ABSTRACT

Title of Dissertation: MOLECULAR PHYLOGENETICS, BIODIVERSITY AND LIFE HISTORY EVOLUTION OF YPONOMEUTOIDEA (LEPIDOPTERA: DITRYSIA), WITH A CATALOG AND AN OVERVIEW OF THE LEPIDOPTERAN FOSSILS

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Yponomeutoidea, one of the earliest-branching superfamilies of advanced (ditrysian) Lepidoptera, comprise about 1,800 species worldwide, including notable pests and models of insect-plant interaction. Yponomeutoids were one of the earliest lepidopteran clades to evolve external feeding and to colonize extensively herbaceous angiosperms. Despite the group’s economic importance, and its value for tracing early lepidopteran evolution, the biodiversity and phylogeny of Yponomeutoidea have been relatively little studied. Even the monophyly and composition of the superfamily have been in doubt. In this dissertation, the most detailed molecular phylogeny to date for Yponomeutoidea is presented (Chapter 1). The resulting phylogeny is compared to previous morphological evidence, and its implications for evolutionary trends in yponomeutoid host association and biogeography are explored. As a prerequisite to divergence dating in the Yponomeutoidea, which is necessarily based on outgroup fossils as none are known for yponomeutoids, a general summary and overview of the lepidopteran fossil record (Chapter 2) is provided, based a recent, comprehensive catalog of known fossils. For chapter 2, all known lepidopteran fossils have been catalogued with annotations of their preservation, specimen deposition, fossil localities and ages (Chapter 3). As a contribution toward better characterization of yponomeutoid biodiversity, taxonomic reviews are provided for the New World genera *Eucalantica* and *Atemelia* (Chapter 4).

The molecular phylogeny estimate (Chapter 1) is based on 8–27 protein coding nuclear genes sequenced in 86 Yponomeutoidea and 53 outgroups. Monophyly for Yponomeutoidea is corroborated. Results from different analyses are highly congruent and relationships within Yponomeutoidea are well supported overall. There is strong support overall for monophyly of families (or major parts thereof) previously recognized on morphological grounds, including Yponomeutidae, Ypsolophidae, Plutellidae, Glyphipterigidae, Argyresthiidae, Attevidae, Praydidae, Heliodinidae, and Bedelliidae. The formerly yponomeutid subfamily Scythropiinae are elevated to family rank (Scythropiidae **stat. rev.**). Host plant family associations of yponomeutoid subfamilies and families are non-random, but show no trends suggesting parallel phylogenesis, and are less

conserved than is mode of feeding (e.g. internal versus external). My analyses reveal previously unrecognized tropical clades in several families, and suggest that previous characterization of yponomeutoids as predominantly Palearctic/ Holarctic was based on insufficient sampling.

MOLECULAR PHYLOGENETICS, BIODIVERSITY AND LIFE HISTORY EVOLUTION OF YPONOMEUTOIDEA (LEPIDOPTERA: DITRYSIA), WITH A CATALOG AND AN OVERVIEW OF THE LEPIDOPTERAN FOSSILS

by

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PREFACE

The Yponomeutoidea are one of 46 superfamilies in the insect order Lepidoptera (the moths and butterflies), and include about 1,800 described species world-wide (van Nieukerken et al., 2011). The yponomeutoids are less familiar than their larger, more conspicuous relatives such as the butterflies (superfamily Papilionoidea), and do not even have a collective common name. However, they are of much importance to understanding the evolution of the Lepidoptera as a whole. Previous morphological studies (e.g. Brock, 1971; Kristensen & Skalski, 1998) suggested that the yponomeutoids are one of the early diverging lineages within Ditrysia. This hypothesis has been confirmed by recent studies based on molecular data (Mutanen et al., 2010; Cho et al., 2011; Regier et al., 2013, in press). At the same time, they are one of the few primitive groups in which some members exhibit a habit characteristic of butterflies and other highly diverse advanced groups, namely, a larva (caterpillar) that feeds externally on the host plant. In contrast, most primitive lepidopterans are leaf miners or other types of internal feeders. Yponomeutoids are also notable for including a number of pest species, an example being the diamondback moth, a world-wide scourge of crops in the cabbage family. To understand the early evolution of the Lepidoptera, as well as to meet the practical need for accurate classification and identification of pest species, we will need much better knowledge of the biodiversity and phylogenetic relationships of yponomeutoids and other primitive lepidopterans than at present. The yponomeutoids are currently an “orphan” group, on which there is no world expert carrying out intensive research. My dissertation study, consisting of four chapters, is intended to fill this gap by: (a) establishing working hypotheses for phylogeny and divergence times within Yponomeutoidea; (b) documenting patterns of yponomeutoid life history trait evolution using a robust phylogeny; and (c) by expanding our knowledge of the species diversity of the Neotropical Yponomeutoidea, which remain poorly studied.

Chapter 1 provides the most robust molecular phylogeny estimate to date for the family-group taxa of Yponomeutoidea, together with a revised classification and new insights into their life history evolution and biogeography. The yponomeutoids are a heterogeneous assemblage of relatively primitive micro-moths, grouped by the most recent treatment (Dugdale *et al.*, 1998a) into eight families (Yponomeutidae, Ypsolophidae, Plutellidae, Acrolepiidae, Heliodinidae, Glyphipterigidae, Lyonetiidae, and Bedelliidae). This chapter addresses (a) whether these families together form a true evolutionary lineage (= monophyletic group); (b) where that putative lineage fits into the larger phylogenetic tree of Lepidoptera; and (c), whether the individual yponomeutoid families themselves are monophyletic groups, and how they are related to each other. The improved estimates of phylogeny are then used to examine questions/patterns of yponomeutoid life history evolution, including the degree of conservation of association with particular host clades; the transition between external and internal feeding; the expansion of host range from arboreal plants to include herbs; and biogeography.

In chapter 2, the lepidopteran fossil record is surveyed with the aim of detecting biases or other possible error sources relevant for divergence time estimation of Lepidoptera. Reliable divergence time estimation is heavily dependent on possession of multiple securely identified fossil constraints which are of appropriate age. Therefore, comprehensive evaluation of the fossil record is a pre-requisite for rigorous molecular dating in any group. In this chapter, all lepidopteran fossils catalogued in Sohn et al. (2012) are categorized by taxonomy, taphonomy, and age groups and then analyzed to discern any pattern.

In chapter 3, a catalog of all known lepidopteran fossils and subfossils is provided with annotations of fossil type, specimen deposition, excavation locality, geological age and remarks of the issues involved in fossil nomenclature and identifications, if any.

In chapter 4, the taxonomic revisions of two yponomeutoid genera, *Eucalantica* and *Atemelia*, are presented. These two examples both show previously underestimated diversity of Yponomeutoidea from the Neotropical Region.

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Chapter 1

A molecular phylogeny for Yponomeutoidea (Insecta, Lepidoptera, Ditrysia) and its implications for classification, biogeography and the evolution of host plant use

Reformatted from Sohn et al. (2013: PLoS ONE 8(1): e55066, doi:10.1371/journal.pone.0055066)

Corrections included.

Introduction

The Yponomeutoidea constitute one of the early radiations in the so-called ditrysian Lepidoptera, the advanced clade that contains the great majority of lepidopteran species. Yponomeutoids include about 1,800 species worldwide, known heretofore mainly from temperate regions (Heppner, 1998; van Nieukerken et al., 2011). Yponomeutoidea are especially important for tracing the early evolution of Lepidoptera-plant interactions because they are one of the earliest groups to evolve external feeding (Powell et al., 1998) and to extensively colonize herbs as well as shrubs and trees (Grimaldi and Engel, 2005). In the modern fauna, those two traits are especially common in the highly diverse lineages of advanced moths, for whose success they may be in part responsible. Some yponomeutoid groups, especially *Yponomeuta*, have served as model systems in studying how insect-plant interactions affect speciation (Menken et al., 1992). Yponomeutoidea also include a number of notable pest species. For example, the diamondback moth (*Plutella xylostella*: Plutellidae) is regarded as the most destructive insect pest of cruciferous vegetables, annually causing about a billion US dollars in economic loss (Talekar & Shelton, 1993). Another notorious pest, the leek moth (*Acrolepiopsis assectella*: Glyphipterigidae), has caused damage to upwards of 70% of leeks and 40–50% of onions in some regions of Europe (Mason et al., 2010). Communal larvae of some species sometimes extensively damage local vegetation or even broader landscapes. The small ermine moths (*Yponomeuta* spp.) cause complete defoliation of some trees in northern Europe (e.g. Leather, 1986; Alonso et al., 2000) and the U.S. (e.g. the introduced *Y. malinellus*: Hoebeke, 1987).

Despite their value for tracing the early evolution of Lepidoptera and their importance as pests, the Yponomeutoidea have received relatively little attention from systematists, and their biodiversity remains poorly understood. Especially problematic is the lack of a robust phylogeny, including a synapomorphy-based definition for the superfamily itself. Until the early 20th century, the taxa currently placed in Yponomeutoidea comprised scattered suprageneric groups of Tineina or Tineae, two collective microlepidopteran group names no longer in use (e.g. Zeller, 1839; Bruand, 1851; Stainton, 1854; Meyrick, 1928), or Tineidae (e.g. Staudinger & Rebel, 1901; Handlirsch, 1925). Although Stephens (1829) had already distinguished them from other microlepidopteran groups, it was Fracker (1915) who first erected a superfamily for Yponomeutoidea. However, as it lacked unambiguously defining characters, the group remained highly heterogeneous and included many genera that now belong to other superfamilies. A succession of subsequent authors advanced increasingly restrictive re-definitions of Yponomeutoidea (e.g. Meyrick, 1928; Börner, 1939; Friese, 1960; Common, 1970; Brock, 1971; Heppner, 1977; Kuznetzov & Stekolnikov, 1977), but failed to achieve a stable classification because they lacked explicit analyses of phylogenetic relationships (Table 1). Kyrki (1984, 1990), in the first cladistic study, significantly modernized the classification of Yponomeutoidea, in which he included only seven families: Yponomeutidae, Ypsolophidae, Plutellidae, Glyphipterigidae, Heliodinidae, Bedelliidae and Lyonetiidae. However, the lack of robustness of Kyrki's phylogeny hindered acceptance of his classification, leaving other hypotheses, such as those of Moriuti (1977) and Heppner (1998), still in contention (Fig. 1). Disagreements on the phylogeny of Yponomeutoidea, in turn, have helped to obscure inter-relationships of the basal lepidopteran groups and hindered testing of evolutionary hypotheses bearing on them.

Recent molecular studies of higher phylogeny in Lepidoptera have begun to clarify the phylogenetic position, definition and internal relationships of Yponomeutoidea (Regier et al. 2009; Mutanen et al. 2010; Cho et al. 2011). The results of Mutanen et al. (2010), who included 23 yponomeutoids in an analysis of 350 lepidopterans sequenced for 8 genes (6.3 kb), were the basis for the revised 10-family classification (Table 1) of van Nieukerken et al. (2011). Here, in the first molecular study aimed specifically at Yponomeutoidea, we greatly expand previous taxon and gene sampling, providing the most comprehensive examination and robust hypothesis to date of phylogeny in this superfamily. We compare our results to all previous classification systems, then trace evolutionary trends in yponomeutoid host associations and biogeography on the new phylogeny.

Materials and Methods

Taxon sampling

A total of 86 species currently assigned to Yponomeutoidea were included in our analyses. These represent all 17 suprageneric groups recognized by Kyrki (1984), and all 10 families recognized by van Nieukerken et al. (2011) as well as all subfamilies and tribes therein. The sample collectively spans nearly all zoogeographical regions, including 37 species from the Palearctic, 21 from the Neotropics, 17 from the Nearctic, seven from the Australian region, two from the Oriental region, and two from the Ethiopian region. All yponomeutoid genera for which material could be obtained were included, each represented by a single species except that two or more species were sampled for several broadly distributed, species-rich genera.

The definition of Yponomeutoidea has been considered controversial (Dugdale et al., 1998a). For this reason, our putative outgroups, totaling 53 species belonging to 22 families in 12 superfamilies of ditrysian Lepidoptera (see Supplement S1), included all superfamilies that were historically associated with Yponomeutoidea or at least contain genera that were once placed within Yponomeutoidea. Among these are Choreutoidea, Copromorphoidea, Epermenioidea, Galacticoidea, Gelechioidea, Schreckensteinoidea, Urodoidea, and Zygaenoidea. Inclusion of these taxa provides an additional test of the monophyly of Yponomeutoidea in the restricted modern sense. We also included two superfamilies, Tortricoidea and Pterophoroidea, which have never been considered close to yponomeutoids. In contrast to all previous hypotheses, recent molecular studies (Regier et al., 2009; Mutanen et al., 2010; Cho et al., 2011) have strongly supported Gracillarioidea as the closest relatives to Yponomeutoidea sensu Kyrki (1984, 1990). For this reason we sampled gracillarioids especially densely, taking exemplars from most of the known families and subfamilies. We included comparably dense sampling of Tineoidea, which have long been considered, now with increasing molecular evidence (Mutanen et al., 2010 and J. Regier et al., unpublished results), to contain the earliest-branching lineages within the Ditrysia (Davis 1998). Finally, to root the entire tree, we added a representative of Tischeriidae, long regarded, also with increasing molecular evidence (Mutanen et al., 2010; J. Regier et al., unpublished results), to be among the closest relatives to Ditrysia.

Specimen preparation and identification

The specimens for this study, obtained by our own collecting as well as from collaborators around the world (see Acknowledgments), are stored in 100% ethanol at -80° C as part of the ATOLep frozen tissue collection at the University of Maryland, College Park, USA (details at http://www.leptree.net/collection). For extraction of nucleic acids we used the legs, head and thorax, or the entire body (always excluding the wings), depending on the size of the specimen. As vouchers we preserved both wings and abdomen for large or medium-sized moths, and wings only for very small ones. Wing voucher images for most of our specimens are available at the Leptree website (http://www.leptree.net/voucher_image_list). Partial COI sequences corresponding to DNA 'barcodes' were generated for each specimen either by the authors or as part of the All-Leps Barcode of Life project (http://www.lepbarcoding.org). Using these sequences, we performed an independent check of the primary identifications of all specimens by searching for matching barcode sequences in the BOLD (Barcode of Life Data system, http://www.boldsystems.org).

Gene sampling

The sequences initially sampled for this study consisted of eight nuclear genes (Supplment S1), totaling 8,096 bp, for nearly all ingroup taxa (83/86 = 96.5%) and all outgroup taxa. These eight are a subset of the 26 genes sequenced in a study of ditrysian phylogeny by Cho et al. (2011), 25 of which were also analyzed in Bombycoidea by Zwick et al. (2011). The eight gene subset was chosen on the basis of its relatively high amplification success rates and phylogenetic utility. The eight genes are: *Gelsolin* (603 bp), *histidyl tRNA synthetase* (447 bp), *AMP deaminase* (768 bp), *glucose phosphate dehydrogenase* (621 bp), *Acetyl-coA carboxylase* (501 bp), *CAD* (2,929 bp), *DDC* (1,281 bp) and *enolase* (1,135 bp). Three species (*Argyresthia austerella*, *Digitivalva hemiglypha*, and *Prays atomocella*), each with close relatives in the eight gene data set, were sequenced for only the five genes (6.6 kb) studied in Ditrysia by Regier et al. (2009), namely, *CAD*, *DDC*, *enolase*, *period*, and *wingless* (Supplement S1).

Because the initial 8-gene analyses yielded little strong support for deeper nodes, we subsequently added 11–19 more nuclear genes (totaling up to 27 genes and 19,386 bp) for a taxon subset consisting of 28 ingroups and 43 outgroups (Supplement S1), amounting to 51% of the total of 139 taxa. The 27 genes include the 26 used by Cho et al. (2011), plus one additional gene, *α-spectrin*. All 27 are included in the set of 68 genes studied by Regier et al. (2008b) across the arthropods. The great majority of taxa (54/65) for which more than eight genes were assayed were sequenced for just the 19 gene set that has recently proven useful in resolving relationships in other superfamilies, including Gracillarioidea (Kawahara et al. 2011), Tortricoidea (Regier et al. 2012a) and Pyraloidea (Regier et al. 2012b). These same studies have also shown that augmentation of the initial gene sample in only a subset of taxa, following Cho et al. (2011), is an effective and cost-efficient means for obtaining stronger support at deeper nodes. Partial gene augmentation introduces blocks of nonrandomly missing data that could have adverse effects on phylogeny estimation (Lemmon et al., 2009; Simmons, 2012). To test this possibility, we compared the results from the 8+19 gene, deliberately incomplete matrix to those from a 4-gene data set (*glucose phosphate dehydrogenase*, *CAD*, *DDC* and *enolase*) that exhibit a relatively low percentage of missing data (21.5%) among our 139 taxa, due to inadvertent failures of amplification or sequencing.

Gene extraction, sequencing and alignment

A detailed protocol of all laboratory procedures is provided by Regier et al. (2008b). Further descriptions, including gene amplification strategies, PCR primer sequences, sequence assembly and alignment methods, can be found in Regier (1998) and Regier et al. (2008a; 2009). To summarize, total RNAs were extracted from an excised tissue using the SV Total RNA Isolation System (Promega Co.). The targeted regions of the mRNAs were amplified using Reverse Transcriptase (RT)-PCR, yielding cDNA. Nested PCR for further purification and/or M13 re-amplification for increasing volume were attempted as necessary. Purified amplicons were sequenced on a 3730 DNA Analyzer (Applied Biosystems) at the Center for Biosystems Research at the University of Maryland, College Park. The resulting ABI files and contigs were checked for error manually and then edited and assembled using Geneious Pro 5.3.4 (Biomatters Ltd.). The data were rechecked for error by inspection of the genetic distances among them determined in PAUP* 4.0b8 (Swofford, 2002). The final sequences for each gene were aligned using the "Translation Align" option in Geneious. The final alignments were concatenated with Geneious, separately for the 8-gene and 8–27 gene analyses, and the combined data sets were visually checked. Regions of uncertain alignment, totaling 1,509 characters, were masked and excluded from subsequent analyses. GenBank accession numbers and the percentage sequence completeness for each gene in each taxon are given in Supplement S1.

Character partition and data set design

It is well known that rates of sequence evolution vary among codon positions, reflecting in part different ratios of synonymous versus nonsynonymous substitutions (Brown, 1985; Griffiths, 1999). Previous empirical studies (e.g. Regier et al., 2008b, 2009; Cho et al., 2011) have shown that partitioning data to reflect this variation, or eliminating synonymous change entirely, can reduce or eliminate phylogenetic error due to among-lineage compositional heterogeneity, but at the cost of discarding potentially informative synonymous signal. To gauge the potential effects of differing evolutionary properties between synonymous and non-synonymous substitution on phylogeny inference, we carried out separate analyses using a variety of character coding and/or data partition schemes. These analyses are: (a) “nt123”, i.e., all codon positions included and unpartitioned; (b) “degen1” (Regier et al, 2010; Zwick, 2010, electronic source), i.e., all synonymous differences degenerated, leaving only non-synonymous differences among taxa; (c) “nt123 partitioned” (Regier et al., 2009), i.e., all codon positions partitioned into mostly non-synonymously evolving (“noLRall1+nt2”) versus mostly synonymously- evolving ones (“LRall1+nt3”); and, (d) “codon” analysis (Ren et al., 2005; Holder et al., 2008), in which the character states are codons and synonymous and nonsynonymous changes are modeled separately. For the codon analyses (only), a 91 taxon set including only Yponomeutoidea and Gracillarioidea was used, rather than the full 139 taxon data set, to reduce the computational burden. Increased numbers of discrete rate categories in the gamma-distributed rate heterogeneity distribution (‘numratecats’ in the GARLI configuration) can also dramatically increase computational time. To avoid this problem, we used trial runs to estimate a minimum number of categories beyond which further increase yields no significant improvement in tree likelihood scores. We determined this number to be three categories. As a third approach to accommodating differences between synonymous and non-synonymous change, we also partitioned the data into first plus second codon positions (“nt12”, supplementary figure S3) versus third codon positions (“nt3”, supplementary figure S4).

Phylogenetic analyses

The best substitution model for each data set was determined using jModelTest (Posada, 2008), which in nearly all cases selected GTR+Γ+I, i.e., the General-Time-Reversible model with among-site rate variation accomodated using a gamma distribution plus separate estimation of a proportion of invariable sites. Phylogenetic analyses were conducted with maximum likelihood (ML) methods as implemented in GARLI 2.0 (Zwickl, 2011), which includes partitioned models. Default settings of the program were used, except that starting tree topology was specified as random; the frequencies with which to log the best score (‘logevery’) and to save the best tree to file (‘saveevery’) were set to 100,000 and 100,000 respectively; and, the number of generations without topology improvement required for termination (‘genthreshfortopoterm’) was set to 5,000. The best tree from 150 independent search replicates was saved, and visualized using FigTree v1.3.1 (Rambaut, 2009). To evaluate the robustness of the resulting trees, bootstrap (BP) values were calculated from 1000 pseudoreplicates, each based on 15 heuristic search replicates except that only a single heuristic search replicate was carried out for each pseudoreplicate in the single-gene bootstrap analyses. Because these analyses are so computation-intensive, they were carried out by Grid parallel computing (Cummings & Huskamp, 2005), using the Lattice Project (Bazinet & Cummings, 2009, 2011). For purposes of discussion, we will refer to BP values of 70–79% as “moderate”, 80–89% as “strong”, and ≥ 90% as “very strong” support. These conventions, also adopted in previous studies (e.g. Kawahara et al., 2011; Cho et al., 2011), are arbitrary and hence serve heuristic purposes only.

Rogue taxon analyses

Despite the addition of 11–19 genes to the initial 8-gene data set, some deeper nodes in even our best-supported trees have low bootstrap values. One possible cause of low support is the sensitivity of bootstrap values to taxa of unstable placement (Sanderson and Shaffer, 2002), termed “rogues” by Wilkinson (1994). Multiple approaches have been suggested for detecting and removing the effects of rogue taxa (reviewed in Aberer, 2011). We investigated the potential contribution of rogue taxa (Table 2) to low bootstrap values in our data set using the RogueNaRok (RNR) approach of Aberer et al. (2011; a pun on Ragnarök, the judgement of the gods in Norse mythology). The key feature of RNR is a new optimality criterion for rogue taxon removal, the “Relative Bipartition Information Criterion” (RBIC) (Aberer 2011; Aberer and Stamatakis 2011). The RBIC strikes a balance between improving per-node support in the reduced bootstrap consensus tree (with rogues deleted) and retaining total information by minimizing the loss of bipartitions in the bootstrap consensus tree that results from such deletions. Aberer and Stamatakis (2011) compared multiple heuristic approaches to maximizing the RBIC. The best results came from their single-taxon algorithm (STA), which begins by removing taxa one at a time to find the taxon (if any) whose deletion most improves the RBIC. After that taxon is removed, one removes each remaining taxon again, to find the next most “roguish” taxon. The process is repeated until the optimality score stops improving. The RogueNaRok algorithm is a fast generalization of the STA, which allows for “deletion sets” – groups of taxa deleted simultaneously – of varying sizes.

To identify rogue taxa, we used the on-line version of RogueNaRok (RNR) at http://193.197.73.70:8080/rnr/roguenarok, which is built on RAxML [60]. Bootstrap files were first generated and submitted to RNR, which identified possible rogue taxa (i.e. ones whose removal increases the RBIC). The reduced data set was then analyzed with RAxML, and the bootstrap outputs again submitted to RNR. This procedure was repeated until RNR no longer identified any additional rogues. Finally, the putatively rogue-free data sets were subjected to bootstrap analyses using GARLI, to make them directly comparable to the original analyses. This procedure was carried out only for the nt123, 8–27 gene data set, which gave the highest initial bootstrap support overall. In our initial RNR analyses, most of the rogue taxa detected were among the more distant outgroups. This result might stem from increased uncertainty in position due to lower sampling density among these taxa, and might in turn impede detection of more subtle rogue taxon effects within the ingroup, which is what we are most interested in. To circumvent this possibility, we also conducted separate RNR analyses on data sets containing Yponomeutoidea (86 taxa) and Gracillarioidea (11 taxa) only.

Significance tests of discord with previous hypotheses

Our results appear to contradict a number of prior hypotheses about phylogenetic relationships in Yponomeutoidea, including several depicted in Figure 1. We used the Approximately Unbiased (AU) test of Shimodaira (2002) to determine whether our data significantly reject those previous hypotheses, against the alternative that the discrepancy can be explained by sampling error in the sequence data. The test determines whether the best tree possible under the constraint of monophyly, no matter what its topology may be otherwise, is a significantly worse fit to the data than the best tree without that constraint. Table 3 lists the 12 groups tested for significance of non-monophyly. For each combination of one character set and one apparently non-monophlyetic previous grouping, we performed a GARLI analysis consisting of 150 replicate tree searches, under the constraint of monophyly for the group in question. The constrained tree was then compared to the previously-obtained unconstrained tree. The site likelihoods of the best constrained and unconstrained trees were then estimated with PAUP* (Swofford, 2002), and the trees and site likelihoods for all comparisons combined into a single input file for the CONSEL 0.20 package

(Shimodaira and Hasegawa, 2001; Shimodaira, 2011, electronic source) with which the Approximately Unbiased test was conducted.

Host plant associations and biogeography

To explore the evolutionary history of Yponomeutoidea with respect to larval host plant associations and biogeography, we compiled data from the literature on these features for all described yponomeutoid species. Given current uncertainty about the limits of the superfamily, we considered only genera whose placements within Yponomeutoidea are secure. Host records were retrieved primarily from the HOSTS website (Robinson et al., 2010). These data were checked for possible error and supplemented by records from other sources. All suspicious records, possibly representing misidentification of larvae, misidentification of hosts, or confusion with adult-habitat association, were excluded. Individual host records were combined into lists of plant families or higher clades used by each of the 16 major yponomeutoid lineages identified on our molecular phylogeny. Higher classification of host plants follows APG III (2009) for angiosperms and Fu et al. (2004) for gymnosperms. Host ranges of individual yponomeutoid species were categorized as either oligophagous (feeding on plants in a single order) or polyphagous (feeding on plants in more than one order). The predominant growth form of hosts for each yponomeutoid lineage was categorized as arboreal (trees and shrubs), herbaceous, or scandent (vines and lianas), and alternatively as woody versus herbaceous. We also scored site and mode of feeding. Finally, for each lineage we tabulated the proportions of species and genera for which at least one host plant record is available, using species and generic diversity estimates from van Nieukerken et al. (2011) or the first author's unpublished data.

Information on yponomeutoid distributions across major biogeographical regions was assembled from global reviews (e.g. Meyrick, 1914; Gershenson & Ulenberg, 1998; Gaedike, 1997) and local checklists (e.g. Friese, 1960; Heppner & Duckworth, 1983; Heppner, 1984; Karsholt & Razowski, 1996; Edwards, 1996; Nielsen, 1996). Distributions due to human-caused dispersal (accidental or deliberate introduction) were excluded when discernable from non-anthropogenic causes. Data for individual species were compiled into summaries of numbers of species occurring in each region for each major yponomeutoid lineage, as described previously for host plant records. For species occurring in more than one region, each region was counted independently, thus some species were counted more than once. Our compilations are based primarily on described species, but undescribed species were included in several cases where they represent significant expansion of the known distribution of the lineage.

Generalization of host and distribution records by higher taxonomic groups often neglects variation, incompleteness, and bias in such data, introducing errors. For this reason, we did not attempt any formal statistical approach, although we did compute (by hand) parsimony optimizations of predominant feeding mode and host plant growth on a simplified version, reduced to major lineages, of the molecular phylogeny. Our goal was simply to provide a first phylogeny-based summary of evolutionary trends in yponomeutoid host-use evolution and biogeography.

Results

The best-score ML tree found in 150 GARLI searches for the 8–27 gene, 139-taxon nt123 analysis is shown in Figures 2 and 3. Figure 2 shows just the Yponomeutoidea as recovered here (79 taxa), while Figure 3 shows the outgroup region of the tree. Bootstrap values for five different combinations of character coding (nt123, nt123 partitioned, degen1) and gene sample (8 genes only vs. 8+19 genes), plus nt123 with rogue taxa removed, are superimposed on each node of this tree. Overall, the tree is well supported: 65 of the 78 nodes in Figures 2 and 3, or 83%, had strong bootstrap support (≥80%) from at least one analysis. Figure 4 shows the same topology in a phylogram format, with thickened branches denoting bootstrap support of ≥70% from at least one of the bootstrap analyses summarized in Figures 2 and 3.

The most robust phylogenies came from the nt123 analysis of the 8–27 gene deliberately incomplete data set (Fig. 2; Table 4). Within Yponomeutoidea (Fig. 2; 79 taxa) this analysis yielded 59 very strongly supported (BP ≥ 90%), 4 strongly supported (BP=80–89%) and 3 moderately supported (BP =70–79%) nodes, for a sum of 66 nodes (of 78 total), or 85%, with BP ≥ 70%. The results for the partitioned nt123 analysis were nearly identical: 58 nodes with BP ≥ 90%, 4 nodes with BP=80–89% and 3 with BP =70–79%. The 8–27 gene degen1 analysis yielded 37 nodes with BP ≥ 90%, 6 with BP=80–89% and 4 with BP =70–79%, for a total of 47/78=60% of nodes with BP ≥ 70%. The codon model results were intermediate between those from nt123 and degen1 but closer to the former, with 54 nodes of BP ≥ 90%, 3 of BP=80–89% and 2 of BP =70–79%, for a total of 59/78=76% of nodes with BP ≥ 70%. The nt123 unpartitioned and nt123 partitioned trees were nearly identical, disagreeing at only three nodes weakly supported in each. The degen1 tree disagreed with the nt123 tree at 18 nodes, of which 8 were very strongly supported, 2 strongly supported, one moderately supported and 7 poorly supported (BP ≤ 60 %) in the nt123 tree. In only two cases, however, was a node strongly supported in the degen1 analysis but not present in the nt123 tree, while in no case was a node strongly supported in one tree and strongly contradicted in the other.

The 8-gene and 8–27 gene nt123 trees were almost entirely congruent, differing in only 2 weakly supported nodes. Of the matching nodes between the two analyses, 12 were better supported in the 8-gene analysis, with a mean difference of +3.33% and a range of 1–11%, while the 19+ gene analysis yielded higher support at 16 nodes, with a mean difference of +7.56% and a range of 1–23%. The 8-gene analysis yielded 55 nodes with BP ≥ 90%, 5 with BP=80–89% and 3 with BP =70–79%, for a total of 63/78=81% of nodes with BP ≥ 70%, only slightly lower than the 19+ gene analysis. However, a few nodes showed substantial increase in support with increased gene sampling. Among these are three that subtend multiple families: Heliodinidae + Bedelliidae + *Scythropia* (Fig. 2, **node 2**; BP =90/67, 19+ genes/8 genes); Bedelliidae + *Scythropia* (Fig. 2, **node 1**; BP =86/69); and Yponomeutoidea (Fig. 2, **node 10**; BP=76/66).

Our rogue taxon analysis using RogueNaRok (Aberer et al. 2011) identified 16 rogue taxa for the 8–27 gene nt123 data set as a whole (Table 2). All but one (Yponomeutidae: *Xylosaris lichineuta*) proved to lie among the outgroups, although several others were thought by some previous authors to belong to Yponomeutoidea (Table 2). Two additional rogue taxa, both yponomeutoids (Lyonetiidae: *Perileucoptera* and Yponomeutidae: *Swammerdamia*), were discovered when only Yponomeutoidea and Gracillarioidea were analyzed. We found no significant correlation between rogue status and sequence data incompleteness (Table 2: SC index). Removal of the 18 rogue taxa resulted in increased bootstrap values for 14 nodes and decreases for 17 nodes in the tree for Yponomeutoidea (Fig. 2). However, 77% of these changes were very small (≤3%). When only changes of > 3% are counted, there are just two decreases in support in the rogue-pruned analysis, one of 5% and one of 6%. In contrast, five nodes showed increases, ranging from 7% to 23%. Among the nodes undergoing the strongest improvements in support are Yponomeutoidea (Fig. 2, **node 10**; BP=99/76, after/before rogue removal); the YPGAL clade (Fig. 2, **node 16**; BP=77/67); and the AL clade (Fig. 2, **node 11**; BP=76/69). Half of the increase in bootstrap values across all affected nodes can be explained by deletion of *Perileucoptera coffeella* alone (data not shown).

Discussion

Phylogenetic signal sources, partial gene sample augmentation and rogue taxon analysis

Our results exemplify the ability of combined analyses of multiple genes to produce robust phylogeny estimates even when there is little strong signal from any individual gene (Regier & Zwick, 2011); none of the deeper nodes with substantial support (BP ≥70) in the concatenated analysis (Fig. 2) were strongly supported by any of the initial 8 genes (Supplementary figure S5) or the 11 additional genes sampled for a subset of taxa (data not shown). The utility of concatenated analysis can be undermined when individual gene trees conflict with each other or with the species tree (Liu & Pearl, 2007). Our individual gene trees showed little evidence of strong conflict (Supplementary figure S5), reinforcing the value of combined analysis for this data set, and implying that the low to modest support for some "backbone" nodes is not in general the result of conflict among gene trees. In a few instances noted below, however, there is indirect evidence that inter-gene conflict may be influencing bootstrap values.

We also see minimal evidence overall of spurious signal resulting from heterogeneity and convergence in base composition. Compositional heterogeneity is especially common at sites undergoing synonymous substitution (Regier and Zwick 2011), and our data are no exception; there is highly significant variation in composition across taxa in both nt3 and nt1+nt2, while heterogeneity is minor with synonymous differences removed (the degen1 data set). Conflicting signal due to compositional heterogeneity, in addition to substitutional saturation, may contribute to the inability of nt3 alone (Supplementary figure S4) to provide notable support to *any* of the among-family relationships that receive moderate to strong bootstraps from the full data set (nt123), despite providing a great majority of the total evolutionary change inferred from that data set and strongly supporting many individual families and sub-clades thereof. If composition had major effects on phylogenetic inference, however, we might expect to see repeated instances of conflicting moderate to strong bootstrap values between the total data set (nt123), dominated by synonymous change, and non-synonymous change only, as estimated by the degen1 analysis. No such cases were found, although several examples of lesser conflict are pointed out below. Rather than conflicting, the signals from synonymous and non-synonymous change appear to be largely complementary.

Our results provide another instance in which deliberately unequal gene sample augmentation markedly improves support for deeper nodes without introducing any apparent artifacts due to large blocks of non-random missing data. Nt123 analyses of the 8-gene “complete” matrix (27% inadvertently missing data due to sporadic failures of amplification or sequencing) and the deliberately-incomplete 8–27 gene matrix (55% missing data) yielded nearly identical topologies and similar bootstrap values. The 8–27 gene analysis produced higher support overall, however, and markedly increased bootstraps for several deeper nodes, including Yponomeutoidea (Fig. 2, **node 10**). Similar findings have been reported in several recent studies of Lepidoptera (Cho et al., 2011; Kawahara et al., 2011; Zwick et al., 2011).

The potential for even a few “rogue” taxa to substantially reduce bootstrap support, obscuring otherwise strong signal on relationships among the remaining taxa, is now widely recognized (Wilkinson, 1995, 1996). Despite multiple proposals, however, it has been unclear how to best identify such taxa and evaluate their effect. We believe that the RogueNaRok procedure of Aberer et al. (2011) is an important advance toward solving this problem. It sets out a very reasonable and explicit optimality criterion for deciding which and how many potential rogue taxa should be removed, balancing the increased support gained by deleting those taxa against the information lost through their deletion, and provides well-tested heuristic algorithms for estimating an optimal set of taxa to delete. Application of RogueNaRok following our 8–27 gene, 139-taxon nt123 analysis identified 18 rogue taxa meriting deletion. Removal of these taxa resulted in substantial bootstrap support increases for five nodes, most notably an increase from 76 to 99% for Yponomeutoidea. We predict that RogueNaRok will prove widely useful in phylogenetic studies of large taxon sets.

Monophyly, composition and phylogenetic position of Yponomeutoidea

In this and subsequent sections we evaluate the implications of our molecular results for current understanding of the phylogeny of yponomeutoids, and for their classification. Our exposition proceeds from the base to the tips of the tree in Figure 2, and makes repeated reference to the node numbers labeled on that tree. Representative adult habitus images for nearly all of the 16 families and subfamilies discussed below are provided in Figure 5. The species diversities, geographic distributions and larval feeding habits of these families and subfamilies are summarized in Figures 6 and 7.

All of our molecular analyses support monophyly for Yponomeutoidea (Fig. 2, **node 11**) in approximately the sense of Kyrki (1984; 1990). Bootstrap support is moderate (BP=76%, nt123) for the full data set but rises to very strong (BP=99, nt123) when the 18 rogue taxa are removed. Kyrki (1984) initially proposed a single synapomorphy for Yponomeutoidea, the presence of posterior expansions on the 8th abdominal pleuron ("pleural lobes") in males. He later added another possible synapomorphy, a transverse ridge on the second abdominal sternite (Kyrki, 1990). On this basis he included seven families: Yponomeutidae, Plutellidae (including Acrolepiidae, later separated by Dugdale et al. 1998a), Ypsolophidae, Glyphipterigidae, Heliodinidae, Lyonetiidae, and Bedelliidae. This hypothesis had been questioned because it requires independent losses of the two synapomorphies in some of the included groups (Dugdale et al., 1998a). In our results, the main remaining question about the composition of Yponomeutoidea concerns Lyonetiidae. Our analyses always separate Lyonetiinae from Cemiostominae, placing the former inside Yponomeutoidea but the latter outside, among the gracillarioids. However, the position of *Perileucoptera*, our sole cemiostomine, is exceptionally unstable. It is identified as a rogue taxon by the RNR analysis, and our AU test cannot reject the monophyly of Lyonetiidae (Table 3).

Among the out-groups included in our analyses, Gracillarioidea sensu van Nieukerken et al. (2011), i.e. with Douglasiidae excluded, were strongly supported (Fig. 3, **node 67**; BP 85–97, all analyses) as the closest relatives to Yponomeutoidea. This clade has been strongly supported in almost all previous molecular studies (e.g. Regier et al., 2009; Kawahara et al. 2011; Cho et al., 2011). However, the deeper divergences within Yponomeutoidea + Gracillarioidea (the G.B.R.Y. clade of Kawahara et al., 2011) are very weakly supported. Like Kawahara et al. (2011), we find no molecular evidence for monophyly of Gracillarioidea. Eventually it may be reasonable to merge Gracillarioidea into an Yponomeutoidea *sensu lato*, but such a change is beyond the scope of the present study.

Our results support several earlier morphology-based proposals that excluded a variety of taxa from membership in, or close relatedness to, Yponomeutoidea. Galacticoidea, Urodoidea and Schreckensteinioidea, once placed in Yponomeutoidea (Kyrki, 1988; Minet 1983, 1986; summary in Dugdale et al., 1998b), are decisively excluded from Yponomeutoidea + Gracillarioidea, here (Fig. 3, **node 67**) and in all other recent molecular studies. Removal of the putative yponomeutid genus *Nosymna* Walker, 1864 to Zygaenoidea by Heppner (1995) is also confirmed by our analyses (Fig. 3, **node 66**), as is the exclusion of *Cycloplasis* Clemens, 1864 from Heliodinidae by Hsu and Powell (2005). Our results place *Cycloplasis* in Apoditrysia + Gelechioidea (Fig. 3, **node 65**; BP=71–83, all analyses). Two genera previously placed in Lyonetiidae, *Philonome*

Chambers, 1872 and *Corythophora* auct Braun, 1915, are here strongly supported as belonging to Tineoidea (Fig. 3, **node 63**; BP=90, nt123).

Basal split within Yponomeutoidea

Within Yponomeutoidea (Fig. 2, **node 11**), our results provide moderate to strong support for most nodes above the family level, allowing us to construct a working hypothesis of higher phylogeny across the superfamily. In presenting this hypothesis below, we make repeated use of informal clade names based primarily on the first letters of the names of the included families.

In the tree of Fig. 2, the basal split is between a ‘PAHSB clade’ (Fig. 2, **node 4**; maximum BP = 75, nt123 partitioned) consisting of Praydidae, Attevidae, Heliodinidae, Bedelliidae and *Scythropia*, and a ‘YYPGAL clade’ (Fig. 2, **node 17**; maximum BP = 77, rogue-pruned nt123) consisting of Yponomeutidae, Ypsolophidae, Plutellidae, Glyphipterigidae, Argyresthiidae and Lyonetiidae. Because bootstrap support for these clades is modest at best, and they are contradicted, albeit very weakly, by degen1, we regard them as provisional. Neither clade has ever been proposed on the basis of morphology. However, our working hypothesis, including this basal split, fits the molecular data much better than any of the alternative proposals for among-family relationships shown in Figure 1, all of which are decisively rejected (P<0.001) by the AU test (Table 3).

Relationships within the PAHSB clade

This clade (Fig. 2, **node 4**), for which no morphological synapomorphies are yet known, contains five relatively small yponomeutoid groups. It divides basally into a 'PA clade' (Fig. 2, **node 5**; maximum BP=82, nt123 partitioned) containing the Praydidae and Attevidae, and an 'HSB clade' (Fig. 2, **node 2**; BP = 90, nt123) consisting of Heliodinidae, Bedelliidae and *Scythropia*. The latter was previously treated as a subfamily of Yponomeutidae.

The PA clade receives moderate to strong support from nearly all of our analyses, except that it is very weakly contradicted by degen1 ($BP \leq 38$). The groups based on *Prays* and *Atteva*, here treated as families following van Nieukerken et al. (2011), were treated as subfamilies of Yponomeutidae by Kyrki (1990), while others have regarded the *Prays* group as closer to Plutellidae than to Yponomeutidae (Pierce and Metcalfe, 1935; Friese, 1960; Moriuti, 1977); Heppner (1998) treated it as a subfamily of Plutellidae. All of these hypotheses are strongly contradicted by our results.

While previous ideas about their phylogenetic position receive no support, the molecular data do corroborate Kyrki's (1990) assertion of a close relationship between the *Prays* and *Atteva* groups, based on two synapomorphies, the lack of a pecten on the antennal scape and the presence of a larval cranial seta P_1 that lies on or above the line defined by setae Af_2–P_2. A possible additional synapomorphy is the presence of less than four segments in the maxillary palp. Ulenberg (2009) also recovered the pairing of the *Prays* and *Atteva* groups within Yponomeutidae, in a parsimony analysis using Kyrki's (1990) characters. These putative synapomorphies might be doubted because they are reductions or homoplasious, but the molecular results suggest that they are real. We nonetheless treat these groups as separate families because the molecular evidence is not yet completely incontrovertible.

Monophyly of the Praydidae, here represented by *Prays* and *Atemelia*, is very strongly supported by our data (Fig. 2, **node 7**; BP= 100, all analyses). The members of this group are easily distinguished from other yponomeutoids by an unusually broad male 8th sternum and by female apophyses anteriores lacking a branched costa at the base (Friese, 1960; Moriuti, 1977). Our data also strongly resolve the relationships among the four *Prays* species sampled (Fig. 2, **nodes 9, 10**; BP=89–100, all analyses). Praydidae, comprising 3 genera and 47 species, are a cosmopolitan group that is most diverse in the Old World. The larvae are initially endophagous feeders in leaves, buds or shoots of woody dicots of diverse families; in some species, older larvae feed externally in webs (Dugdale et al. 1998a).

The two species of *Atteva* included in our sample are likewise strongly grouped (Fig. 2, **node 6**; BP=100). The Attevidae can be defined by four autapomorphies (Kyrki, 1984): the presence of chaetosema; reduction of the hindleg tibia and tarsus, especially in the male; the presence of two subventral setae on the larval meso- and metathorax; and concealment of the labial palps in the pupa. Attevidae are a predominantly pan-tropical group of 52 described species in a single genus *Atteva*, most diverse in the Oriental region. The larvae are communal leaf webbers on woody dicots, with >90% of records from Simaroubaceae (Dugdale et al., 1998a).

Monophyly of the probable sister group to the PA clade, the HSB clade (Fig. 2, **node 2**; maximum BP=90, nt123), is supported by all of our analyses. The grouping of Heliodinidae, Bedelliidae and *Scythropia* has not been previously proposed. The closest antecedents are the grouping of Heliodinidae, Bedelliidae and Lyonetiidae by Kyrki (1990) and that of Lyonetiidae (including Bedelliinae), Acrolepiidae, and Heliodinidae by Heppner (1998). Kyrki (1990) proposed three possible synapomorphies for Heliodinidae + Bedelliidae: larva with a long spinneret; larval seta V_1 not apparent on the thorax; and pupa without a cocoon. It is not known whether *Scythropia* shares any of these traits. The search for morphological synapomorphies of the strongly-supported HSB clade merits further effort.

The molecular data strongly favor monophyly for Heliodinidae as sampled here (Fig. 2, **node 3**; BP=100, all analyses), corroborating the re-definition of this family by Hsu and Powell (2005). Kyrki (1984) suggested four synapomorphies for heliodinids: in the adult, smooth scaling on the head and absence of the CuP vein in forewing; and in the pupa, strong lateral ridges and stiff, long lateral and dorsal bristles. Only the last trait, however, is limited to the re-defined Heliodinidae. In their cladistic analyses, Hsu and Powell (2005) found three additional synapomorphies: female apophyses anteriores with ventral branches originating from a fused medial sclerite; male tegumen greatly expanded posteriorly, forming a conical or tubular sclerotized sac; and the forewing M vein with two branches. Adult diurnality is another possible synapomorphy (Dugdale et al. 1998a). Our data strongly resolve two of the three nodes subtending the five heliodinid genera sampled and yield relationships among these genera that are entirely concordant with the morphological cladistic analysis of Hsu and Powell (2005). Heliodinidae are a widespread but primarily New World group of 13 genera and 69 described species (van Nieukerken et al., 2011). The larvae are variable in feeding habits, with most species feeding internally in leaves, stems or fruits, while others are externally-feeding leaf webbers, all on herbaceous plants. The great majority of records (>85%) are from Caryophyllales, primarily Nyctaginaceae (Hsu and Powell, 2005)).

The apparent sister group to Heliodinidae is the strongly supported pairing of *Bedellia* + *Scythropia* (Fig. 2, **node 1**), favored in all of our analyses, with bootstraps as high as 86% (8–27 gene nt123). This is an entirely new hypothesis. No morphological synapomorphies are apparent, but a search for these would be worthwhile, given the strength of the molecular evidence. Bedelliidae are often confused with Lyonetiidae or Gracillariidae (see Kuroko [1964] for detailed history). Heppner (2011) recently transferred *Philonome* and *Euprora* to Bedelliidae (Bedelliinae auct), but our analyses very strongly place these genera in Tineidae instead (Fig. 3). Kyrki (1984, 1990) maintained separate family status for *Bedellia.* The widespread contrasting view, that *Bedellia* constitutes a subfamily of Lyonetiidae (Kuroko, 1964; Kuznetzov et al., 1988; Seksyayeva, 1994; Heppner, 1998), is unsupported by clear morphological synapomorphies and is likewise strongly rejected by our analyses, including the AU test (Table 3, #12). Bedelliidae are a monogeneric, cosmopolitan group of 16 species, most diverse in the Old World (van Nieukerken et al., 2011). The larvae are leaf miners in herbaceous plants, with 70% of records from Convolvulaceae (Dugdale et al., 1998a).

The position of *Scythropia* has likewise been controversial. Kyrki (1990) suggested that it constitutes the first-diverging subfamily of Yponomeutidae, while others, such as Friese (1960), Moriuti (1977), and Heppner (1998), grouped this genus with Plutellidae. Our results strongly contradict all previous hypotheses about the systematic position of *Scythropia*. We are reluctant to combine it with Bedelliidae, given the current complete absence of morphological support for such a pairing, and therefore hereby elevate Scythropiinae to Scythropiidae **stat. rev.** Larvae of the single, Palearctic species, *Scythropia crataegella*, are initially leaf miners and subsequently feed externally in a communal web, on *Crataegus* and sometimes other woody Rosaceae (Dugdale et al. 1998a).

Relationships within the YYPGAL clade

The majority of yponomeutoid species belong to the provisional YYPGAL clade (Fig. 2, **node 17**). This group is monophyletic in all analyses except degen1, where it is only very weakly contradicted (BP<20; tree not shown). However, bootstrap support is moderate at best (BP = 77, rogue-pruned nt123). Limited support for this node may result in part from conflict among gene trees, as suggested by the fact that the bootstrap value for 8–27 genes is lower than that for 8 genes (67 vs. 72%). No grouping like the YYPGAL clade has been proposed previously, and no morphological synapomorphies are apparent.

Within the YYPGAL clade there are three main sub-clades, each with moderate or strong support: an ‘AL clade’ consisting of Argyresthiidae and Lyonetiidae (Fig. 2, **node 12**; maximum BP=76, rogue-pruned nt123); Yponomeutidae (Fig. 2, **node 18**; BP ≥ 97, all analyses); and a ‘YPG clade’ consisting of Ypsolophidae, Plutellidae and Glyphipterigidae (Fig. 2, **node 36**; BP ≥ 97, all analyses). Relationships among these three entities, however, are less clear. All analyses favor grouping of Yponomeutidae plus the YPG clade to the exclusion of the AL clade (Fig. 2, **node 35**), with the weakly supported exception of degen1. However, bootstrap support for this relationship never exceeds 65%, and is higher for 8 genes than for 8–27 (63 versus 56%), again suggesting the presence of inter-gene conflict.

Relationships within the AL clade

The AL clade (Fig. 2, **node 12**) comprises Argyresthiidae plus Lyonetiidae: Lyonetiinae. It is monophyletic in all of our analyses except degen1, where it is only very weakly contradicted (BP<20; tree not shown). However, bootstrap support is moderate at best (BP = 77, rogue-pruned nt123). Limited support for this node may result in part from conflict among gene trees, as suggested by the fact that the bootstrap value for 8–27 genes is lower than that for 8 genes (69 vs. 72%). Grouping of these two taxa has never been proposed previously, and no morphological synapomorphies are apparent. In view of all the evidence, we regard this clade as only provisionally established. However, Kyrki’s (1990) inclusion of Argyresthiidae as a subfamily of Yponomeutidae can be confidently ruled out.

Monophyly for Argyresthiidae as sampled here is very strongly supported (Fig. 2, **node 13**; BP=100, all analyses). The family had been thought to be monobasic, defined by unique features of the male genitalia including a laterally produced vinculum and sensilla ornaments on the socii (Dugdale et al., 1998a). Our results, however, very strongly favor inclusion of a well-supported clade of several Neotropical yponomeutoids (Fig. 2, **node 15**; BP=100, all analyses) that were originally assigned to, but later excluded from, Acrolepiinae (Gaedike, 1997). These species are morphologically divergent from typical *Argyresthia*, which will necessitate a reevaluation of the currently hypothesized argyresthiid synapomorphies. Argyresthiidae are a cosmopolitan group of 157 described species, most species-rich in the Holarctic. The larvae are typically leaf miners or borers in flower buds, seeds or twigs of trees and shrubs (Dugdale et al. 1998a). About half of the records are from conifers.

Monophyly of the subfamily Lyonetiinae as sampled here (Fig. 2, **node 13**), comprising two species each of *Lyonetia* and *Phyllobrostis,* is supported by all but one of our analyses, with bootstraps up to 92%, although the two genera are separated by several nodes in the degen1 tree (BP ≤ 64). A close relationship between *Lyonetia* and *Phyllobrostis*, to the exclusion of *Leucoptera* (Cemiostominae), was also supported by a cladistic analysis of morphology (Mey, 2006). Lyonetiinae are a cosmopolitan group of 5 genera and 67 described species (van Nieukerken et al., 2011). The larvae are typically leaf miners on woody dicots, of diverse families (Dugdale et al., 1998a).

The Cemiostominae, in contrast, are one of the most problematic groups in our study. *Perileucoptera*, our sole representative, was identified as a rogue taxon. Cemiostomines differ from Lyonetiinae in many features, e.g. in having shorter antennae, different forewing pattern elements, and spine-like setae on the adult abdomen, leading some authors (e.g. Börner, 1939; Gerasimov, 1952) to place them in their own family. Kyrki (1990), however, proposed uniting Cemiostominae and Lyonetiinae into a single family, citing as a possible synapomorphy the shared possession of an "eye cap" formed by scales on the antennal scape. Our molecular analyses nearly always separated the two subfamilies, excluding Cemiostominae but not Lyonetiinae from Yponomeutoidea, concordant with the view of Börner (1939). However, bootstrap support for Yponomeutoidea is modest at best except when *Perileucoptera* is excluded from the analysis, and support for alternative positions among the Gracillarioidea for *Perileucoptera* had very low support. Moreover, the four-gene nt123 analysis (Supplementary figure S2) grouped Lyonetiinae with Cemiostominae, albeit with very weak support. Finally, our AU test cannot reject the monophyly of Lyonetiinae + Cemiostominae as sampled here (Table 3: # 11). Mutanen et al. (2011) also failed to recover Cemiostominae (represented by *Leucoptera*) + Lyonetiinae. Their analysis places *Leucoptera* as sister group to *Atteva* with 76% bootstrap support. Given the weak and conflicting molecular evidence on the placement of *Perileucoptera*, we tentatively retain Cemiostominae as a subfamily of Lyonetiidae pending further investigation. Although the composition of this family remains in doubt, our results do strongly confirm Kyrki's (1984) placement of Lyonetiidae in or near Yponomeutoidea: both subfamilies fall within the strongly supported clade Yponomeutoidea + Gracillarioidea (Fig. 3, **node 67**; BP 85–97, all analyses). The Cemiostominae are a cosmopolitan group of about 6 genera and 120 described species; the larvae are typically leaf miners in woody dicots of diverse families (Dugdale et al. 1998a).

Composition of and relationships within Yponomeutidae

Different authors have hypothesized very different compositions for Yponomeutidae (Table 1). Our analyses very strongly support a circumscription of this family (Fig. 2, **node 18**; BP = 97–100, all analyses) that corresponds exactly to Yponomeutinae sensu Moriuti (1977). Moriuti (1977) proposed two synapomorphies for this group, the presence of spine-like setae on the adult abdominal tergites, and a seta V_1 on the larval head that is as large as a long tactile seta. Kyrki (1990; and see also Ulenberg, 2009), in contrast, assigned six subfamilies to Yponomeutidae, three of which are now the separate families Argyresthiidae, Attevidae and Praydidae (van Nieukerken et al., 2011). Kyrki's hypothesis for Yponomeutidae has gained little support even from other morphological studies (Dugdale et al., 1998a), and is soundly rejected by our AU test (Table 3: # 4). Yponomeutidae as delimited here are a cosmopolitan group of 32 genera and 297 described species, most diverse in the Palearctic. The larvae are usually communal leaf webbers, although some species of *Zelleria* mine pine needles (Dugdale et al., 1998a). A very diverse array of host families is used, mostly woody but some herbaceous.

Within his concept of Yponomeutinae, here treated as a family (Fig. 2, **node 18**), Moriuti (1977) recognized two tribes, Yponomeutini and Saridoscelini, which we treat as subfamilies. One of these, here treated as Saridoscelinae, was previously restricted to *Saridoscelis*. The molecular data, however, very strongly indicate that *Saridoscelis* is the sister group to *Eucalantica*, an yponomeutoid genus of previously unsettled position (Fig. 2, **node 20**; BP=100, all analyses). We therefore hereby re-define Saridoscelinae to include *Eucalantica*. Moriuti (1977), followed by Kyrki (1990) and Dugdale et al. (1998a), proposed two synapomorphies for *Saridoscelis*, a unique modification of the male 8th abdominal sternite, and the presence of three branches in the M vein of the hindwing. In *Eucalantica* the condition of the male 8th abdominal sternite is ambiguous; it may or may not share a derived modification with *Saridoscelis*. The number of hindwing M veins is sufficiently homoplasious in Yponomeutoidea that this character too is ambiguous evidence on the grouping of these two genera (J. Sohn, unpublished). Thus, further search is needed for morphological synapomorphies of the Saridoscelinae as here re-defined.

Within his concept of Yponomeutini, here treated as a subfamily, Moriuti (1977) recognized two subtribes, here treated as the tribes Yponomeutini and Niphonymphini. The molecular evidence on monophyly of Yponomeutinae as defined here is somewhat complex due to conflicting results regarding the position of our representative of Niphonymphini, *Thecobathra*. In the nt123 and nt123 partitioned analyses, *Thecobathra* groups with Saridoscelinae, but with weak support (Fig. 2, **node 19**; BP 51–59). On the other hand, analyses emphasizing non-synonymous change (degen1 and codon model) place it as sister group to Yponomeutini, with strong support (BP=82, degen1). Previous morphological studies have also supported monophyly for Niphonymphini + Yponomeutini, equivalent to Yponomeutidae sensu Friese (1960) and Yponomeutini sensu Moriuti (1977). The 8–27 gene degen1 result, being stronger and concordant with morphology, seems more persuasive than the nt123 placement for *Thecobathra*. We therefore provisionally recognize a subfamily Yponomeutinae composed of Niphonymphini + Yponomeutini.

Our analyses provide robust, consistent evidence on the initial divergences within Yponomeutini as sampled here. *Metanomeuta* branches off first (Fig. 2, **node 21**; BP=100, nt123), followed by *Paraswammerdamia* (Fig. 2, **node 22**; BP = 99, nt123). *Yponomeuta* is strongly paired with *Teinoptila* (Fig. 2, **node 23**; BP ≥94, all analyses), and relationships among the four sampled species of *Yponomeuta* (Fig. 2, **nodes 24, 25, 26**) are also very strongly resolved. The remaining Yponomeutini comprise an assemblage whose monophyly is weakly supported by nt123 (Fig. 2, **node 28**; BP=56, nt123) and weakly contradicted by degen1, which allies *Klausius* instead with *Teinoptila* + *Yponomeuta* (BP=57, tree not shown). The remainder of the assemblage (Fig. 2, **node 28**) divides into two strongly supported clades, one consisting of *Cedestis* + *Zelleria retiniella* (Fig. 2, **node 29**; BP=100, nt123), and the other (Fig. 2, **node 32**; BP=90, nt123) containing additional species of *Zelleria* plus three other genera, relationships among which are not clearly resolved. These results strongly contradict all previous hypotheses about relationships within Yponomeutini, including Kloet & Hincks (1945), Moriuti (1977), Heppner (1998) and Ulenberg (2009). In addition, our data provide strong evidence for polyphyly of *Zelleria* (Fig. 2, **nodes 30, 34**). Clearly there is much further work to be done on the systematics of Yponomeutini.

Relationships within the YPG clade

In our analyses, the sister group to Yponomeutidae consists of Ypsolophidae, Plutellidae and Glyphipterigidae. Grouping of the latter three families, the 'YPG clade', is very strongly supported (Fig. 2, **node 36**; BP = 98–100, all analyses). This clade has never been proposed previously, and no morphological synapomorphies are known. The basal split within the YPG clade, also very strongly supported, unites Plutellidae and Glyphipterigidae to the exclusion of Ypsolophidae (Fig. 2, **node 45**; BP ≥99, all analyses).

Monophyly of Ypsolophidae including *Ochsenheimeria* is very strongly supported by our data (Fig. 2, **node 37**; BP=100, all analyses). A similar result was reported by Mutanen et al. (2010). The enigmatic *Ochsenheimeria* group was long assigned to Tineoidea before Kyrki (1984) allied it with Yponomeutoidea. Kyrki (1990) proposed eight synapomorphies for Ypsolophidae including Ochsenheimeriinae: hindwing veins with Rs and M_1 stalked or coincident; male genitalia with tegumen deeply bilobed at the anterior margin; tuba analis membranous and densely setose; phallus with two cornuti or cornutal zones; female genitalia with long anterior and posterior apophyses; termination of ductus seminalis on ductus bursae close to ostium; signum elongate, band-like, usually with two transverse ridges; and, pupal cremaster without setae. Heppner's (1998) placement of Ochsenheimeriinae (raised to the family level) as sister group to all other yponomeutoids (Fig. 1B) is strongly rejected by our data. Our data likewise reject proposals by Moriuti (1977) and Heppner (1998) to merge Ypsolophidae minus Ochsenheimeriinae into Plutellidae.

Within Ypsolophidae sensu Kyrki, our data provide somewhat contradictory evidence on the basal split. In all analyses that include synonymous change, Ypsolophinae are monophyletic, excluding *Ochsenheimeria*, with very strong support (Fig. 2, **node 38**; BP= 100, nt123). In contrast, under degen1, *Ochsenheimeria* is nested two nodes deep within Ypsolophinae, as sister group to *Bhadorcosma*, with 68% bootstrap support, contradicting two groupings (Fig. 2, **nodes 38, 39**) that have ≥99% bootstrap under nt123. While the signal from nt123 is stronger, we cannot confidently rule out the hypothesis of a paraphyletic Ypsolophinae (Dugdale et al. 1998a) until this striking conflict is explained. Apart from the position of *Ochsenheimeria,* however, our data provide very strong resolution of all relationships within Ypsolophinae as sampled here (Fig. 2, **nodes 39, 40, 41**; BP = ≥99, nt123). *Ypsolopha* is always paraphyletic in our trees, with respect to either *Bhadorcosma* and *Ochsenheimeria* (degen1) or *Bhadorcosma* alone (all other analyses). Ypsolophidae are a cosmopolitan group of 5 genera and160 described species, most diverse in the Palearctic (van Nieukerken et al., 2011). The larvae of Ypsolophinae are most often leaf webbers on woody plants, of many different families, while those of Ochsenheimeriinae are leaf miners and borers in Poaceae, Cyperaceae and Juncaceae (Poales).

Relationships within the PG clade

A sister group relationship between Plutellidae and Glyphipterigidae, very strongly supported by our data (Fig. 2, **node 45**; BP ≥99, all analyses), has not been previously proposed. Given the exceptionally robust molecular evidence, a search for morphological synapomorphies seems warranted. Two possible candidates, hypothesized by Kyrki (1990; but see Dugdale et al. 1998a) to unite Plutellinae and Acrolepiinae (now part of Glyphipterigidae), are lamellae postvaginales of the female genitalia consisting of two setose lobes, and loosely meshed cocoons.

Our analyses provide strong and consistent support for monophyly of Plutellidae (Fig. 2, **node 42**; BP=93, nt123). Like Mutanen et al. (2010), we find that the so-called “mega-plutellids” of New Zealand and Tasmania, here represented by *Proditrix* and *Doxophyrtis*, are actually nested within Glyphipterigidae: Orthoteliinae, as sister group to *Orthotelia* (Fig. 2, **node 49**; BP=100, all analyses). Within Plutellidae sensu stricto (van Nieukerken et al. 2011) as sampled here, our data strongly support a basal split between a North Temperate “core” group consisting of *Plutella* and allies (Fig. 2, **node 44**; BP=100, all analyses), and a tropical lineage (Fig. 2, **node 43**; BP ≥93, all analyses) here represented by the Namibian *Deryaxenistis* and an undescribed genus from Mexico. The plutellid association for *Deryaxenistis*, previously tentative (Mey 2007, 2011a), is here strongly confirmed. We suspect that this tropical plutellid lineage is greatly under-explored. Its characterization will probably result in a new morphological definition for the family. Kyrki (1984) characterized Plutellidae in the restricted sense (*Plutella*-group auct) by male genitalia with curved gnathal processes surrounding the anal tube. This feature, however, is not found in the tropical clade, which may deserve subfamily status. Plutellidae are a cosmopolitan group of 48 genera and150 described species, most diverse in the Australoceanian region (van Nieukerken et al., 2011). The larvae are typically skeletonizing leaf webbers (Dugdale et al., 1998a). More than half of the host records are from Brassicales.

The monophyly of Glyphipterigidae is very strongly supported in all of our analyses (Fig. 2, **node 52**; BP=98, nt123) except degen1 and the codon model. The conflict concerns a newly-discovered, strongly-supported Neotropical clade of probable Orthoteliinae (Fig. 2, **node 47**; BP = 96, nt123). Under degen1, this clade branches off at the base of the PG clade in the ML tree, but with very weak support; the bootstrap value is actually higher (49%) for glyphipterigid monophyly. Like Mutanen et al. (2010), we find Glyphipterigidae to consist of three subfamilies, Glyphipteriginae, Acrolepiinae and Orthoteliinae. Previous hypotheses based on morphology have sometimes included both Glyphipteriginae and Orthoteliinae (Table 1), but never Acrolepiinae, which have been variously treated as a subfamily of Plutellidae (Kyrki, 1990) or as a family related to Lyonetiidae and Heliodinidae (Heppner, 1998). Morphological synapomorphies for Glyphipterigidae in the new sense (van Nieukerken et al., 2011) have yet to be discovered. Kyrki & Itämie (1986) and Kyrki (1990) proposed eight synapomorphies for Glyphipterigidae excluding Acrolepiinae. Three of these – antenna without a pecten, male genitalia without teguminal processes, and larva endophagous – are also common in Acrolepiinae. These traits are also widespread in other lepidopteran lineages, however, leaving their phylogenetic significance uncertain. Within Glyphipterigidae, our data very strongly group Acrolepiinae with Glyphipteriginae to the exclusion of Orthoteliinae (Fig. 2, **node 53**; BP ≥95, all analyses). Mutanen et al. (2010) reported a similar result.

Our analyses favor a broad concept of the formerly monobasic Orthoteliinae (Fig. 2, **node 46**) that includes both the New Zealand/Tasmanian "mega-plutellids" (Fig. 2, **node 50**), as proposed by Heppner (2005) and corroborated also by Mutanen et al. (2010), and an assemblage of undescribed genera and species from the Neotropical region. This definition of the subfamily is strongly supported (Fig. 2, **node 46**; 89≤BP≤93) by all analyses except degen1 and the codon model, which, as noted earlier, very weakly place a subclade of Neotropical species (Fig. 2, **node 47**) at the base of either Glyphipterigidae or the PG clade (BP <<50; trees not shown). No morphological synapomorphies are apparent for Orthoteliinae in the new sense.

Within Orthoteliinae, the "mega-plutellids" (Fig. 2, **node 50**) appear closely related to the monobasic Palearctic type genus *Orthotelia* (Fig. 2, **node 49**; BP= 100, all analyses), while the Neotropical fauna may prove to constitute the paraphyletic basal lineages of the subfamily. One undescribed genus from Chile ("CL67") is strongly supported as the nearest relative to the core group that includes *Orthotelia* (Fig. 2, **node 48**; 81 ≤BP ≤96, all analyses), while the remaining Neotropical exemplars form a strongly supported clade (Fig. 2, **node 47**; BP=96, nt123) that is sister group to all other orthoteliines. Further exploration of the Neotropical biodiversity of Orthoteliinae is clearly desirable. Within the mega-plutellid group (Fig. 2, **node 50**), no analysis yielded strong support for monophyly of *Proditrix* (Fig. 2, **node 51**; BP≤ 52, all analyses), while degen1 grouped *Doxophyrtis* + *Proditrix nielseni* to the exclusion of *P. gahniae*, with 86% bootstrap (denoted by dotted arrow in Fig. 2). Thus, *Proditrix* may be paraphyletic with respect to *Doxophyrtis*. The Orthoteliinae as here delimited contain 6 genera and 14 described species. The species with known hostplants are typically borers within monocots (>90% of host records).

Monophyly for Acrolepiinae is very strongly supported by our data (Fig. 2, **node 40**; BP=100, all analyses). Kyrki (1984) proposed four synapomorphies for acrolepiines (Dugdale et al. 1998a): reduction of the tegumen, teguminal processes, and gnathos; basal widening of the phallus; stalking of hindwing veins M_1+M_2; and stalking of hindwing veins M_3+CuA_1. However, the first of these, involving reduction of the tegumen, is also common in Glyphipteriginae. In addition, stalking of M_3+CuA_1 is found in *Sericostola* (Glyphipteriginae), though not in other glyphipterigine genera for which wing venation is known. Among Acrolepiinae as sampled here, our data strongly favor the grouping of *Acrolepiopsis* + *Digitivalva* (Fig. 2, **node 55**; BP=100, all analyses) to the exclusion of *Acrolepia* (Fig. 2, **node 56**; BP=87–100, all analyses). Acrolepiinae are a cosmopolitan group of 4 genera and 87 described species, most diverse in the Palearctic. The larvae are internal feeders in leaves, stems, flower buds and seeds of herbaceous plants, either monocots (*Acrolepiopsis*) or asterids (*Digitivalva*, *Acrolepia*).

Our analyses very strongly support monophyly for Glyphipteriginae as sampled here (Fig. 2, **node 57**; BP=100, all analyses). Kyrki & Itämie (1986) proposed three possible synapomorphies for Glyphipteriginae (Dugdale et al. 1998a): a conical male 8th abdominal segment with an enlarged tergum; a vestigial M-stem and CuP in the forewing venation; and approximation (not stalking) of hindwing veins M_3 and CuA_1. Dugdale et al. (1998a) note that adult diurnality and a characteristic rhythmic raising and lowering of the wings while at rest may be additional synapomorphies. All divergences within Glyphipteriginae as sampled here are strongly to very strongly supported by nt123 (Fig. 2, **nodes 57–62**; BP 80–100, nt123), and contradicted in only two instances, weakly, by degen1. In our tree, *Glyphipterix quadragintapunctata* is the sister group to a strongly supported clade comprising all remaining Glyphipteriginae including the four other *Glyphipterix* species sampled (Fig. 2, **node 58**; BP=100, all analyses). The two other genera sampled, *Diploschizia* and *Lepidotarphius,* each have sister groups consisting nearly or entirely of subsets of *Glyphipterix* species, rendering *Glyphipterix* paraphyletic with respect to both. According to Dugdale et al. (1998a), about two thirds of the species of glyphipterigines are placed in the cosmopolitan type genus, while many of the 20+ other genera are monobasic. Thus, *Glyphipterix* might prove paraphyletic with respect to other genera as well. Glyphipteriginae are a cosmopolitan group of 25 genera and 397 described species, most diverse in the Australoceanian and Oriental regions. The larvae are typically endophagous in the leaves or stems of commelinid monocots.

Host plant associations

Previous hypotheses about life history evolution and biogeography of Yponomeutoidea (e.g. Friese, 1960; Moriuti, 1977; Powell et al., 1998; Grimaldi and Engel, 2005; Ulenberg, 2009) have been few, and their evaluation has been hampered by the lack of a robust phylogeny. In this and the next section we review trends in these features in light of our molecular phylogeny, as summarized in Figures 6 and 7.

To characterize the evolution of larval host plant associations, we sought to assess the degree of conservatism with respect to the new ypnomeutoid phylogeny, of mode of feeding, diet breadth (diversity of plant taxa used by individual species), host plant growth form, and host plant taxon membership at the family level and above. We also sought to infer the ancestral conditions and evolutionary directionality of these traits, for Yponomeutoidea as a whole and for subgroups thereof.

Larval feeding mode in the broad sense of internal versus external feeding is strongly conserved at the subfamily level and family level in yponomeutoids (Figure 7). Of the 16 subfamily or family clades identified by our phylogeny, only two show substantial variation in this trait. In Heliodinidae, internal feeding is numerically dominant but several early branching are external feeders, possibly representing the ancestral habit (Hsu and Powell, 2005). In Yponomeutidae external feeding is nearly universal, whereas internal feeding, specifically mining in conifer needles, is restricted to several species of the derived genera *Zelleria* and *Cedestis* (Friese, 1960; Dugdale et al. 1998a). Despite this stability at the family and subfamily level, however, transitions between internal and external feeding are frequent enough to obscure the deeper-level history of this trait within Yponomeutoidea. For example, parsimony optimization across the entire phylogeny is unable to assign an unambiguous state to any ancestor below the family level (Figure 7). In this frequency of transition between internal and external feeding, Yponomeutoidea contrast strikingly with their nearest relatives, the possibly paraphyletic Gracillarioidea, within which internal feeding is universal.

Although here scored as “external feeding”, Scythropiidae (monospecific), as well as some species of Praydidae, Yponomeutidae, Heliodinidae and possibly other families, actually show an intermediate condition, in which initially leaf-mining larvae subsequently switch to become external leaf webbers. Analogous ontogenetic shifts from internal to external feeding are seen in a number of non-ditrysian groups as well (Powell et al., 1998), and may represent a pathway by which external feeding arises over evolutionary time as well. External feeding in yponomeutoids, as in most other so-called microlepidopterans, is not fully equivalent to that seen in Macroheterocera (sensu van Nieukerken et al. 2011), in that the larvae are not fully exposed, but rather concealed in some way, e.g. by leaf webbing. Nonetheless, given the multiple evolutionary transitions between internal and external feeding now identified, Yponomeutoidea offer promising material for further studies of the causes and consequences of this fundamental feature of evolution in Lepidoptera and other holometabolous insect phytophages (Winkler and Mitter, 2008).

A second aspect of yponomeutoid larval host use that shows striking phylogenetic conservatism is diet breadth. Oligophagy, defined as using plants of a single order, appears to be nearly universal, characterizing >96% of the 448 yponomeutoid species for which we found host records. Moreover, nearly all oligophagous yponomeutoids use only one plant family. We may be under-estimating the incidence of polyphagy, defined as using two or more plant orders, because for many species only a single host record exists. On the other hand, it also is possible that some of the 14 species that have been recorded from two or more plant families represent undetected host-specific sibling species complexes. Whatever the exact incidence of polyphagy in Yponomeutoidea turns out to be, it clearly seems to be dramatically less than that reported for many groups of Apoditrysia, particularly in Macroheterocera (Powell et al., 1998; Menken et al., 2009). Nonetheless, yponomeutoids, like many other insect herbivore clades in which individual species are mostly oligophagous, collectively use an enormous range of host plant families (see below). It may be that models of diversification of insect herbivore species and host associations that depend on plasticity of host use (e.g. Janz, 2011) are less applicable to clades of oligophages such as yponomeutoids than to lepidopteran groups with greater mean diet breadth.

A third phylogenetically conserved aspect of yponomeutid host use is growth form of the host plant. Nearly all of the 16 subfamily/family clades supported by our molecular analyses feed on either woody or herbaceous plants, but not both (Fig. 6). The main exceptions are in Plutellidae and Yponomeutini. Most Plutellidae feed on Brassicales or other herbaceous taxa, but eight species of *Chrysorthenches* have been recorded from Podocarpaceae. Most Yponomeutini feed on woody plants, but about 20% feed on herbaceous Saxifragales. Parsimony optimization of herbaceous versus woody plant use on the molecular phylogeny (see Figure 6), when the nearest outgroups, Gracillarioidea, are included, reconstructs an ancestral association with woody plants, followed by relatively few independent origins of herb feeding, in Yponomeutini, the HSB clade and the YPG clade.

Finally, association with particular plant families, orders or more inclusive clades is conserved to a variable but always obviously non-random extent, within and sometimes between the 16 major yponomeutoid clades. There is some suggestion that host-taxon conservatism is stronger among herb feeders than among woody plant feeders, as previously reported for other lepidopterans (Janz and Nylin, 1998; Menken et al., 2009). Most of the taxa with pronounced fidelity to single or closely-related plant families are herb feeders (Fig. 6). For example, Bedelliidae are nearly restricted to Convolvulaceae; Heliodinidae feed almost exclusively on Nyctaginaceae or other Caryophyllales; Ochsenheimeriinae are known only from Poales; and, the great majority of Glyphipteriginae feed on commelinid monocots.

Among woody-plant feeders, the only comparable example is Attevidae, which feed almost exclusively on Simaroubaceae. Larger woody-plant-feeding clades are typically spread across many plant families and orders, with several, most notably Argyresthiidae, Ypsolophinae and Yponomeutini, using conifers as well as angiosperms as hosts. The Lyonetiinae, for example are recorded from 17 plant families in 10 orders, belonging to major clades (APG III, 2009) including magnoliids, basal eudicot lineages, basal core eudicot lineages, rosids and asterids (Fig. 6). As with other woody-plant-feeding clades, they are most often associated with rosids, particularly Rosales and Fabales, orders that are especially characteristic of north temperate forests. A few woody-plant feeding clades or subclades thereof show unusually frequent association with particular plant clades. The most notable example is *Yponomeuta*, in which 29 of the 42 species with recorded hosts feed on Celastraceae. Several other genera of Yponomeutini also include species feeding on Celastraceae. Our phylogeny, in which the Celastraceae-restricted *Teinoptila* is strongly supported as the sister group to *Yponomeuta*, is consistent with the conclusion of Turner et al. (2010) that Celastraceae is the ancestral host for *Yponomeuta*. However, Celastraceae are unlikely to be the ancestral hosts for Yponomeutidae as a whole (contra Ulenberg, 2009), as neither Niphonymphini nor Saridoscelinae feed on this family.

Biogeography

Yponomeutoidea have been conventionally considered to be a primarily North Temperate group that is most diverse in the Palearctic region. Tabulation of the zoogeographical composition of the 16 tribe, subfamily and family clades supported by our phylogeny (Figure 7) suggests that this view needs modification.

It is indeed the case that in a majority of lineages, nine of 16, species diversity is highest in the Palearctic, equaling or exceeding 50% of total diversity in five of these. However, half of the lineages, eight of 16, are now known to be at least represented in all major zoogeographic regions. Four other yponomeutoid groups have more restricted distributions but are still widespread: Ypsolophinae are nearly absent from the Southern Hemisphere; Ochsenheimeriinae and Niphonymphini are restricted to the Old World; Attevidae are pantropical, extending into the Nearctic Region. Two groups show strongly disjunct distributions. In Saridoscelinae, one of the two genera occurs in the Palearctic and Oriental regions, whereas the other is restricted to the Nearctic and Neotropical regions. Orthoteliinae are found in the Australian region, in Europe, and as demonstrated here for the first time, in the Neotropical region. On-going taxonomic revisions in Ypsolophinae, Yponomeutini, and Argyresthiidae by the first author show that in these groups, Neotropical species diversity has been significantly underestimated. The same may hold true for tropical diversity of yponomeutoids in general.

Summary and conclusions

Phylogeny and classification.

Our molecular results offer substantial clarification of yponomeutoid relationships at multiple levels of classification:

(1) We find consistent support, rising to very strong (BP = 99%) when rogue taxa are removed, for monophyly of a concept of Yponomeutoidea close to that of Kyrki (1984, 1990).

(2) With one exception, our data are consistent with recognition of all 10 yponomeutoid families included in the classification of van Nieukerken et al. (2011), and strongly support monophyly for eight of the nine families for which multiple representatives were sampled. We also find strong support for recognition of an 11th family, Scythropiidae **stat. rev.**, which was previously subordinate within Yponomeutidae.

The chief remaining uncertainty about yponomeutoid family-level classification concerns the subfamily Cemiostominae of Lyonetiidae. Our sole cemiostomine, *Perileucoptera*, is grouped (albeit weakly) with Lyonetiinae in the four-gene nt123 analysis, but is excluded entirely from Yponomeutoidea in all other analyses, suggesting conflict among genes. Such conflict may also underlie the inability of our AU test to reject monophyly for *Perileucoptera* + Lyonetiinae for the full data set, and the identification of *Perileucoptera* as a rogue taxon by RogueNaRok. We leave Cemiostominae in Lyonetiidae until its position is clarified, by further taxon sampling and perhaps gene tree/species tree analysis.

(3) There is strong support for tribal and/or subfamily divisions within the three largest families, and for inter-generic relationships within all families for which two or more genera were sampled (Fig. 2).

(4) We present a new working hypothesis for relationships among yponomeutoid families (Fig. 2) in which 7 of 8 nodes have at least moderate support (BP ≥70), and 4 of 8 have strong support (BP ≥80), in one or more analyses. It differs markedly from, and fits our data decisively better than, all previous hypotheses.

Our proposed classification and phylogeny are summarized in the following phylogenetically indented list, in which each taxon is taken to be the sister group of all following taxa at the same level of indentation, provided there is no intervening taxon with lesser indentation. Asterisks denote levels of bootstrap support for our proposed supra-familial clades (*, **, *** = BP ≥ 70, 80, 90, respectively, in at least one analysis).

- Superfamily Yponomeutoidea
  - ‘YYPGAL Clade’*
    - ‘YYPG Clade’:
      - Family Yponomeutidae
        - Subfamily Yponomeutinae
          - Tribe Yponomeutini
          - Tribe Niphonymphini
        - Subfamily Saridoscelinae

- ‘YPG Clade’***:
  - Family Ypsolophidae
    - Subfamily Ypsolophinae
    - Subfamily Ochsenheimeriinae
  - ‘PG Clade’***:
    - Family Plutellidae
    - Family Glyphipterigidae
      - Subfamily Orthoteliinae
      - Subfamily Glyphipteriginae
      - Subfamily Acrolepiinae
- ‘AL Clade’*:
  - Family Argyresthiidae
  - Family Lyonetiidae
    - Subfamily Lyonetiinae
    - Subfamily Cemiostominae

‘PAHSB Clade’*:

- ‘PA Clade’**:
  - Family Attevidae
  - Family Praydidae
- ‘HSB Clade’***
  - Family Heliodinidae
  - Family Bedelliidae

Family Scythropiidae **stat. rev.**

Host associations.

Yponomeutoidea show notable conservatism on the new phylogeny with respect to four aspects of larval host plant use:

(1) **Internal versus external feeding** is strongly conserved at the family level, varying notably only within Heliodinidae and, to a much lesser extent, Yponomeutidae. Parsimony optimization on the molecular phylogeny (Figure 7) points to an internal feeding as the ancestral yponomeutoid condition, with external feeders arising several times independently. This transition may typically pass through an intermediate stage seen in several extant groups, in which larvae mine leaves in the first instar and subsequently switch to external feeding, living in a communal web and skeletonizing leaves.

(2) **Diet breadth** is remarkably conserved across yponomeutoids (Figure 7), with oligophagy, defined as using plants of a single order, characterizing 96% of all species with recorded hosts (albeit uncorrected for singleton records). Moreover, nearly all oligophagous yponomeutoids use only one plant family. It seems therefore possible that at least some of the 14 species that have been recorded from two or more plant families, whose rate of incidence is highest in Lyonetiinae (17%) and Ortholeliinae (20%), will prove to represent undetected host-specific sibling species complexes.

(3) **Growth form of host plants used** is also markedly conserved: with a few exceptions, the 16 family-group taxa supported by our phylogeny feed on

either woody plants or herbaceous plants, but not both (Fig. 6). Parsimony optimization of herbaceous versus woody plant use on the molecular phylogeny (Figure 6), when the nearest outgroups, Gracillarioidea, are included, reconstructs an ancestral association with woody plants, followed by several independent origins of herb feeding, in Yponomeutini, the HSB clade and the YPG clade.

(4) **Taxonomic affinity of host plants used**, at the level of plant family, order or more inclusive clade is conserved to a variable but always notable extent within each of the 16 family-group yponomeutoid clades (Figure 7). Most of the clades that are restricted mainly to a single plant family or order are herb feeders; woody plant feeders appear to shift somewhat more readily among plant orders, albeit typically within the rosid plant clade.

Given these strong initial phylogenetic patterns, yponomeutoids appear to provide promising material for future more detailed studies of the evolution and evolutionary consequences of host plant use in early-diverging ditrysian Lepidoptera.

Biogeography.

Our tabulation of yponomeutoid distributions in light of the molecular phylogeny shows that Yponomeutoidea are considerably more diverse outside the Palearctic than has previously been appreciated. Half (8) of the 16 family-group clades supported here are now known to occur in all major zoogeographic regions. The known distribution is expanded most markedly by our findings for two groups: Plutellidae, in which the North Temperate “core” group is shown to have a tropical sister lineage; and, the formerly monobasic, exclusively Palearctic Orthoteliinae, which are shown to include both Australoceanic and Neotropical lineages. From these results, in conjunction with recent revisionary studies, it seems likely that tropical and southern continent biodiversity of Yponomeutoidea, particularly that of the Neotropical Region, has been heretofore considerably under-estimated.

Table 1. Previous classifications of Yponomeutoidea. Nomenclature follows the original. Families are indicated in bold.

Common (1970)	Moriuti (1977)	Heppner (1998)	Kyrki (1990)	van Nieukerken et al. (2011)
Yponomeutidae Plutellinae Yponomeutinae Amphitherinae Argyresthinae **Glyphipterigidae** **Heliodinidae** **Aegeriidae** **Douglasiidae** **Epermeniidae**	**Yponomeutidae** Yponomeutinae Yponomeutini Yponomeutina Niphonymphina Saridoscelini Praydinae Plutellinae Scythropiini Plutellini **Argyresthiidae**	**Yponomeutidae** Yponomeutinae Saridoscelinae Cedestinae **Attevidae** **Argyresthiidae** **Plutellidae** Ypsolophinae Plutellinae Scythropiinae Praydinae **Acrolepiidae** **Ochsenheimeriidae** **Glyphipterigidae** Orthoteliinae Glyphipteriginae **Heliodinidae** **Lyonetiidae** Cemiostominae Lyonetiinae Bedelliinae	**Yponomeutidae** Yponomeutinae Saridoscelinae Scythropiinae Attevinae Praydinae Argyresthiinae **Plutellidae** Plutellinae Acrolepiinae **Ypsolophidae** Ypsolophinae Ochsenheimeriinae **Glyphipterigidae** Orthoteliinae Glyphipteriginae **Heliodinidae** **Lyonetiidae** Cemiostominae Lyonetiinae **Bedelliidae**	**Yponomeutidae** Yponomeutinae Saridoscelinae Scythropiinae **Attevidae** **Praydidae** **Argyresthiidae** **Plutellidae** **Ypsolophidae** Ypsolophinae Ochsenheimeriinae **Glyphipterigidae** Acrolepiinae Orthoteliinae Glyphipteriginae **Heliodinidae** **Lyonetiidae** Cemiostominae Lyonetiinae **Bedelliidae**

Table 2. Rogue taxa identified by the RogueNaRok (RNR) analyses, listed in the order in which they were identified and removed. The RBIC (relative bipartition information content) for the reduced consensus tree, after pruning all taxa up to and including any given rogue taxon, is shown in the last column. Ingroup rogue taxa are shown in bold.

Rogue taxon set*	Rogue taxon	Code name	SC** (%)	Raw Improvement***	RBIC
A	*Copromorpha* sp.	Cmpa	12	0.906667	0.767598
	Xyrosaris lichneuta	Xlic	29.2	0.74	0.773039
	Cycloplasis panicifoliella	Cpan	26.2	0.666667	0.777941
	Hybroma servulella	Hybs	67.0	0.58	0.782206
	Epermenia sinjovi	Esji	30.6	0.26	0.784118
	Philonome clemensella	Pmsa	26.7	0.246667	0.785931
	Opogona thiadelia	Othi	64.1	0.113333	0.786765
	Emmelina monodactyla	Emon	86.9	0.093333	0.787451
	Klimeschia transversella	Ktr	66.4	0.906667	0.794118
	Hemerophila felis	Hfel	90.8	0.186667	0.79549
	Nemapogon cloacella	Nclo	55.1	0.013333	0.795588
B	*Narycia duplicella*	Nard	34.1	0.373333	0.867413
	Euclemensia bassettella	Cole	81.6	0.146667	0.868587
	Bucculatrix sp.	Bucc	56.9	0.033333	0.868853
C	*Homadaula anisocentra*	Hani	64.7	0.82	0.870656
	"*Wockia*" sp.	MX60	19.1	0.2	0.879016
D	***Perileucoptera coffeella***	Leuco	43.2	0.12	0.874545
	Swammerdamia glaucella	Swgl	33.7	0.046667	0.875076

* Rogue taxon sets = rogue taxa identified on each successive one-at-a-time pass through the taxa. Each such pass, after the first pass, starts from a reduced taxon set from which all previously-identified rogues have been removed. Following the removal of rogue taxon sets A–C, no further rogue taxa could be identified in the entire data set. Rogue taxon set D was identified in an independent analysis of just Yponomeutoidea + Gracillarioidea, excluding other outgroups.

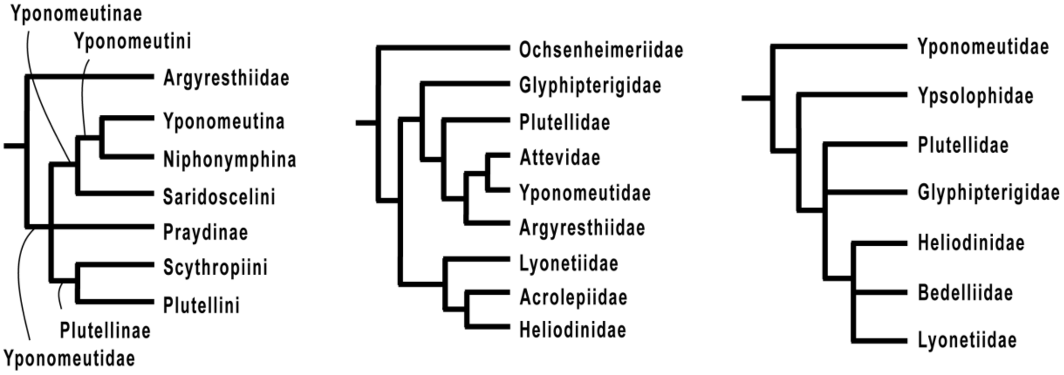
A: 139 taxa x 8–27 genes. Initial score = 0.760931, # of partitions in reduced consensus tree = 973
B: 128 taxa (11 rogue taxa deleted from A). Initial score = 0.864427, # of partitions = 443
C: 125 taxa (3 rogue taxa deleted from B). Initial score = 0.870656, # of partitions = 337
D: 91 taxa (Yponomeutoidea+Gracillarioidea). Initial score = 0.873182, # of partitions = 272
** SC (sequence data completeness) = (# of nucleotides actually sequenced/ total # of targeted nucleotides) x 100
***Raw Improvement: the improvement in support (sum of all bootstrap values) for the reduced consensus tree, if the taxon in question is pruned AND all previously identified rogue taxa are also pruned.

Table 3. Results of Approximately Unbiased (AU) tests for significance of rejection of 12 previous phylogenetic hypotheses. All analyses are based on the 8–27 gene nt123 and degen1 data sets. P values < 0.05 in bold.

#	Constraint group	Source	nt123 (*p*)	degen1 (*p*)
1	Yponomeutoidea *sensu* Kyrki (Fig. 1)	Kyrki (1990)	**0.001**	**<0.001**
2	Yponomeutoidea *sensu* Heppner (Fig. 1)	Heppner (1998)	**<0.001**	**<0.001**
3	Yponomeutidae s. l. (Fig. 1)	Moriuti (1977)	**<0.001**	**<0.001**
4	Yponomeutidae *sensu* Kyrki (Table 1)	Kyrki (1990)	**<0.001**	**<0.001**
5	Cedestinae	Friese (1960)	**<0.001**	**0.002**
6	Yponomeutidae B1 group	Friese (1960)	**0.001**	**0.001**
7	Plutellidae+Praydidae	Heppner (1998)	**<0.001**	**<0.001**
8	Plutellidae+*Scythropia*	Heppner (1998)	**<0.001**	**0.002**
9	Plutellidae *sensu* Heppner (Table 1)	Heppner (1998)	**<0.001**	**<0.001**
10	#9+*Ochsenheimeria*	Heppner (1998)	**<0.001**	**<0.001**
11	Lyonetiinae+Cemiostominae	Kyrki (1990)	0.259	0.180
12	Lyonetiidae+Bedelliidae	Kuroko (1964)	**0.005**	**0.005**

Table 4. Bootstrap supports for selected clades. Dashes indicate unrecovered clades. Node numbers corresponding to Figure 2 (a & b for alternative topologies).

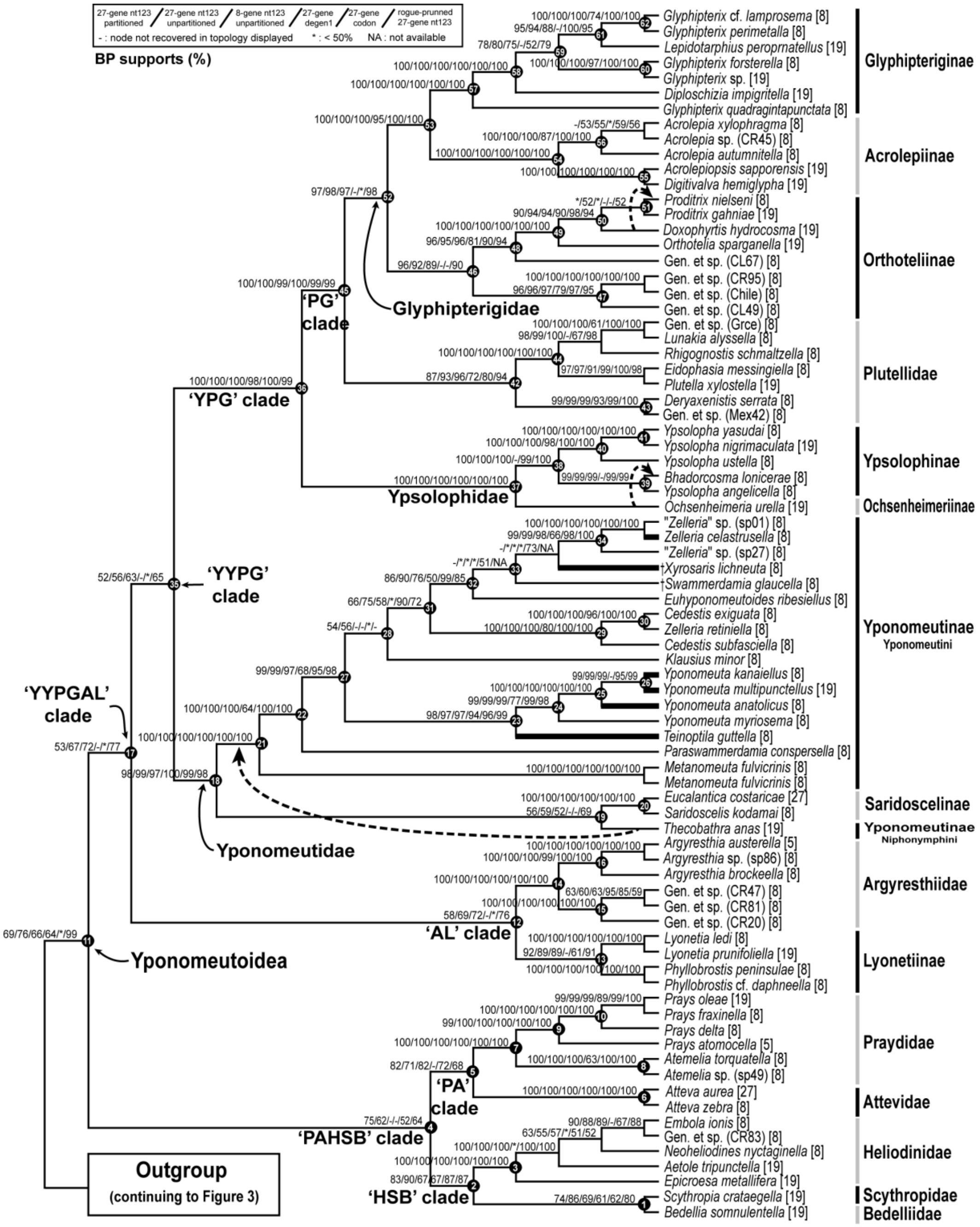
Node #	Selected Clade	4-gene nt123	8-gene nt123	8–27 gene nt123	8–27 gene partition	8–27 gene degen1	8–27 gene Codon	8–27 gene & no-rogue nt123
1	*Bedellia*+*Scythropia*	<50	69	86	74	61	62	80
2	‘H·S·B’ clade	56	67	90	83	67	87	87
3	Heliodinidae	100	100	100	100	100	100	100
4	‘P·A·H·S·B’ clade	–	–	62	75	–	52	64
5	‘P·A’ clade	96	82	71	82	–	72	68
6	Attevidae	100	100	100	100	100	100	100
7	Praydidae	100	100	100	100	100	100	100
8	*Atemelia*	100	100	100	100	100	100	100
9	*Prays*	89	100	100	99	100	100	100
11	Yponomeutoidea (excl. Cemiostomiinae)	–	66	76	69	64	<50	99
12	‘A·L’ clade	–	72	69	58	–	<50	76
13	Lyonetiidae (Lyonetiinae)	89	89	89	92	–	61	91
14	Argyresthiidae	100	100	100	100	100	100	100
15	“*Dasycarea*” group	100	100	100	100	100	100	100
16	*Argyresthia*	100	100	100	100	100	100	100
17	‘Y·Y·P·G·A·L’ clade	–	72	67	53	–	<50	77
18	Yponomeutidae	98	97	99	98	100	99	98
19	Saridoscelinae+*Thecobathra*	<50	52	59	56	–	–	69
20	Saridoscelinae	100	100	100	100	100	100	100
21a	Yponomeutini	100	100	100	100	100	100	100
21b	Yponomeutini+ *Thecobathra*	–	–	–	–	82	52	–
23	*Yponomeuta* group	99	97	97	98	94	96	99
29	*Cedestis*+*Zelleria* (part)	100	100	100	100	80	100	100
31	Node 29+32	–	58	75	66	<50	90	72
32	*Zelleria* (part)+*Xyrosaris*+*Swammerdamia*+*Euhyponomeutoides*	–	76	90	86	50	99	85
35	‘Y·Y·P·G’ clade	–	63	56	52	–	<50	65
36	‘Y·P·G’ clade	96	100	100	100	98	100	99
37	Ypsolophidae	100	100	100	100	100	100	100
38	Ypsolophinae	100	100	100	100	–	99	100
39	*Bhadorcosma*+*Ypsolopa angelicella*	96	99	99	99	–	99	99
42	Plutellidae	92	96	93	87	72	80	94
43	*Deryaxenistis* group	97	99	99	99	93	99	100
44	Core Plutellidae	100	100	100	100	100	100	100
45	‘P·G’ clade	95	99	100	100	100	99	99
46	Orthoteliinae	86	89	92	96	–	–	90
47	Neotropical Orthoteliinae	99	96	96	97	79	97	95
48	Core Orthoteliinae	90	96	95	96	81	90	94
51a	*Proditrix*	<50	<50	52	<50	–	–	52
51b	*Doxophytis*+*Proditrix nielseni*	–	–	–	–	86	56	–
52	Glyphipterigidae	98	97	98	97	–	<50	98
53	Glyphipteriginae+Acrolepiinae	96	100	100	100	95	100	100
54	Acrolepiinae	100	100	100	100	100	100	100
57	Glyphipteriginae	100	100	100	100	100	100	100
59	*Glyphipterix* (part)+*Lepidotarphius*	–	75	80	78	–	52	79



A. Moriuti (1977) B. Heppner (1998) C. Kyrki (1990)

Figure 1. Previous hypotheses of phylogenetic relationships in Yponomeutoidea. A. Moriuti (1977), B. Heppner (1998), C. Kyrki (1990). All figures are redrawn with nomenclature following the original.

Figure 2. The best ML tree found for nt123 analysis of the deliberately incomplete 8–27 gene, 139-taxon data set, showing Yponomeutoidea only. Bootstrap supports shown above branches: partitioned 8–27 gene nt123/unpartitioned 8–27 gene nt123/8-gene nt123/8–27 gene degen1/8–27 gene codon model/rogue-pruned 8–27 gene nt123 (121 taxa). ‘-’ = node not recovered in the ML tree for that analysis. ‘*’= bootstrap value <50%. ‘NA’= bootstrap value undefined because data were obtained for ≤ 1 taxon in that clade for that analysis. Dotted lines indicate alternative topologies strongly supported by either degen1 or the codon model. Node numbers for selected nodes (solid circles) are provided to facilitate discussion. Thickened terminal branches denote yponomeutoid species feeding on Celastraceae.


27-gene nt123 partitioned / 27-gene nt123 unpartitioned / 8-gene nt123 unpartitioned / 27-gene degen1 / 27-gene codon / rogue-prunned 27-gene nt123
- : node not recovered in topology displayed
* : < 50%
NA : not available
BP supports (%)
100/100/100/74/100/100
95/94/88/-/100/95
78/80/75/-/52/79
100/100/100/97/100/100
100/100/100/100/100/100
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100/100/100/95/100/100
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100/100/100/87/100/100
100/100/100/100/100/100
100/100/100/100/100/100
97/98/97/-/*/98
/52//-/-/52
90/94/94/90/98/94
100/100/100/100/100/100
96/95/96/81/90/94
96/92/89/-/-/90
100/100/100/100/100/100
96/96/97/79/97/95
100/100/99/100/99/99
100/100/100/61/100/100
98/99/100/-/67/98
100/100/100/100/100/100
97/97/91/99/100/98
87/93/96/72/80/94
99/99/99/93/99/100
100/100/100/98/100/99
100/100/100/100/100/100
100/100/100/98/100/100
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100/100/100/80/100/100
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99/99/99/-/95/99
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100/100/100/100/100/100
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53/67/72/-/*/77
98/99/97/100/99/98
100/100/100/100/100/100
100/100/100/100/100/100
56/59/52/-/-/69
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99/100/100/100/100/100
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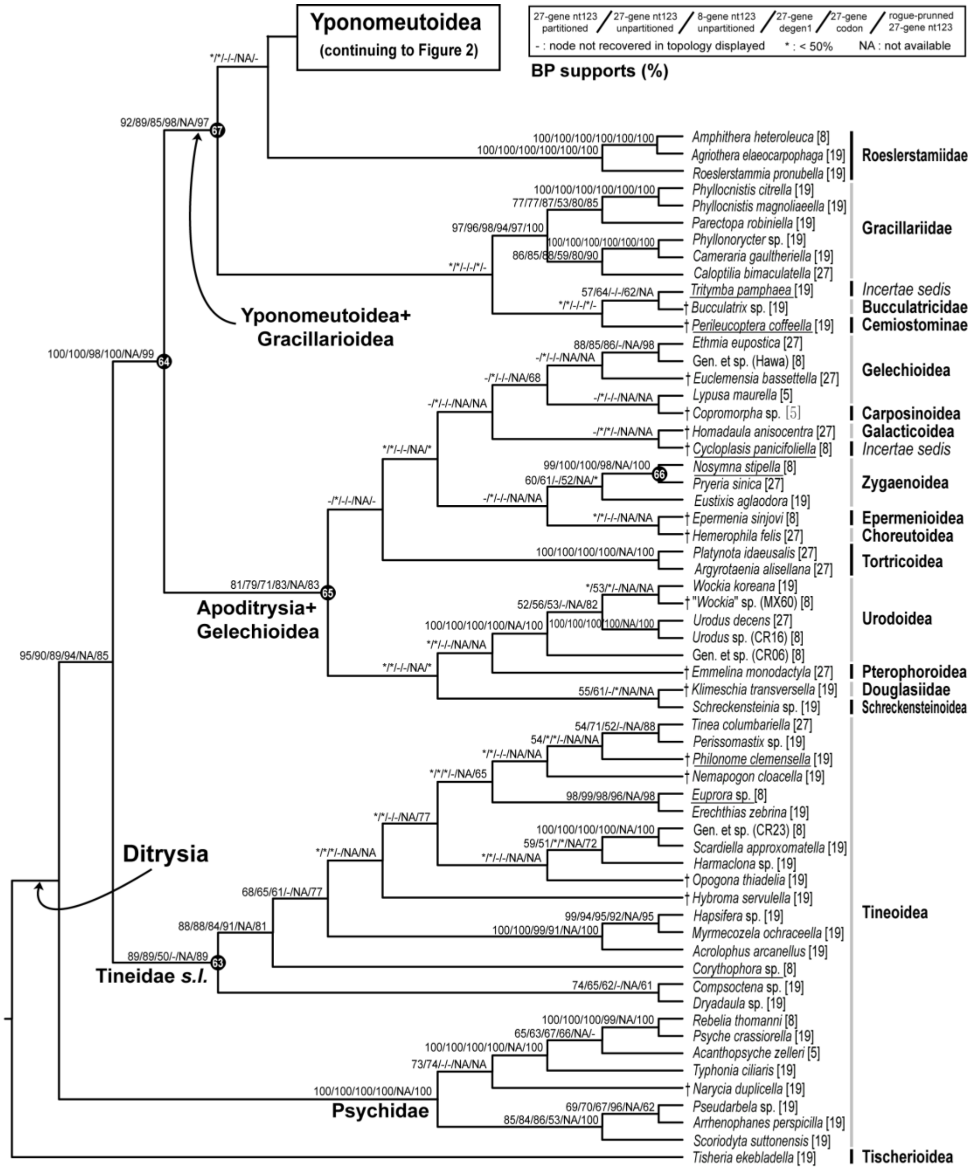
100/100/100/*/100/100
100/100/100/100/100/100
83/90/67/67/87/87
74/86/69/61/62/80
Glyphipterix cf. lamprosema [8]
Glyphipterix perimetalla [8]
Lepidotarphius peroprnatellus [19]
Glyphipterix forsterella [8]
Glyphipterix sp. [19]
Diploschizia impigritella [19]
Glyphipterix quadragintapunctata [8]
Acrolepia xylophragma [8]
Acrolepia sp. (CR45) [8]
Acrolepia autumnitella [8]
Acrolepiopsis sapporensis [19]
Digitivalva hemiglypha [19]
Proditrix nielseni [8]
Proditrix gahniae [19]
Doxophyrtis hydrocosma [19]
Orthotelia sparganella [19]
Gen. et sp. (CL67) [8]
Gen. et sp. (CR95) [8]
Gen. et sp. (Chile) [8]
Gen. et sp. (CL49) [8]
Gen. et sp. (Grce) [8]
Lunakia alyssella [8]
Rhigognostis schmaltzella [8]
Eidophasia messingiella [8]
Plutella xylostella [19]
Deryaxenistis serrata [8]
Gen. et sp. (Mex42) [8]
Ypsolopha yasudai [8]
Ypsolopha nigrimaculata [19]
Ypsolopha ustella [8]
Bhadorcosma lonicerae [8]
Ypsolopha angelicella [8]
Ochsenheimeria urella [19]
"Zelleria" sp. (sp01) [8]
Zelleria celastrusella [8]
"Zelleria" sp. (sp27) [8]
†Xyrosaris lichneuta [8]
†Swammerdamia glaucella [8]
Euhyponomeutoides ribesiellus [8]
Cedestis exiguata [8]
Zelleria retiniella [8]
Cedestis subfasciella [8]
Klausius minor [8]
Yponomeuta kanaiellus [8]
Yponomeuta multipunctellus [19]
Yponomeuta anatolicus [8]
Yponomeuta myriosema [8]
Teinoptila guttella [8]
Paraswammerdamia conspersella [8]
Metanomeuta fulvicrinis [8]
Metanomeuta fulvicrinis [8]
Eucalantica costaricae [27]
Saridoscelis kodamai [8]
Thecobathra anas [19]
Argyresthia austerella [5]
Argyresthia sp. (sp86) [8]
Argyresthia brockeella [8]
Gen. et sp. (CR47) [8]
Gen. et sp. (CR81) [8]
Gen. et sp. (CR20) [8]
Lyonetia ledi [8]
Lyonetia prunifoliella [19]
Phyllobrostis peninsulae [8]
Phyllobrostis cf. daphneella [8]
Prays oleae [19]
Prays fraxinella [8]
Prays delta [8]
Prays atomocella [5]
Atemelia torquatella [8]
Atemelia sp. (sp49) [8]
Atteva aurea [27]
Atteva zebra [8]
Embola ionis [8]
Gen. et sp. (CR83) [8]
Neoheliodines nyctaginella [8]
Aetole tripunctella [19]
Epicroesa metallifera [19]
Scythropia crataegella [19]
Bedellia somnulentella [19]
Glyphipteriginae
Acrolepiinae
Orthoteliinae
Plutellidae
Ypsolophinae
Ochsenheimeriinae
Yponomeutinae
Yponomeutini
Saridoscelinae
Yponomeutinae
Niphonymphini
Argyresthiidae
Lyonetiinae
Praydidae
Attevidae
Heliodinidae
Scythropidae
Bedelliidae
Glyphipterigidae
'PG' clade
'YPG' clade
Ypsolophidae
'YYPG' clade
'YYPGAL' clade
Yponomeutidae
'AL' clade
Yponomeutoidea
'PA' clade
'PAHSB' clade
'HSB' clade
Outgroup
(continuing to Figure 3)

Figure 3. The best ML tree found for nt123 analysis of the deliberately incomplete 8–27 gene, 139-taxon data set (continued from Fig. 2), showing outgroups only. See Figure 2 for notes on bootstrap supports and node numbers. Terminal taxa shown in pink were initially thought to be yponomeutoids.


Yponomeutoidea
(continuing to Figure 2)
27-gene nt123 partitioned / 27-gene nt123 unpartitioned / 8-gene nt123 unpartitioned / 27-gene degen1 / 27-gene codon / rogue-pruned 27-gene nt123
- : node not recovered in topology displayed
* : < 50%
NA : not available
BP supports (%)
//-/-/NA/-
92/89/85/98/NA/97
67
100/100/100/100/100/100
100/100/100/100/100/100
Amphithera heteroleuca [8]
Agriothera elaeocarpophaga [19]
Roeslerstammia pronubella [19]
Roeslerstamiidae
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77/77/87/53/80/85
Phyllocnistis citrella [19]
Phyllocnistis magnoliaeella [19]
Parectopa robiniella [19]
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Phyllonorycter sp. [19]
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Cameraria gaultheriella [19]
Caloptilia bimaculatella [27]
Gracillariidae
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57/64/-/-/62/NA
Tritymba pamphaea [19]
Incertae sedis
//-/-/*/-
† Bucculatrix sp. [19]
Bucculatricidae
† Perileucoptera coffeella [19]
Cemiostominae
Yponomeutoidea+
Gracillarioidea
100/100/98/100/NA/99
64
88/85/86/-/NA/98
Ethmia eupostica [27]
-/*/-/-/NA/NA
Gen. et sp. (Hawa) [8]
-/*/-/-/NA/68
† Euclemensia bassettella [27]
Gelechioidea
-/*/-/-/NA/NA
Lypusa maurella [5]
-/*/-/-/NA/NA
† Copromorpha sp. [5]
Carposinoidea
-/*/*/-/NA/NA
† Homadaula anisocentra [27]
Galacticoidea
† Cycloplasis panicifoliella [8]
Incertae sedis
//-/-/NA/*
99/100/100/98/NA/100
Nosymna stipella [8]
66
60/61/-/52/NA/*
Pryeria sinica [27]
Zygaenoidea
-/*/-/-/NA/NA
Eustixis aglaodora [19]
-/*/-/-/NA/-
//-/-/NA/NA
† Epermenia sinjovi [8]
Epermenioidea
† Hemerophila felis [27]
Choreutoidea
100/100/100/100/NA/100
Platynota idaeusalis [27]
Argyrotaenia alisellana [27]
Tortricoidea
81/79/71/83/NA/83
65
Apoditrysia+
Gelechioidea
/53//-/NA/NA
Wockia koreana [19]
52/56/53/-/NA/82
† "Wockia" sp. (MX60) [8]
100/100/100/100/NA/100
100/100/100/100/NA/100
Urodus decens [27]
Urodus sp. (CR16) [8]
Gen. et sp. (CR06) [8]
Urodoidea
//-/-/NA/NA
//-/-/NA/*
† Emmelina monodactyla [27]
Pterophoroidea
55/61/-/*/NA/NA
† Klimeschia transversella [19]
Douglasiidae
Schreckensteinia sp. [19]
Schreckensteinoidea
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Tinea columbariella [27]
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Perissomastix sp. [19]
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† Philonome clemensella [19]
//*/-/NA/65
† Nemapogon cloacella [19]
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Erechthias zebrina [19]
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Gen. et sp. (CR23) [8]
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Scardiella approxomatella [19]
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//-/-/NA/NA
Harmaclona sp. [19]
† Opogona thiadelia [19]
Ditrysia
† Hybroma servulella [19]
68/65/61/-/NA/77
99/94/95/92/NA/95
Hapsifera sp. [19]
100/100/99/91/NA/100
Myrmecozela ochraceella [19]
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Acrolophus arcanellus [19]
Tineoidea
Corythophora sp. [8]
89/89/50/-/NA/89
63
Tineidae s.l.
74/65/62/-/NA/61
Compsoctena sp. [19]
Dryadaula sp. [19]
100/100/100/99/NA/100
Rebelia thomanni [8]
65/63/67/66/NA/-
Psyche crassiorella [19]
100/100/100/100/NA/100
Acanthopsyche zelleri [5]
73/74/-/-/NA/NA
Typhonia ciliaris [19]
100/100/100/100/NA/100
† Narycia duplicella [19]
69/70/67/96/NA/62
Pseudarbela sp. [19]
Psychidae
85/84/86/53/NA/100
Arrhenophanes perspicilla [19]
Scoriodyta suttonensis [19]
Tisheria ekebladella [19]
Tischerioidea

Figure 4. Phylogram representation of ML tree shown in Figures 2 and 3. Branch lengths are proportional to total number of substitutions per site. Thickened branches are supported by ≥70% bootstrap in at least one analysis summarized in Figures 2 and 3.

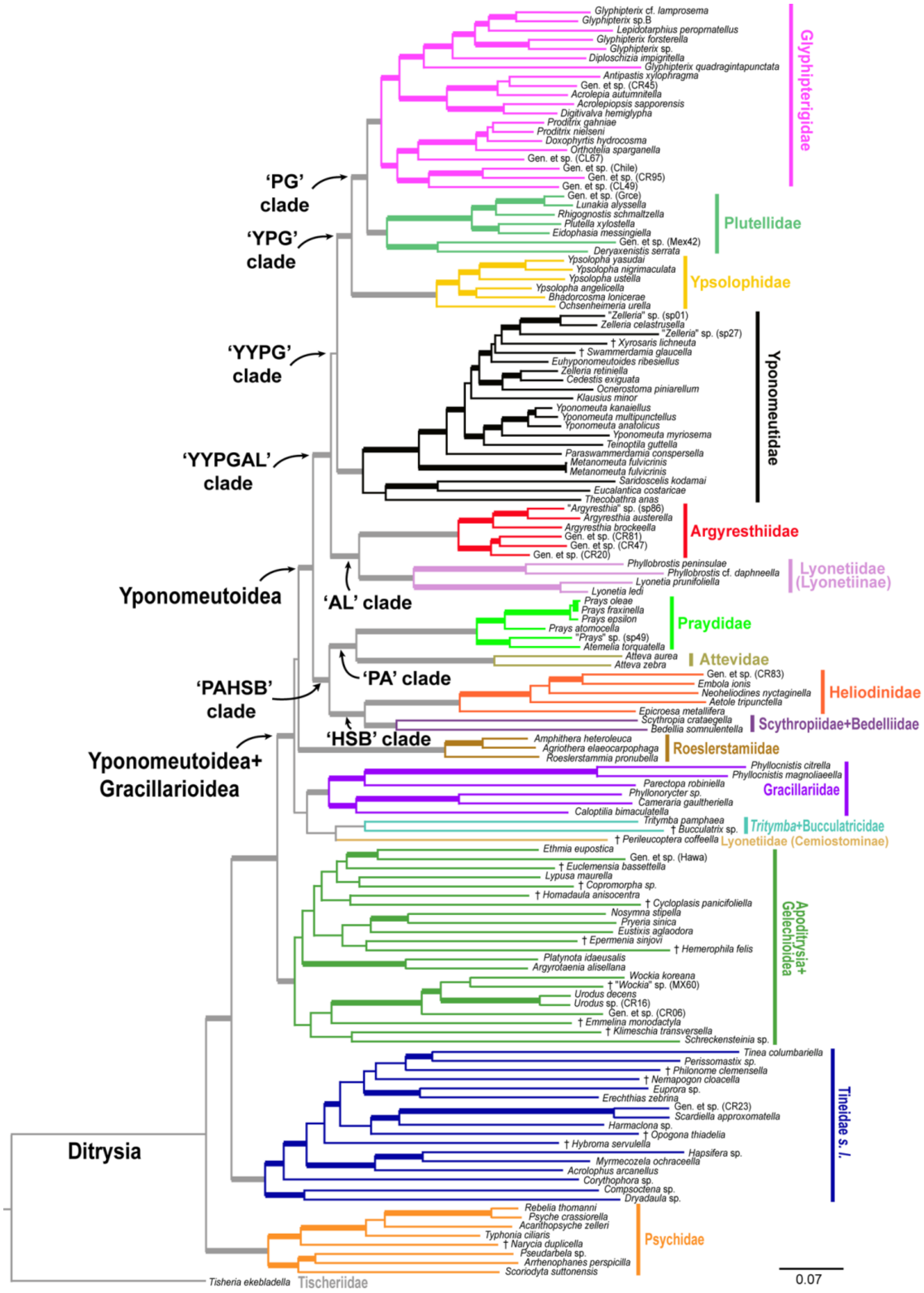

Glyphipterix cf. lamprosema
Glyphipterix sp.B
Lepidotarphius perornatellus
Glyphipterix forsterella
Glyphipterix sp.
Diploschizia impigritella
Glyphipterix quadragintapunctata
Antipastis xylophragma
Gen. et sp. (CR45)
Acrolepia autumnitella
Acrolepiopsis sapporensis
Digitivalva hemiglypha
Proditrix gahniae
Proditrix nielseni
Doxophyrtis hydrocosma
Orthotelia sparganella
Gen. et sp. (CL67)
Gen. et sp. (Chile)
Gen. et sp. (CR95)
Gen. et sp. (CL49)
Glyphipterigidae
Gen. et sp. (Grce)
Lunakia alyssella
Rhigognostis schmaltzella
Plutella xylostella
Eidophasia messingiella
Gen. et sp. (Mex42)
Deryaxenistis serrata
Plutellidae
Ypsolopha yasudai
Ypsolopha nigrimaculata
Ypsolopha ustella
Ypsolopha angelicella
Bhadorcosma lonicerae
Ochsenheimeria urella
Ypsolophidae
"Zelleria" sp. (sp01)
Zelleria celastrusella
"Zelleria" sp. (sp27)
† Xyrosaris lichneuta
† Swammerdamia glaucella
Euhyponomeutoides ribesiellus
Zelleria retiniella
Cedestis exiguata
Ocnerostoma piniarellum
Klausius minor
Yponomeuta kanaiellus
Yponomeuta multipunctellus
Yponomeuta anatolicus
Yponomeuta myriosema
Teinoptila guttella
Paraswammerdamia conspersella
Metanomeuta fulvicrinis
Metanomeuta fulvicrinis
Saridoscelis kodamai
Eucalantica costaricae
Thecobathra anas
Yponomeutidae
"Argyresthia" sp. (sp86)
Argyresthia austerella
Argyresthia brockeella
Gen. et sp. (CR81)
Gen. et sp. (CR47)
Gen. et sp. (CR20)
Argyresthiidae
Phyllobrostis peninsulae
Phyllobrostis cf. daphneella
Lyonetia prunifoliella
Lyonetia ledi
Lyonetiidae (Lyonetiinae)
Prays oleae
Prays fraxinella
Prays epsilon
Prays atomocella
"Prays" sp. (sp49)
Atemelia torquatella
Praydidae
Atteva aurea
Atteva zebra
Attevidae
Gen. et sp. (CR83)
Embola ionis
Neoheliodines nyctaginella
Aetole tripunctella
Epicroesa metallifera
Heliodinidae
Scythropia crataegella
Bedellia somnulentella
Scythropiidae+Bedelliidae
Amphithera heteroleuca
Agriothera elaeocarpophaga
Roeslerstammia pronubella
Roeslerstamiidae
Phyllocnistis citrella
Phyllocnistis magnoliaeella
Parectopa robiniella
Phyllonorycter sp.
Cameraria gaultheriella
Caloptilia bimaculatella
Gracillariidae
Tritymba pamphaea
† Bucculatrix sp.
Tritymba+Bucculatricidae
† Perileucoptera coffeella
Lyonetiidae (Cemiostominae)
Ethmia eupostica
Gen. et sp. (Hawa)
† Euclemensia bassettella
Lypusa maurella
† Copromorpha sp.
† Homadaula anisocentra
† Cycloplasis panicifoliella
Nosymna stipella
Pryeria sinica
Eustixis aglaodora
† Epermenia sinjovi
† Hemerophila felis
Platynota idaeusalis
Argyrotaenia alisellana
Wockia koreana
† "Wockia" sp. (MX60)
Urodus decens
Urodus sp. (CR16)
Gen. et sp. (CR06)
† Emmelina monodactyla
† Klimeschia transversella
Schreckensteinia sp.
Apoditrysia+ Gelechioidea
Tinea columbariella
Perissomastix sp.
† Philonome clemensella
† Nemapogon cloacella
Euprora sp.
Erechthias zebrina
Gen. et sp. (CR23)
Scardiella approxomatella
Harmaclona sp.
† Opogona thiadelia
† Hybroma servulella
Hapsifera sp.
Myrmecozela ochraceella
Acrolophus arcanellus
Corythophora sp.
Compsoctena sp.
Dryadaula sp.
Tineidae s. l.
Rebelia thomanni
Psyche crassiorella
Acanthopsyche zelleri
Typhonia ciliaris
† Narycia duplicella
Pseudarbela sp.
Arrhenophanes perspicilla
Scoriodyta suttonensis
Psychidae
Tisheria ekebladella
Tischeriidae
0.07
'PG' clade
'YPG' clade
'YYPG' clade
'YYPGAL' clade
Yponomeutoidea
'AL' clade
'PA' clade
'PAHSB' clade
'HSB' clade
Yponomeutoidea+ Gracillarioidea
Ditrysia

Figure 5. Representative adult habitus images of all yponomeutoid families and subfamilies recognized in this study. Scale bar = 5 mm. A. Glyphipterigidae: Glyphipteriginae, *Glyphipterix bifasciata* (Walsingham); B. Glyphipterigidae: Acrolepiinae, *Acrolepia xylophragma* (Meyrick); C. Glyphipterigidae: Orthoteliinae, *Orthotelia sparganella* (Thunberg); D. Plutellidae, *Plutella xylostella* (Linnaeus); E. Ypsolophidae: Ypsolophinae, *Ypsolopha blandella* (Christoph); F. Ypsolophidae: Ochsenheimeriinae, *Ochsenheimeria vacculella* Fisher von Roeslerstamm; G. Yponomeutidae: Yponomeutinae, *Yponomeuta padellus* Linnaeus; H. Yponomeutidae: Saridoscelinae, *Saridoscelis kodamai* Moriuti; I. Argyresthiidae, *Argyresthia brockeella* (Hübner); J. Lyonetiidae: Lyonetiinae, *Lyonetia ledi* Wocke; K. Lyonetiidae: Cemiostominae, *Leucoptera spartifoliella* (Hübner); L. Praydidae, *Prays fraxinella* (Bjerkander); M. Attevidae, *Atteva aurea* (Fitch); N. Heliodinidae, *Embola ciccella* (Barnes et Busck); O. Bedelliidae, *Bedellia somnulentella* (Zeller); P. Scythropiidae **stat. rev.**, *Scythropia crataegella* (Linnaeus).

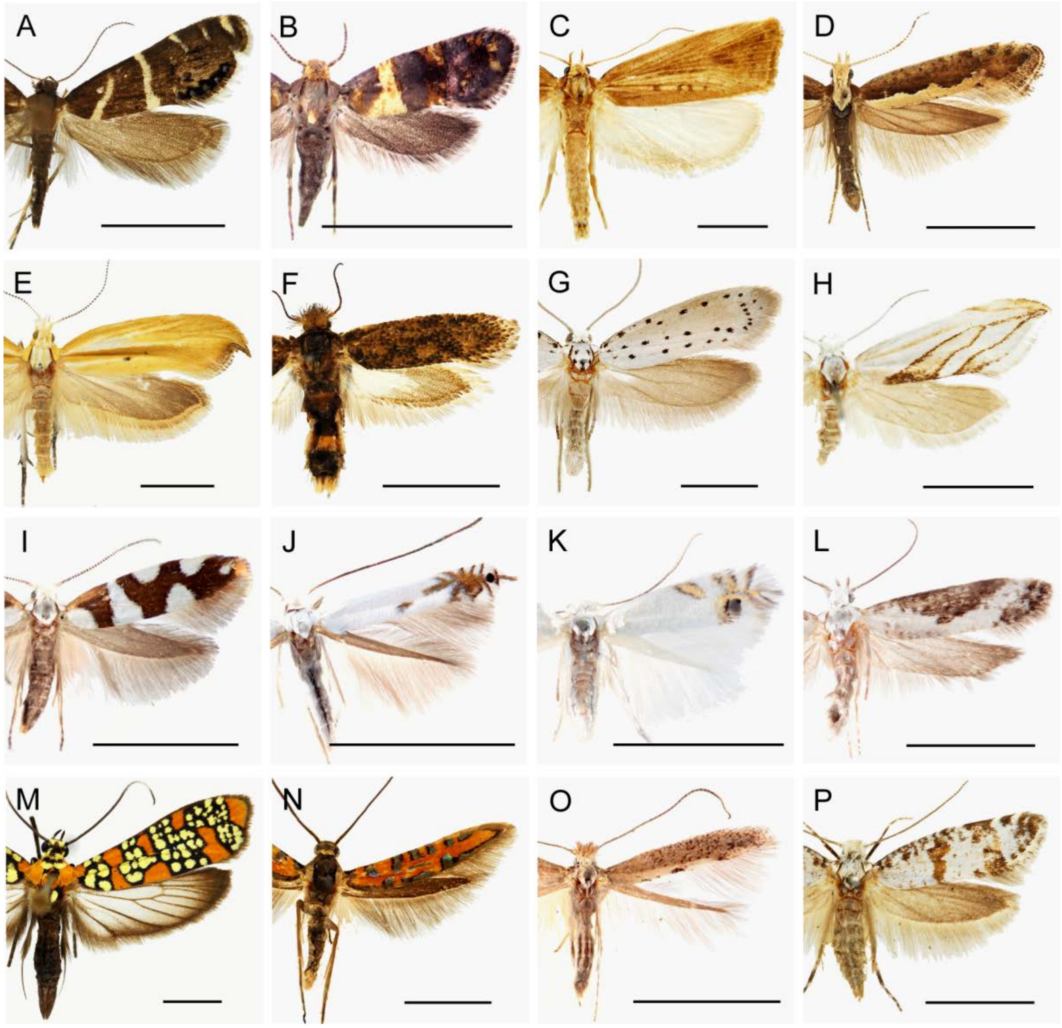
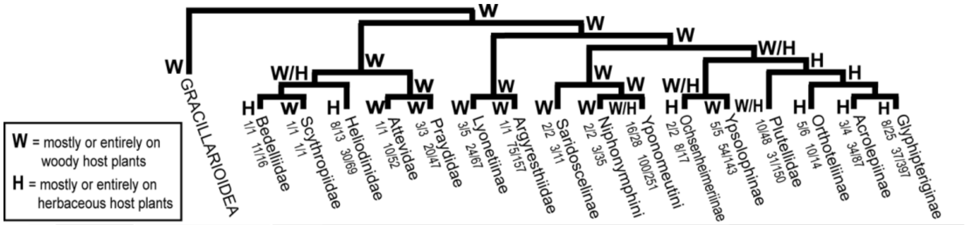
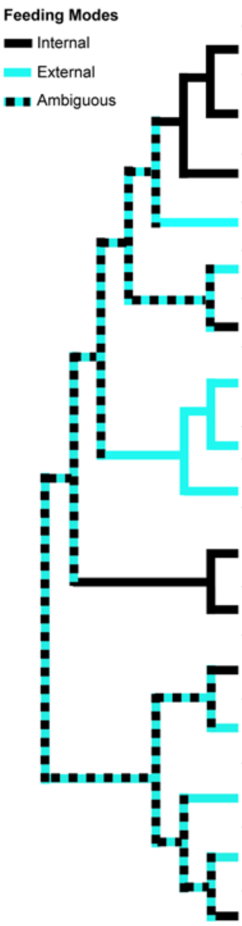

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P

Figure 6. Host plant families of 16 major yponomeutoid lineages. The cladogram is simplified from figure 2, annotated with predominant growth form of host plants (‘W’ for woody plants vs. ‘H’ for herbaceous plants). Fractions below yponomeutoid taxon names denote host record completeness for genera and species (in that order), calculated from the number of genera or species with host records relative to the total number of known genera or species. Host plant families used by each lineage are denoted by gray cells showing the numbers of species feeding on that plant family. Symbols denote the dominant growth-forms of each plant family: shaded circles = trees and shrubs; open circles = herbs; and shaded stars = veins and lianas. Capital letters next to host plant orders denote membership in clades above the order level: A – magnoliids, B – commelinids, C – fabids, D – malvids, E – lamiids, F – campanulids, G – Gnetophyta, and H – Pinophyta.



				Bedelliidae 1/1 11/16	Scythropiidae 1/1 1/1	Heliodinidae 8/13 30/69	Attevidae 1/1 10/52	Praydidae 3/3 20/47	Lyonetiinae 3/5 24/67	Argyresthiidae 1/1 75/157	Saridoscelinae 2/2 3/11	Niphonymphini 2/2 3/35	Yponomeutini 16/28 100/251	Ochsenheimeriinae 2/2 8/17	Ypsolophinae 5/5 54/143	Plutellidae 10/48 31/150	Orthoteliinae 5/6 10/14	Acrolepiinae 3/4 34/87	Glyphipteriginae 8/25 37/397
	A	Laurales	● Lauraceae						1										
		Magnoliales	● Annonaceae						1										
		Piperales	○ Piperaceae			1													1
Monocots		Alismatales	○ Araceae																1
		Asparagales	○ Amaryllidaceae															3	
			○ Asteliaceae														1		
			○ Iridaceae														1		
		Dioscoreales	★ Dioscoreaceae												1			6	
		Liliales	○ Liliaceae														1	5	
			★ Smilacaceae															3	1
		Pandanales	● Pandanaceae														1		
	B	Arecales	● Arecaceae														1		
		Poales	○ Cyperaceae											2		2	3		12
			○ Juncaceae																11
			○ Poaceae	2										5		1	3		4
			○ Typhaceae														1		
		Zingiberales	○ Zingiberaceae																1
		Proteales	● Proteaceae						2										
		Ranunculales	● Berberidaceae												1				
		Saxifragales	● Altingiaceae									1							
			○ Crassulaceae										3						2
			● Grossulariaceae						1				3						
			○ Saxifragaceae										12						
		Caryophyllales	○ Aizoaceae			1													
			○ Amaranthaceae			1													
			○ Nyctaginaceae			22													
			○ Phytolaccaceae			1													
			○ Portulacaceae			3													
		Santalales	● Loranthaceae										3						
			● Santalaceae										3						
Rosids	C	Celastrales	● Celastraceae										35		3				
		Fabales	○ Fabaceae													1			
			● Betulaceae					1	3	4			3		2				
			● Fagaceae						3	4		2	1		12				
			● Juglandaceae					1											
			● Myricaceae						2	1					1				
		Malpighiales	● Salicaceae						3	1			3		8				
		Rosales	★ Cannabaceae						1										
			● Rhamnaceae						1				2						
			● Rosaceae		1				6	14			15		10				
			● Ulmaceae					1	1	1					2				
			○ Urticaceae	1															3
	D	Brassicales	○ Brassicaceae													16			
			○ Capparaceae													2			
		Malvales	● Dipterocarpaceae						1										
			● Malvaceae												1				
			● Thymelaeaceae						5										
		Myrtales	● Myrtaceae						1	1			1						
			○ Onagraceae			1													
		Sapindales	● Burseraceae					1											
			● Rutaceae					7											
			● Sapindaceae							1					4				
			● Simaroubaceae				9												
Asterids		Ericales	● Ericaceae						2	3	3		4				1		
			● Theaceae						2										
	E	Gentianales	● Rubiaceae										1						
		Lamiales	○ Lamiaceae															1	
			● Oleaceae					7					5						
		Solanales	★ Convolvulaceae	8															
			○ Solanaceae															6	1
	F	Apiales	● Araliaceae			1	1												
		Asterales	○ Asteraceae															12	
		Dipsacales	● Caprifoliaceae					3							8	2			
	G	Ephedrales	● Ephedraceae												10				
	H	Cupressales	● Cupressaceae							29									
		Pinales	● Podocarpaceae													7			
			● Pinaceae							19			8		4				

Figure 7. Species diversity, feeding mode, diet breadth and geographic distribution of 16 major yponomeutoid lineages. The tree topology is that of Figure 6. Branch colors indicate predominant feeding modes: black = internal feeding; blue = external feeding; alternating black and blue = state ambiguous under parsimony optimization.



Taxon	# of spp.*	Predominant feeding mode	Predominant diet breadth (%)**	Geographic distribution (%)***
Glyphipterigidae Glyphipteriginae	397	leaf miners or stemborers; herbs, 78% on monocots	Oligophagous (37/37 = 100%)	AO (25) OR (21) NT (19) PA (16) NA (11) ET (8)
Glyphipterigidae Acrolepiinae	87	leaf miners or borers in stems, flower buds, seeds; monocots and asterid herbs	Oligophagous (33/34 = 97%)	PA (50.57) ET (14) NT (9) OR (8) NA (7) AO(5)
Glyphipterigidae Ortholeliinae	14	borers in stems and tiller bases; monocots	Oligophagous (8/10 = 80%)	AO (93) PA (7)NT****
Plutellidae	150	leaf webbers; >50% on Brassicales	Oligophagous (31/31 = 100%)	AO (39) PA (21) OR (14) ET (11) NT (9) NA(6)
Ypsolophidae Ypsolophinae	143	leaf webbers; trees and shrubs, many families	Oligophagous (51/54 = 94%)	PA (66) NA (25) OR (5) NT (3) ET (1)
Ypsolophidae Ochsenheimeriinae	17	leaf miners or stem borers; Poales	Oligophagous (8/8 = 100%)	PA (94) OR (6)
Yponomeutidae Yponomeutini	251	leaf webbers, a few pine needle miners; mostly trees and shrubs, many families	Oligophagous (100/100= 100%)	PA (50) OR (17) AO (15) ET (9) NA (7) NT (2)
Yponomeutidae Niphonymphini	35	leaf webbers; Fabales	Oligophagous (3/3 = 100%)	PA (57) OR (32) ET (5) NA (3) AO (3)
Yponomeutidae Saridoscelinae	11	leaf webbers; shrubs, all Ericaceae	Oligophagous (3/3 = 100%)	NT (41) PA (25) NA (17) OR (17)
Argyresthiidae	157	leaf miners or borers in flower buds, seeds; trees and shrubs, > 60% on conifers	Oligophagous (75/75 = 100%)	PA (49) NA (30) ET (10) OR (6) NT (4) AO (1)
Lyonetiidae Lyonetiinae	67	leaf miners ; woody dicots, mostly rosids	Oligophagous (20/24 = 83%)	PA (27) OR (21) AO (18) NT (13) ET (12) NA (9)
Praydidae	47	leaf miners or borers in flower buds or shoots; woody dicots	Oligophagous (19/20 = 95%)	PA (36) OR (20) AO (18) ET (16) NA (6) NT (4)
Attevidae	52	leaf webbers; woody dicots, >90% on Simaroubaceae	Oligophagous (10/10 = 100%)	OR (36) NT (32) AO (28) ET (2) NA (2)
Heliodinidae	69	Leaf miners, some are leaf webbers (ancestral); >85% on Caryophyllales	Oligophagous (30/30 = 100%)	NA (47) NT (42) AO (8) PA (3)
Scythropiidae	1	leaf miners then webbers in later instars; woody Rosaceae	Oligophagous (1/1 = 100%)	PA (100)
Bedelliidae	16	leaf miners; herbs, >70% on Convolvulaceae	Oligophagous (11/11 = 100%)	AO (42) OR (19) PA (19) ET (8) NA (8) NT (4)

* only described species counted.

** the number of oligophagous species/ the number of total species whose hosts are known.

*** AO: Australoceanian, ET: Ethiopian, NA: Nearctic, NT: Neotropical, OR: Oriental, PA: Palearctic.

**** based on the undescribed species included in our analyses

Supplement S1-1. A spreadsheet showing the included species with annotations of their classification, collecting locality, and host plant families.

IN-GROUP						
superfamily	Family	Subfamily	Genus	Species	Country	Host plant family
Yponomeutoidea	Bedellidae		*Bedellia*	*somnulentella*	USA	Convolvulaceae
Yponomeutoidea	Glyphipterigidae	Acrolepiinae	*Acrolepia*	*autumnitella*	UK	Solanaceae
Yponomeutoidea	Glyphipterigidae	Acrolepiinae	*Acrolepia*	*xylophragma*	Costa Rica	Solanaceae
Yponomeutoidea	Glyphipterigidae	Acrolepiinae	*Acrolepia*	sp.	Costa Rica	N/A
Yponomeutoidea	Glyphipterigidae	Acrolepiinae	*Acrolepiopsis*	*sapporensis*	Korea	Amaryllidaceae
Yponomeutoidea	Glyphipterigidae	Acrolepiinae	*Digitivalva*	*hemiglypha*	Korea	N/A
Yponomeutoidea	Glyphipterigidae	Glyphipteriginae	*Diploschizia*	*impigritella*	USA	Cyperaceae
Yponomeutoidea	Glyphipterigidae	Glyphipteriginae	*Glyphipterix*	*forsterella*	UK	Cyperaceae
Yponomeutoidea	Glyphipterigidae	Glyphipteriginae	*Glyphipterix*	sp.	Costa Rica	N/A
Yponomeutoidea	Glyphipterigidae	Glyphipteriginae	*Glyphipterix*	*quadragintapunctata*	USA	N/A
Yponomeutoidea	Glyphipterigidae	Glyphipteriginae	*Glyphipterix*	cf. *lamprosema*	Australia	N/A
Yponomeutoidea	Glyphipterigidae	Glyphipteriginae	*Glyphipterix*	*perimetalla*	Australia	N/A
Yponomeutoidea	Glyphipterigidae	Glyphipteriginae	*Lepidotarphius*	*peroprnatellus*	Korea	Araceae
Yponomeutoidea	Glyphipterigidae	Orthoteliinae	*Orthotelia*	*sparganella*	Finland	Iridaceae, Poaceae, Typhaceae
Yponomeutoidea	Glyphipterigidae	Orthoteliinae	*Proditrix*	*gahniae*	Australia	Cyperacedae
Yponomeutoidea	Glyphipterigidae	Orthoteliinae	*Proditrix*	*nielseni*	Australia	Ericaceae
Yponomeutoidea	Heliodinidae	putative	*Cycloplasis*	*panicifoliella*	USA	Poaceae
Yponomeutoidea	Heliodinidae		*Aetole*	*tripunctella*	USA	Nyctaginaceae
Yponomeutoidea	Heliodinidae		*Embola*	*ionis*	USA	Nyctaginaceae
Yponomeutoidea	Heliodinidae		*Epicroesa*	*metallifera*	Taiwan	Nyctaginaceae
Yponomeutoidea	Heliodinidae		Gen.	sp.	Costa Rica	N/A

Yponomeutoidea	Heliodinidae		*Neoheliodines*	*nyctaginella*	USA	Nyctaginaceae
Yponomeutoidea	Lyonetiidae	Cemiostominae	*Perileucoptera*	*coffeella*	Colombia	Rubiaceae
Yponomeutoidea	Lyonetiidae	Lyonetiinae	*Lyonetia*	*ledi*	Korea	Ericaceae, Myricaceae
Yponomeutoidea	Lyonetiidae	Lyonetiinae	*Lyonetia*	*prunifoliella*	USA	Betulaceae, Rosaceae
Yponomeutoidea	Lyonetiidae	putative	*Corythophora*	sp.	Costa Rica	N/A
Yponomeutoidea	Lyonetiidae	putative	*Euprora*	sp.	Mexico	N/A
Yponomeutoidea	Lyonetiidae	putative	*Philonome*	*clemensella*	USA	N/A
Yponomeutoidea	Lyonetiidae	putative	*Phyllobrostis*	cf. *daphneella*	Spain	N/A
Yponomeutoidea	Lyonetiidae	putative	*Phyllobrostis*	*peninsulae*	South Africa	N/A
Yponomeutoidea	Plutellidae		*Deryaraxenistis*	*serrata*	Namibia	N/A
Yponomeutoidea	Plutellidae		*Doxophyrtis*	*hydrocosma*	Australia	Arecaceae
Yponomeutoidea	Plutellidae		*Eidophasia*	*messingiella*	Finland	Brassicaceae
Yponomeutoidea	Plutellidae		Gen.	sp.	Greece	N/A
Yponomeutoidea	Plutellidae		*Lunakia*	*alyssella*	Greece	Brassicaceae
Yponomeutoidea	Plutellidae		*Plutella*	*xylostella*	USA	Brassicaceae
Yponomeutoidea	Plutellidae		*Rhigognostis*	*schmaltzella*	Finland	Brassicaceae
Yponomeutoidea	Plutellidae		*Tritymba*	*pamphaea*	Australia	N/A
Yponomeutoidea	Yponomeutidae	Argyresthiinae	*Argyresthia*	sp.	Costa Rica	N/A
Yponomeutoidea	Yponomeutidae	Argyresthiinae	*Argyresthia*	*austerella*	USA	N/A
Yponomeutoidea	Yponomeutidae	Argyresthiinae	*Argyresthia*	*brockeella*	China	Betulaceae
Yponomeutoidea	Yponomeutidae	Attevinae	*Atteva*	*aurea*	USA	Simaroubaceae
Yponomeutoidea	Yponomeutidae	Attevinae	*Atteva*	*zebra*	Costa Rica	Simaroubaceae
Yponomeutoidea	Yponomeutidae	Praydinae	*Atemelia*	n. sp.	Costa Rica	N/A
Yponomeutoidea	Yponomeutidae	Praydinae	*Atemelia*	*torquatella*	Finland	Betulaceae, Ulmaceae
Yponomeutoidea	Yponomeutidae	Praydinae	*Prays*	*fraxinella*	UK	Oleaceae
Yponomeutoidea	Yponomeutidae	Praydinae	*Prays*	*delta*	Korea	Oleaceae
Yponomeutoidea	Yponomeutidae	Praydinae	*Prays*	*atomocella*	USA	Rutaceae
Yponomeutoidea	Yponomeutidae	Praydinae	*Prays*	*oleae*	Spain	Oleaceae
Yponomeutoidea	Yponomeutidae	Saridoscelinae	*Saridoscelis*	*kodamai*	Japan	Ericaceae

Yponomeutoidea	Yponomeutidae	Scythropiinae	*Scythropia*	*crataegella*	Finland	Rosaceae
Yponomeutoidea	Yponomeutidae	uncertain	*Eucalantica*	*costaricae*	Costa Rica	N/A
Yponomeutoidea	Yponomeutidae	uncertain	New genus	sp.	Costa Rica	N/A
Yponomeutoidea	Yponomeutidae	uncertain	New genus	sp.	Costa Rica	N/A
Yponomeutoidea	Yponomeutidae	uncertain	New genus	sp.	Costa Rica	N/A
Yponomeutoidea	Yponomeutidae	Yponomeutinae	"*Xyrosaris*"	sp.	Costa Rica	N/A
Yponomeutoidea	Yponomeutidae	Yponomeutinae	"*Zelleria*"	sp.	Costa Rica	N/A
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Cedestis*	*exiguata*	Korea	N/A
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Cedestis*	*subfasciella*	Finland	Pinaceae
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Euhyponomeutoides*	*ribesiellus*	Finland	N/A
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Klausius*	*minor*	Korea	N/A
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Metanomeuta*	*fulvicrinis*	Korea	N/A
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Metanomeuta*	*fulvicrinis*	Korea	N/A
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Paraswammerdamia*	*conspersella*	Finland	Ericaceae
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Swammerdamia*	*glaucella*	Korea	N/A
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Teinoptila*	*guttella*	Japan	Celastraceae
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Thecobathra*	*anas*	Japan	Fagaceae
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Xyrosaris*	*lichneuta*	Korea	Celastraceae
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Yponomeuta*	*anatolica*	Korea	Celastraceae
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Yponomeuta*	*kanaiella*	Korea	Celastraceae
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Yponomeuta*	*multipunctella*	USA	Celastraceae
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Yponomeuta*	*myriosema*	Australia	N/A
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Zelleria*	*celastrusella*	USA	Celastraceae
Yponomeutoidea	Yponomeutidae	Yponomeutinae	*Zelleria*	*retiniella*	USA	N/A
Yponomeutoidea	Ypsolophidae	Ochsenheimeriinae	*Ochsenheimeria*	*urella*	Finland	Poaceae
Yponomeutoidea	Ypsolophidae	Ypsolophinae	*Bhadorcosma*	*lonicerae*	Japan	Caprifoliaceae
Yponomeutoidea	Ypsolophidae	Ypsolophinae	*Ypsolopha*	*nigrimaculata*	Korea	N/A
Yponomeutoidea	Ypsolophidae	Ypsolophinae	*Ypsolopha*	*angelicella*	USA	N/A
Yponomeutoidea	Ypsolophidae	Ypsolophinae	*Ypsolopha*	*ustella*	UK	Fagaceae

Yponomeutoidea	Ypsolophidae	Ypsolophinae	*Ypsolopha*	*yasudai*	Korea	N/A
Yponomeutoidea	uncertain		New genus	sp.	Chile	N/A
Yponomeutoidea	uncertain		New genus	sp.	Costa Rica	N/A
Yponomeutoidea	uncertain		New genus	sp.	Mexico	N/A
“Yponomeutoidea”	“Yponomeutidae”	putative	*Nosymna*	*stipella*	Thailand	N/A
“Yponomeutoidea”	uncertain				Chile	N/A
“Yponomeutoidea”	uncertain				Chile	N/A
OUT-GROUP						
superfamily	Family	Subfamily	Genus	Species	Country	
Choreutoidea	Choreutidae	Choreutinae	*Hemerophila*	*felis*	Costa Rica	N/A
Copromorpoidea	Copromorphidae		*Copromorpha*	sp.	Madagascar	N/A
Epermenioidea	Epermeniidae		*Epermenia*	*sinjovi*	Korea	Apiaceae
Galacticoidea	Galacticidae		*Homadaula*	*anisocentra*	USA	Fabaceae
Gelechioidea	Cosmopterigidae	Antequerinae	*Euclemensia*	*bassettella*	USA	scale insects
Gelechioidea	Ethmiidae	Ethmiinae	*Ethmia*	*eupostica*	Australia	N/A
Gelechioidea	Lypusidae		*Lypusa*	*maurella*	Sweden	N/A
Gelechioidea	uncertain		Gen.	sp.	Hawaii Isl.	N/A
Gracillarioidea	Bucculatricidae		*Bucculatrix*	sp.	USA	N/A
Gracillarioidea	Douglasiidae		*Klimeschia*	*transversella*	Sweden	N/A
Gracillarioidea	Gracillariidae	Gracillariinae	*Caloptilia*	*bimaculatella*	USA	Sapindaceae
Gracillarioidea	Gracillariidae	Gracillariinae	*Parectopa*	*robiniella*	USA	Fabaceae
Gracillarioidea	Gracillariidae	Lithocolletinae	*Cameraria*	*gaultheriella*	USA	Ericaceae
Gracillarioidea	Gracillariidae	Lithocolletinae	*Phyllonorycter*	sp.	USA	N/A
Gracillarioidea	Gracillariidae	Phyllocnistinae	*Phyllocnistis*	*citrella*	Spain	Clusiaceae, Lauraceae, Loranthaceae, Rutaceae
Gracillarioidea	Gracillariidae	Phyllocnistinae	*Phyllocnistis*	*magnoliaeella*	USA	Magnoliaceae
Gracillarioidea	Roeslerstamiidae		*Agriothera*	*elaeocarpophaga*	Japan	Elaeaocarpaceae
Gracillarioidea	Roeslerstamiidae		*Roeslerstammia*	*pronubella*	Japan	N/A
Gracillarioidea	Roeslerstamiidae		*Amphithera*	*heteroleuca*	Australia	Elaeaocarpaceae

Pterophoroidea	Pterophoridae	Pterophorinae	*Emmelina*	*monodactyla*	USA	Asteraceae, Chenopodiaceae, Convolvulaceae, Ericaceae, Polygonaceae, Solanaceae
Schreckensteinoidea	Schreckensteiniidae		*Schreckensteinia*	sp.	Costa Rica	N/A
Tineoidea	Acrolophidae		*Acrolophus*	*arcanellus*	USA	N/A
Tineoidea	Arrhenophanidae		*Arrhenophanes*	*perspicilla*	Costa Rica	fungi
Tineoidea	Eriocottidae	Compsoctetinae	*Compsoctena*	sp.	n/a	N/A
Tineoidea	Psychidae	Epichnopteryginae	*Rebelia*	*thomanni*	Italy	N/A
Tineoidea	Psychidae	Naryciinae	*Narycia*	*duplicella*	n/a	N/A
Tineoidea	Psychidae	Oiketicinae	*Acanthopsyche*	*zelleri*	Croatia	N/A
Tineoidea	Psychidae	Pseudarbelinae	*Pseudarbela*	sp.	Borneo	N/A
Tineoidea	Psychidae	Psychinae	*Psyche*	*crassiorella*	Switzerland	Betulaceae, Grossulariaceae, Poaceae, Rosaceae, Salicaceae
Tineoidea	Psychidae	Scoriodytinae	*Scoriodyta*	*suttonensis*	New Zealand	N/A
Tineoidea	Psychidae	Typhoniinae	*Typhonia*	*ciliaris*	Switzerland	N/A
Tineoidea	Tineidae	Dryadaulinae	*Dryadaula*	sp.	USA	N/A
Tineoidea	Tineidae	Erechthiinae	*Erechthias*	*zebrina*	Costa Rica	Dipterocarpaceae, Fabaceae, Myrtaceae, Palmae
Tineoidea	Tineidae	Hapsiferinae	*Hapsifera*	sp.	Kenya	N/A
Tineoidea	Tineidae	Harmacloninae	*Harmaclona*	sp.	Fr. Guiana	N/A
Tineoidea	Tineidae	Hieroxestinae	*Opogona*	*thiadelia*	Japan	N/A
Tineoidea	Tineidae	Meessiinae	*Hybroma*	*servulella*	USA	N/A
Tineoidea	Tineidae	Myrmecozelinae	*Myrmecozela*	*ochraceella*	Sweden	N/A
Tineoidea	Tineidae	Nemapogoninae	*Nemapogon*	*cloacella*	Sweden	fungi
Tineoidea	Tineidae	Perissomasticinae	*Perissomastix*	sp.	n/a	N/A
Tineoidea	Tineidae	Scardiinae	*Scardiella*	*approxomatella*	USA	N/A
Tineoidea	Tineidae	Tineinae	*Tinea*	*columbariella*	Australia	organic debries
Tineoidea	Tineidae		Gen.	sp.	Costa Rica	N/A
Tischerioidea	Tischeriidae		*Tischeria*	*ekebladella*	Sweden	Fagaceae
Tortricoidea	Tortricidae	Tortricinae	*Argyrotaenia*	*alisellana*	USA	Fagaceae

Tortricoidea	Tortricidae	Tortricinae	*Platynota*	*idaeusalis*	USA	Asteraceae, Caprifoliaceae, Fabaceae, Ericaceae, Moraceae, Oleaceae, Papaveraceae, Pinaceae, Rhamnaceae, Rosaceae, Salicaceae, Solanaceae
Urodoidea	Urodidae		Gen.	sp.	Costa Rica	N/A
Urodoidea	Urodidae		*Urodus*	sp.	Costa Rica	N/A
Urodoidea	Urodidae		"*Wockia*"	sp.	Mexico	N/A
Urodoidea	Urodidae		*Urodus*	*decens*	Costa Rica	N/A
Urodoidea	Urodidae		*Wockia*	*koreana*	Korea	N/A
Zygaenoidea	Lacturidae		*Eustixis*	*aglaodora*	Australia	N/A
Zygaenoidea	Zygaenidae	Zygaeninae	*Pryeria*	*sinica*	USA	Celastraceae

Supplement S1-2. A spreadsheet showing the included species with annotations of their classification, identification check with DNA barcodes, and sequence data completeness (fraction of total target sequence actually obtained).

IN-GROUP								
superfamily	Family	Genus	Species	Acc. No.	Code	BOLD Compatibility (%)	Seq. com-pleteness (%)	# genes attempted
Yponomeutoidea	Bedellidae	*Bedellia*	*somnulentella*	DRD-01-0150	Bsmu	100	71.4	19
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	*autumnitella*	ISI-08-0827	Acau	100	10.9	8
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	*xylophragma*	KN-06-1146	Axpg	no hit	27.2	8
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	sp.	SJC-08-2145	CR45	no hit	37	8
Yponomeutoidea	Glyphipterigidae	*Acrolepiopsis*	*sapporensis*	JCS-06-0177	Asap	100	62.4	19
Yponomeutoidea	Glyphipterigidae	*Digitivalva*	*hemiglypha*	SWC-06-0204	Dhem	no hit	65.1	19
Yponomeutoidea	Glyphipterigidae	*Diploschizia*	*impigritella*	TH-08-6101	Dimp	99.85	64.2	19
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*forsterella*	ISI-08-0802	Gfor	100	7.22	8
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	sp.	KN-06-0535	Glpx	no hit	46.8	19
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*quadragintapunctata*	TH-08-6093	Glqu	no hit	37.1	8
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	cf. *lamprosema*	AZ-07-5001	Gly01	no hit	36.5	8
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*perimetalla*	AZ-07-5002&5003	Gly02	99.08	26.1	8
Yponomeutoidea	Glyphipterigidae	*Lepidotarphius*	*peroprnatellus*	SWC-07-2003	Lpts	N/A	72	19
Yponomeutoidea	Glyphipterigidae	*Orthotelia*	*sparganella*	JCS-09-0112	Ospa	100	61.5	19
Yponomeutoidea	Glyphipterigidae	*Proditrix*	*gahniae*	MM-09-1003	Pgah	no hit	58.3	19
Yponomeutoidea	Glyphipterigidae	*Proditrix*	*nielseni*	JCS-09-0111	Prsp	no hit	13.8	8
Yponomeutoidea	Heliodinidae	*Cycloplasis*	*panicifoliella*	TH-08-6110	Cpan	N/A	26.2	8
Yponomeutoidea	Heliodinidae	*Aetole*	*tripunctella*	TH-08-6088	Aetr	no hit	66.4	19
Yponomeutoidea	Heliodinidae	*Embola*	*ionis*	TH-08-6090	Eion	99.85	32.9	8
Yponomeutoidea	Heliodinidae	*Epicroesa*	*metallifera*	LS-06-0061	Emet	no hit	57.4	19

Yponomeutoidea	Heliodinidae	Gen.	sp.	JCS-08-2083	CR83	chorJanzen01[misidentified as Choreutidae] (99.24)	33.3	8
Yponomeutoidea	Heliodinidae	*Neoheliodines*	*nyctaginella*	TH-08-6089	Nnyc	unidentified Heliodinidae (95.57)	25.4	8
Yponomeutoidea	Lyonetiidae	*Perileucoptera*	*coffeella*	CWM-07-2322	Leuco	no hit; 100 with other specimen in Leptree stock	43.2	19
Yponomeutoidea	Lyonetiidae	*Lyonetia*	*ledi*	JCS-08-1021	Lled	94.16	10.8	8
Yponomeutoidea	Lyonetiidae	*Lyonetia*	*prunifoliella*	DRD-05-0253	Lpfe	100	47.7	19
Yponomeutoidea	Lyonetiidae	*Corythophora*	sp.	JCS-09-0105	Cory	*Corythopora* sp. (89.51)	27.8	8
Yponomeutoidea	Lyonetiidae	*Euprora*	sp.	JCS-09-2071	Eumx	Tineidae, *Erechtias* (90.21)	34.3	8
Yponomeutoidea	Lyonetiidae	*Philonome*	*clemensella*	TH-08-6182	Pmsa	N/A	26.7	19
Yponomeutoidea	Lyonetiidae	*Phyllobrostis*	cf. *daphneella*	LK-09-5000	Phlk	no hit	10.9	8
Yponomeutoidea	Lyonetiidae	*Phyllobrostis*	*peninsulae*	WM-09-3001	Phsp	no hit	18.9	8
Yponomeutoidea	Plutellidae	*Deryaraxenistis*	*serrata*	WM-08-4006-1	Pxse	no hit	17.7	8
Yponomeutoidea	Plutellidae	*Doxophyrtis*	*hydrocosma*	MM-09-1002	Dhyd	100	37.4	19
Yponomeutoidea	Plutellidae	*Eidophasia*	*messingiella*	MM-08-6879	Emnl	100	24.5	8
Yponomeutoidea	Plutellidae	Gen.	sp.	JCS-09-0110	Grce	no hit	13.1	8
Yponomeutoidea	Plutellidae	*Lunakia*	*alyssella*	JCS-09-0109	Luna	*Eidophasia syenitella* (97.85)	10	8
Yponomeutoidea	Plutellidae	*Plutella*	*xylostella*	JWB-05-0013	Pxy	99.85	62.3	19
Yponomeutoidea	Plutellidae	*Rhigognostis*	*schmaltzella*	MM-08-8908	Rsze	100	35.9	8
Yponomeutoidea	Plutellidae	*Tritymba*	*pamphaea*	MM-08-7513	Tpph	N/A	28.1	19
Yponomeutoidea	Yponomeutidae	*Argyresthia*	sp.	SJC-08-2086	sp86	no hit	35.8	8
Yponomeutoidea	Yponomeutidae	*Argyresthia*	*austerella*	TH-08-6095	Aase	*Argyresthia sp.* (99.23)	24.6	5
Yponomeutoidea	Yponomeutidae	*Argyresthia*	*brockeella*	JCS-08-3014	Abck	99.08	39.4	8

Yponomeutoidea	Yponomeutidae	*Atteva*	*aurea*	JWB-05-0041	Atpu2	99.66	80.1	27
Yponomeutoidea	Yponomeutidae	*Atteva*	*zebra*	05-srnp-33966	Atze	100	32.2	8
Yponomeutoidea	Yponomeutidae	*Atemelia*	n. sp.	SJC-08-2149	sp49	no hit	39.5	8
Yponomeutoidea	Yponomeutidae	*Atemelia*	*torquatella*	MM-08-6266	Aotl	100	37.8	8
Yponomeutoidea	Yponomeutidae	*Prays*	*fraxinella*	ISI-08-0822	Pfra2	100	13.7	8
Yponomeutoidea	Yponomeutidae	*Prays*	*delta*	JCS-08-1022	Ppes	*Prays ruficeps* (94.78)	28.4	8
Yponomeutoidea	Yponomeutidae	*Prays*	*atomocella*	TH-08-6084	Prays	100	31.4	5
Yponomeutoidea	Yponomeutidae	*Prays*	*oleae*	JBA-06-0101	Pryo	*Prays fraxinella* [misid?] (99.69)	62.8	19
Yponomeutoidea	Yponomeutidae	*Saridoscelis*	*kodamai*	SJC-08-4039	Skod	no hit	18.5	8
Yponomeutoidea	Yponomeutidae	*Scythropia*	*crataegella*	MM-08-6730	Sytg	N/A	40.3	19
Yponomeutoidea	Yponomeutidae	*Eucalantica*	*costaricae*	DA-03-3364	Ysp	*Eucalantica polita* (91.9)	84.4	27
Yponomeutoidea	Yponomeutidae	New genus	sp.	SJC-08-2120	CR20	no hit	32.9	8
Yponomeutoidea	Yponomeutidae	New genus	sp.	SJC-08-2147	CR47	no hit	36.5	8
Yponomeutoidea	Yponomeutidae	New genus	sp.	SJC-08-2081	CR81	no hit	35.9	8
Yponomeutoidea	Yponomeutidae	"*Xyrosaris*"	sp.	SJC-08-2227	sp27	no hit	35.8	8
Yponomeutoidea	Yponomeutidae	"*Zelleria*"	sp.	SJC-08-2101	sp01	no hit	32.9	8
Yponomeutoidea	Yponomeutidae	*Cedestis*	*exiguata*	JCS-08-1025	Cexi	no hit; 99.69 with other specimen in Leptree stock	34.2	8
Yponomeutoidea	Yponomeutidae	*Cedestis*	*subfasciella*	MM-08-3997	Opin1	100	35.7	8
Yponomeutoidea	Yponomeutidae	*Euhyponomeutoides*	*ribesiellus*	MM-08-6137	Eryt	100	17.6	8
Yponomeutoidea	Yponomeutidae	*Klausius*	*minor*	JCS-08-1008	Kmin	no hit	28.5	8
Yponomeutoidea	Yponomeutidae	*Metanomeuta*	*fulvicrinis*	JCS-09-0113	Mefu	no hit	18.5	8
Yponomeutoidea	Yponomeutidae	*Metanomeuta*	*fulvicrinis*	SWC-06-0221	Cvag	no hit	64.6	8
Yponomeutoidea	Yponomeutidae	*Paraswammerdamia*	*conspersella*	MM-08-2617	Pcpa	99.85	13.8	8
Yponomeutoidea	Yponomeutidae	*Swammerdamia*	*glaucella*	SJC-08-3046	Swgl	no hit	33.7	8

Yponomeutoidea	Yponomeutidae	*Teinoptila*	*guttella*	UJ-09-1003	Tegu	no hit; 100 with other specimens in Leptree stock	31.5	8
Yponomeutoidea	Yponomeutidae	*Thecobathra*	*anas*	AYK-04-5640	Tan	no hit	68.3	19
Yponomeutoidea	Yponomeutidae	*Xyrosaris*	*lichneuta*	JCS-08-1006	Xlic	no hit	29.2	8
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*anatolica*	JCS-08-1045	Yana	96.77	35.9	8
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*kanaiella*	JCS-08-1047	Ykan	*Y. evonymella* (94.62)	31.9	8
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*multipunctella*	JWB-06-1126	Ymul	99.69	54.3	19
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*myriosema*	AZ-08-0503	Yrsm	99.85	35.7	8
Yponomeutoidea	Yponomeutidae	*Zelleria*	*celastrusella*	TH-08-6085-1	Zcll	no hit	32.9	8
Yponomeutoidea	Yponomeutidae	*Zelleria*	*retiniella*	JCS-09-2012	Zere	99.84	30.2	8
Yponomeutoidea	Ypsolophidae	*Ochsenheimeria*	*urella*	MM-08-0008	Oure	97.29	66.1	19
Yponomeutoidea	Ypsolophidae	*Bhadorcosma*	*lonicerae*	SJC-08-4041	Bhlo	no hit	34.8	8
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*nigrimaculata*	JCS-06-0102	Yni	no hit; 100 with *Crinopteryx familiella* [possibly contamination]	68.3	19
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*angelicella*	JCS-DNA-009	Ypan	100	30.6	8
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*ustella*	ISI-08-0825	Ypus	100	13.1	8
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*yasudai*	JCS-08-1048	Yyas	*Ypsolopha falcella* (98.62)	35.7	8
Yponomeutoidea	uncertain	New genus	sp.	AYK-04-0528-25	Chile	no hit	37.8	8
Yponomeutoidea	uncertain	New genus	sp.	SJC-08-2095	CR95	no hit	32.6	8
Yponomeutoidea	uncertain	New genus	sp.	SJC-08-4042	Mex42	no hit	16	8
“Yponomeutoidea”	“Yponomeutidae”	*Nosymna*	*stipella*	KC-5005-012	Nost	no hit	36.6	8
“Yponomeutoidea”	uncertain			LP-92-0049	CL49	no hit	29.6	8
“Yponomeutoidea”	uncertain			LP-92-0167-1	CL67	no hit	25.1	8
OUT-GROUP								

superfamily	Family	Genus	Species	Acc. No.	Code	BOLD Compatibility (%)	Seq. completeness (%)	# genes attempted
Choreutoidea	Choreutidae	*Hemerophila*	*felis*	DRD-01-0218	Hfel	100	90.8	27
Copromorpoidea	Copromorphidae	*Copromorpha*	sp.	DCL-07-0010	Cmpa	unidentified Copromorphidae (91.06)	12	5
Epermenioidea	Epermeniidae	*Epermenia*	*sinjovi*	JCS-08-1020	Esji	*Epermenia infracta* (93.12)	30.6	8
Galacticoidea	Galacticidae	*Homadaula*	*anisocentra*	JWB-05-0026	Hani	100	64.7	19
Gelechioidea	Cosmopterigidae	*Euclemensia*	*bassettella*	JWB-05-0044	Cole	99.85	81.6	27
Gelechioidea	Ethmiidae	*Ethmia*	*eupostica*	MJM-96-0277	Eeu	*Ethmia pusiella* (94.34)	88.6	27
Gelechioidea	Lypusidae	*Lypusa*	*maurella*	DRD-07-4102	Lmau	100	24.3	5
Gelechioidea	uncertain	Gen.	sp.	AZ-07-3279	Hawa	Cosmopterigidae, *Limnaecia* (91.59)	32.9	8
Gracillarioidea	Bucculatricidae	*Bucculatrix*	sp.	DRD-05-0270	Bucc	*Bucculatrix* sp. (99.85)	56.9	19
Gracillarioidea	Douglasiidae	*Klimeschia*	*transversella*	DRD-01-0017	Ktr	100	66.4	19
Gracillarioidea	Gracillariidae	*Caloptilia*	*bimaculatella*	DRD-05-0248	Cbim	100	84.1	27
Gracillarioidea	Gracillariidae	*Parectopa*	*robiniella*	DRD-01-0009	Prbn	99.69	51.2	19
Gracillarioidea	Gracillariidae	*Cameraria*	*gaultheriella*	DRD-01-0113v	Caga	100	62	19
Gracillarioidea	Gracillariidae	*Phyllonorycter*	sp.	TPF-89-1114	Phyl	*Phyllonorycter hostis*, *P. mespilella* and *P. pomonella* (99.84)	58	19
Gracillarioidea	Gracillariidae	*Phyllocnistis*	*citrella*	JBA-06-0025	Phcn	100	68.9	19
Gracillarioidea	Gracillariidae	*Phyllocnistis*	*magnoliaeella*	DRD-05-0244	Pmgl	100	58.7	19
Gracillarioidea	Roeslerstamiidae	*Agriothera*	*elaeocarpophaga*	DRD-01-0143	Agel	no hit	57.9	19
Gracillarioidea	Roeslerstamiidae	*Roeslerstammia*	*pronubella*	DRD-01-0142	Rstm	*R. erxlebella* (94.28)	60.7	19

Gracillarioidea	Roeslerstamiidae	*Amphithera*	*heteroleuca*	AZ-07-2289	AU89	99.85	37.2	8
Pterophoroidea	Pterophoridae	*Emmelina*	*monodactyla*	CWM-05-1000	Emon	100	86.9	27
Schreckensteinoidea	Schreckensteiniidae	*Schreckensteinia*	sp.	KN-06-3401	Sktn	*S. festaliella* (94.32)	68	19
Tineoidea	Acrolophidae	*Acrolophus*	*arcanellus*	DRD-06-1339	Arca	100	42.9	19
Tineoidea	Arrhenophanidae	*Arrhenophanes*	*perspicilla*	DRD-01-0063	Arrp	91.55	45.9	19
Tineoidea	Eriocottidae	*Compsoctena*	sp.	MF-06-3006	Comp	*Compsoctena* sp. (89.91)	57.2	19
Tineoidea	Psychidae	*Rebelia*	*thomanni*	DRD-01-0110	Rtnn	N/A	13.7	8
Tineoidea	Psychidae	*Narycia*	*duplicella*	DRD-01-0035	Nard	100	34.1	19
Tineoidea	Psychidae	*Acanthopsyche*	*zelleri*	DRD-01-0042	Azri	100	17.8	5
Tineoidea	Psychidae	*Pseudarbela*	sp.	DCL-07-0001	Pdba	no hit	43.5	19
Tineoidea	Psychidae	*Psyche*	*crassiorella*	DRD-06-1334	Pcra	99.08	14.7	19
Tineoidea	Psychidae	*Scoriodyta*	*suttonensis*	DRD-06-0281	Scdy	no hit	55.3	19
Tineoidea	Psychidae	*Typhonia*	*ciliaris*	DRD-06-0059	Tycl	100	44.8	19
Tineoidea	Tineidae	*Dryadaula*	sp.	TH-08-6188	Drya	N/A	30.3	19
Tineoidea	Tineidae	*Erechthias*	*zebrina*	DRD-05-0256	Ezeb	99.85	51.7	19
Tineoidea	Tineidae	*Hapsifera*	sp.	DA-05-0010	Haps	no hit	51.7	19
Tineoidea	Tineidae	*Harmaclona*	sp.	BL-08-0107	Harm	no hit	23.1	19
Tineoidea	Tineidae	*Opogona*	*thiadelia*	DRD-05-0147	Othi	*Opogona* sp.20 (92.47)	64.1	19
Tineoidea	Tineidae	*Hybroma*	*servulella*	DRD-07-0289	Hybs	100	67	19
Tineoidea	Tineidae	*Myrmecozela*	*ochraceella*	DRD-07-4103	Moch	100	69.9	19
Tineoidea	Tineidae	*Nemapogon*	*cloacella*	DRD-01-0015	Nclo	99.85	55.1	19
Tineoidea	Tineidae	*Perissomastix*	sp.	MF-06-3005	Peri	no hit	58.6	19
Tineoidea	Tineidae	*Scardiella*	*approxomatella*	DRD-01-0003	Sapp	99.85	60.9	19
Tineoidea	Tineidae	*Tinea*	*columbariella*	EN-91-0006	Tco2	100	81.5	27
Tineoidea	Tineidae	Gen.	sp.	JCS-07-1123	CR23	*Scardiella approximatella* (91.51)	24.7	8
Tischerioidea	Tischeriidae	*Tischeria*	*ekebladella*	DRD-01-0019	Tgkb	100	41.8	19

Tortricoidea	Tortricidae	*Argyrotaenia*	*alisellana*	CWM-94-0262	Arga	99.85	87.5	27
Tortricoidea	Tortricidae	*Platynota*	*idaeusalis*	JWB-05-0029	Pida2	100	91.3	27
Urodoidea	Urodidae	Gen.	sp.	JCS-07-5006	CR06	no hit	10.8	8
Urodoidea	Urodidae	*Urodus*	sp.	JCS-07-1016	CR16	*Urodus* sp. (100)	27.5	8
Urodoidea	Urodidae	"*Wockia*"	sp.	JCS-09-2060	MX60	*Wockia* sp. (95.41)	19.1	8
Urodoidea	Urodidae	*Urodus*	*decens*	DA-03-3349	Ursp	99.69	88.2	27
Urodoidea	Urodidae	*Wockia*	*koreana*	JCS-07-0084	Woc	*Wockia asperipunctella* (89.31)	34.3	19
Zygaenoidea	Lacturidae	*Eustixis*	*aglaodora*	AZ-07-2761	Eust	100	14.8	19
Zygaenoidea	Zygaenidae	*Pryeria*	*sinica*	JWB-05-0045-1	Psin	*Phauda UB02* (94.95)	91.9	27

Supplement S1-3. A spreadsheet showing the included species with annotations of their classification and GenBank accession numbers for *109fin*, *265fin*, *268fin*, *3007fin* and *acc*. The genes sampled for the 4-gene nt123 analysis are shown in bold.

IN-GROUP								
superfamily	Family	Genus	Species	109fin	265fin	268fin	**3007fin**	acc
Yponomeutoidea	Bedellidae	*Bedellia*	*somnulentella*	JQ787725	JQ788104	JQ789021	JQ786285	JQ789906
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	*autumnitella*				KC242955	
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	*xylophragma*					
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	sp.	JQ787727	JQ788107	JQ789024	JQ786288	JQ789909
Yponomeutoidea	Glyphipterigidae	*Acrolepiopsis*	*sapporensis*	JQ787706	JQ788083	JQ789002	JQ786266	
Yponomeutoidea	Glyphipterigidae	*Digitivalva*	*hemiglypha*	JQ787782	JQ788163	JQ789072	JQ786350	JQ789968
Yponomeutoidea	Glyphipterigidae	*Diploschizia*	*impigritella*	JQ787785	JQ788166		JQ786353	JQ789971
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*forsterella*				KC242963	
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	sp.	JQ787832	JQ788213		JQ786403	JQ790018
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*quadragintapunctata*	KC242921	KC242934	KC242949	KC242964	KC242988
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	cf. *lamprosema*	KC242922	KC242935	KC242950	KC242965	KC242989
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*perimetalla*		KC242936		KC242966	KC242990
Yponomeutoidea	Glyphipterigidae	*Lepidotarphius*	*peroprnatellus*	JQ787879	JQ788258	JQ789150	JQ786456	JQ790068
Yponomeutoidea	Glyphipterigidae	*Orthotelia*	*sparganella*	JQ787926	JQ788303	JQ789187	JQ786508	JQ790117
Yponomeutoidea	Glyphipterigidae	*Proditrix*	*gahniae*	JQ787945	JQ788322	JQ789205	JQ786530	JQ790138
Yponomeutoidea	Glyphipterigidae	*Proditrix*	*nielseni*				KC242975	
Yponomeutoidea	Heliodinidae	*Cycloplasis*	*panicifoliella*					
Yponomeutoidea	Heliodinidae	*Aetole*	*tripunctella*	JQ787679	JQ788060		JQ786238	JQ789862
Yponomeutoidea	Heliodinidae	*Embola*	*ionis*					
Yponomeutoidea	Heliodinidae	*Epicroesa*	*metallifera*	JQ787802	JQ788186	JQ789088	JQ786372	JQ789989
Yponomeutoidea	Heliodinidae	Gen.	sp.	KC242918	KC242931		KC242960	KC242985
Yponomeutoidea	Heliodinidae	*Neoheliodines*	*nyctaginella*					

Yponomeutoidea	Lyonetiidae	*Perileucoptera*	*coffeella*	JQ787874	JQ788253		JQ786450	JQ790064
Yponomeutoidea	Lyonetiidae	*Lyonetia*	*ledi*		JQ788256		JQ786453	
Yponomeutoidea	Lyonetiidae	*Lyonetia*	*prunifoliella*	JQ787878	JQ788257	JQ789149	JQ786455	JQ790067
Yponomeutoidea	Lyonetiidae	*Corythophora*	sp.	KC242919	KC242932		KC242961	KC242986
Yponomeutoidea	Lyonetiidae	*Euprora*	sp.	KC242920	KC242933	KC242948	KC242962	KC242987
Yponomeutoidea	Lyonetiidae	*Philonome*	*clemensella*					
Yponomeutoidea	Lyonetiidae	*Phyllobrostis*	cf. *daphneella*				KC242973	
Yponomeutoidea	Lyonetiidae	*Phyllobrostis*	*peninsulae*				KC242974	KC242995
Yponomeutoidea	Plutellidae	*Deryaraxenistis*	*serrata*		KC242940		KC242976	KC242996
Yponomeutoidea	Plutellidae	*Doxophyrtis*	*hydrocosma*	JQ787783	JQ788164	JQ789073	JQ786351	JQ789969
Yponomeutoidea	Plutellidae	*Eidophasia*	*messingiella*		JQ788187	JQ789089		
Yponomeutoidea	Plutellidae	Gen.	sp.				KC242967	
Yponomeutoidea	Plutellidae	*Lunakia*	*alyssella*					
Yponomeutoidea	Plutellidae	*Plutella*	*xylostella*	JQ787987	JQ788366	JQ789242	JQ786575	JQ790181
Yponomeutoidea	Plutellidae	*Rhigognostis*	*schmaltzella*	JQ787991	JQ788370	JQ789246	JQ786580	JQ790185
Yponomeutoidea	Plutellidae	*Tritymba*	*pamphaea*					
Yponomeutoidea	Yponomeutidae	*Argyresthia*	sp.	JQ788050	JQ788431	JQ789299	JQ786647	JQ790253
Yponomeutoidea	Yponomeutidae	*Argyresthia*	*austerella*					
Yponomeutoidea	Yponomeutidae	*Argyresthia*	*brockeella*	JQ787672	JQ788053	JQ788973	JQ786228	JQ789854
Yponomeutoidea	Yponomeutidae	*Atteva*	*aurea*	GU575557	GU575750		GU575902	GU576133
Yponomeutoidea	Yponomeutidae	*Atteva*	*zebra*	KC242914	KC242926	KC242944	KC242956	
Yponomeutoidea	Yponomeutidae	*Atemelia*	n. sp.	JQ788049	JQ788430	JQ789298	JQ786646	JQ790252
Yponomeutoidea	Yponomeutidae	*Atemelia*	*torquatella*	JQ787699	JQ788076	JQ788995	JQ786258	JQ789880
Yponomeutoidea	Yponomeutidae	*Prays*	*fraxinella*				KC242972	
Yponomeutoidea	Yponomeutidae	*Prays*	*delta*	JQ787963			JQ786550	JQ790156
Yponomeutoidea	Yponomeutidae	*Prays*	*atomocella*					
Yponomeutoidea	Yponomeutidae	*Prays*	*oleae*	JQ787972	JQ788349		JQ786559	JQ790166
Yponomeutoidea	Yponomeutidae	*Saridoscelis*	*kodamai*				JQ786592	JQ790197
Yponomeutoidea	Yponomeutidae	*Scythropia*	*crataegella*	JQ788012				JQ790208

Yponomeutoidea	Yponomeutidae	*Eucalantica*	*costaricae*	GU575589	GU575782	GU575821	GU575933	GU576166
Yponomeutoidea	Yponomeutidae	New genus	sp.		JQ788106	JQ789023	JQ786287	JQ789908
Yponomeutoidea	Yponomeutidae	New genus	sp.		JQ788108	JQ789025	JQ786289	JQ789910
Yponomeutoidea	Yponomeutidae	New genus	sp.	JQ787728	JQ788109	JQ789026	JQ786290	JQ789911
Yponomeutoidea	Yponomeutidae	"*Xyrosaris*"	sp.	JQ788048	JQ788429	JQ789297	JQ786645	JQ790251
Yponomeutoidea	Yponomeutidae	"*Zelleria*"	sp.		JQ788428	JQ789296	JQ786644	JQ790250
Yponomeutoidea	Yponomeutidae	*Cedestis*	*exiguata*	JQ787741	JQ788123	JQ789036	JQ786303	JQ789925
Yponomeutoidea	Yponomeutidae	*Cedestis*	*subfasciella*	JQ787923	JQ788301		JQ786504	JQ790114
Yponomeutoidea	Yponomeutidae	*Euhyponomeutoides*	*ribesiellus*			JQ789097	JQ786381	
Yponomeutoidea	Yponomeutidae	*Klausius*	*minor*	JQ787869	JQ788248		JQ786445	JQ790059
Yponomeutoidea	Yponomeutidae	*Metanomeuta*	*fulvicrinis*				KC242970	KC242993
Yponomeutoidea	Yponomeutidae	*Metanomeuta*	*fulvicrinis*		JQ788151	JQ789061	JQ786335	JQ789955
Yponomeutoidea	Yponomeutidae	*Paraswammerdamia*	*conspersella*				JQ786522	
Yponomeutoidea	Yponomeutidae	*Swammerdamia*	*glaucella*	JQ788010		JQ789262	JQ786602	JQ790206
Yponomeutoidea	Yponomeutidae	*Teinoptila*	*guttella*			KC242952	KC242977	KC242997
Yponomeutoidea	Yponomeutidae	*Thecobathra*	*anas*		JQ788392	JQ789265	JQ786606	JQ790210
Yponomeutoidea	Yponomeutidae	*Xyrosaris*	*lichneuta*	JQ788039	JQ788417		JQ786634	JQ790239
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*anatolica*	JQ788042	JQ788420	JQ789291	JQ786636	JQ790242
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*kanaiella*	JQ788043	JQ788421		JQ786637	JQ790243
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*multipunctella*	JQ788044	JQ788422	JQ789292	JQ786638	JQ790244
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*myriosema*	JQ788046	JQ788424		JQ786640	JQ790246
Yponomeutoidea	Yponomeutidae	*Zelleria*	*celastrusella*		JQ788426	JQ789294	JQ786642	JQ790248
Yponomeutoidea	Yponomeutidae	*Zelleria*	*retiniella*		KC242942	KC242953	KC242980	KC242999
Yponomeutoidea	Ypsolophidae	*Ochsenheimeria*	*urella*	JQ787929	JQ788305		JQ786511	JQ790120
Yponomeutoidea	Ypsolophidae	*Bhadorcosma*	*lonicerae*	JQ787722		JQ789018	JQ786280	
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*nigrimaculata*	JQ788045	JQ788423	JQ789293	JQ786639	JQ790245
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*angelicella*	KC242925			KC242978	KC242998
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*ustella*				KC242979	
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*yasudai*	JQ788047	JQ788425		JQ786641	JQ790247

Yponomeutoidea	uncertain	New genus	sp.	JQ787743	JQ788125	JQ789038	JQ786306	JQ789928
Yponomeutoidea	uncertain	New genus	sp.	JQ787729	JQ788110			JQ789912
Yponomeutoidea	uncertain	New genus	sp.				JQ786472	
“Yponomeutoidea”	“Yponomeutidae”	*Nosymna*	*stipella*	KC242924	KC242939	KC242951	KC242971	KC242994
“Yponomeutoidea”	uncertain			KC242915	KC242927	KC242945	KC242957	KC242982
“Yponomeutoidea”	uncertain				KC242928		KC242958	
OUT-GROUP								
superfamily	Family	Genus	Species	109fin	265fin	268fin	3007fin	acc
Choreutoidea	Choreutidae	*Hemerophila*	*felis*	GU575569	GU575762	GU575801	GU575915	GU576146
Copromorpoidea	Copromorphidae	*Copromorpha*	sp.					
Epermenioidea	Epermeniidae	*Epermenia*	*sinjovi*	JQ787813			JQ786384	JQ789999
Galacticoidea	Galacticidae	*Homadaula*	*anisocentra*		JQ788220	JQ789114	JQ786411	JQ790026
Gelechioidea	Cosmopterigidae	*Euclemensia*	*bassettella*			GU575792	GU575906	GU576137
Gelechioidea	Ethmiidae	*Ethmia*	*eupostica*	GU575565	GU575758	GU575797	GU575911	GU576142
Gelechioidea	Lypusidae	*Lypusa*	*maurella*					
Gelechioidea	uncertain	Gen.	sp.	KC242923	KC242937		KC242968	KC242991
Gracillarioidea	Bucculatricidae	*Bucculatrix*	sp.		JN124901		JN124940	JN125020
Gracillarioidea	Douglasiidae	*Klimeschia*	*transversella*	JN124851	JN124911	JN124930	JN124955	JN125033
Gracillarioidea	Gracillariidae	*Caloptilia*	*bimaculatella*	GU575559	GU575752	GU575790	GU575904	GU576135
Gracillarioidea	Gracillariidae	*Parectopa*	*robiniella*	JN124860	JN124918	JN124933	JN124965	JN125043
Gracillarioidea	Gracillariidae	*Cameraria*	*gaultheriella*	JN124845	JN124902	JN124923	JN124941	JN125021
Gracillarioidea	Gracillariidae	*Phyllonorycter*	sp.	JN124858	JN124915		JN124961	JN125039
Gracillarioidea	Gracillariidae	*Phyllocnistis*	*citrella*	JN124857	JN124914	JN124932		JN125038
Gracillarioidea	Gracillariidae	*Phyllocnistis*	*magnoliaeella*	JN124859	JN124916		JN124963	JN125041
Gracillarioidea	Roeslerstamiidae	*Agriothera*	*elaeocarpophaga*	JN124844	JN124899	JN124921	JN124936	JN125019
Gracillarioidea	Roeslerstamiidae	*Roeslerstammia*	*pronubella*	JN124861	JN124920		JN124968	JN125044
Gracillarioidea	Roeslerstamiidae	*Amphithera*	*heteroleuca*	KC242913		KC242943	KC242954	KC242981
Pterophoroidea	Pterophoridae	*Emmelina*	*monodactyla*	GU575566	GU575759	GU575798	GU575912	GU576143

Schreckensteinoidea	Schreckensteiniidae	*Schreckensteinia*	sp.	JQ788002	JQ788382	JQ789256	JQ786593	JQ790198
Tineoidea	Acrolophidae	*Acrolophus*	*arcanellus*	JQ787703	JQ788080	JQ788999	JQ786262	JQ789884
Tineoidea	Arrhenophanidae	*Arrhenophanes*	*perspicilla*	JQ787705	JQ788082	JQ789001	JQ786265	JQ789886
Tineoidea	Eriocottidae	*Compsoctena*	sp.	JQ787752	JQ788133	JQ789047	JQ786316	JQ789938
Tineoidea	Psychidae	*Rebelia*	*thomanni*				JQ786581	
Tineoidea	Psychidae	*Narycia*	*duplicella*	JQ787908	JQ788285		JQ786489	
Tineoidea	Psychidae	*Acanthopsyche*	*zelleri*					
Tineoidea	Psychidae	*Pseudarbela*	sp.	JQ787939	JQ788317		JQ786524	JQ790132
Tineoidea	Psychidae	*Psyche*	*crassiorella*		JQ788315			JQ790130
Tineoidea	Psychidae	*Scoriodyta*	*suttonensis*	JQ787993	JQ788372	JQ789248	JQ786582	JQ790187
Tineoidea	Psychidae	*Typhonia*	*ciliaris*		JQ788407		JQ786622	JQ790228
Tineoidea	Tineidae	*Dryadaula*	sp.					
Tineoidea	Tineidae	*Erechthias*	*zebrina*	JQ787825	JQ788207	JQ789103	JQ786395	JQ790010
Tineoidea	Tineidae	*Hapsifera*	sp.	JQ787839	JQ788221	JQ789115	JQ786412	JQ790027
Tineoidea	Tineidae	*Harmaclona*	sp.					
Tineoidea	Tineidae	*Opogona*	*thiadelia*	JQ787927	JQ788304	JQ789188	JQ786509	JQ790118
Tineoidea	Tineidae	*Hybroma*	*servulella*	JQ787858	JQ788238	JQ789131	JQ786434	JQ790049
Tineoidea	Tineidae	*Myrmecozela*	*ochraceella*	JQ787899	JQ788278	JQ789168	JQ786480	JQ790092
Tineoidea	Tineidae	*Nemapogon*	*cloacella*	JQ787910	JQ788287		JQ786491	JQ790101
Tineoidea	Tineidae	*Perissomastix*	sp.	JQ787942	JQ788320	JQ789202	JQ786527	JQ790135
Tineoidea	Tineidae	*Scardiella*	*approxomatella*	JQ787992	JQ788371	JQ789247		JQ790186
Tineoidea	Tineidae	*Tinea*	*columbariella*	GU575585	GU575778	GU575817		GU576162
Tineoidea	Tineidae	Gen.	sp.	KC242917	KC242930	KC242947		KC242984
Tischerioidea	Tischeriidae	*Tischeria*	*ekebladella*	JQ788017	JQ788396		JQ786611	JQ790215
Tortricoidea	Tortricidae	*Argyrotaenia*	*alisellana*	GU575556	GU575749	GU575788	GU575901	GU576132
Tortricoidea	Tortricidae	*Platynota*	*idaeusalis*	GU575576	GU575769	GU575808	GU575922	GU576153
Urodoidea	Urodidae	Gen.	sp.					
Urodoidea	Urodidae	*Urodus*	sp.	KC242916	KC242929	KC242946	KC242959	KC242983
Urodoidea	Urodidae	"*Wockia*"	sp.		KC242938		KC242969	KC242992

Urodoidea	Urodidae	*Urodus*	*decens*	GU575588	GU575781	GU575820		GU576165
Urodoidea	Urodidae	*Wockia*	*koreana*	JQ788038	JQ788416	JQ789288	JQ786632	JQ790238
Zygaenoidea	Lacturidae	*Eustixis*	*aglaodora*					
Zygaenoidea	Zygaenidae	*Pryeria*	*sinica*	GU575580	GU575773	GU575812	GU575926	GU576157

Supplement S1-4. A spreadsheet showing the included species with annotations of their classification and GenBank accession numbers for *CAD*, *DDC*, *enolase*, *period* and *wingless*. The genes sampled for the 4-gene nt123 analysis are shown in bold.

IN-GROUP								
superfamily	Family	Genus	Species	**CAD**	**DDC**	**enolase**	period	wingless
Yponomeutoidea	Bedellidae	*Bedellia*	*somnulentella*	JQ784362	JQ785724	JQ789380		JQ786705
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	*autumnitella*	KC243012				
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	*xylophragma*	JQ784340	JQ785703	JQ789361	JQ785297	
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	sp.	JQ784366	JQ785728	JQ789384		
Yponomeutoidea	Glyphipterigidae	*Acrolepiopsis*	*sapporensis*	JQ784326		JQ789349	JQ785291	
Yponomeutoidea	Glyphipterigidae	*Digitivalva*	*hemiglypha*	JQ784455	JQ785808	JQ789468	JQ785367	
Yponomeutoidea	Glyphipterigidae	*Diploschizia*	*impigritella*	JQ784458	JQ785810	JQ789469	JQ785369	
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*forsterella*	KC243022				
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	sp.	JQ784544	JQ785887			
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*quadragintapunctata*	KC243023	KC243048	KC243069		
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	cf. *lamprosema*	KC243024	KC243049	KC243070		
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*perimetalla*	KC243025	KC243050	KC243071		
Yponomeutoidea	Glyphipterigidae	*Lepidotarphius*	*peroprnatellus*	JQ784629	JQ785968	JQ789611	JQ785476	JQ786896
Yponomeutoidea	Glyphipterigidae	*Orthotelia*	*sparganella*	JQ784707	JQ786037	JQ789678		JQ786953
Yponomeutoidea	Glyphipterigidae	*Proditrix*	*gahniae*	JQ784734	JQ786059	JQ789700		JQ786970
Yponomeutoidea	Glyphipterigidae	*Proditrix*	*nielseni*	KC243035				
Yponomeutoidea	Heliodinidae	*Cycloplasis*	*panicifoliella*	JQ784416	JQ785773	JQ789431	JQ785343	JQ786738
Yponomeutoidea	Heliodinidae	*Aetole*	*tripunctella*	JQ784290	JQ785660	JQ789314	JQ785263	JQ786660
Yponomeutoidea	Heliodinidae	*Embola*	*ionis*	JQ784489	JQ785838	JQ789493	JQ785386	JQ786788
Yponomeutoidea	Heliodinidae	*Epicroesa*	*metallifera*	JQ784492		JQ789495	JQ785387	JQ786791
Yponomeutoidea	Heliodinidae	Gen.	sp.	KC243019	KC243046	KC243066		
Yponomeutoidea	Heliodinidae	*Neoheliodines*	*nyctaginella*	JQ784685	JQ786017	JQ789657		JQ786939

Yponomeutoidea	Lyonetiidae	*Perileucoptera*	*coffeella*	JQ784618		JQ789601		
Yponomeutoidea	Lyonetiidae	*Lyonetia*	*ledi*			JQ789606		
Yponomeutoidea	Lyonetiidae	*Lyonetia*	*prunifoliella*	JQ784627		JQ789609	JQ785474	
Yponomeutoidea	Lyonetiidae	*Corythophora*	sp.	KC243020		KC243067		
Yponomeutoidea	Lyonetiidae	*Euprora*	sp.	KC243021	KC243047	KC243068		
Yponomeutoidea	Lyonetiidae	*Philonome*	*clemensella*	JQ784749		JQ789712	JQ785546	JQ786982
Yponomeutoidea	Lyonetiidae	*Phyllobrostis*	cf. *daphneella*	KC243033				
Yponomeutoidea	Lyonetiidae	*Phyllobrostis*	*peninsulae*	KC243034		KC243074		
Yponomeutoidea	Plutellidae	*Deryaraxenistis*	*serrata*	KC243036	KC243056			
Yponomeutoidea	Plutellidae	*Doxophyrtis*	*hydrocosma*	JQ784456	JQ785809			JQ786762
Yponomeutoidea	Plutellidae	*Eidophasia*	*messingiella*	JQ784495	JQ785843	JQ789497		
Yponomeutoidea	Plutellidae	Gen.	sp.	KC243026	KC243051			
Yponomeutoidea	Plutellidae	*Lunakia*	*alyssella*	KC243028	KC243053			
Yponomeutoidea	Plutellidae	*Plutella*	*xylostella*	JQ784791	JQ786110	JQ789743	JQ785568	
Yponomeutoidea	Plutellidae	*Rhigognostis*	*schmaltzella*	JQ784804	JQ786122	JQ789753		
Yponomeutoidea	Plutellidae	*Tritymba*	*pamphaea*	JQ784870	JQ786183	JQ789813	JQ785618	JQ787068
Yponomeutoidea	Yponomeutidae	*Argyresthia*	sp.	JQ784913	JQ786224	JQ789851		
Yponomeutoidea	Yponomeutidae	*Argyresthia*	*austerella*	JQ784280	JQ785651	JQ789305		
Yponomeutoidea	Yponomeutidae	*Argyresthia*	*brockeella*	JQ784281	JQ785652	JQ789306		
Yponomeutoidea	Yponomeutidae	*Atteva*	*aurea*	GQ283513	GQ283600	GQ283677	GQ283760	GQ283829
Yponomeutoidea	Yponomeutidae	*Atteva*	*zebra*	KC243013	KC243042	KC243062		
Yponomeutoidea	Yponomeutidae	*Atemelia*	n. sp.	JQ784912	JQ786223	JQ789850		
Yponomeutoidea	Yponomeutidae	*Atemelia*	*torquatella*	JQ784319	JQ785684	JQ789341		
Yponomeutoidea	Yponomeutidae	*Prays*	*fraxinella*	KC243032				
Yponomeutoidea	Yponomeutidae	*Prays*	*delta*	JQ784761		JQ789719		
Yponomeutoidea	Yponomeutidae	*Prays*	*atomocella*	JQ784767	JQ786089	JQ789724	JQ785559	JQ786996
Yponomeutoidea	Yponomeutidae	*Prays*	*oleae*	JQ784772	JQ786094	JQ789728		JQ786999
Yponomeutoidea	Yponomeutidae	*Saridoscelis*	*kodamai*	JQ784824	JQ786141			
Yponomeutoidea	Yponomeutidae	*Scythropia*	*crataegella*	JQ784843	JQ786159	JQ789788		

Yponomeutoidea	Yponomeutidae	*Eucalantica*	*costaricae*	GQ283589	GQ283666	GQ283749		GQ283903
Yponomeutoidea	Yponomeutidae	New genus	sp.	JQ784365	JQ785727	JQ789383		
Yponomeutoidea	Yponomeutidae	New genus	sp.	JQ784367	JQ785729	JQ789385		
Yponomeutoidea	Yponomeutidae	New genus	sp.	JQ784368	JQ785730	JQ789386		
Yponomeutoidea	Yponomeutidae	"*Xyrosaris*"	sp.	JQ784911	JQ786222	JQ789849		
Yponomeutoidea	Yponomeutidae	"*Zelleria*"	sp.	JQ784910	JQ786221	JQ789848		
Yponomeutoidea	Yponomeutidae	*Cedestis*	*exiguata*	JQ784386	JQ785748	JQ789401		
Yponomeutoidea	Yponomeutidae	*Cedestis*	*subfasciella*	JQ784702	JQ786034	JQ789674		
Yponomeutoidea	Yponomeutidae	*Euhyponomeutoides*	*ribesiellus*	JQ784510				
Yponomeutoidea	Yponomeutidae	*Klausius*	*minor*	JQ784611	JQ785953	JQ789595		
Yponomeutoidea	Yponomeutidae	*Metanomeuta*	*fulvicrinis*	KC243030	KC243054			
Yponomeutoidea	Yponomeutidae	*Metanomeuta*	*fulvicrinis*	JQ784436	JQ785792	JQ789449		
Yponomeutoidea	Yponomeutidae	*Paraswammerdamia*	*conspersella*	JQ784723				
Yponomeutoidea	Yponomeutidae	*Swammerdamia*	*glaucella*	JQ784839	JQ786155	JQ789785		
Yponomeutoidea	Yponomeutidae	*Teinoptila*	*guttella*	KC243037	KC243057	KC243075		
Yponomeutoidea	Yponomeutidae	*Thecobathra*	*anas*	JQ784846	JQ786163	JQ789792	JQ785606	JQ787050
Yponomeutoidea	Yponomeutidae	*Xyrosaris*	*lichneuta*	JQ784894	JQ786205	JQ789832		
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*anatolica*	JQ784898	JQ786209	JQ789836		
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*kanaiella*	JQ784899	JQ786210	JQ789837		
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*multipunctella*		JQ786211	JQ789838	JQ785637	
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*myriosema*	JQ784901	JQ786213	JQ789840		
Yponomeutoidea	Yponomeutidae	*Zelleria*	*celastrusella*	JQ784906	JQ786218	JQ789845		
Yponomeutoidea	Yponomeutidae	*Zelleria*	*retiniella*	KC243040	KC243060	KC243077		
Yponomeutoidea	Ypsolophidae	*Ochsenheimeria*	*urella*	JQ784709	JQ786040	JQ789681	JQ785522	JQ786955
Yponomeutoidea	Ypsolophidae	*Bhadorcosma*	*lonicerae*	JQ784352	JQ785714	JQ789370		
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*nigrimaculata*	JQ784900	JQ786212	JQ789839	JQ785638	JQ787089
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*angelicella*	KC243038	KC243058	KC243076		
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*ustella*	KC243039	KC243059			
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*yasudai*	JQ784902	JQ786214	JQ789841		

Yponomeutoidea	uncertain	New genus	sp.	JQ784392	JQ785754	JQ789409		
Yponomeutoidea	uncertain	New genus	sp.	JQ784369	JQ785731	JQ789387		
Yponomeutoidea	uncertain	New genus	sp.	JQ784645	JQ785983			
“Yponomeutoidea”	“Yponomeutidae”	*Nosymna*	*stipella*	KC243031	KC243055	KC243073		
“Yponomeutoidea”	uncertain			KC243014	KC243043	KC243063		
“Yponomeutoidea”	uncertain			KC243015		KC243064		
OUT-GROUP								
superfamily	Family	Genus	Species	CAD	DDC	enolase	period	wingless
Choreutoidea	Choreutidae	*Hemerophila*	*felis*	GQ283543	GQ283626	GQ283705	GQ283784	GQ283857
Copromorpoidea	Copromorphidae	*Copromorpha*	sp.	JQ784399	JQ785759			JQ786725
Epermenioidea	Epermeniidae	*Epermenia*	*sinjovi*	JQ784513	JQ785858	JQ789511		
Galacticoidea	Galacticidae	*Homadaula*	*anisocentra*	JQ784556	JQ785899	JQ789548	JQ785421	JQ786838
Gelechioidea	Cosmopterigidae	*Euclemensia*	*bassettella*	GQ283521	GQ283608	GQ283685	GQ283766	GQ283837
Gelechioidea	Ethmiidae	*Ethmia*	*eupostica*	GQ283535	GQ283621	GQ283699	GQ283778	GQ283849
Gelechioidea	Lypusidae	*Lypusa*	*maurella*	JQ784624	JQ785964	JQ789607	JQ785471	
Gelechioidea	uncertain	Gen.	sp.	KC243027	KC243052	KC243072		
Gracillarioidea	Bucculatricidae	*Bucculatrix*	sp.	JN125053	JN125091	JN125135		JN125199
Gracillarioidea	Douglasiidae	*Klimeschia*	*transversella*	JN125071		JN125147	JN125194	JN125204
Gracillarioidea	Gracillariidae	*Caloptilia*	*bimaculatella*	GQ283517	GQ283604	GQ283681		GQ283833
Gracillarioidea	Gracillariidae	*Parectopa*	*robiniella*	JN125083	JN125102	JN125155		
Gracillarioidea	Gracillariidae	*Cameraria*	*gaultheriella*	JN125054		JN125136		JN125200
Gracillarioidea	Gracillariidae	*Phyllonorycter*	sp.	JN125079		JN125153		JN125206
Gracillarioidea	Gracillariidae	*Phyllocnistis*	*citrella*	JN125078	JN125101	JN125152	JN125195	JN125205
Gracillarioidea	Gracillariidae	*Phyllocnistis*	*magnoliaeella*	JN125081		JN125154	JN125196	JN125207
Gracillarioidea	Roeslerstamiidae	*Agriothera*	*elaeocarpophaga*	JN125048		JN125133		
Gracillarioidea	Roeslerstamiidae	*Roeslerstammia*	*pronubella*	JN125086	JN125104	JN125157		JN125208
Gracillarioidea	Roeslerstamiidae	*Amphithera*	*heteroleuca*	KC243011	KC243041	KC243061		
Pterophoroidea	Pterophoridae	*Emmelina*	*monodactyla*	GQ283536	GQ283622	GQ283700	GQ283779	GQ283850

Schreckensteinoidea	Schreckensteiniidae	*Schreckensteinia*	sp.	JQ784825	JQ786142	JQ789772	JQ785591	JQ787034
Tineoidea	Acrolophidae	*Acrolophus*	*arcanellus*		JQ785687	JQ789344		JQ786683
Tineoidea	Arrhenophanidae	*Arrhenophanes*	*perspicilla*	JQ784325	JQ785691	JQ789348		
Tineoidea	Eriocottidae	*Compsoctena*	sp.	JQ784405		JQ789420		JQ786728
Tineoidea	Psychidae	*Rebelia*	*thomanni*	JQ784805				
Tineoidea	Psychidae	*Narycia*	*duplicella*	JQ784673	JQ786006	JQ789646		
Tineoidea	Psychidae	*Acanthopsyche*	*zelleri*	JQ784344	JQ785707		JQ785299	
Tineoidea	Psychidae	*Pseudarbela*	sp.	JQ784727	JQ786051		JQ785531	
Tineoidea	Psychidae	*Psyche*	*crassiorella*	JQ784724				
Tineoidea	Psychidae	*Scoriodyta*	*suttonensis*	JQ784811	JQ786128	JQ789759	JQ785580	
Tineoidea	Psychidae	*Typhonia*	*ciliaris*	JQ784878	JQ786190		JQ785623	JQ787074
Tineoidea	Tineidae	*Dryadaula*	sp.	JQ784470	JQ785822	JQ789479	JQ785377	JQ786773
Tineoidea	Tineidae	*Erechthias*	*zebrina*	JQ784532	JQ785875	JQ789526		
Tineoidea	Tineidae	*Hapsifera*	sp.	JQ784559	JQ785902	JQ789550		
Tineoidea	Tineidae	*Harmaclona*	sp.	JQ784560	JQ785903	JQ789551	JQ785423	JQ786841
Tineoidea	Tineidae	*Opogona*	*thiadelia*	JQ784708	JQ786038	JQ789679	JQ785520	JQ786954
Tineoidea	Tineidae	*Hybroma*	*servulella*	JQ784592	JQ785935	JQ789576	JQ785448	JQ786867
Tineoidea	Tineidae	*Myrmecozela*	*ochraceella*	JQ784660	JQ785996	JQ789635	JQ785493	JQ786919
Tineoidea	Tineidae	*Nemapogon*	*cloacella*	JQ784675	JQ786008	JQ789648		JQ786933
Tineoidea	Tineidae	*Perissomastix*	sp.	JQ784732	JQ786057			JQ786968
Tineoidea	Tineidae	*Scardiella*	*approxomatella*	JQ784808	JQ786125	JQ789756	JQ785578	JQ787023
Tineoidea	Tineidae	*Tinea*	*columbariella*	GQ283585	GQ283662	GQ283745	GQ283816	GQ283899
Tineoidea	Tineidae	Gen.	sp.	KC243018	KC243046			
Tischerioidea	Tischeriidae	*Tischeria*	*ekebladella*	JQ784854	JQ786170			JQ787057
Tortricoidea	Tortricidae	*Argyrotaenia*	*alisellana*	GQ283512	GQ283599	GQ283676	GQ283759	GQ283828
Tortricoidea	Tortricidae	*Platynota*	*idaeusalis*	GQ283566	GQ283645	GQ283727	GQ283802	GQ283880
Urodoidea	Urodidae	Gen.	sp.	KC243016				
Urodoidea	Urodidae	*Urodus*	sp.	KC243017	KC243044	KC243065		
Urodoidea	Urodidae	"*Wockia*"	sp.	KC243029				

Urodoidea	Urodidae	*Urodus*	*decens*	GQ283588	GQ283665	GQ283748	GQ283819	GQ283902
Urodoidea	Urodidae	*Wockia*	*koreana*	JQ784891		JQ789830		
Zygaenoidea	Lacturidae	*Eustixis*	*aglaodora*	JQ784524				JQ786811
Zygaenoidea	Zygaenidae	*Pryeria*	*sinica*	GQ283576	GQ283654	GQ283737	GQ283808	GQ283890

Supplement S1-5. A spreadsheet showing the included species with annotations of their classification and GenBank accession numbers for *36fin*, *40fin*, *42fin*, *44fin* and *69fin*.

IN-GROUP								
superfamily	Family	Genus	Species	36fin	40fin	42fin	44fin	69fin
Yponomeutoidea	Bedellidae	*Bedellia*	*somnulentella*		JQ787139	JQ788468		
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	*autumnitella*					
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	*xylophragma*					
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	sp.					
Yponomeutoidea	Glyphipterigidae	*Acrolepiopsis*	*sapporensis*		JQ787124	JQ788454		
Yponomeutoidea	Glyphipterigidae	*Digitivalva*	*hemiglypha*		JQ787176	JQ788503		
Yponomeutoidea	Glyphipterigidae	*Diploschizia*	*impigritella*		JQ787178	JQ788505		
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*forsterella*					
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	sp.		JQ787209			
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*quadragintapunctata*					
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	cf. *lamprosema*					
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*perimetalla*					
Yponomeutoidea	Glyphipterigidae	*Lepidotarphius*	*peroprnatellus*		JQ787250	JQ788567		
Yponomeutoidea	Glyphipterigidae	*Orthotelia*	*sparganella*		JQ787285	JQ788600		
Yponomeutoidea	Glyphipterigidae	*Proditrix*	*gahniae*		JQ787301			
Yponomeutoidea	Glyphipterigidae	*Proditrix*	*nielseni*					
Yponomeutoidea	Heliodinidae	*Cycloplasis*	*panicifoliella*					
Yponomeutoidea	Heliodinidae	*Aetole*	*tripunctella*		JQ787103	JQ788436		
Yponomeutoidea	Heliodinidae	*Embola*	*ionis*					
Yponomeutoidea	Heliodinidae	*Epicroesa*	*metallifera*		JQ787192			
Yponomeutoidea	Heliodinidae	Gen.	sp.					
Yponomeutoidea	Heliodinidae	*Neoheliodines*	*nyctaginella*					

Yponomeutoidea	Lyonetiidae	*Perileucoptera*	*coffeella*					
Yponomeutoidea	Lyonetiidae	*Lyonetia*	*ledi*					
Yponomeutoidea	Lyonetiidae	*Lyonetia*	*prunifoliella*					
Yponomeutoidea	Lyonetiidae	*Corythophora*	sp.					
Yponomeutoidea	Lyonetiidae	*Euprora*	sp.					
Yponomeutoidea	Lyonetiidae	*Philonome*	*clemensella*					
Yponomeutoidea	Lyonetiidae	*Phyllobrostis*	cf. *daphneella*					
Yponomeutoidea	Lyonetiidae	*Phyllobrostis*	*peninsulae*					
Yponomeutoidea	Plutellidae	*Deryaraxenistis*	*serrata*					
Yponomeutoidea	Plutellidae	*Doxophyrtis*	*hydrocosma*					
Yponomeutoidea	Plutellidae	*Eidophasia*	*messingiella*					
Yponomeutoidea	Plutellidae	Gen.	sp.					
Yponomeutoidea	Plutellidae	*Lunakia*	*alyssella*					
Yponomeutoidea	Plutellidae	*Plutella*	*xylostella*		JQ787336	JQ788636		
Yponomeutoidea	Plutellidae	*Rhigognostis*	*schmaltzella*					
Yponomeutoidea	Plutellidae	*Tritymba*	*pamphaea*					
Yponomeutoidea	Yponomeutidae	*Argyresthia*	sp.					
Yponomeutoidea	Yponomeutidae	*Argyresthia*	*austerella*					
Yponomeutoidea	Yponomeutidae	*Argyresthia*	*brockeella*					
Yponomeutoidea	Yponomeutidae	*Atteva*	*aurea*	GU575397	GU575427	GU575464	GU575496	
Yponomeutoidea	Yponomeutidae	*Atteva*	*zebra*					
Yponomeutoidea	Yponomeutidae	*Atemelia*	n. sp.					
Yponomeutoidea	Yponomeutidae	*Atemelia*	*torquatella*					
Yponomeutoidea	Yponomeutidae	*Prays*	*fraxinella*					
Yponomeutoidea	Yponomeutidae	*Prays*	*delta*					
Yponomeutoidea	Yponomeutidae	*Prays*	*atomocella*					
Yponomeutoidea	Yponomeutidae	*Prays*	*oleae*		JQ787326	JQ788626		
Yponomeutoidea	Yponomeutidae	*Saridoscelis*	*kodamai*					
Yponomeutoidea	Yponomeutidae	*Scythropia*	*crataegella*		JQ787361			

Yponomeutoidea	Yponomeutidae	*Eucalantica*	*costaricae*	GU575421	GU575457	GU575491		GU575549
Yponomeutoidea	Yponomeutidae	New genus	sp.					
Yponomeutoidea	Yponomeutidae	New genus	sp.					
Yponomeutoidea	Yponomeutidae	New genus	sp.					
Yponomeutoidea	Yponomeutidae	"*Xyrosaris*"	sp.					
Yponomeutoidea	Yponomeutidae	"*Zelleria*"	sp.					
Yponomeutoidea	Yponomeutidae	*Cedestis*	*exiguata*					
Yponomeutoidea	Yponomeutidae	*Cedestis*	*subfasciella*					
Yponomeutoidea	Yponomeutidae	*Euhyponomeutoides*	*ribesiellus*					
Yponomeutoidea	Yponomeutidae	*Klausius*	*minor*					
Yponomeutoidea	Yponomeutidae	*Metanomeuta*	*fulvicrinis*					
Yponomeutoidea	Yponomeutidae	*Metanomeuta*	*fulvicrinis*					
Yponomeutoidea	Yponomeutidae	*Paraswammerdamia*	*conspersella*					
Yponomeutoidea	Yponomeutidae	*Swammerdamia*	*glaucella*					
Yponomeutoidea	Yponomeutidae	*Teinoptila*	*guttella*					
Yponomeutoidea	Yponomeutidae	*Thecobathra*	*anas*		JQ787363	JQ788658		
Yponomeutoidea	Yponomeutidae	*Xyrosaris*	*lichneuta*					
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*anatolica*					
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*kanaiella*					
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*multipunctella*		JQ787384	JQ788676		
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*myriosema*					
Yponomeutoidea	Yponomeutidae	*Zelleria*	*celastrusella*					
Yponomeutoidea	Yponomeutidae	*Zelleria*	*retiniella*					
Yponomeutoidea	Ypsolophidae	*Ochsenheimeria*	*urella*		JQ787287	JQ788603		
Yponomeutoidea	Ypsolophidae	*Bhadorcosma*	*lonicerae*					
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*nigrimaculata*		JQ787385	JQ788677		
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*angelicella*					
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*ustella*					
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*yasudai*					

Yponomeutoidea	uncertain	New genus	sp.					
Yponomeutoidea	uncertain	New genus	sp.					
Yponomeutoidea	uncertain	New genus	sp.					
“Yponomeutoidea”	“Yponomeutidae”	*Nosymna*	*stipella*					
“Yponomeutoidea”	uncertain							
“Yponomeutoidea”	uncertain							
OUT-GROUP								
superfamily	Family	Genus	Species	36fin	40fin	42fin	44fin	69fin
Choreutoidea	Choreutidae	*Hemerophila*	*felis*	GU575408	GU575439	GU575475	GU575504	GU575533
Copromorpoidea	Copromorphidae	*Copromorpha*	sp.					
Epermenioidea	Epermeniidae	*Epermenia*	*sinjovi*					
Galacticoidea	Galacticidae	*Homadaula*	*anisocentra*			JQ788535		
Gelechioidea	Cosmopterigidae	*Euclemensia*	*bassettella*	GU575399	GU575431	GU575466	GU575497	GU575527
Gelechioidea	Ethmiidae	*Ethmia*	*eupostica*	GU575404	GU575436	GU575471		
Gelechioidea	Lypusidae	*Lypusa*	*maurella*					
Gelechioidea	uncertain	Gen.	sp.					
Gracillarioidea	Bucculatricidae	*Bucculatrix*	sp.		JN124823	JN124835		
Gracillarioidea	Douglasiidae	*Klimeschia*	*transversella*		JN124828	JN124839		
Gracillarioidea	Gracillariidae	*Caloptilia*	*bimaculatella*	GU575398	GU575429	GU575465		GU575526
Gracillarioidea	Gracillariidae	*Parectopa*	*robiniella*					
Gracillarioidea	Gracillariidae	*Cameraria*	*gaultheriella*		JN124824	JN124836		
Gracillarioidea	Gracillariidae	*Phyllonorycter*	sp.		JN124830	JN124841		
Gracillarioidea	Gracillariidae	*Phyllocnistis*	*citrella*		JN124829	JN124840		
Gracillarioidea	Gracillariidae	*Phyllocnistis*	*magnoliaeella*		JN124831			
Gracillarioidea	Roeslerstamiidae	*Agriothera*	*elaeocarpophaga*		JN124822	JN124834		
Gracillarioidea	Roeslerstamiidae	*Roeslerstammia*	*pronubella*		JN124832	JN124842		
Gracillarioidea	Roeslerstamiidae	*Amphithera*	*heteroleuca*					
Pterophoroidea	Pterophoridae	*Emmelina*	*monodactyla*	GU575405	GU575437	GU575472	GU575502	GU575531

Schreckensteinoidea	Schreckensteiniidae	*Schreckensteinia*	sp.		JQ787352	JQ788649		
Tineoidea	Acrolophidae	*Acrolophus*	*arcanellus*		JQ787123			
Tineoidea	Arrhenophanidae	*Arrhenophanes*	*perspicilla*			JQ788453		
Tineoidea	Eriocottidae	*Compsoctena*	sp.		JQ787153	JQ788481		
Tineoidea	Psychidae	*Rebelia*	*thomanni*					
Tineoidea	Psychidae	*Narycia*	*duplicella*					
Tineoidea	Psychidae	*Acanthopsyche*	*zelleri*					
Tineoidea	Psychidae	*Pseudarbela*	sp.		JQ787297			
Tineoidea	Psychidae	*Psyche*	*crassiorella*					
Tineoidea	Psychidae	*Scoriodyta*	*suttonensis*		JQ787342			
Tineoidea	Psychidae	*Typhonia*	*ciliaris*					
Tineoidea	Tineidae	*Dryadaula*	sp.					
Tineoidea	Tineidae	*Erechthias*	*zebrina*					
Tineoidea	Tineidae	*Hapsifera*	sp.		JQ787215			
Tineoidea	Tineidae	*Harmaclona*	sp.					
Tineoidea	Tineidae	*Opogona*	*thiadelia*			JQ788601		
Tineoidea	Tineidae	*Hybroma*	*servulella*		JQ787232	JQ788549		
Tineoidea	Tineidae	*Myrmecozela*	*ochraceella*		JQ787267	JQ788582		
Tineoidea	Tineidae	*Nemapogon*	*cloacella*		JQ787275			
Tineoidea	Tineidae	*Perissomastix*	sp.		JQ787300			
Tineoidea	Tineidae	*Scardiella*	*approxomatella*		JQ787341			
Tineoidea	Tineidae	*Tinea*	*columbariella*	GU575419	GU575454	GU575489	GU575518	
Tineoidea	Tineidae	Gen.	sp.					
Tischerioidea	Tischeriidae	*Tischeria*	*ekebladella*					
Tortricoidea	Tortricidae	*Argyrotaenia*	*alisellana*	GU575396		GU575463	GU575495	GU575524
Tortricoidea	Tortricidae	*Platynota*	*idaeusalis*	GU575412	GU575445	GU575481	GU575511	
Urodoidea	Urodidae	Gen.	sp.					
Urodoidea	Urodidae	*Urodus*	sp.					
Urodoidea	Urodidae	"*Wockia*"	sp.					

Urodoidea	Urodidae	*Urodus*	*decens*	GU575420	GU575456	GU575490	GU575520	GU575548
Urodoidea	Urodidae	*Wockia*	*koreana*					
Zygaenoidea	Lacturidae	*Eustixis*	*aglaodora*					
Zygaenoidea	Zygaenidae	*Pryeria*	*sinica*	GU575415	GU575449	GU575484	GU575513	GU575543

Supplement S1-6. A spreadsheet showing the included species with annotations of their classification and GenBank accession numbers for *113fin*, *192fin*, *197fin*, *262fin* and *270fin*.

IN-GROUP								
superfamily	Family	Genus	Species	113fin	192fin	197fin	262fin	270fin
Yponomeutoidea	Bedellidae	*Bedellia*	*somnulentella*		JQ790284	JQ783997	JQ784963	
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	*autumnitella*					
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	*xylophragma*					
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	sp.					
Yponomeutoidea	Glyphipterigidae	*Acrolepiopsis*	*sapporensis*		JQ790270	JQ783980	JQ784945	
Yponomeutoidea	Glyphipterigidae	*Digitivalva*	*hemiglypha*		JQ790318	JQ784042	JQ785008	
Yponomeutoidea	Glyphipterigidae	*Diploschizia*	*impigritella*		JQ790321	JQ784044	JQ785011	
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*forsterella*					
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	sp.		JQ790352	JQ784081	JQ785053	
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*quadragintapunctata*					
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	cf. *lamprosema*					
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*perimetalla*					
Yponomeutoidea	Glyphipterigidae	*Lepidotarphius*	*peroprnatellus*		JQ790388	JQ784125	JQ785100	
Yponomeutoidea	Glyphipterigidae	*Orthotelia*	*sparganella*		JQ790426	JQ784169	JQ785144	
Yponomeutoidea	Glyphipterigidae	*Proditrix*	*gahniae*		JQ790440	JQ784186	JQ785163	
Yponomeutoidea	Glyphipterigidae	*Proditrix*	*nielseni*					
Yponomeutoidea	Heliodinidae	*Cycloplasis*	*panicifoliella*					
Yponomeutoidea	Heliodinidae	*Aetole*	*tripunctella*		JQ790258	JQ783959	JQ784922	
Yponomeutoidea	Heliodinidae	*Embola*	*ionis*					
Yponomeutoidea	Heliodinidae	*Epicroesa*	*metallifera*		JQ790333	JQ784057	JQ785027	
Yponomeutoidea	Heliodinidae	Gen.	sp.					
Yponomeutoidea	Heliodinidae	*Neoheliodines*	*nyctaginella*					

Yponomeutoidea	Lyonetiidae	*Perileucoptera*	*coffeella*		JQ790385	JQ784120	JQ785095	
Yponomeutoidea	Lyonetiidae	*Lyonetia*	*ledi*					
Yponomeutoidea	Lyonetiidae	*Lyonetia*	*prunifoliella*			JQ784124	JQ785099	
Yponomeutoidea	Lyonetiidae	*Corythophora*	sp.					
Yponomeutoidea	Lyonetiidae	*Euprora*	sp.					
Yponomeutoidea	Lyonetiidae	*Philonome*	*clemensella*					
Yponomeutoidea	Lyonetiidae	*Phyllobrostis*	cf. *daphneella*					
Yponomeutoidea	Lyonetiidae	*Phyllobrostis*	*peninsulae*					
Yponomeutoidea	Plutellidae	*Deryaraxenistis*	*serrata*					
Yponomeutoidea	Plutellidae	*Doxophyrtis*	*hydrocosma*		JQ790319		JQ785009	
Yponomeutoidea	Plutellidae	*Eidophasia*	*messingiella*					
Yponomeutoidea	Plutellidae	Gen.	sp.					
Yponomeutoidea	Plutellidae	*Lunakia*	*alyssella*					
Yponomeutoidea	Plutellidae	*Plutella*	*xylostella*			JQ784222	JQ785198	
Yponomeutoidea	Plutellidae	*Rhigognostis*	*schmaltzella*					
Yponomeutoidea	Plutellidae	*Tritymba*	*pamphaea*					
Yponomeutoidea	Yponomeutidae	*Argyresthia*	sp.					
Yponomeutoidea	Yponomeutidae	*Argyresthia*	*austerella*					
Yponomeutoidea	Yponomeutidae	*Argyresthia*	*brockeella*					
Yponomeutoidea	Yponomeutidae	*Atteva*	*aurea*	GU575596	GU575635	GU575670	GU575710	GU575827
Yponomeutoidea	Yponomeutidae	*Atteva*	*zebra*					
Yponomeutoidea	Yponomeutidae	*Atemelia*	n. sp.					
Yponomeutoidea	Yponomeutidae	*Atemelia*	*torquatella*					
Yponomeutoidea	Yponomeutidae	*Prays*	*fraxinella*					
Yponomeutoidea	Yponomeutidae	*Prays*	*delta*					
Yponomeutoidea	Yponomeutidae	*Prays*	*atomocella*					
Yponomeutoidea	Yponomeutidae	*Prays*	*oleae*		JQ790462	JQ784211	JQ785187	
Yponomeutoidea	Yponomeutidae	*Saridoscelis*	*kodamai*					
Yponomeutoidea	Yponomeutidae	*Scythropia*	*crataegella*		JQ790492	JQ784245	JQ785222	

Yponomeutoidea	Yponomeutidae	*Eucalantica*	*costaricae*	GU575628	GU575663	GU575702	GU575743	
Yponomeutoidea	Yponomeutidae	New genus	sp.					
Yponomeutoidea	Yponomeutidae	New genus	sp.					
Yponomeutoidea	Yponomeutidae	New genus	sp.					
Yponomeutoidea	Yponomeutidae	"*Xyrosaris*"	sp.					
Yponomeutoidea	Yponomeutidae	"*Zelleria*"	sp.					
Yponomeutoidea	Yponomeutidae	*Cedestis*	*exiguata*					
Yponomeutoidea	Yponomeutidae	*Cedestis*	*subfasciella*					
Yponomeutoidea	Yponomeutidae	*Euhyponomeutoides*	*ribesiellus*					
Yponomeutoidea	Yponomeutidae	*Klausius*	*minor*					
Yponomeutoidea	Yponomeutidae	*Metanomeuta*	*fulvicrinis*					
Yponomeutoidea	Yponomeutidae	*Metanomeuta*	*fulvicrinis*					
Yponomeutoidea	Yponomeutidae	*Paraswammerdamia*	*conspersella*					
Yponomeutoidea	Yponomeutidae	*Swammerdamia*	*glaucella*					
Yponomeutoidea	Yponomeutidae	*Teinoptila*	*guttella*					
Yponomeutoidea	Yponomeutidae	*Thecobathra*	*anas*		JQ790493	JQ784247	JQ785224	
Yponomeutoidea	Yponomeutidae	*Xyrosaris*	*lichneuta*					
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*anatolica*					
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*kanaiella*					
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*multipunctella*			JQ784269	JQ785252	
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*myriosema*					
Yponomeutoidea	Yponomeutidae	*Zelleria*	*celastrusella*					
Yponomeutoidea	Yponomeutidae	*Zelleria*	*retiniella*					
Yponomeutoidea	Ypsolophidae	*Ochsenheimeria*	*urella*		JQ790428	JQ784172	JQ785147	
Yponomeutoidea	Ypsolophidae	*Bhadorcosma*	*lonicerae*					
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*nigrimaculata*		JQ790512	JQ784270	JQ785253	
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*angelicella*					
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*ustella*					
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*yasudai*					

Yponomeutoidea	uncertain	New genus	sp.					
Yponomeutoidea	uncertain	New genus	sp.					
Yponomeutoidea	uncertain	New genus	sp.					
“Yponomeutoidea”	“Yponomeutidae”	*Nosymna*	*stipella*					
“Yponomeutoidea”	uncertain							
“Yponomeutoidea”	uncertain							
OUT-GROUP								
superfamily	Family	Genus	Species	113fin	192fin	197fin	262fin	270fin
Choreutoidea	Choreutidae	*Hemerophila*	*felis*	GU575609	GU575644	GU575683	GU575723	GU575838
Copromorpoidea	Copromorphidae	*Copromorpha*	sp.					
Epermenioidea	Epermeniidae	*Epermenia*	*sinjovi*					
Galacticoidea	Galacticidae	*Homadaula*	*anisocentra*			JQ784086	JQ785059	
Gelechioidea	Cosmopterigidae	*Euclemensia*	*bassettella*	GU575600	GU575639	GU575674	GU575714	GU575830
Gelechioidea	Ethmiidae	*Ethmia*	*eupostica*	GU575605	GU575642	GU575679	GU575719	GU575835
Gelechioidea	Lypusidae	*Lypusa*	*maurella*					
Gelechioidea	uncertain	Gen.	sp.					
Gracillarioidea	Bucculatricidae	*Bucculatrix*	sp.		JN124864	JN124876	JN124887	
Gracillarioidea	Douglasiidae	*Klimeschia*	*transversella*		JN124869	JN124880	JN124892	
Gracillarioidea	Gracillariidae	*Caloptilia*	*bimaculatella*	GU575598	GU575637	GU575672	GU575712	GU575829
Gracillarioidea	Gracillariidae	*Parectopa*	*robiniella*		JN124873	JN124884	JN124896	
Gracillarioidea	Gracillariidae	*Cameraria*	*gaultheriella*		JN124865	JN124877	JN124888	
Gracillarioidea	Gracillariidae	*Phyllonorycter*	sp.		JN124871	JN124882	JN124894	
Gracillarioidea	Gracillariidae	*Phyllocnistis*	*citrella*		JN124870	JN124881	JN124893	
Gracillarioidea	Gracillariidae	*Phyllocnistis*	*magnoliaeella*		JN124872	JN124883	JN124895	
Gracillarioidea	Roeslerstamiidae	*Agriothera*	*elaeocarpophaga*			JN124875	JN124886	
Gracillarioidea	Roeslerstamiidae	*Roeslerstammia*	*pronubella*			JN124885	JN124897	
Gracillarioidea	Roeslerstamiidae	*Amphithera*	*heteroleuca*					
Pterophoroidea	Pterophoridae	*Emmelina*	*monodactyla*	GU575606	GU575643	GU575680	GU575720	GU575836

Schreckensteinoidea	Schreckensteiniidae	*Schreckensteinia*	sp.		JQ790484	JQ784236	JQ785212	
Tineoidea	Acrolophidae	*Acrolophus*	*arcanellus*		JQ790268	JQ783977	JQ784942	
Tineoidea	Arrhenophanidae	*Arrhenophanes*	*perspicilla*			JQ783979		
Tineoidea	Eriocottidae	*Compsoctena*	sp.			JQ784012	JQ784980	
Tineoidea	Psychidae	*Rebelia*	*thomanni*					
Tineoidea	Psychidae	*Narycia*	*duplicella*		JQ790412		JQ785129	
Tineoidea	Psychidae	*Acanthopsyche*	*zelleri*					
Tineoidea	Psychidae	*Pseudarbela*	sp.		JQ790434			
Tineoidea	Psychidae	*Psyche*	*crassiorella*				JQ785156	
Tineoidea	Psychidae	*Scoriodyta*	*suttonensis*		JQ790476			
Tineoidea	Psychidae	*Typhonia*	*ciliaris*				JQ785240	
Tineoidea	Tineidae	*Dryadaula*	sp.					
Tineoidea	Tineidae	*Erechthias*	*zebrina*				JQ785046	
Tineoidea	Tineidae	*Hapsifera*	sp.			JQ784087	JQ785060	
Tineoidea	Tineidae	*Harmaclona*	sp.					
Tineoidea	Tineidae	*Opogona*	*thiadelia*			JQ784170	JQ785145	
Tineoidea	Tineidae	*Hybroma*	*servulella*		JQ790371	JQ784106	JQ785079	
Tineoidea	Tineidae	*Myrmecozela*	*ochraceella*		JQ790404	JQ784147	JQ785120	
Tineoidea	Tineidae	*Nemapogon*	*cloacella*		JQ790414	JQ784154		
Tineoidea	Tineidae	*Perissomastix*	sp.		JQ790437	JQ784183	JQ785160	
Tineoidea	Tineidae	*Scardiella*	*approxomatella*		JQ790475	JQ784226	JQ785202	
Tineoidea	Tineidae	*Tinea*	*columbariella*	GU575624	GU575660	GU575699	GU575739	
Tineoidea	Tineidae	Gen.	sp.					
Tischerioidea	Tischeriidae	*Tischeria*	*ekebladella*			JQ784251	JQ785228	
Tortricoidea	Tortricidae	*Argyrotaenia*	*alisellana*	GU575595	GU575634	GU575669	GU575709	GU575826
Tortricoidea	Tortricidae	*Platynota*	*idaeusalis*	GU575615	GU575651	GU575690	GU575730	GU575844
Urodoidea	Urodidae	Gen.	sp.					
Urodoidea	Urodidae	*Urodus*	sp.					
Urodoidea	Urodidae	"*Wockia*"	sp.					

Urodoidea	Urodidae	*Urodus*	*decens*	GU575627	GU575662	GU575701	GU575742	GU575854
Urodoidea	Urodidae	*Wockia*	*koreana*					
Zygaenoidea	Lacturidae	*Eustixis*	*aglaodora*					
Zygaenoidea	Zygaenidae	*Pryeria*	*sinica*	GU575619	GU575655	GU575694	GU575734	

Supplement S1-6. A spreadsheet showing the included species with annotations of their classification and GenBank accession numbers for *3006fin*, *3017fin*, *3059fin*, *3070fin* and *8028fin*.

IN-GROUP								
superfamily	Family	Genus	Species	3006fin	3017fin	3059fin	3070fin	8028fin
Yponomeutoidea	Bedellidae	*Bedellia*	*somnulentella*		JQ788723		JQ783394	JQ787428
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	*autumnitella*					
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	*xylophragma*					
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	sp.					
Yponomeutoidea	Glyphipterigidae	*Acrolepiopsis*	*sapporensis*		JQ788705		JQ783377	JQ787413
Yponomeutoidea	Glyphipterigidae	*Digitivalva*	*hemiglypha*		JQ788759		JQ783436	JQ787464
Yponomeutoidea	Glyphipterigidae	*Diploschizia*	*impigritella*		JQ788761		JQ783438	JQ787466
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*forsterella*					
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	sp.		JQ788795		JQ783478	
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*quadragintapunctata*					
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	cf. *lamprosema*					
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*perimetalla*					
Yponomeutoidea	Glyphipterigidae	*Lepidotarphius*	*peroprnatellus*		JQ788835		JQ783519	JQ787541
Yponomeutoidea	Glyphipterigidae	*Orthotelia*	*sparganella*		JQ788875		JQ783561	JQ787579
Yponomeutoidea	Glyphipterigidae	*Proditrix*	*gahniae*				JQ783579	
Yponomeutoidea	Glyphipterigidae	*Proditrix*	*nielseni*					
Yponomeutoidea	Heliodinidae	*Cycloplasis*	*panicifoliella*					
Yponomeutoidea	Heliodinidae	*Aetole*	*tripunctella*		JQ788684		JQ783358	JQ787394
Yponomeutoidea	Heliodinidae	*Embola*	*ionis*					
Yponomeutoidea	Heliodinidae	*Epicroesa*	*metallifera*		JQ788774		JQ783455	JQ787480
Yponomeutoidea	Heliodinidae	Gen.	sp.					
Yponomeutoidea	Heliodinidae	*Neoheliodines*	*nyctaginella*					

Yponomeutoidea	Lyonetiidae	*Perileucoptera*	*coffeella*		JQ788831		JQ783516	
Yponomeutoidea	Lyonetiidae	*Lyonetia*	*ledi*					
Yponomeutoidea	Lyonetiidae	*Lyonetia*	*prunifoliella*		JQ788834			JQ787540
Yponomeutoidea	Lyonetiidae	*Corythophora*	sp.					
Yponomeutoidea	Lyonetiidae	*Euprora*	sp.					
Yponomeutoidea	Lyonetiidae	*Philonome*	*clemensella*					
Yponomeutoidea	Lyonetiidae	*Phyllobrostis*	cf. *daphneella*					
Yponomeutoidea	Lyonetiidae	*Phyllobrostis*	*peninsulae*					
Yponomeutoidea	Plutellidae	*Deryaraxenistis*	*serrata*					
Yponomeutoidea	Plutellidae	*Doxophyrtis*	*hydrocosma*					
Yponomeutoidea	Plutellidae	*Eidophasia*	*messingiella*					
Yponomeutoidea	Plutellidae	Gen.	sp.					
Yponomeutoidea	Plutellidae	*Lunakia*	*alyssella*					
Yponomeutoidea	Plutellidae	*Plutella*	*xylostella*		JQ788920		JQ783607	JQ787621
Yponomeutoidea	Plutellidae	*Rhigognostis*	*schmaltzella*					
Yponomeutoidea	Plutellidae	*Tritymba*	*pamphaea*					
Yponomeutoidea	Yponomeutidae	*Argyresthia*	sp.					
Yponomeutoidea	Yponomeutidae	*Argyresthia*	*austerella*					
Yponomeutoidea	Yponomeutidae	*Argyresthia*	*brockeella*					
Yponomeutoidea	Yponomeutidae	*Atteva*	*aurea*	GU575861	GU575938	GU575976	GU576015	GU576053
Yponomeutoidea	Yponomeutidae	*Atteva*	*zebra*					
Yponomeutoidea	Yponomeutidae	*Atemelia*	n. sp.					
Yponomeutoidea	Yponomeutidae	*Atemelia*	*torquatella*					
Yponomeutoidea	Yponomeutidae	*Prays*	*fraxinella*					
Yponomeutoidea	Yponomeutidae	*Prays*	*delta*					
Yponomeutoidea	Yponomeutidae	*Prays*	*atomocella*					
Yponomeutoidea	Yponomeutidae	*Prays*	*oleae*		JQ788910		JQ783597	JQ787612
Yponomeutoidea	Yponomeutidae	*Saridoscelis*	*kodamai*					
Yponomeutoidea	Yponomeutidae	*Scythropia*	*crataegella*		JQ788943		JQ783626	

Yponomeutoidea	Yponomeutidae	*Eucalantica*	*costaricae*	GU575894	GU575968	GU576008	GU576045	GU576084
Yponomeutoidea	Yponomeutidae	New genus	sp.					
Yponomeutoidea	Yponomeutidae	New genus	sp.					
Yponomeutoidea	Yponomeutidae	New genus	sp.					
Yponomeutoidea	Yponomeutidae	"*Xyrosaris*"	sp.					
Yponomeutoidea	Yponomeutidae	"*Zelleria*"	sp.					
Yponomeutoidea	Yponomeutidae	*Cedestis*	*exiguata*					
Yponomeutoidea	Yponomeutidae	*Cedestis*	*subfasciella*					
Yponomeutoidea	Yponomeutidae	*Euhyponomeutoides*	*ribesiellus*					
Yponomeutoidea	Yponomeutidae	*Klausius*	*minor*					
Yponomeutoidea	Yponomeutidae	*Metanomeuta*	*fulvicrinis*					
Yponomeutoidea	Yponomeutidae	*Metanomeuta*	*fulvicrinis*					
Yponomeutoidea	Yponomeutidae	*Paraswammerdamia*	*conspersella*					
Yponomeutoidea	Yponomeutidae	*Swammerdamia*	*glaucella*					
Yponomeutoidea	Yponomeutidae	*Teinoptila*	*guttella*					
Yponomeutoidea	Yponomeutidae	*Thecobathra*	*anas*		JQ788944		JQ783628	JQ787645
Yponomeutoidea	Yponomeutidae	*Xyrosaris*	*lichneuta*					
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*anatolica*					
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*kanaiella*					
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*multipunctella*		JQ788969		JQ783653	JQ787667
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*myriosema*					
Yponomeutoidea	Yponomeutidae	*Zelleria*	*celastrusella*					
Yponomeutoidea	Yponomeutidae	*Zelleria*	*retiniella*					
Yponomeutoidea	Ypsolophidae	*Ochsenheimeria*	*urella*		JQ788878		JQ783562	JQ787581
Yponomeutoidea	Ypsolophidae	*Bhadorcosma*	*lonicerae*					
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*nigrimaculata*		JQ788970			JQ787668
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*angelicella*					
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*ustella*					
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*yasudai*					

Yponomeutoidea	uncertain	New genus	sp.					
Yponomeutoidea	uncertain	New genus	sp.					
Yponomeutoidea	uncertain	New genus	sp.					
“Yponomeutoidea”	“Yponomeutidae”	*Nosymna*	*stipella*					
“Yponomeutoidea”	uncertain							
“Yponomeutoidea”	uncertain							
OUT-GROUP								
superfamily	Family	Genus	Species	3006fin	3017fin	3059fin	3070fin	8028fin
Choreutoidea	Choreutidae	*Hemerophila*	*felis*	GU575874	GU575951	GU575988		GU576065
Copromorpoidea	Copromorphidae	*Copromorpha*	sp.					
Epermenioidea	Epermeniidae	*Epermenia*	*sinjovi*					
Galacticoidea	Galacticidae	*Homadaula*	*anisocentra*		JQ788800		JQ783483	JQ787506
Gelechioidea	Cosmopterigidae	*Euclemensia*	*bassettella*	GU575865	GU575942	GU575980	GU576019	
Gelechioidea	Ethmiidae	*Ethmia*	*eupostica*	GU575870	GU575947	GU575984	GU576024	GU576061
Gelechioidea	Lypusidae	*Lypusa*	*maurella*					
Gelechioidea	uncertain	Gen.	sp.					
Gracillarioidea	Bucculatricidae	*Bucculatrix*	sp.		JN124972			JN124997
Gracillarioidea	Douglasiidae	*Klimeschia*	*transversella*		JN124977		JN124989	JN125001
Gracillarioidea	Gracillariidae	*Caloptilia*	*bimaculatella*	GU575863	GU575940	GU575978	GU576017	GU576055
Gracillarioidea	Gracillariidae	*Parectopa*	*robiniella*				JN124993	
Gracillarioidea	Gracillariidae	*Cameraria*	*gaultheriella*		JN124973		JN124985	JN124998
Gracillarioidea	Gracillariidae	*Phyllonorycter*	sp.		JN124979		JN124991	JN125003
Gracillarioidea	Gracillariidae	*Phyllocnistis*	*citrella*		JN124978		JN124990	JN125002
Gracillarioidea	Gracillariidae	*Phyllocnistis*	*magnoliaeella*		JN124980		JN124992	JN125004
Gracillarioidea	Roeslerstamiidae	*Agriothera*	*elaeocarpophaga*		JN124971		JN124984	JN124996
Gracillarioidea	Roeslerstamiidae	*Roeslerstammia*	*pronubella*		JN124981		JN124994	JN125005
Gracillarioidea	Roeslerstamiidae	*Amphithera*	*heteroleuca*					
Pterophoroidea	Pterophoridae	*Emmelina*	*monodactyla*	GU575871	GU575948	GU575985	GU576025	GU576062

Schreckensteinoidea	Schreckensteiniidae	*Schreckensteinia*	sp.		JQ788934		JQ783618	JQ787636
Tineoidea	Acrolophidae	*Acrolophus*	*arcanellus*		JQ788702			JQ787411
Tineoidea	Arrhenophanidae	*Arrhenophanes*	*perspicilla*				JQ783376	
Tineoidea	Eriocottidae	*Compsoctena*	sp.		JQ788736		JQ783409	JQ787440
Tineoidea	Psychidae	*Rebelia*	*thomanni*					
Tineoidea	Psychidae	*Narycia*	*duplicella*				JQ783546	JQ787568
Tineoidea	Psychidae	*Acanthopsyche*	*zelleri*					
Tineoidea	Psychidae	*Pseudarbela*	sp.				JQ783573	
Tineoidea	Psychidae	*Psyche*	*crassiorella*				JQ783572	
Tineoidea	Psychidae	*Scoriodyta*	*suttonensis*		JQ788925			JQ787626
Tineoidea	Psychidae	*Typhonia*	*ciliaris*		JQ788958		JQ783642	JQ787656
Tineoidea	Tineidae	*Dryadaula*	sp.					
Tineoidea	Tineidae	*Erechthias*	*zebrina*		JQ788789			JQ787495
Tineoidea	Tineidae	*Hapsifera*	sp.				JQ783484	JQ787507
Tineoidea	Tineidae	*Harmaclona*	sp.					
Tineoidea	Tineidae	*Opogona*	*thiadelia*		JQ788876			JQ787580
Tineoidea	Tineidae	*Hybroma*	*servulella*		JQ788817			
Tineoidea	Tineidae	*Myrmecozela*	*ochraceella*		JQ788853		JQ783538	JQ787561
Tineoidea	Tineidae	*Nemapogon*	*cloacella*		JQ788862		JQ783547	
Tineoidea	Tineidae	*Perissomastix*	sp.		JQ788887		JQ783576	JQ787590
Tineoidea	Tineidae	*Scardiella*	*approxomatella*		JQ788924			JQ787625
Tineoidea	Tineidae	*Tinea*	*columbariella*	GU575890		GU576004	GU576041	GU576080
Tineoidea	Tineidae	Gen.	sp.					
Tischerioidea	Tischeriidae	*Tischeria*	*ekebladella*				JQ783631	
Tortricoidea	Tortricidae	*Argyrotaenia*	*alisellana*	GU575860		GU575975	GU576014	GU576052
Tortricoidea	Tortricidae	*Platynota*	*idaeusalis*	GU575881	GU575958	GU575995	GU576032	GU576072
Urodoidea	Urodidae	Gen.	sp.					
Urodoidea	Urodidae	*Urodus*	sp.					
Urodoidea	Urodidae	"*Wockia*"	sp.					

Urodoidea	Urodidae	*Urodus*	*decens*	GU575893	GU575967	GU576007	GU576044	GU576083
Urodoidea	Urodidae	*Wockia*	*koreana*					
Zygaenoidea	Lacturidae	*Eustixis*	*aglaodora*				JQ783473	JQ787493
Zygaenoidea	Zygaenidae	*Pryeria*	*sinica*	GU575885	GU575961	GU575999	GU576036	GU576075

Supplement S1-7. A spreadsheet showing the included species with annotations of their classification and GenBank accession numbers for *8091fin* and *aspec*.

IN-GROUP					
superfamily	Family	Genus	Species	8091fin	aspec
Yponomeutoidea	Bedellidae	*Bedellia*	*somnulentella*	JQ783695	
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	*autumnitella*		
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	*xylophragma*		
Yponomeutoidea	Glyphipterigidae	*Acrolepia*	sp.		
Yponomeutoidea	Glyphipterigidae	*Acrolepiopsis*	*sapporensis*	JQ783681	
Yponomeutoidea	Glyphipterigidae	*Digitivalva*	*hemiglypha*	JQ783734	
Yponomeutoidea	Glyphipterigidae	*Diploschizia*	*impigritella*	JQ783736	
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*forsterella*		
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	sp.		
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*quadragintapunctata*		
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	cf. *lamprosema*		
Yponomeutoidea	Glyphipterigidae	*Glyphipterix*	*perimetalla*		
Yponomeutoidea	Glyphipterigidae	*Lepidotarphius*	*peroprnatellus*	JQ783816	
Yponomeutoidea	Glyphipterigidae	*Orthotelia*	*sparganella*		
Yponomeutoidea	Glyphipterigidae	*Proditrix*	*gahniae*	JQ783872	
Yponomeutoidea	Glyphipterigidae	*Proditrix*	*nielseni*		
Yponomeutoidea	Heliodinidae	*Cycloplasis*	*panicifoliella*		
Yponomeutoidea	Heliodinidae	*Aetole*	*tripunctella*	JQ783661	
Yponomeutoidea	Heliodinidae	*Embola*	*ionis*		
Yponomeutoidea	Heliodinidae	*Epicroesa*	*metallifera*		
Yponomeutoidea	Heliodinidae	Gen.	sp.		
Yponomeutoidea	Heliodinidae	*Neoheliodines*	*nyctaginella*		

Yponomeutoidea	Lyonetiidae	*Perileucoptera*	*coffeella*	JQ783812	
Yponomeutoidea	Lyonetiidae	*Lyonetia*	*ledi*		
Yponomeutoidea	Lyonetiidae	*Lyonetia*	*prunifoliella*	JQ783815	
Yponomeutoidea	Lyonetiidae	*Corythophora*	sp.		
Yponomeutoidea	Lyonetiidae	*Euprora*	sp.		
Yponomeutoidea	Lyonetiidae	*Philonome*	*clemensella*		
Yponomeutoidea	Lyonetiidae	*Phyllobrostis*	cf. *daphneella*		
Yponomeutoidea	Lyonetiidae	*Phyllobrostis*	*peninsulae*		
Yponomeutoidea	Plutellidae	*Deryaraxenistis*	*serrata*		
Yponomeutoidea	Plutellidae	*Doxophyrtis*	*hydrocosma*		
Yponomeutoidea	Plutellidae	*Eidophasia*	*messingiella*		
Yponomeutoidea	Plutellidae	Gen.	sp.		
Yponomeutoidea	Plutellidae	*Lunakia*	*alyssella*		
Yponomeutoidea	Plutellidae	*Plutella*	*xylostella*		
Yponomeutoidea	Plutellidae	*Rhigognostis*	*schmaltzella*		
Yponomeutoidea	Plutellidae	*Tritymba*	*pamphaea*		
Yponomeutoidea	Yponomeutidae	*Argyresthia*	sp.		
Yponomeutoidea	Yponomeutidae	*Argyresthia*	*austerella*		
Yponomeutoidea	Yponomeutidae	*Argyresthia*	*brockeella*		
Yponomeutoidea	Yponomeutidae	*Atteva*	*aurea*	GU576092	KC243001
Yponomeutoidea	Yponomeutidae	*Atteva*	*zebra*		
Yponomeutoidea	Yponomeutidae	*Atemelia*	n. sp.		
Yponomeutoidea	Yponomeutidae	*Atemelia*	*torquatella*		
Yponomeutoidea	Yponomeutidae	*Prays*	*fraxinella*		
Yponomeutoidea	Yponomeutidae	*Prays*	*delta*		
Yponomeutoidea	Yponomeutidae	*Prays*	*atomocella*		
Yponomeutoidea	Yponomeutidae	*Prays*	*oleae*	JQ783892	
Yponomeutoidea	Yponomeutidae	*Saridoscelis*	*kodamai*		
Yponomeutoidea	Yponomeutidae	*Scythropia*	*crataegella*	JQ783925	

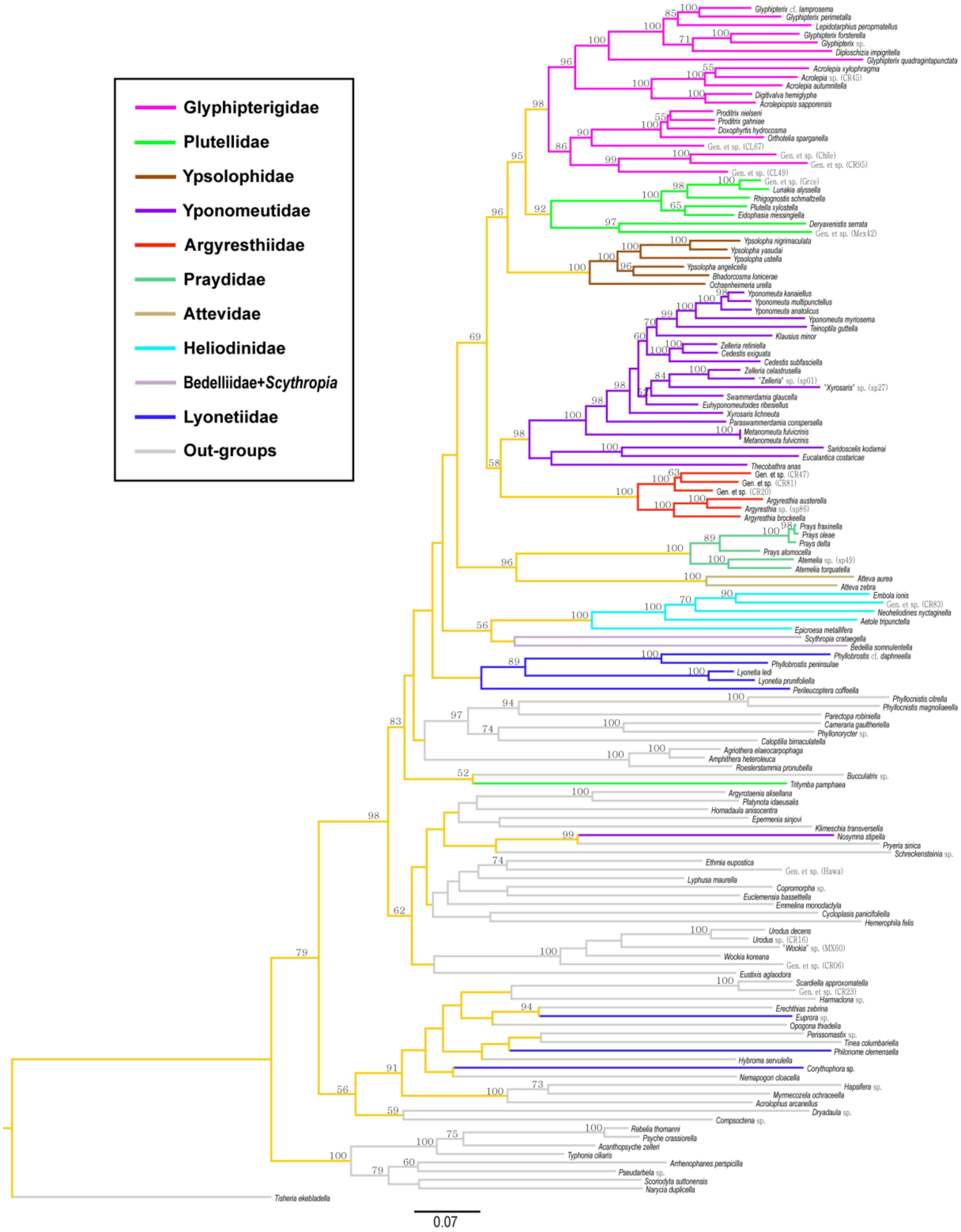
Yponomeutoidea	Yponomeutidae	*Eucalantica*	*costaricae*	GU576125	KC243010
Yponomeutoidea	Yponomeutidae	New genus	sp.		
Yponomeutoidea	Yponomeutidae	New genus	sp.		
Yponomeutoidea	Yponomeutidae	New genus	sp.		
Yponomeutoidea	Yponomeutidae	"*Xyrosaris*"	sp.		
Yponomeutoidea	Yponomeutidae	"*Zelleria*"	sp.		
Yponomeutoidea	Yponomeutidae	*Cedestis*	*exiguata*		
Yponomeutoidea	Yponomeutidae	*Cedestis*	*subfasciella*		
Yponomeutoidea	Yponomeutidae	*Euhyponomeutoides*	*ribesiellus*		
Yponomeutoidea	Yponomeutidae	*Klausius*	*minor*		
Yponomeutoidea	Yponomeutidae	*Metanomeuta*	*fulvicrinis*		
Yponomeutoidea	Yponomeutidae	*Metanomeuta*	*fulvicrinis*		
Yponomeutoidea	Yponomeutidae	*Paraswammerdamia*	*conspersella*		
Yponomeutoidea	Yponomeutidae	*Swammerdamia*	*glaucella*		
Yponomeutoidea	Yponomeutidae	*Teinoptila*	*guttella*		
Yponomeutoidea	Yponomeutidae	*Thecobathra*	*anas*	JQ783927	
Yponomeutoidea	Yponomeutidae	*Xyrosaris*	*lichneuta*		
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*anatolica*		
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*kanaiella*		
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*multipunctella*	JQ783950	
Yponomeutoidea	Yponomeutidae	*Yponomeuta*	*myriosema*		
Yponomeutoidea	Yponomeutidae	*Zelleria*	*celastrusella*		
Yponomeutoidea	Yponomeutidae	*Zelleria*	*retiniella*		
Yponomeutoidea	Ypsolophidae	*Ochsenheimeria*	*urella*	JQ783858	
Yponomeutoidea	Ypsolophidae	*Bhadorcosma*	*lonicerae*		
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*nigrimaculata*	JQ783951	
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*angelicella*		
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*ustella*		
Yponomeutoidea	Ypsolophidae	*Ypsolopha*	*yasudai*		

Yponomeutoidea	uncertain	New genus	sp.		
Yponomeutoidea	uncertain	New genus	sp.		
Yponomeutoidea	uncertain	New genus	sp.		
“Yponomeutoidea”	“Yponomeutidae”	*Nosymna*	*stipella*		
“Yponomeutoidea”	uncertain				
“Yponomeutoidea”	uncertain				
OUT-GROUP					
superfamily	Family	Genus	Species	8091fin	aspec
Choreutoidea	Choreutidae	*Hemerophila*	*felis*	GU576105	KC243005
Copromorpoidea	Copromorphidae	*Copromorpha*	sp.		
Epermenioidea	Epermeniidae	*Epermenia*	*sinjovi*		
Galacticoidea	Galacticidae	*Homadaula*	*anisocentra*	JQ783776	
Gelechioidea	Cosmopterigidae	*Euclemensia*	*bassettella*	GU576096	KC243003
Gelechioidea	Ethmiidae	*Ethmia*	*eupostica*	GU576101	KC243004
Gelechioidea	Lypusidae	*Lypusa*	*maurella*		
Gelechioidea	uncertain	Gen.	sp.		
Gracillarioidea	Bucculatricidae	*Bucculatrix*	sp.	JN125008	
Gracillarioidea	Douglasiidae	*Klimeschia*	*transversella*	JN125012	
Gracillarioidea	Gracillariidae	*Caloptilia*	*bimaculatella*	GU576094	KC243002
Gracillarioidea	Gracillariidae	*Parectopa*	*robiniella*	JN125016	
Gracillarioidea	Gracillariidae	*Cameraria*	*gaultheriella*	JN125009	
Gracillarioidea	Gracillariidae	*Phyllonorycter*	sp.	JN125014	
Gracillarioidea	Gracillariidae	*Phyllocnistis*	*citrella*	JN125013	
Gracillarioidea	Gracillariidae	*Phyllocnistis*	*magnoliaeella*	JN125015	
Gracillarioidea	Roeslerstamiidae	*Agriothera*	*elaeocarpophaga*	JN125007	
Gracillarioidea	Roeslerstamiidae	*Roeslerstammia*	*pronubella*	JN125017	
Gracillarioidea	Roeslerstamiidae	*Amphithera*	*heteroleuca*		
Pterophoroidea	Pterophoridae	*Emmelina*	*monodactyla*	GU576102	

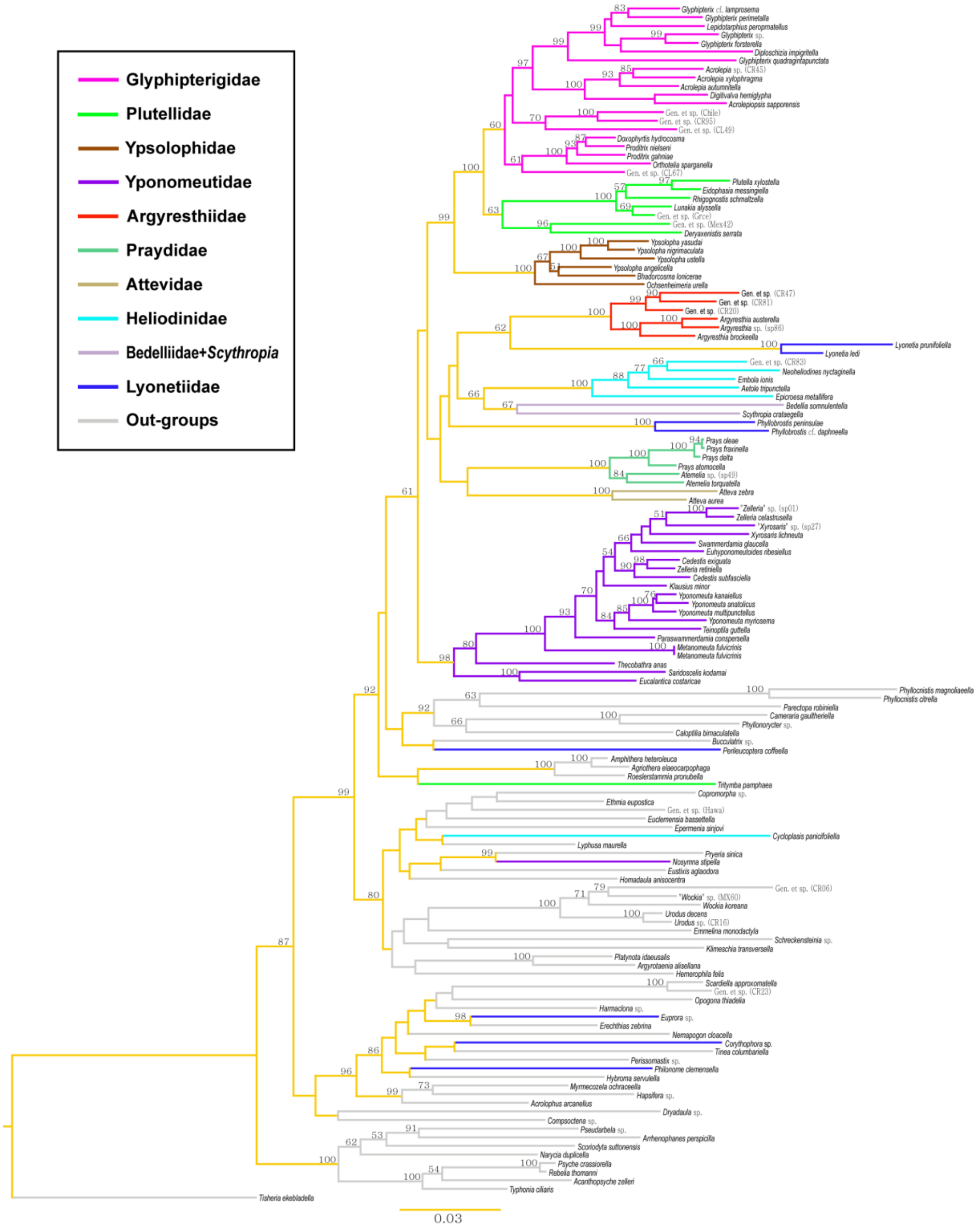
Schreckensteinoidea	Schreckensteiniidae	*Schreckensteinia*	sp.	JQ783916	
Tineoidea	Acrolophidae	*Acrolophus*	*arcanellus*		
Tineoidea	Arrhenophanidae	*Arrhenophanes*	*perspicilla*	JQ783680	
Tineoidea	Eriocottidae	*Compsoctena*	sp.	JQ783709	
Tineoidea	Psychidae	*Rebelia*	*thomanni*		
Tineoidea	Psychidae	*Narycia*	*duplicella*	JQ783842	
Tineoidea	Psychidae	*Acanthopsyche*	*zelleri*		
Tineoidea	Psychidae	*Pseudarbela*	sp.	JQ783867	
Tineoidea	Psychidae	*Psyche*	*crassiorella*		
Tineoidea	Psychidae	*Scoriodyta*	*suttonensis*	JQ783906	
Tineoidea	Psychidae	*Typhonia*	*ciliaris*		
Tineoidea	Tineidae	*Dryadaula*	sp.		
Tineoidea	Tineidae	*Erechthias*	*zebrina*		
Tineoidea	Tineidae	*Hapsifera*	sp.	JQ783777	
Tineoidea	Tineidae	*Harmaclona*	sp.		
Tineoidea	Tineidae	*Opogona*	*thiadelia*	JQ783856	
Tineoidea	Tineidae	*Hybroma*	*servulella*	JQ783797	
Tineoidea	Tineidae	*Myrmecozela*	*ochraceella*	JQ783836	
Tineoidea	Tineidae	*Nemapogon*	*cloacella*	JQ783843	
Tineoidea	Tineidae	*Perissomastix*	sp.	JQ783870	
Tineoidea	Tineidae	*Scardiella*	*approxomatella*	JQ783905	
Tineoidea	Tineidae	*Tinea*	*columbariella*	GU576121	KC243008
Tineoidea	Tineidae	Gen.	sp.		
Tischerioidea	Tischeriidae	*Tischeria*	*ekebladella*	JQ783931	
Tortricoidea	Tortricidae	*Argyrotaenia*	*alisellana*	GU576091	KC243000
Tortricoidea	Tortricidae	*Platynota*	*idaeusalis*	GU576112	KC243006
Urodoidea	Urodidae	Gen.	sp.		
Urodoidea	Urodidae	*Urodus*	sp.		
Urodoidea	Urodidae	"*Wockia*"	sp.		

Urodoidea	Urodidae	*Urodus*	*decens*	GU576124	KC243009
Urodoidea	Urodidae	*Wockia*	*koreana*		
Zygaenoidea	Lacturidae	*Eustixis*	*aglaodora*		
Zygaenoidea	Zygaenidae	*Pryeria*	*sinica*	GU576116	KC243007

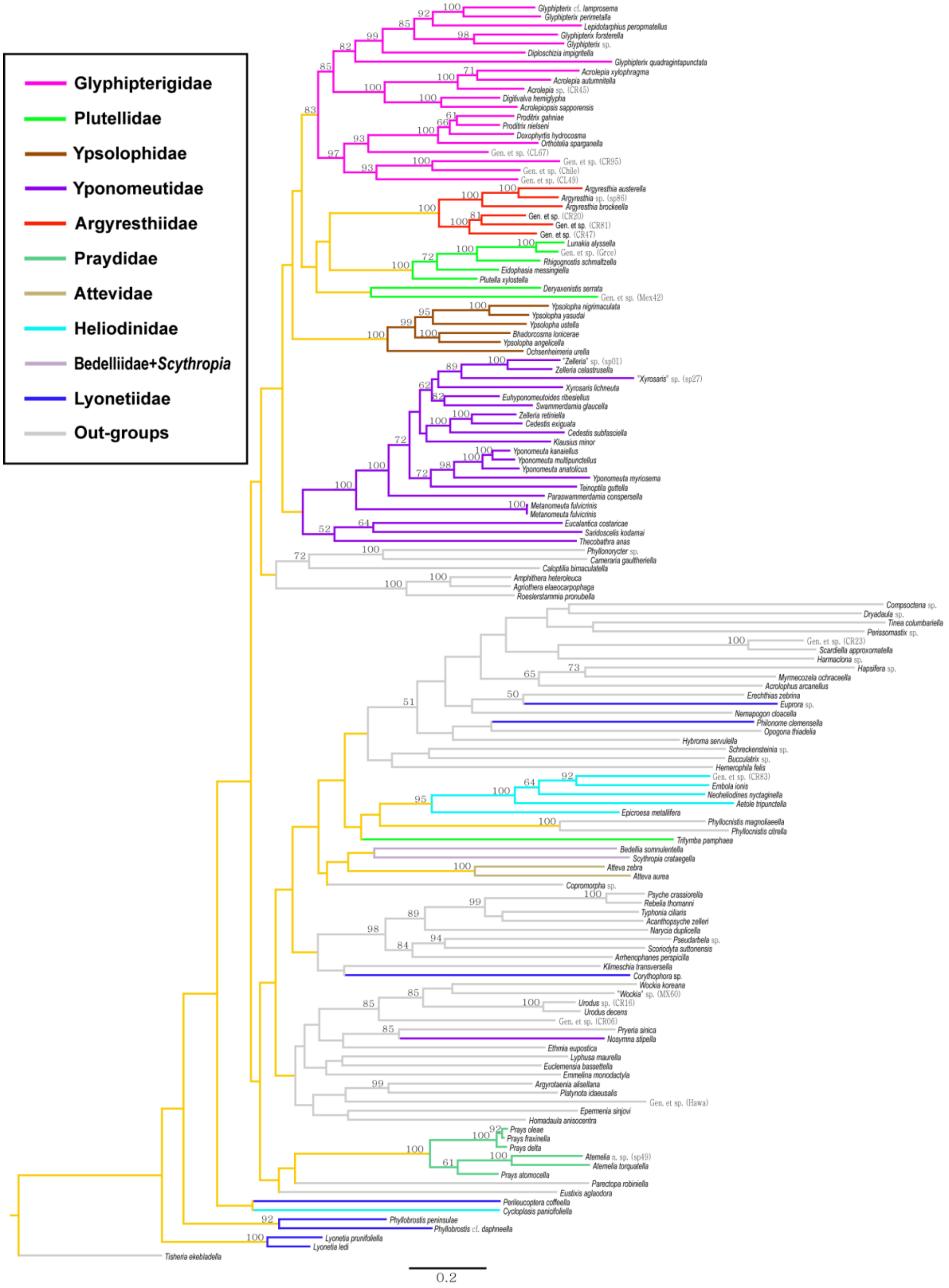
Supplementary figure S2. The best maximum likelihood tree found in nt123 analysis of the 4-gene, 139-taxon data set. The four genes are listed in Supplement 1. The tree is rooted with *Tischeria ekebladella*. Bootstrap values, when >50%, are shown above branches.



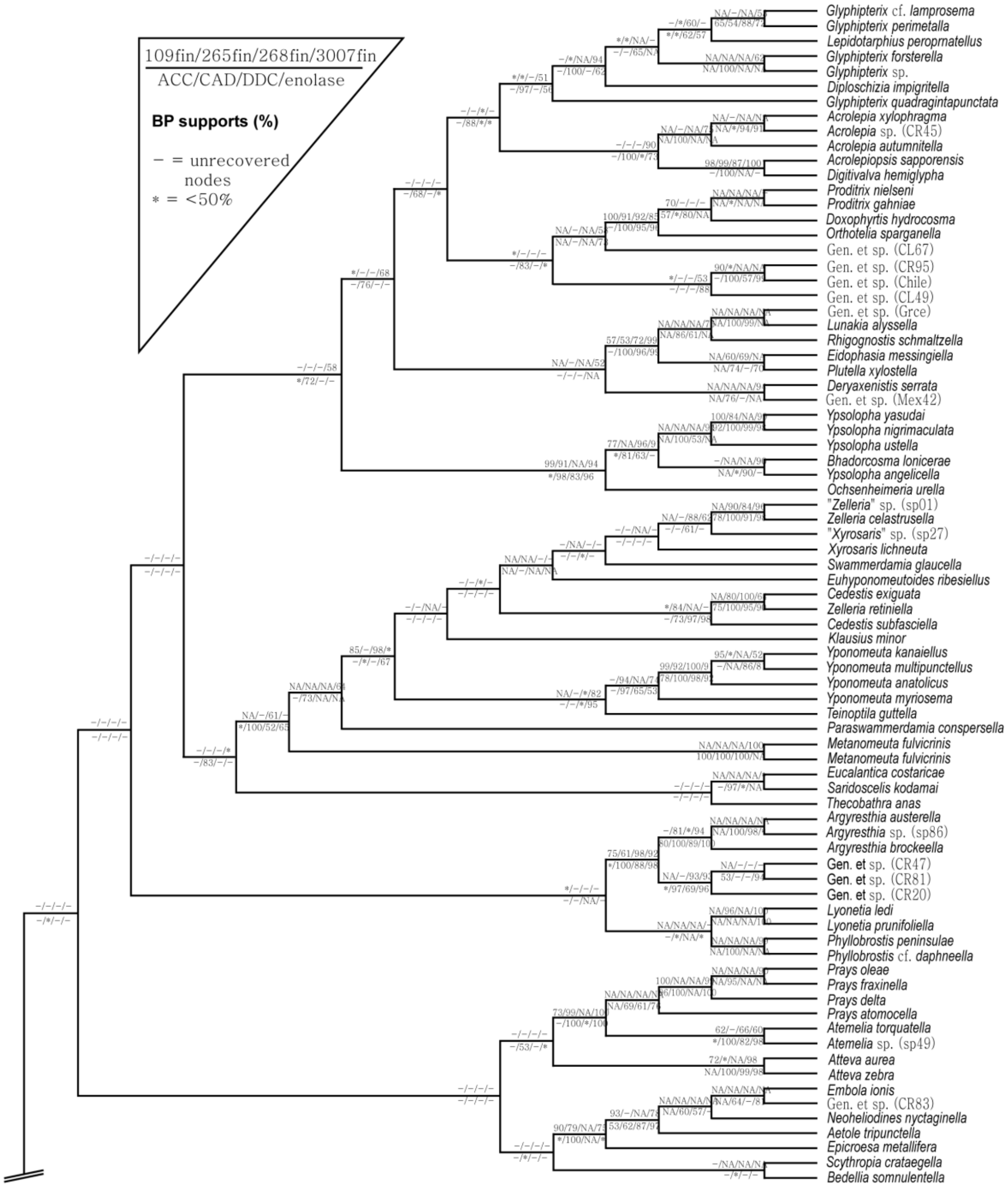
Supplementary figure S3. The best ML tree found for nt12 (only) analysis of the 8–27 gene, 139-taxon data set, rooted with *Tischeria ekebladella*. Bootstrap values, when >50%, are shown above branches.



Supplementary figure S4. The best ML tree for nt3 (only) analysis of the 8–27 gene, 139-taxon data set, rooted with *Tischeria ekebladella*. Bootstrap values, when >50%, are shown above branches.



Supplementary figure S5. The best ML cladogram from Figure 2, with bootstrap values for the initial 8 genes (nt123 analysis). Values for 109fin, 205fin, 208fin, and 3007fin are shown above branch, in that order; values for ACC, CAD, DDC and enolase are shown below branches. ‘-’ = node not recovered in the ML tree for that analysis. ‘*’= bootstrap value <50%. ‘NA’= bootstrap value undefined because sequence was obtained for ≤ 1 taxon for that that gene in that clade. Bootstrap supports for groups with missing taxa are calculated from the remaining taxa.


109fin/265fin/268fin/3007fin
ACC/CAD/DDC/enolase
BP supports (%)
− = unrecovered nodes
∗ = <50%
Glyphipterix cf. lamprosema
Glyphipterix perimetalla
Lepidotarphius perornatellus
Glyphipterix forsterella
Glyphipterix sp.
Diploschizia impigritella
Glyphipterix quadragintapunctata
Acrolepia xylophragma
Acrolepia sp. (CR45)
Acrolepia autumnitella
Acrolepiopsis sapporensis
Digitivalva hemiglypha
Proditrix nielseni
Proditrix gahniae
Doxophyrtis hydrocosma
Orthotelia sparganella
Gen. et sp. (CL67)
Gen. et sp. (CR95)
Gen. et sp. (Chile)
Gen. et sp. (CL49)
Gen. et sp. (Grce)
Lunakia alyssella
Rhigognostis schmaltzella
Eidophasia messingiella
Plutella xylostella
Deryaxenistis serrata
Gen. et sp. (Mex42)
Ypsolopha yasudai
Ypsolopha nigrimaculata
Ypsolopha ustella
Bhadorcosma lonicerae
Ypsolopha angelicella
Ochsenheimeria urella
"Zelleria" sp. (sp01)
Zelleria celastrusella
"Xyrosaris" sp. (sp27)
Xyrosaris lichneuta
Swammerdamia glaucella
Euhyponomeutoides ribesiellus
Cedestis exiguata
Zelleria retiniella
Cedestis subfasciella
Klausius minor
Yponomeuta kanaiellus
Yponomeuta multipunctellus
Yponomeuta anatolicus
Yponomeuta myriosema
Teinoptila guttella
Paraswammerdamia conspersella
Metanomeuta fulvicrinis
Metanomeuta fulvicrinis
Eucalantica costaricae
Saridoscelis kodamai
Thecobathra anas
Argyresthia austerella
Argyresthia sp. (sp86)
Argyresthia brockeella
Gen. et sp. (CR47)
Gen. et sp. (CR81)
Gen. et sp. (CR20)
Lyonetia ledi
Lyonetia prunifoliella
Phyllobrostis peninsulae
Phyllobrostis cf. daphneella
Prays oleae
Prays fraxinella
Prays delta
Prays atomocella
Atemelia torquatella
Atemelia sp. (sp49)
Atteva aurea
Atteva zebra
Embola ionis
Gen. et sp. (CR83)
Neoheliodines nyctaginella
Aetole tripunctella
Epicroesa metallifera
Scythropia crataegella
Bedellia somnulentella

Chapter 2

An overview of the lepidopteran fossil record: diversity, taphonomy and implications for divergence-time estimates

Reformatted from Sohn et al. (2013, in submission)

Introduction

The Lepidoptera, including moths, butterflies and skippers, are one of the most speciose lineages on the Earth, currently consisting of somewhat over 160,000 described species and possibly approximating a half million total species (Kristensen et al., 2007). The elevated species diversity of Lepidoptera represents nearly 3 % of the extant world biota (Gaston, 1991; Hammond, 1992). Lepidopterans provide fundamental roles in terrestrial ecosystems, principally through larvae as herbivores and adults as pollinators (Scoble, 1992; Proctor et al., 1996), and at higher trophic levels lepidopterans serve as an important food source for other animals (Lacki et al., 2007). On an aesthetic note, many butterflies provide an important source of inspiration (Kritsky and Cherry, 2000), and perhaps as a result, are one of the most extensively studied animal groups. In spite of lepidopteran importance in global biodiversity, the evolutionary history of Lepidoptera remains largely unknown. This mostly is attributable to their poor fossil record that contrasts to other, much better represented, major insect orders (Kapoor, 1981; Labandeira and Sepkoski 1993; Kristensen & Skalski, 1998; Kozlov et al., 2002). Explanations for this paucity of lepidopteran fossils historically have been couched in evolutionary hypotheses involving the extant fauna (Carpenter, 1992; Kristensen, 1997; Kristensen et al., 2007). Partly as a consequence, there have been few attempts to estimate divergence-time dates for lepidopterans (e.g. Wahlberg et al. 2003; Braby et al., 2006). Such studies have been criticized by contemporary researchers, notably de Jong (2007), due to ambiguities in fossil calibrations. Because of these calibration issues, a systematic overview of the lepidopteran fossil record is a prerequisite for establishing credible divergence-time estimates.

Robust molecular dating requires multiple, reliably-identified fossils, each of which is sufficiently old to address a relevant divergence event in a deep-time phylogeny (Donoghue and Benton, 2007; Pyron, 2010). These requirements often are difficult to meet for the depauperate lepidopteran fossil record. Modeling the uncertainties involved in the fossil calibrations could be a possible alternative (Ho and Phillips, 2009). However, there are major concerns of the lepidopteran fossil record that involve taxonomic and geochronologic biases as well as the reliability of fossil identifications (Skalski, 1976a; Kozlov et al., 2002). Such factors can significantly affect the resulting divergence time estimates from molecular dating analyses (Donoghue and Benton, 2007). These data biases and identification issues in the lepidopteran fossil record have not been thoroughly explored.

The earliest fossil reliably identified as a member of the Lepidoptera is *Archaeolepis mane* Whalley, from a Lower Jurassic calcareous flatstone deposit in England (Whalley, 1985; Grimaldi and Engel, 2005). A limited number of other lepidopteran fossils are known from the Middle Jurassic (Ansorge, 2002), reviewed by Skalski (1990a) and Kristensen and Skalski (1998), although the greatest amount of material originates from mid Cenozoic compression-impression and amber-copal deposits (Grimaldi and Engel, 2005; de Jong, 2007). Prevailing views regarding such a geochronologic bias have postulated that the Lepidoptera, of all insect orders, evolved most recently (Carpenter, 1930; Riek, 1970; Ollerton, 1999; Grimaldi and Engel, 2005), and in particular diversified, perhaps in concert, with angiosperms (Carpenter and Burnham, 1985; Kristensen, 1997; Powell et al., 1998). These proposals, nevertheless, have been based on anecdotal information rather than systematic approaches to the lepidopteran fossil record, such as a well-documented Trichoptera + Lepidoptera sister-group relationship (Whiting, 2002) combined with a Middle Triassic Trichoptera earliest fossil record (Shcherbakov, 2008). The recent compilation of documented fossil Lepidoptera (Sohn et al., 2012) expands the compass of such studies, although these data have not been subjected to statistical analysis.

The aim of this paper is to provide an overview of the lepidopteran fossil record based on data from Sohn et al. (2012), including statistical summaries of preservational categories, age distributions, and taxonomic composition. The biases and other issues originating from the data are discussed for identifying aspects of the lepidopteran fossil record that undoubtedly will be addressed by future molecular dating analyses. The resulting patterns are compared with previous views, allowing an updated revision of lepidopteran evolution.

Materials and Methods

Data collection

Data for our analyses came from Sohn et al. (2012) which provide a comprehensive compilation of known lepidopteran fossils. This catalog includes 4,593 fossil specimens reliably assigned to Lepidoptera. The total number was based on a conservative, cumulative enumeration of fossil taxonomic entries such that ambiguous accounts were kept to a minimum. For example, taxonomic accounts listing multiple specimens were counted as two specimens and records where the absence of documentation specifying the number of taxa was counted as one specimen. When body and trace fossils rarely occurred together in the same matrix, for example a psychid larva within its case, they were counted as two specimens.

The retrieved data were categorized by preservational type, geochronologic age and taxonomic affinities, as defined in Sohn et al. (2012). Preservational types followed, with modification, the eight categories of Sohn et al. (2012). They are: (1), amber and copal combined into a single amber-copal category; (2), asphaltum and tar sands; (3), compression and impression fossils; (4); gut contents and coprolites of insectivorous animals; (5), peat and lignite; (6), salt deposits; (7), sieved residues; and (8), silica or other types of permineralization (Labandeira, 1999). Each preservational type for the 4,593 fossil occurrences (Sohn et al., 2012) were subdivided into two categories, body and trace fossils. A body fossil is defined as consisting of the entire or partial body, frequently wings, of a lepidopteran egg, larva, pupa or adult in fossil matrix. By contrast, a trace fossil consists of plant damage, a teratology or disturbance caused by a lepidopteran, consisting principally of leaf-mines, other feeding damage (Labandeira et al., 2007), or any product derived from lepidopteran activity, such as larval domicile cases and more rarely, frass. Body and trace fossils ambiguously affiliated with Lepidoptera were excluded. This initial characterization of the fossil data based on preservational type, abundance, age and locality is provided in Figure 1A–C.

The 4,561 body- and trace fossils of known geological age were divided into temporally delimited bins at the epoch level of resolution and further divided by their preservational type. Age determinations are provided in Sohn et al. (2012). Each fossil age date was given as the midpoint of an epoch or stage interval, which was chosen for graphical representation. The geological time scale of Gradstein et al. (2004), the international standard, was used. We combined fossil and subfossil occurrences of Pleistocene and Holocene age into a single time interval in Figure 1C (each count available in Table 1). The number of fossil deposits in each age interval was calculated based on data from the primary geological or paleoentomological literature. Because of the spatiotemporal scale involved in plotting the data, multiple occurrences of similarly dated lepidopteran fossils, within about five million years of each other, were combined into a single, composite data point indicated in Appendix 1.

The next step was to establish family-level diversity data for the Lepidoptera and Amphiesmenoptera (Lepidoptera + Trichoptera) lineages from the Early Permian to the present-day (Fig. 2). In this analysis, we compared separate Lepidoptera family diversity curves from 1994 (Labandeira, 1994) to that of a 2012 updated version, sourced in Sohn et al. (2012). For analogous comparison to the family-level diversity of the Lepidoptera and Amphiesmenoptera, we plotted from Labandeira (1994) analogous family-level diversities for the four major, ordinal-level, holometabolous lineages (Trichoptera, Coleoptera, Diptera, Hymenoptera) for the same Early Permian to present-day interval (Fig. 3). Collectively, these data provided a family-level assessment of improvements in capturing lepidopteran fossil diversity during the last 18 years, as well as comparisons to the family-level diversities of other, exceptionally diverse, major holometabolous lineages.

Last, the taxonomic affinities of fossil occurrences were tabulated and assigned to lepidopteran superfamilies, following the assignments of Sohn et al. (2012) and the classification system of van Nieukerken et al. (2011). It is important to note that our tabulations for superfamily composition did not distinguish between securely identified fossils (grey data points in Fig. 4) from those whose taxonomic assignment was more questionable (black encircled data points in Fig. 4). The total number of fossils for each superfamily was partitioned into their respective preservational types (Table 2).

Calibrating lineage divergence times

Lepidopteran fossils were sorted by superfamilies and plotted onto a cladogram assembled from the results of recent molecular phylogenetic studies (Mutanen et al., 2010; Cho et al., 2011; J. Regier and colleagues, 2012, unpublished). Weakly supported clades were collapsed into polytomies. Divergence times of superfamily-level lineages were adjusted based on the earliest fossil occurrences of their sister-groups and closely related lineages. For nodes unrepresented by the fossil record, divergences were a compromise based on Labandeira et al. (1994), and Grimaldi and Engel (2005), or otherwise defined arbitrarily from adjacent nodes. Fossil occurrences data sources are tabulated in Appendix 1. Occasionally occurrences involve morphotypes with uncertain taxonomic affiliation, such as trace-fossil affiliations identified with extant analogs, or body fossils whose original affiliations have been questioned subsequently in the literature.

Estimation of family-level diversity

It has been known for some time that insect diversity analyses at the family level are suitable for inferring fossil diversity studies at other levels (Labandeira, 2005), a procedure that parallels methods such as the higher taxon approach (Balmford et al., 1996) used for estimating diversity in modern ecosystems. From the fossil data, we assessed the earliest occurrences of lepidopteran families through geologic time. The raw data initially used by Labandeira & Sepkoski (1993) were based on a compilation (Labandeira, 1994), with supplemental updates. To understand the lepidopteran fossil record, we considered only those holometabolous orders with comparably elevated extant diversity, such as Coleoptera, Diptera and Hymenoptera, and the closely related Trichoptera of the

Amphiesmenoptera (Lepidoptera + Trichoptera). The data were plotted and statistically analyzed, using Microsoft® Office Excel 2010. Linear and exponential regressions were chosen to model the relationship among variables.

Results

Taphonomic and taxonomic trends

We assessed the influence of taphonomy and taxonomic affiliation on the lepidopteran fossil record. Our analyses involve 4,593 specimens assigned to the Lepidoptera, sourced from the latest catalog of fossil and subfossil specimens (Sohn et al., 2012), including updated corrections. These data contain 328 specimens that have been attributed to 236 described fossil lepidopteran species. Of the 4,593 specimens, 985 (21.4%) were assigned to a superfamily, based on judgments and reasoning in the primary literature. Of the total number of specimens, 4,262 (92.8 %) were body fossils and 331 (7.2 %) specimens were trace fossils. When the body-fossil fraction of 4,262 specimens were sorted by preservational type, 52.0 % (2,218) were compression-impression fossils and 40.0 % (1,646) were inclusions in amber and copal; both preservational modes represented 92.0 % of all lepidopteran body fossils (Fig. 1A). Of the remaining body fossils, 7.0 % (298) were sieved residues, representing mostly Pliocene–Pleistocene glacial deposits; all other types of preservation, consisting of asphaltum and tar sands, gut contents and coprolites, peat and lignites, salt deposits, and silica and other types of permineralization, accounted for approximately 1 % (100) of body-fossil preservational types (Fig. 1A).

The preservational types of trace fossils consisted principally of compression-impression fossils, representing 55.6 % (184) of the total, whereas amber-copal inclusions contributed 34.1 % (113), and accounting for 89.7% of all specimens

(Fig. 1B; Table 1). In addition, the most frequent occurrence of trace fossils were leaf mines, representing 57.1 % (178), followed by larval cases (33.5 %, 111), and larval frass (9.4 %, 31). Leaf-mine fossils were overwhelmingly preserved as compressions or impressions (55.0 %, 176), whereas fossilized larval cases and frass were recovered almost exclusively from amber (34.4 %, 110); silica and other forms of permineralization constituted a subordinate preservational type (9.4 %, 30), and all other preservational types were minor (1.2 %, 4) (Fig. 1B).

The 4,561 lepidopteran fossils whose age is known spanned a time interval ranging from the Early Jurassic to the Holocene, or about 195 million years. During this interval, there are two high peaks in their frequency distribution of specimen occurrences (Fig. 1C). One elevated mode of 1,901 specimens is in the Paleocene, and the other subequal mode of 1,824 specimens occurs during the Eocene. A minor peak of 340 specimens occurs in the Pleistocene to Holocene. Other than these three peaks, the number of recovered lepidopteran fossils consistently was less than 120 specimens. By comparison, the composition of preservational types significantly varied through time, five of which (Early Jurassic, Middle Jurassic, Late Jurassic; Late Paleocene; Oligocene) consisted predominantly or near entirely of compression-impression body fossils (Fig. 1C; Table 1). The 1,730 Mid-Eocene fossils overwhelmingly consisted of body inclusions in amber (Table 1).

The 145 localities where lepidopteran fossils have been found have fluctuated extensively through geologic time. Localities with the most elevated frequency of occurrences correspond to: (1), Eocene; (2) Miocene; and (3) Pleistocene +

Holocene (Fig. 1C). Among these maxima, the Miocene peak was the highest (31 occurrences), followed by the Eocene and the Pleistocene + Holocene (22 and 23 occurrences respectively).

A total of 985 lepidopteran fossils have been assigned to 23 extant superfamilies (Table 2), of which the 214 Tineoidea affiliations were most numerous, followed by Papilionoidea (142), Noctuoidea (110), and Nepticuloidea (103). Nevertheless, the fossil preservational type varies by superfamily; in most cases, one or two preservation types were dominant (Table 2). There are seven superfamilies—Bombycoidea, Cossoidea, Hepialoidea, Noctuoidea, Pterophoroidea, Pyraloidea, and Zygaenoidea—whose preservational types predominantly or exclusively occur in lacustrine deposits. By contrast, there are nine superfamilies—Adeloidea, Gelechioidea, Lophocoronoidea, Micropterigoidea, Mnesarchaeoidea, Tineoidea, Thyridoidea, Tortricoidea, and Yponomeutoidea—that are represented entirely or predominantly in amber and copal resins, typically representing forested ecosystems. Leaf mines were overwhelmingly represented by the three superfamilies of Gracillarioidea, Nepticuloidea and Tischerioidea.

The family-level diversity of Lepidoptera increases significantly toward the recent, and the highest diversity values of the Pliocene–Pleistocene remain significantly lower than their extant family diversity (Fig. 2). Our data show a relatively low linear correlation (Table 3, $R^2 = 0.729$) expressing a fluctuation of diversity for lepidopteran families. This relationship has a better fit under an exponential model (Table 3, $R^2=0.9027$). The Trichoptera alone and the Amphiesmenoptera

(Trichoptera + Lepidoptera) also exhibit a family-level diversity increase that is poorly fitted to a linear regression (Table 3, $R^2 = 0.8302$ and 0.7138 respectively). By contrast, for the Hymenoptera and Diptera, family-level increases assume a linear trajectory (Fig. 3 and Table 3, $R^2 = 0.9588$ and 0.9109 respectively). The Coleoptera demonstrates that both linear and exponential models robustly explain their family diversity increase (Fig. 3 and Table 3).

Discussion

Lepidopteran fossil abundance

It is generally considered that lepidopterans are relatively scarce among insect fossils (Labandeira and Sepkoski, 1993; Kozlov et al., 2002; Grimaldi and Engel, 2005; Kristensen et al., 2007), and represent a Lagerstätten-driven record consisting of deposits that are exceptionally well preserved or are very abundant in specimens (Seilacher et al., 1985). This widely accepted perception, however, is seldom based on actual counts of existing lepidopteran fossils. Kristensen and Skalski (1998) were the first to provide figures of the total number of known lepidopteran fossils, which they estimated at 600 to 700 specimens. We calculated the number of existing lepidopteran fossils from the latest catalog (Sohn et al., 2012) and arrived at 4,593 specimens. This number is somewhat more than seven times larger that of Kristensen and Skalski's (1998) estimate, which we average to an estimate midpoint of 650 specimens. Part of this significant increase is attributable to greater activity in finding new lepidopteran fossils since Kristensen and Skalski's (1998) findings. For example, Rust (1998, 1999) reported over 1,000 new lepidopteran fossils from the late Paleocene Fur Formation of Denmark. Another possible explanation is that Sohn et al. (2012) included several historical collections, which currently cannot be located and was not counted by Kristensen and Skalski (1998). Given these considerations, Kristensen and Skalski (1998) seem to have significantly underestimated the total number of the lepidopteran fossils.

Lepidopteran taphonomy

In spite of the recent remarkable increase in the total number of lepidopteran fossils, the lineage appears considerably less abundant than the other, hyperdiverse insect orders of Coleoptera, Diptera and Hymenoptera, which together with the Lepidoptera, constitute the “big four” of Grimaldi and Engel (2005). However, lepidopterans in most amber deposits constitute less than 1% of whole-insect inclusions (Penney, 2010). This depauperate lepidopteran fauna apparently is due to their fragile bodies (Labandeira and Sepkoski, 1993). In fact, actualistic taphonomic simulations of extant lepidopterans suggest that submerged bodies and wings of Lepidoptera were easily dismembered and underwent rapid decomposition (Duncan, 1997). The buoyancy of their bodies encourages predation by ants, thus rendering unlikely the chances for fossilization in lacustrine deposits (Smith, 1998; Grimaldi & Engel, 2005). The proportional representation of lepidopterans in amber appears low, as many lepidopterans are strong fliers and avoid being trapped in plant resin (Skalski, 1976a). The paucity of name-bearing lepidopteran fossils is another reason for their general absence, initially commented by Kristensen and Skalski (1998), who predicted that about one-third, or about 220 taxa, of all known lepidopteran fossils have been described and named. This absolute number of the name-bearing fossil species is nearly identical to our count (236), and is far less than Diptera, which comprises 3,245 described fossil species (Evenhuis, 2004, electronic source). The predicted proportion, however, does seem to be inflated since our data show that only about

7 % of the total fossil lepidopteran specimens have been formally described and named.

Earlier examinations indicated that lepidopteran fossils occur principally as amber inclusions and larval leaf-mine compressions and impressions (Grimaldi and Engel, 2005). Our data suggest that compression-impression fossils and amber-copal inclusions collectively account for 91% of all lepidopteran specimens. Kristensen and Skalski (1998) estimated that approximately 500 out of 650 fossils are preserved as amber or copal. This proportion is significantly different from our estimate that demonstrates that compression-impression fossils are 13 % more abundant than resin-originating body fossils (Fig. 1A). In addition, the proportion of compression-impression fossils increases significantly when all trace fossils are included, as especially leaf mines are considerably more documented in fine-grained sediments than they are as inclusions in amber or copal (Fig. 1B). This difference in representation appears partly due to recent collections, such as compression-impression material retrieved from the Danish Fur Formation, that were not included in Kristensen and Skalski’s (1998) account. The third most frequent preservational type for the lepidopteran fossils are sieved residues, corresponding to 7 % of total specimens. Sieved residues are disarticulated cuticular sclerites or body fragments that originate from unconsolidated matrix, typically from late Pliocene to Holocene deposits associated with glacial environments (Elias, 1992).

Trace fossils likely associated with lepidopterans consist predominantly leaf mines and larval cases (Fig. 1B). These two types of trace fossils differ remarkably in preservational type and their occurrence in the sedimentary record. Leaf-mine fossils predominate as compressions or impressions of foliage, and rarely are present as leaf fossils in amber (Sutherland, 2009), a pattern reflecting the considerably greater foliar surface areas available in fine-grained slabs of sedimentary matrix, when compared to an amber record of miniscule, entombed leaf fragments. Alternatively, some mid Cenozoic deposits, such as Baltic Amber, contain a surprising abundance of larval cases, such as psychid moths (Sobczyk and Kobbert, 2009). Other lepidopteran feeding damage include relatively rare feeding guilds, such as wood borings and external foliage feeding (Labandeira et al., 2007), although attribution to a lepidopteran culprit rarely is possible. Occasionally, fossilized larval frass, preserved as small coprolites, have long been misidentified as seeds or even small fruits (Lancucka-Srodoniowa, 1964), although surface features of such structures can readily distinguish the two apart (Solomon, 1977). These considerations suggest that a thorough review of seeds and other plant reproductive structures may reveal additional misidentifications, potentially increasing the proportion of taxonomically affiliated larval frass in the lepidopteran fossil record.

Lepidopteran fossils show extreme age bias toward the early Paleogene Period, accounting for about 80% of their total fossil occurrences (Fig. 1C). A large proportion of compression-impression occurrences from only a few deposits are preserved during the Paleocene Epoch, especially late Paleocene (58.7–55.8 Ma: Table 1). The Eocene Epoch, especially mid-Eocene (48.6–37.2 Ma: Table 1), by contrast, has a high level of occurrences that represent varied preservational types originating from eleven, geographically disparate and major fossil localities that includes compression-impression material and especially amber. A small peak of occurrences during the Miocene Epoch notably corresponds to the highest number of fossil localities. Fossils from this interval represent a variety of preservational types, but are dominated by compression-impression fossils. The Quaternary Period also shows a small peak, predominantly comprising sieved residues. Generally, the numbers of fossil specimens and fossil localities are not congruent, except for the Eocene, the Miocene and the Pleistocene + Holocene intervals, recording a scarcity of lepidopteran fossils during much of the intervening time.

Taxonomic composition of lepidopteran fossils

Labandeira (1994) estimated that 63.4 % of all extant insect families are represented by at least one occurrence in the fossil record. This percentage is higher than for major holometabolous orders, but for the Lepidoptera, the capture rate of extant families was even lower, at 42.0 %. This low percentage is consistent with Labandeira (1994), and show that only 985 or 21.4% of the total lepidopteran fossil specimens have been placed into 23 (Table 2) of the 42 extant lepidopteran superfamilies (Fig. 4), for a capture rate of 54.8 %. These taxonomically assigned fossils predominantly were amber-copal inclusions (38.4%), followed by the compression-impression body fossils (19.0%), and leaf mines (16.6%). These proportions contrast significantly to the preservational composition of all lepidopteran fossils, reflecting that amber fossils are more amenable to superfamily-level identification than other preservational types. It is highly likely that the low capture rates of lepidopteran superfamilies (and families) are attributable to the difficulty of identifying fossils, especially specimens from compression-impression material, rather than recording an intrinsically depauperate fauna.

The representation of lepidopteran superfamilies in the fossil record varies considerably, and likely depends on biological peculiarities such as the habitat frequented, extent of geographically delimited population size, flight ability, and other mostly dispersal-related attributes of particular lineages. For example, relatively abundant fossils of Tineoidea often occur as inclusions in amber, with arboreal detritivorous and exophytic feeding patterns that provide opportunities for entrapment in plant resins. Leaf-mine fossils of Nepticuloidea also are strongly associated with an arboreal existence, but unlike tineoid taxa, feature herbivorous and endophytic feeding habits. Consequently, there is preferential occurrence of nepticuloids in compression-impression deposits. The fossil records of leaf-mining superfamilies are heavily dependent of expanses of foliar surfaces in bedding planes, although identifications of leaf mine taxa have been questioned by some (Kristensen and Skalski, 1998; Grimaldi, 1999; Grimaldi and Engel, 2005). In taphonomically different settings, noctuoid fossils may have inflated abundances, since their preservation as scales, sclerites and other cuticular fragments in vertebrate gut contents and coprolites (Richter and Storch, 1980), can be derived from the same individual prey item. The relatively large proportion of fossil Papilionoidea fossils is surprising, given that this group accounts for only about 15% of the extant macrolepidopteran fauna (Grimaldi and Engel, 2005). This disproportionate abundance likely is due to elevated anthropogenic interest, as is the case for extant butterflies. Fossils of the Bombycoidea, Cossoidea, Hepialoidea, Noctuoidea, Pterophoroidea, Pyraloidea and Zygaenoidea predominantly or exclusively are from compressed sedimentary matrices. Members of these superfamilies, except for the Pterophoridae, possess relatively large body sizes and consequently have robust flight musculature, allowing resistance to resin entrapment and explaining their rarity in amber. Among macrolepidopteran superfamilies, the Geometroidea are exceptional in having near equivalent numbers of specimens from fine-grained sedimentary matrices as well as fossil resins, although only a limited number of fossils are known for the group. This equivalence may be spurious, as the proportion of amber with geometrid fossils probably will increase, if the many fossils known in Dominican amber are described (pers. comm. to J.-C. Sohn, 2010–2012). The macrolepidopteran Geometroidea and especially microlepidopteran lineages are considerably enriched in amber deposits. The Gelechioidea, Tineoidea and Tortricoidea are relatively more abundant in amber than in fine-grained clastic matrices. These patterns of representation are consistent with Skalski's (1976a) observation that two families, Tineidae and Oecophoridae (auct.), constitute approximately 30 % of all lepidopteran inclusions in amber.

Our data show that the taxonomic representation in the lepidopteran fossil record is biased toward a few superfamilies, and is roughly proportional to their extant diversity, except for the Papilionoidea. The fossils of each superfamily also are subject to preservational bias and, consequently a distributional bias based on fossil age. These biases indicate that lepidopteran fossil data are very incomplete, and appropriate interpretation would require correction factors. For example, amber deposits with insect inclusions predating the mid Early Cretaceous at ca 120 Ma are virtually absent, limiting coverage of older lepidopteran history (Azar et al., 2010). Such a geochronological limitation needs to be taken into account for interpreting the fossil record, especially of microlepidopteran superfamilies whose taxa are predominantly entombed in amber.

Lepidopteran diversity in the fossil record

Labandeira & Sepkoski (1993) found that lepidopteran family diversity, when projected over geologic time, deviates from the expected pattern of insects that display a gradual and proportional increase toward their current diversities. As calculated from Labandeira (1994), the diversity increase of lepidopteran families is indeed nonlinear, significantly differing from other major holometabolous insect orders, which exhibit gradual, linear increases through time (Figs. 2 & 3). This deviation seems to be related to the low capture rate of fossil lepidopteran families. We tested if the recent increase in the number of the lepidopteran fossils (Sohn et al., 2012) would negate such a deviation (Table 3). Our linear regression result yielded a slightly lower value (R^2=0.729) than one estimated for Labandeira (1994). Therefore, despite of recent updates to the lepidopteran fossil record, their unusual evolutionary pattern of family-level diversity evolution still holds. This absence of change indicates that most additional fossil taxa since Labandeira (1994) were ones where family-level assignments already had a fossil record or otherwise lacked a family assignment. Indeed, the differences between Labandeira’s (1994) and our estimate are principally attributable to changes in the family-level classification system of the Lepidoptera. The unusual family-level diversity increase in the Lepidoptera seems to be common feature of the Amphiesmenoptera, as our data incorporating the Trichoptera with the Lepidoptera resulted in a further lowering of the linear regression estimate (Table 3).

The fluctuation in lepidopteran family-level diversity is better explained by exponential models (Table 3), rather than by linear regression. Either solution supports a putative recent diversification of the Lepidoptera (Riek, 1970; Kapoor, 1981; Ollerton, 1999; Grimaldi and Engel, 2005). However, this pattern requires careful interpretation. For example, in comparison to other insect orders, the Lepidoptera exhibits weak family diversity peaks during the Paleocene (ca 65.5–55.8 Ma) and the Miocene (ca 23.0–5.3 Ma). It is known that many lepidopteran fossils are recorded from these strata, such as the late Paleocene Fur Formation and early Miocene Dominican amber. However, these elevated diversities perhaps could be better explained by the pull-of-the-recent (Raup, 1979; Jablonski et al., 2003), which is a phenomenon whereby a more complete fossil record toward the present day also predilects for a greater taxonomic representation of fossil taxa. Our superfamily-level assignments do not reflect a wealth of primary specimen data, and consequently there are few, additional, family-level identifications based on new specimens since the 1994 compilation. Future studies attempting to resolve the taxonomic identities of unstudied lepidopteran fossils likely will fill in existing gaps in the fossil record. In addition, it is likely that the lepidopteran fossil record will increasingly track a more familiar linear increase in family diversity, as demonstrated for other insect orders.

Lepidopteran divergence in the fossil record

Fossil occurrences of lepidopteran superfamily-level lineages are depicted on a phylogeny (Fig. 4) that reflects recent developments in molecular phylogenetic methods (Regier et al., 2009; Mutanen et al., 2010; Cho et al., 2011). Similar, but morphologically based phylogenies, calibrated by key fossil occurrences, were constructed by Labandeira et al. (1994), Grimaldi (1999), and lately, Grimaldi and Engel (2005). Most approaches date the origin of Lepidoptera approximately to the Sinemurian Stage (196.5–189.6 Ma) of the Early Jurassic (Fig. 4: occurrence no. 1), based on the fossil, *Archaeolepis mane* (Whalley, 1985), the earliest known lepidopteran. Thereafter, during later Early Jurassic to earlier Middle Jurassic, several lineages with robust mandibulate mouthparts originated in succession (Rasnitsyn, 1983; Kozlov, 1988; Ansorge, 2002; Huang et al., 2010), eventually giving rise to a preglossatan clade provided with mouthparts characterized by a short, tubular siphon, the Glossata (Kristensen, 1997). In contrast to the afore-mentioned hypothesis whereby the divergence of the Glossata and earlier clades was accomplished by 160 Ma, Grimaldi and Engel

(2005) propose an alternative hypothesis. Their hypothesis states that such divergence events occurred considerably later, centered in the mid Late Jurassic to the Berriasian, the earliest stage of the Cretaceous, and perhaps coincident with initial angiosperm diversification (Grimaldi, 1999; Friis et al., 2011). These two scenarios differ from each other in how to treat putative early lepidopteran specimens, including 180 million-year-old mandibulate forms from Grimmen (Ansorge, 2002), and approximately 155 million-year-old specimens from Karatau (Kazakhstan), particularly the basal moth *Protolepis cuprealata* Kozlov 1989, that controversially may have had a short siphon for imbibition of fluid food (Kristensen and Skalski, 1998). If verified, *Protolepis* would represent the earliest known member of the Glossata.

The former view considers an initial short fuse followed by diversification of basal lepidopteran groups during the first 25 million years of the lepidopteran fossil record (Labandeira et al., 1994; Fig. 4). By contrast, the latter view maintains an initial 35 m.y. interval of stasis, or a long fuse, followed by a relatively rapid, 15 m.y. interval of rapid cladogenesis from 155 to 140 Ma, toward the end of which the Glossata evolved (Grimaldi and Engel, 2005). One possible advantage with the former view is that it is free from an assumption that the early evolution of the Lepidoptera was contemporaneous with initial angiosperm diversification. For the origin of the Glossata, similar to the placements of Labandeira et al. (1994) and Grimaldi (1999), we position the event between 175 and 165 Ma. Grimaldi and Engel (2005), in the other, suggested that their evolution occurred later by about 20 Ma. This difference is contingent on whether the allegedly earliest glossatan, *Protolepis cuprealata,* is included or not. Grimaldi and Engel (2005) thought that an undescribed larva in Lebanese amber (120 Ma, mid Early Cretaceous) is the earliest Glossata. A recent molecular estimate of the divergence of Zeugloptera from Glossata (Imada et al., 2011) resulted in a confidence interval spanning 170 to 135 Ma, consistent with both proposals.

The occurrence of the Apoditrysia clade is considerably older (Labandeira et al. 1994; Fig. 4), than the timing proposed by Grimaldi (1999), and Grimaldi and Engel (2005). This temporal difference is attributable to a major change in the recent phylogenetic status of the Gelechioidea as an apoditrysian superfamily, two fossils of which are new gelechioid fossils dated at 110 Ma (Fig. 4, data points 72–74). In addition, Grimaldi and Engel (2005) proposed that the Macrolepidoptera, including the Papilionoidea (butterflies and skippers), diverged during the early Cenozoic. This view recently has been challenged because of the revised position of the Papilionoidea within the Obtectomera in a recent classification of the Lepidoptera (van Nieukerken et al., 2011). Accordingly, the Macroheterocera clade in our phylogenetic reconstruction evolved during the early Late Cretaceous, differing from Grimaldi and Engel (2005), who instead proposed an early Paleocene origin. This difference in timing resulted from the inclusion of likely geometroid (Fig. 4, data points 95 and 96) and noctuoid (Fig. 4, data point 106) fossils in our study. By way of comparison, Kozlov et al. (2002) observed that the relative dominance of microlepidopteran over macrolepidopteran fossils in the Eocene was reversed during the late Oligocene and early Miocene, raising the possibility that microlepidopteran diversity increased only after the Eocene. We did not recover such a turnover in our data, which includes more lepidopteran fossil specimens than those used by Kozlov et al. (2002). Overall, our summary in Figure 4 agrees with Labandeira et al. (1994), and suggests that diversification of major lepidopteran clades occurred earlier than previously thought. This earlier shift in origin necessitates reconsideration of major lepidopteran cladogenetic events occurring synchronously with initial angiosperm diversification during a 45-m.y. interval from 135–90 Ma (Friis et al., 2011).

Implications of new divergence-time estimates

Fossil Lepidoptera have been conventionally perceived as consisting of a depauperate fossil record. Although this perception often was based on the sparseness of lepidopteran fossils, there have been no studies that have evaluated the record with tabulations of specimen abundances based on locality, higher-level taxa, preservational mode, and other relevant variables. We scrutinized the entire lepidopteran fossil record, taking a systematic approach. Our analyses show that the recent increase in the number of discovered fossil specimens does not improve paleontological resolution for establishing divergences among the lepidopteran superfamilies. There are a few major taphonomic or research biases observed from our fossil data that may account for this pattern.

As the availability of fossil identifications increase, the most common preservational mode characterizing lepidopteran identifications is amber. This type of preservation could be problematic in that amber fossils cover a shorter time window than compression-impression fossils, with the oldest insect-bearing ambers extending only to about 120 Ma, effectively rendering older occurrences of fossils available only as compressions or impressions (Labandeira, 1999; Penney, 2010; but see Schmidt et al., 2012). Consequently, superfamily-level diversity of Lepidoptera prior to the Late Cretaceous is likely to be underestimated because of the absence of available amber fossil deposits. Another factor is that lepidopteran fossil occurrences in general are extremely biased toward the Paleogene Period. This enrichment may be due to the increased, idiosyncratic, preservational potential of lepidopteran fossils during the Paleogene, or possibly related to the pull-of-the-recent (Raup, 1979). Such a bias would draw downward the occurrence of superfamilies on both sides of the Paleogene, causing the appearance of explosive diversification rather than a dramatic increase in preservational potential. Last, the availability and density of fossil occurrences for establishing the presence of lepidopteran superfamilies appears highly variable across time, habitats and lineages. Such a bias requires that divergences of several superfamily-level lineages lacking relevant fossils for establishment in the fossil record, rather be inferred from sister groups with identifiable fossils or even cladogenetically related, more distant lineages. These three biases often are interrelated, and collectively present a sporadic and incomplete record, as shown by the prevalence of ghost lineages occupying dotted vertical lines lacking fossils in Figure 4.

Divergence time estimation of molecular phylogenies has become common in evolutionary studies. This advance critically depends on the quality of the fossil record. A poor fossil record of Lepidoptera may be of minimal use for such analyses. Recent progress in molecular dating methods nevertheless would allow for establishing uncertainties in fossil calibrations (Warnock et al., 2012). From our overview of the lepidopteran fossil record, we propose three important requirements for considering such uncertainties and hence for devising reliable divergence-time estimates for lineages.

First, divergence time estimates of lineages should adopt at least one calibration point. Such points ideally correspond to the earliest fossil occurrences of particular lineages. For lepidopteran fossils, such an approach may need correction factors for differential preservation that would incorporate sedimentological correlates associated with the probability of fossil presence, general occurrence patterns based on taxonomy, and the tendency for a better fossil record toward the recent. An example of a taphonomically driven preservation potential are several microlepidopteran clades whose fossils entirely or largely originate from Paleogene and Neogene amber deposits. It is very possible that earlier fossil occurrences of these microlepidopteran clades are significantly older than the stated divergence events, in part because fossils almost always represent minimum dates, but also attributable to amber deposits absent in earlier time intervals. In Bayesian divergence time estimation, using vague prior probability intervals with the fossil age set to a minimum is a practical way to overcome this problem. A second way of evaluating divergence-time estimates is to establish confidence intervals for lineages with nonrandom distributions of sampling intensity or fossil occurrences with variable preservation potential (Marshall, 1997). The establishment of a confidence interval, based in part on the density of fossil occurrences and sampling intensity under particular conditions of preservation, can provide the time of origin of a fossil lineage using an appropriate modification of classical confidence-interval techniques (e.g., Labandeira et al., 2002b). Consequently, each fossil calibration needs to be carefully evaluated for consideration of possible data bias.

Second, choices involved in placement of the fossils onto a phylogeny significantly affect resulting divergence time estimates (Pyron, 2010). Typically, reliable identification needs to be based on apomorphic characters. However, such characters often are unavailable for lepidopteran fossils, resulting in substantial uncertainty regarding their systematic position. Amber or copal inclusions usually preserve more body structures useful for identification than do other preservation types. As our examination shows, any interpretation involving a particular preservational type will emphasize a limited facet of lepidopteran evolutionary history. Therefore, fossils representing a variety of preservational types need to be considered, even if some are subject to taxonomic uncertainty. Molecular dating analyses that include such uncertainty consequently need to test several alternative fossil placements (Pyron, 2010), or alternatively adopt both “early but risky” and “safe but late” fossil constraint strategies (Sauquet et al., 2012).

Third, lineage-specific fossil densities depicted in Figure 4 may provide another useful criterion for evaluating fossil calibrations. Such data would address the effects of sampling the fossil record, and can assist in resolving discrepancies between molecular estimates and paleontological evidence (Brocklehurst et al. 2012). We show that some lepidopteran superfamily-level lineages have comparatively denser fossil occurrences. It is likely that such groups provide more reliable calibrations than those with a sporadic fossil record. From this perspective, vague prior densities on the ages of calibrated nodes also should be used to detect the ages of lineages with few fossils.

Conclusions

It has been shown that even for fossils assigned to a superfamily, most identifications typically have been questioned by subsequent reviewers (Sohn et al., 2012). Therefore, we encourage researchers to review carefully lepidopteran fossils, especially their relationships with extant taxa, before using them as calibration points for molecular analyses. Our overview reveals that about 78 % of lepidopteran fossils remain unidentified. Plots of fossils onto lepidopteran phylogenies suggest that a high proportion of their evolutionary history currently is undetected in the fossil record. Unstudied lepidopteran fossils may play a pivotal role in supplementing this incomplete fossil record. Therefore, future fossil studies for the Lepidoptera need to focus on increasing the proportion of securely identified fossils. The *Lepidoptera Assembling the Tree of Life* consortium is aware of this requirement, and plans to examine additional undescribed fossils and evaluate the previous identifications with a view toward establishing more robustly calibrated lineages within lepidopteran phylogeny. Such an effort eventually will provide data that are especially useful for constraining the lepidopteran time tree and garner a better understanding of Lepidoptera evolutionary history.

Table 1. The number of trace and body fossils by their preservation type and age. The second row indicates the preservation types: AM, amber and copal; AS, asphaltum and tar sands; CI, compressions and impressions; GC, gut contents and coprolites; PE, peat and lignite; SA, salt deposits; SR, sieved residues; and SI, silica and other forms of permineralization.

	Trace fossils					Body fossils						
Time intervals	CI	AM	SI	SA	PE	CI	AM	SI	SR	GC	AS	PE
Early Jurassic	1	0	0	0	0	14	0	0	0	0	0	0
Middle Jurassic	0	0	0	0	0	5	0	0	0	0	0	0
Late Jurassic	0	0	0	0	0	6	0	0	0	0	0	0
Early Cretaceous	47	0	0	0	0	15	26	0	0	0	0	0
Late Cretaceous	29	0	0	0	0	1	31	1	1	0	0	0
Early Paleocene	4	0	0	0	0	1	0	0	0	0	0	0
Middle Paleocene	0	0	0	0	0	1	0	0	0	0	0	0
Late Paleocene	3	0	0	0	0	1892	0	0	0	0	0	0
Early Eocene	4	0	0	0	0	12	0	0	0	0	0	0
Middle Eocene	28	111	0	0	0	18	1532	37	0	4	0	0
Late Eocene	6	0	0	0	0	67	5	0	0	0	0	0
Early Oligocene	0	0	0	0	0	27	1	1	0	0	0	0
Late Oligocene	2	0	4	0	0	12	0	2	0	0	0	0
Early Miocene	9	2	0	0	0	61	44	2	0	0	0	0
Middle Miocene	15	0	0	1	0	14	1	0	0	0	0	0
Late Miocene	7	0	20	0	0	14	0	0	0	0	0	0
Early Pliocene	2	0	0	0	0	0	0	0	0	0	0	0
Late Pliocene	24	0	0	0	0	52	0	1	0	0	1	0
Pleistocene	0	0	8	0	1	2	18	0	296	0	1	1
Holocene	0	0	0	0	0	3	4	2	4	0	0	0

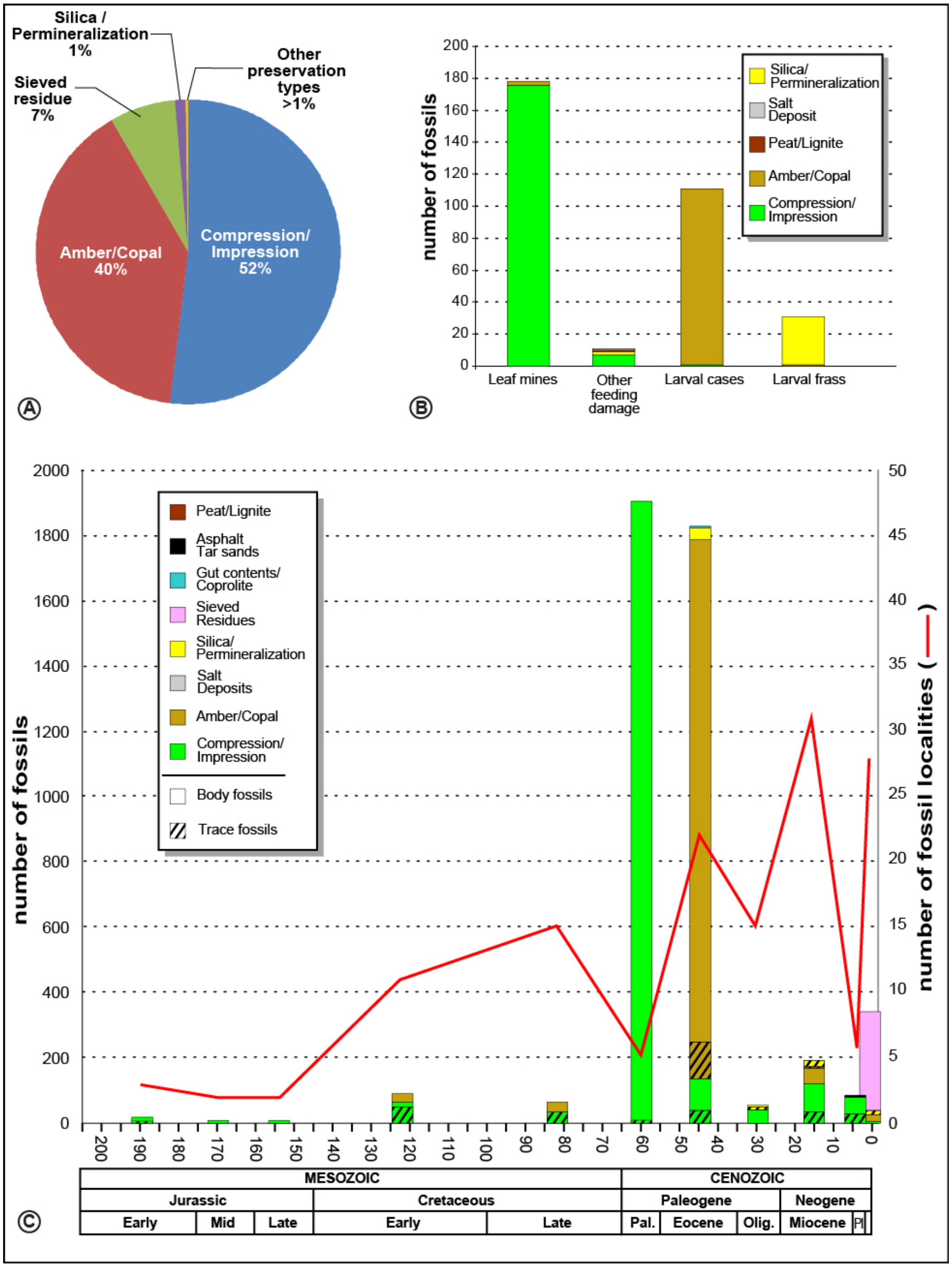
Table 2. Taxonomic and preservational modes of lepidopteran fossils. The numbers of the fossil specimens are shown in each column. The lepidopteran superfamilies are arranged by numerical rank order of total fossil specimens. Preservational mode abbreviations: AM, amber and copal; AS, asphaltum and tar sands; CI, compressions and impressions; GC, gut contents and coprolites; PE, peat and lignite; SA, salt deposits; SR, sieved residues; and SI, silica and other forms of permineralization.

Superfamily	CI	CI&T	AM	AM&T	CO	SI	SI&T	SR	GC	AS	PE&T	**Total**
Tineoidea	3	0	105	96	0	8	1	1	0	0	0	214
Papilionoidea	81	0	50	0	9	0	0	1	1	0	0	142
Noctuoidea	30	0	3	1	6	2	0	67	0	1	0	110
Nepticuloidea	2	97	2	0	2	0	0	0	0	0	0	103
Gelechioidea	3	14	76	0	0	0	0	0	0	0	0	93
Tortricoidea	2	0	78	0	1	0	0	0	0	0	1	82
Bombycoidea	9	0	1	0	0	40	0	1	1	1	0	53
Gracillarioidea	1	39	4	1	0	0	0	0	0	0	0	45
Micropterigoidea	10	0	21	0	0	0	0	0	1	0	0	32
Yponomeutoidea	4	3	14	1	1	0	0	0	0	0	0	23
Adeloidea	0	8	12	0	0	0	0	0	0	0	0	20
Geometroidea	8	0	3	0	4	0	0	2	0	0	0	17
Pyraloidea	8	0	2	0	1	0	0	0	0	0	0	11
Zygaenoidea	9	0	0	0	0	0	0	0	0	1	0	10
Hepialoidea	7	0	0	0	0	2	0	0	0	0	0	9
Cossoidea	5	0	1	0	0	0	0	0	1	0	0	7
Eriocranioidea	2	1	2	0	0	0	0	0	0	0	0	5
Pterophoroidea	3	0	0	0	0	0	0	0	0	0	0	3
Carposinoidea	1	0	1	0	0	0	0	0	0	0	0	2
Lophocoronoidea	0	0	1	0	0	0	0	0	0	0	0	1
Mnesarchaeoidea	0	0	1	0	0	0	0	0	0	0	0	1
Tischerioidea	0	1	0	0	0	0	0	0	0	0	0	1
Thyridoidea	0	0	1	0	0	0	0	0	0	0	0	1

Table 3. Linear and exponential regression equations (y) coefficients (R^2) for Figures 2 and 3.

	linear		Exponential	
	y	R^2	Y	R^2
Lepidoptera (Labandeira, 1994)	2.3187x - 67.702	0.7343	$0.0788e^{0.1249x}$	0.9292
Lepidoptera (Sohn et al., 2012)	2.0147x - 54.575	0.729	$0.1886e^{0.1083x}$	0.9027
Lepidoptera+Trichoptera	1.695x - 23.963	0.7138	$0.7045e^{0.0903x}$	0.9696
Trichoptera	0.4922x - 4.8454	0.8302	$0.9301e^{0.0627x}$	0.9614
Coleoptera	2.4267x - 17.481	0.9417	$6.2521e^{0.0589x}$	0.924
Diptera	2.1594x - 23.443	0.9109	$1.9969e^{0.0794x}$	0.7833
Hymenoptera	2.0268x - 25.753	0.9588	$1.6138e^{0.081x}$	0.7031

Fig. 1. Proportional representation of 4,593 lepidopteran fossils categorized by preservational type, abundance, age, and associated locality, documented in Sohn et al. (2012). (**A**), Proportional representation of preservational types of lepidopteran body fossils (N = 4,262). (**B**), Proportional representation of trace-fossil types in the lepidopteran fossil record (N = 331). (**C**), Frequency distribution of lepidopteran body and trace fossils (N = 4,561) by geochronologic age, preservational type, abundance, and number (N = 145) of lepidopteran-bearing localities. The geochronology at bottom is after Gradstein et al. (2004).


Silica / Permineralization 1%
Other preservation types >1%
Sieved residue 7%
Compression/ Impression 52%
Amber/Copal 40%
Ⓐ
200
180
160
140
120
100
80
60
40
20
0
number of fossils
Silica/ Permineralization
Salt Deposit
Peat/Lignite
Amber/Copal
Compression/ Impression
Leaf mines
Other feeding damage
Larval cases
Larval frass
Ⓑ
2000
1800
1600
1400
1200
1000
800
600
400
200
0
number of fossils
Peat/Lignite
Asphalt Tar sands
Gut contents/ Coprolite
Sieved Residues
Silica/ Permineralization
Salt Deposits
Amber/Copal
Compression/ Impression
Body fossils
Trace fossils
50
45
40
35
30
25
20
15
10
5
0
number of fossil localities (——)
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
MESOZOIC
CENOZOIC
Jurassic
Cretaceous
Paleogene
Neogene
Early
Mid
Late
Early
Late
Pal.
Eocene
Olig.
Miocene
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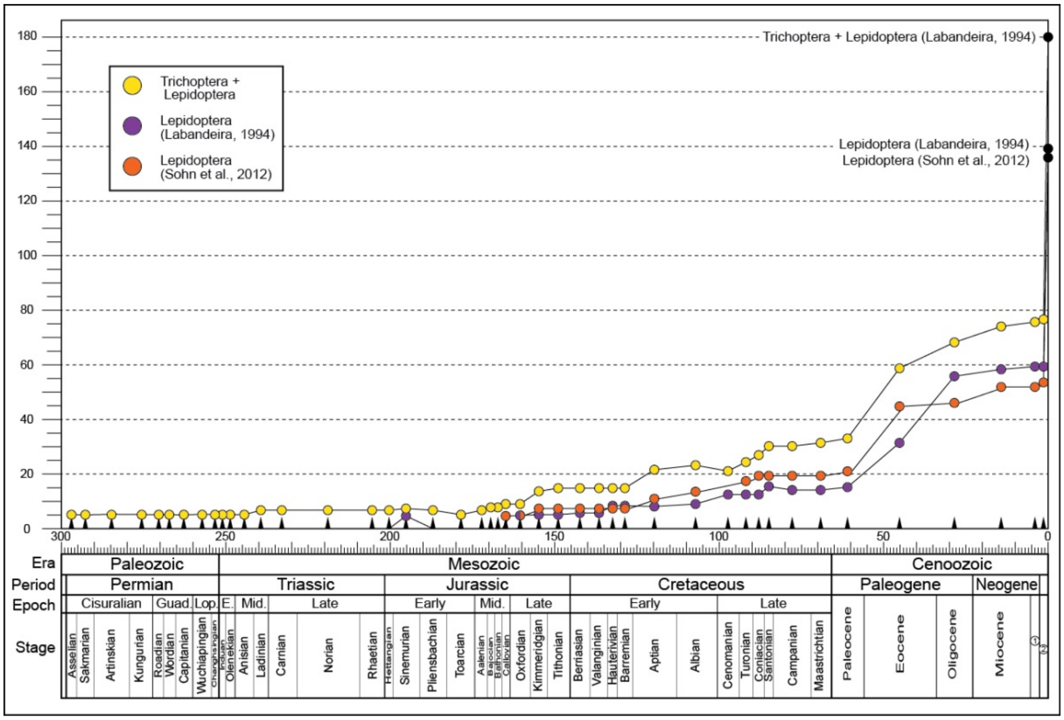
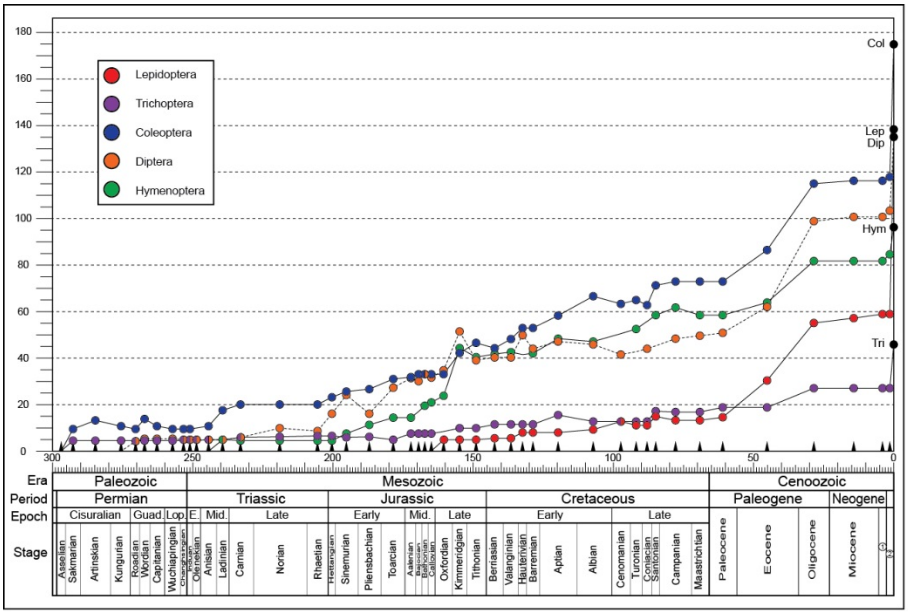


Fig. 2. Family-level diversity of the Lepidoptera and Amphiesmenoptera (Lepidoptera + Trichoptera). Modern data for the Amphiesmenoptera is from Labandeira (1994), shown in orange circles; a mid 1990's understanding of Lepidopteran history is from Labandeira (1994), as red circles; and current understanding of lepidopteran history is from Sohn et al. (2012), as yellow circles. The range-through method tabulating occurrence data was used, with data plotted at stage and epoch midpoints (Labandeira and Sepkoski, 1993); the geochronology at bottom is after Gradstein et al. (2004). Abbreviations: Ma, million years; 1, Asselian; 2, Roadian; 3, Wordian; 4, Induan; 5, Rhaetian; 6, Bathonian; 7, Santonian; 8, Pliocene; and 9, Pleistocene.

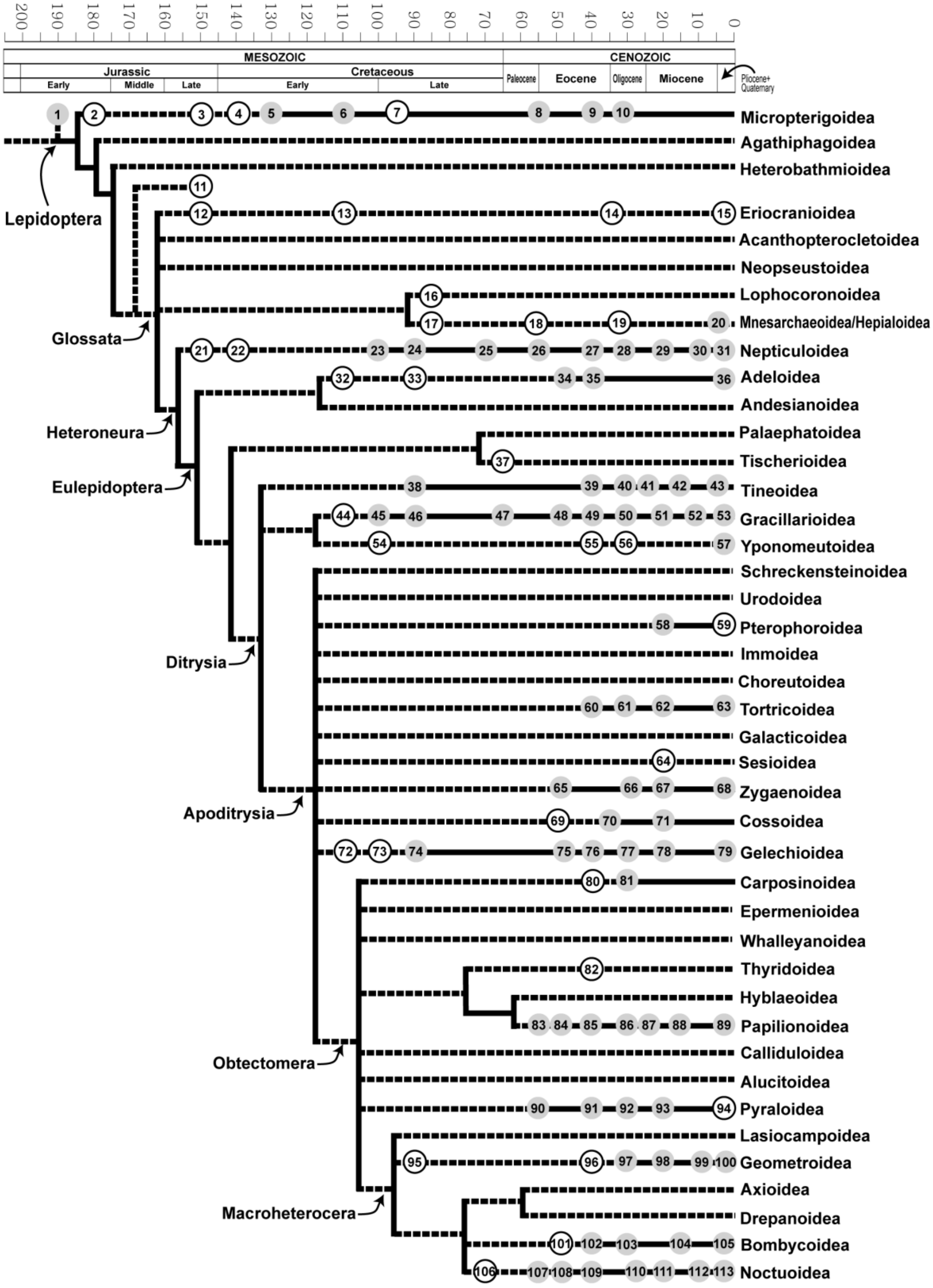


③

④

Fig. 3. Family-level diversity of four major, ordinal-level, holometabolous lineages. Circle symbols for ordinal-level lineages: Lepidoptera, red; Trichoptera, purple; Coleoptera, blue; Diptera, brown; and Hymenoptera, green. All data were sourced from Labandeira (1994). Abbreviation: Ma = million years ago. The range-through method was used, with data plotted at stage and epoch midpoints (Labandeira and Sepkoski, 1993); the geochronology at bottom is after Gradstein et al. (2004). Abbreviations: Ma, million years; 1, Asselian; 2, Roadian; 3, Wordian; 4, Induan; 5, Rhaetian; 6, Bathonian; 7, Santonian; 8, Pliocene; and 9, Pleistocene.

Fig. 4. Cladogram representing the phylogenetic relationships and fossil record of lepidopteran superfamilies. Circles on vertical lines indicate important fossil occurrences, representing from one occurrence to a temporally constrained cluster of multiple occurrences present within an approximate 5 million-year interval. White circles indicate less reliable fossil occurrences; gray circles indicate reliably identified fossil occurrences. Vertical lines with solid branch segments indicate definitive fossil evidence whereas branch segments with dotted lines represent no or unreliable fossil evidence. The numbers within the circles were arbitrarily assigned from lower left to upper right of the cladogram; see Appendix 1 for a numbered list of fossil occurrences.


200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
MESOZOIC
CENOZOIC
Jurassic
Cretaceous
Early
Middle
Late
Early
Late
Paleocene
Eocene
Oligocene
Miocene
Pliocene+ Quaternary
1 2 3 4 5 6 7 8 9 10 Micropterigoidea
Agathiphagoidea
Heterobathmioidea
11
12 13 14 15 Eriocranioidea
Acanthopterocletoidea
Neopseustoidea
16 Lophocoronoidea
17 18 19 20 Mnesarchaeoidea/Hepialoidea
21 22 23 24 25 26 27 28 29 30 31 Nepticuloidea
32 33 34 35 36 Adeloidea
Andesianoidea
Palaephatoidea
37 Tischerioidea
38 39 40 41 42 43 Tineoidea
44 45 46 47 48 49 50 51 52 53 Gracillarioidea
54 55 56 57 Yponomeutoidea
Schreckensteinoidea
Urodoidea
58 59 Pterophoroidea
Immoidea
Choreutoidea
60 61 62 63 Tortricoidea
Galacticoidea
64 Sesioidea
65 66 67 68 Zygaenoidea
69 70 71 Cossoidea
72 73 74 75 76 77 78 79 Gelechioidea
80 81 Carposinoidea
Epermenioidea
Whalleyanoidea
82 Thyridoidea
Hyblaeoidea
83 84 85 86 87 88 89 Papilionoidea
Calliduloidea
Alucitoidea
90 91 92 93 94 Pyraloidea
Lasiocampoidea
95 96 97 98 99 100 Geometroidea
Axioidea
Drepanoidea
101 102 103 104 105 Bombycoidea
106 107 108 109 110 111 112 113 Noctuoidea
Lepidoptera
Glossata
Heteroneura
Eulepidoptera
Ditrysia
Apoditrysia
Obtectomera
Macroheterocera

Appendix 1

The following is a list of fossil occurrences and associated literature sources for Figure 4. For brevity, only taxon names and locality information are shown. This is not an exhaustive list; due to graphical limitations, not all relevant deposits were included below or in Figure 4. More expansive accounts and literature sources for taxa in each record is provided in Sohn et al. (2012).

1. The archaeolepid, *Archaeolepis mane*, from a calcareous flatstone of Dorset, United Kingdom (Whalley, 1985), the earliest, reliably identified lepidopteran.

2. Two undescribed lepidopterans, related to the Micropterigidae, from the Grüne Series of Grimmen, Germany (Ansorge, 2002).

3. *Auliepterix mirabilis*, a micropterygoid specimen, from the Karabastau Formation, Kazakhstan (Kozlov, 1989).

4. *Auliepterix minima*, a micropterygoid specimen, from the Archangel Formation of Mongolia (Kozlov, 1989).

5. The micropterygid, *Palaeosabatinca zherichini*, from the Zaza Formation of Asian Russia (Kozlov, 1988).

6. *Parasabatinca aftimacrai* from the Grès de Base Formation, Lebanon (Whalley, 1978); *P. caldasae* from the Crato Formation, Brazil (Martins-Neto & Vulcano, 1989); *Sabatinca perveta* (Cockerell, 1919) from Burmese amber of an unnamed formation (Rasnitsyn and Ross, 2000), in northern Myanmar; and

an indeterminate genus in Álava Amber from the Nograro Formation, Spain (Martínez-Delclós et al., 1999).

7. Micropterygid wing scale in inclusions from Aquitanian Amber of France (Kühne et al., 1973).

6. The micropterygid *Moleropterix kalbei*, from the Fur Formation of Denmark (Engel & Kinzelbach, 2008).

9. Four described micropterigid species, *Baltimartyria proavittella*, *B. rasnitsyni*, *Micropterix gertraudae* and *M. immensipalpa*, in Baltic Amber from the Prussian Formation of the Baltic Region (Rebel, 1936; Kusnezov, 1941; Kurz & Kurz, 2010; Mey, 2011b).

10. The micropterygid, *Micropterix angelica*, from the Bouldnor Formation of the United Kingdom (Jarzembowski, 1980).

11. The glossatan, *Protolepis cuprealata*, from the Karabastau Formation of Kazakhstan (Kozlov, 1989).

12. An undescribed eriocranoid specimen from the Karabastau Formation of Kazakhstan (Kozlov et al., 2002).

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14. An undescribed specimen in Baltic Amber from the Prussian Formation, Baltic Region (Skalski, 1990b).

15. The eriocranoid, *Eriocranites hercynicus*, from lake sediments of Willershausen in Germany (Kernbach, 1967); and undescribed leaf mines from the Payette Formation, United States (Opler, 1973).

16. An undescribed lophocoronid specimen in Taimyr Amber from the Kheta Formation, European Russia (Skalski, 1979a).

17. An undescribed mnesarchaeoid or hepialioid specimen in Taimyr Amber of the Kheta Formation, from European Russia (Zherikhin & Sukacheva, 1973).

18. The hepialioid, *Prohepialus incertus*, from the “cinerites” of Puy-de-Dôme, France (Piton, 1940).

19. Undescribed mnesarchaoid or hepialioid specimens from the Bouldnor Formation (Jarzembowski, 1976), and the Glen Afton mine (Evans, 1931), of the United Kingdom.

20. The hepialioid specimens *Protohepialus incertus,* from the Puente Formation of California, USA (Skalski, 1990a); and *Oiophassus nycterus*, from the Shanwang Formation, of Shandong, China (Zhang, 1989).

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22. Several undescribed leaf mines, attributed to the Nepticulidae, from the Battle Camp Formation of Queensland, Australia (Rozefelds, 1988).

23. Undescribed nepticulid leaf mines from the Dakota Formation, Kansas and Nebraska, USA (Stephenson, 1991; Labandeira et al., 1994); a *Stigmellites araliae* leaf mine from the Perucher Formation of the Czech Republic (Fritsch, 1982).

24. Five described morphospecies (*Stigmellites kzyldzharicus*, *S. samsonovi*, *S. serpentina*, *S. sharovi*, *S. tyshchenkoi*) from the Beleuty Formation of the Kyzl-Ordinsky Region, Kazakhstan (Kozlov, 1988).

25. Undescribed nepticulid leaf mines from the Meeteetsee Formation of Wyoming, USA (Labandeira, 2002b), and undescribed leaf mines from the Hell Creek Formation of North Dakota, USA (Labandeira et al., 2002b).

26. The nepticulid leaf mines *Stigmellites centennis* and *S. gossi* from the Reading Formation (Jarzembowski, 1989), of late Paleocene age from the United Kingdom; and *Stigmellites messelensis* from the Messel Formation (Straus, 1976), of middle Eocene age, from Germany.

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28. Undescribed nepticulid specimens from the Bouldnor Formation, United Kingdom (Jarzembowski, 1980).

29. The nepticulid leaf mine *Stigmellites fossilis* from the Rott Formation, Germany (Heyden, 1862; Kozlov, 1988); and *Stigmella* (?) *almeidae* from the Tremembé Formation, Brazil (Martins-Neto, 1989).

30. Undescribed nepticulid specimens from bituminous rhythmites at the “La Rinconada” site, Spain (Peñalver and Delclòs, 2004); undescribed nepticulid mines (Liebhold et al., 1982) from the Trapper Creek Formation, Idaho, USA; and various other North American middle Miocene fossil sites (Opler, 1973) of the Pacific Interior, USA.

31. Five described nepticulid species from several fossil sites: *Stigmella ulmivora*, *Stigmellites carpiniorentalis*, *Stigmellites heringi*, *Stigmellites pliotityrellus* and *Stigmellites zelkoviae*, all of the late Pliocene lake sediments of Willershausen, Germany (Kernbach, 1967; Straus, 1977).

32. Adeloid wing scales from Lebanese Amber of the Grès de Base Formation, Lebanon (Whalley, 1978).

33. Feeding trace fossils from the Upper Hatira Formation, Israel (Krassilov and Shuklina, 2008); an undescribed incurvariid specimen from Taimyr Amber of the Kheta Formation, European Russia (Skalski, 1979a).

34. Stereotypical incurvariid leaf-case fossils of earlier middle Eocene age from the Green River Formation of Colorado (Labandeira, 1998), Klondike Mountain Formation of Washington (Labandeira, 2002a), and the Messel Formation of Germany (Labandeira et al., 2007).

35. Eight described adeloid species of later middle Eocene age in Baltic Amber from the Prussian Formation (Rebel, 1934; Rebel, 1936; Kozlov, 1987): *Adela kuznetzovi* and *A. similis*; *Adelites acutitarsellus*, *A. purpurascens*, *A. serraticornellus*, *A. electreellus*; *Prophalonia gigas*; and *Incurvarites alienellus*.

36. Incurvariid leaf mines from the Willershausen lake deposits of Germany (Straus, 1977).

37. An undescribed tischeriid leaf mine from the Ripley Formation of Tennessee, USA (Stephenson, 1991).

38. Undescribed specimens from New Jersey Amber of the Raritan Formation, USA (Grimaldi and Nascimbene, 2010).

39. Approximately twenty described and several undescribed tineoid specimens (Menge, 1856; Rebel, 1934; Kusnezov, 1941; Skalski, 1974, 1977; Jarzembowski, 1980; Kozlov, 1987, 1988; Sobczyk and Kobbert, 2009) from Baltic Amber of the Prussian Formation, in Germany, Poland, Russia and adjacent countries.

40. The tineoids *Paratriaxomasia solentensis* from the Bouldnor Formation, United Kingdom (Jarzembowski, 1980) and *Adelopsyche frustrans* from the Florissant Formation of Colorado, USA (Cockerell, 1926).

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45. Phyllocnistine and gracillariine leaf-mine fossils (Chambers, 1882; Stephenson, 1991; Labandeira et al., 1994), from the Dakota Formation, Kansas and Nebraska, USA.

46. The gracillarioid *Bucculatrix platani* from the Beleuty Formation of Kazakhstan (Kozlov, 1988); undescribed leaf mines from the Frontier Formation of Wyoming, USA (Knowlton, 1917); and leaf mines from the Ora Formation, Israel (Krassilov and Shuklina, 2008).

47. Undescribed gracillarioid leaf mines from the Hell Creek Formation of North Dakota, USA (Labandeira et al., 2002a, 2002b).

48. An undescribed bucculatricid leaf mine from the Wind River Formation, Wyoming, USA (Hickey and Hodges, 1975); and gracillariid leaf mines from the Tufulitas Laguna del Hunco Formation, southern Argentina (Wilf et al., 2005).

49. The body fossil *Gracillariites lithuanicus* and *G. mixtus* from Baltic Amber of the Prussian Formation, Baltic Region (Kozlov, 1987); and undescribed leaf mines (Stephenson, 1991; Jarzembowski, 1995; Labandeira, 2002a), from several middle Eocene deposits of the United Kingdom and USA.

50. Undescribed leaf mines from the Florissant Formation of Colorado, USA (Opler, 1982), and the Bouldnor Formation of the United Kingdom (Jarzembowski, 1980).

51. The leaf mine *Phyllonorycter* (?) *oliveirae* from the Tremembé Formation of southern Brazil (Martins-Neto, 1989) and a leaf mine from Mexican Amber of the Simojovel Formation, Mexico (Poinar and Brown, 2002).

52. Undescribed gracillarioid leaf mines of *Acrocercops*, *Bucculatrix*, *Cameraria* and *Lithocolletis* from several Miocene deposits (Buffalo Canyon, Esmeralda, Latah, Payette, Savage Canyon and Trout Creek Formations) of Idaho, Nevada, Oregon and Washington, western USA (Opler, 1973; Lewis, 1985).

53. Two gracillarioid leaf mines attributed to the extant taxa, *Phyllonorycter maestingella* and *Bucculatrix thoracella*, from the Willershausen lake beds of Germany (Straus, 1977).

54. A putative yponomeutoid leaf mine assigned to the Praydidae from the Dakota Formation, Kansas and Nebraska, USA (Stephenson, 1991).

55. Nine described yponomeutoid species: *Argyresthites balticellus*, *A. succinellus*, *Plutellites acutipenellus*, *P. inversellus*, *P. minorellus*, *P. tenebricus*, *Epinomeuta truncatipennella*, *Scythropites balticellus* and *Prolyonetia cockerelli*, in Baltic Amber from the Prussian Formation of the Baltic Region (Rebel, 1934, 1936; Kusnezov, 1941; Skalski, 1976b, 1977; Kozlov, 1988).

56. Undescribed yponomeutoid specimens of late Eocene to early Oligocene age from the Bouldnor Formation (Jarzembowski, 1980) of the United Kingdom, and from Sicilian Amber (Skalski and Veggiani, 1990), Italy.

57. An undescribed yponomeutoid specimen from East African copal of Zanzibar, Tanzania (Skalski, 1976a).

58. The pterophoroid body fossil, *Merrifieldia oligocenicus,* from the "laminites lacustres" of Aix-en-Provence, France (Bigot et al., 1986).

59. An undescribed pterophoroid body fossil from the "cinerites" deposit of Puy-de-Dôme, France (Piton, 1936).

60. Six described tortricid species: *Electresia zalesskii*; *Tortricibaltia diakonoffi*; *Tortricidrosis inclusa*; *Spatalistiforma submerge*; *Tortricites sadilenkoi*, *T. skalskii*, in Baltic Amber of the Prussian Formation, from the Baltic Region (Kusnezov, 1941; Skalski, 1973a, 1992; Kozlov, 1988).

61. The tortricid species *Tortricites destructus* and *T. florissantanus* from the Florissant Formation of Colorado, USA (Cockerell, 1916; Skalski, 1992; Meyer, 2003).

62. An undescribed tortricid specimen in Mexican Amber from the Simojovel Formation (Skalski, 1973a); and *Polyvena horatis* Poinar and Brown, 1993, and other undescribed fossils (Poinar, 1992; Grimaldi and Engel, 2005) from somewhat younger Dominican Amber, Dominican Republic.

63. Tortricid larval feeding damage attributed to the extant *Retinia resinella* from the Piionso Moor, Finland (Koponen and Nuorteva, 1973).

64. An undescribed sesiid specimen from the "laminites lacustres" of Aix-en-Provence, France (de Serres, 1829; Rasnitsyn and Zherikhin, 2002).

65. Undescribed zygaeniid material, assigned to the Procridinae from the Messel Formation, Germany (McNamara et al., 2011).

66. The zygaeniid *Neurosymploca* (?) *oligocenica* from the Calcaires de Montfuron or Calcaires de Vachères Formation of Céreste, France (Fernández-Rubio and Nel, 2000).

67. An undescribed zygaeniid specimen from the "laminites lacustres" of Aix-en-Provence, France (Leestmans, 1983); the zygaeniids *Zygaena* (?) *miocaenica* and *Zygaenites controversus* from the "dysodile beds" of Randecker Maar, Germany (Burgeff, 1951); and *Zygaena* (?) *turolensis* from the "bituminous

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68. Undescribed limacodid specimen, cf. *Limacodes*, from the oil sands of Trinidad (Blair, 1927).

69. Cossoid cuticular fragments from the Messel Formation, Germany (Richter and Storch, 1980).

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71. Two cossid species, *Kleopathra*, *nemogypsia* and *K. noctodiva*, from the Tremembé Formation, Brazil (Martins-Neto, 1998a).

72. Undescribed gelechiid specimens in Burmese Amber from an unnamed formation in northern Myanmar (Ross et al., 2010).

73. Possible gelechiid leaf mines from the Dakota Formation, Kansas and Nebraska, USA (Stephenson, 1991).

74. Undescribed coleophorid leaf mines from the Upper Hatira Formation of Israel (Krassilov, 2007).

75. The elachistid *Hexerites primalis* from the Green River Formation of Colorado, USA (Kozlov, 1988).

76. Twenty-five described gelechioid species, assigned to cf. *Anybia*, *Borkhausenites*, *Epiborkhausenites*, *Glesseumeyrickia*, cf. *Hofmannophila*, *Microperittia*, *Neoborkhausenites*, *Oecophorinites*, *Palaeodepressaria*, *Palaeoelachista*, *Paraborkhausenites*, *Praemendesia*, in Baltic amber from the Prussian Formation, Baltic Region (Rebel, 1934, 1936; Kusnezov, 1941; Skalski, 1973b, 1976b, 1977, 1979b; Kozlov, 1987; Kupryjanowicz, 2001).

77. The elachastid *Ethmia* (?) *mortuella* from the Florissant Formation of Colorado, USA (Kozlov, 1988; Meyer, 2003).

78. Several undescribed gelechioid specimens in Mexican amber from the Simojovel Formation (Hurd et al., 1962; Skalski, 1976b; Poinar, 1992); and several other gelechioid specimens in Dominican Amber from the La Toca Formation, Dominican Republic (Skalski, 1990b; Poinar, 1992; Grimaldi and Engel, 2005; Peñalver and Grimaldi, 2006).

79. Undescribed gelechiid and coleophorid leaf mines of late Miocene to late Pliocene age in Romania, Germany and Nevada, USA (Opler, 1973; Straus, 1977; Givulescu, 1984), some of which were attributed to the extant taxa, such as *Recurvaria nanella*.

80. An undescribed copromorphid species in Baltic Amber from the Prussian Formation of the Baltic Region (Skalski, 1990b).

81. The copromorphid, *Copromorpha fossilis* from the Bouldnor Formation, United Kingdom (Jarzembowski, 1980).

82. An undescribed thyridid close to the extant *Rhodoneura* in Baltic Amber, from the Prussian Formation of the Baltic Region (Skalski, 1985).

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84. Three described papilionoid species, *Praepapilio colorado, P. gracilis*; *Riodinella nympha* from the Green River Formation of Colorado, USA (Durden and Rose, 1978).

85. Undescribed papilionoid specimens in Baltic Amber from the Prussian Formation of the Baltic Region (Gravenhorst, 1835).

86. Thirteen described species, including the noted *Prodryas persephone* from the late Eocene Florissant Formation, Colorado, USA (Scudder, 1878); *Lithopsyche antiqua* and *Nymphalites zeuneri* from the Bouldnor Formation, United Kingdom (Jarzembowski, 1980); *Lethe* (?) *corbieri* and *Pseudoneorina coulleti* from the “laminites lacustres” of Céreste, France (Nel et al., 1993; Nel and Descimon, 1994); and *Thanatites vetulus* from the Rott Formation of Germany (Scudder, 1875).

87. Eight described papilionoid species, *Pamphilites abditus*, *Aquisextana irenaei, Lethites reynesii*, *Neorinopis sepulta*, *Thaites ruminianus,* and *Coliates proserpina,* from the “laminites lacustres” of Aix-en-Provence, France (Scudder, 1875; Théobald, 1937; Nel and Nel, 1986; Nel et al., 1993); and

Archaeolycorea ferreirai and *Neorinella garciae* from the Trembembé Formation of São Paulo, Brazil (Martins-Neto, 1989; Martins-Neto et al., 1993).

88. Six described papilionoid species: *Voltinia dramba* and *Dynamine alexae* in Dominican Amber from the La Toca Formation, Dominican Republic (Hall et al., 2004; Peñalver and Grimaldi, 2006); *Mylothrites pluto*, *Nymphalites atavus* and *Pontia freyeri* from a lignite deposit in Radoboj, Croatia (Heer, 1849; Scudder, 1875; Rasnitsyn and Zherikhin, 2002); *Miopieris talboti* from the “dysodile beds” of Randecker Maar, Germany (Zeuner, 1942); and *Aglais karaganica* from the Karagan Horizon of the Caucasus, Russia (Nekrutenko, 1965).

89. Late Pleistocene papilionoid specimens identified as extant butterfly species: *Andronymus neander*, *Charaxes candiope* and *Belenois crawshayi* from East African copal of Zanzibar, Tanzania (Skalski, 1976b).

90. An undescribed pyraloid specimen from the Fur Formation of Denmark (Bonde et al., 2008).

91. The pyraloid, *Glendotricha olgae* in Baltic Amber from the Prussian Formation of the Baltic Region (Kusnezov, 1941).

92. The pyraloid, *Pyralites preecei*, from the Bouldnor Formation, United Kingdom (Jarzembowski, 1980).

93. The pyraloids *Petisca dryellina* from the Tremembé Formation of São Paulo, Brazil (Martins-Neto, 1998b); and *Pyralites obscurus* from the "laminites lacustres" of Aix-en-Provence, France (Heer, 1856; Jarzembowski, 1980).

94. The pyraloid *Gallerites keleri* from lacustrine deposits at Willershausen, Germany (Kernbach, 1967).

95. An undescribed geometroid specimen from the Broken River Formation, North Island, New Zealand (Harris and Raine, 2002).

96. An undescribed geometroid specimen from the Klondike Mountain Formation of Washington, USA (Lewis, 1992).

97. Two geometroid specimens, *Geometridites larentiiformis*, from Bouldnor Formation, United Kingdom (Jarzembowski, 1980); and *Hydriomena* (?) *protrita* from the Florissant Formation of Colorado, USA (Cockerell, 1922).

98. An undescribed geometroid specimen from the "laminites lacustres" of Aix-en-Provence, France (Heer, 1961); and two species of *Phalaenites*, *obsoletus* and *crenatus* in a lignite deposit from Radoboj, Croatia (Heer, 1849; Rasnitsyn & Zherikhin, 2002).

99. The geometrid, *Problongos baudiliensis* from a diatomite of Saint-Bauzile, France (Mérit and Mérit, 2008).

100. A specimen of the extant *Hyperythra lutea* from East African copal of Zanzibar, Tanzania (Kozlov, 1988), and other geometroid material from the

late Pliocene to late Pleistocene, including *Geometrides jordani* and *G. repens* from the lacustrine deposits of Willershausen, Germany (Kernbach, 1967); and an indeterminate pupa of the Fossil Insect Research Group for Nojiri-ko Excavation (1990), from the Nojiri-ko Formation of Nagano Prefecture, Japan.

101. Sphingid cuticular fragments from the Messel Formation of Germany (Richter and Storch, 1980).

102. Undescribed saturniid cocoons from the Bouxwiller Formation of Alsace, France (Kunz, 2010) and undescribed sphingid specimens in Baltic Amber from the Prussian Formation, Germany (Berendt, 1830).

103. The saturniid species *Rothschildia* (?) *fossilis* from the Florissant Formation of Colorado, USA (Cockerell, 1914).

104. An undescribed larva, probably Sphingidae from the Hiwegi Formation, Lake Victoria region, Kenya (Leaky, 1952); a sphingid larva from the “dysodile beds” of Randecker Maar, Germany (Zeuner, 1927); and the sphingid adult *Mioclanis shanwangiana* from the Shanwang Formation of Shanwang, China (Zhang et al., 1994).

105. The bombycid species, *Bombycites buechii* and *B. oeningensis*, from the “Molasseformatien” of Oeningen, Switzerland (Heer 1849, Kozlov, 1988).

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107. An undescribed noctuid specimen from the Fur Formation of Denmark (Bonde et al., 2008).

108. Undescribed noctuoid specimens from the Klondike Mountain Formation (Joseph, 1986), of Washington, USA, and an indeterminate noctuoid from the Green River Formation of Wyoming, USA (Scudder, 1867).

109. Undescribed noctuoid specimens, including adults and larval frass in Baltic Amber from the Prussian Formation, Germany (Klebs, 1890, Bachofen-Echt, 1949; Nuorteva and Kinnunen, 2008); and a noctuid wing from the Allenby Formation of British Columbia, Canada (Douglas and Stockey, 1996).

110. The noctuoid *Noctuites incertissimus* from the “cinerites” of Puy-de-Dôme, France (Oustalet, 1870); the arctiid *Oligamatites martynovi* from Kazakhstan (Kusnezov, 1928); the catocalinid *Philodarchia cigana* from the Tremembé Formation of São Paulo, Brazil (Martins-Neto, 1998a); and the noctuoid *Noctuites deperditus* from the “laminites lacustres” of Aix-en-Provence, France (Heer, 1856; Kozlov, 1988).

111. There are approximately 12 early to middle Miocene specimens of noctuids: the seven described noctuoid species, *Noctuites caucasicus*, *N. kaspievi*, *N. kozhantshikovi*, *N. kusnezovi*, *N. maximus* , *N. radobojana*, *N. stavropolicus*, and *Noctuites* sp. from the Chorkraksky and Karagan Horizons, European Russia (Kozlov, 1988); *Noctuites effosus* and *N. haidingeri* from the lignite deposits of Radoboj, Croatia (Heer, 1849); Notodontidae incertae sedis from the Most Formation of the Ùsti Region of the Czech Republic (Prokop, 2003);

Stauropolia nekrutenkoi from an unspecified horizon in the Stavropol Region, Russia (Skalski, 1988); and an indeterminate noctuoid specimen from the "dysodile beds" of Randecker Maar, Germany (Reiss, 1936).

112. The noctuoid specimen, *Noctuites miocenicus* from an unspecified horizon in the Stavropol Region, Russia (Kozhanchikov, 1957); and *Arctiites deletus* from Tuscany, Italy (Rebel, 1898).

113. Two noctuoid species, *Cerurites wagneri* and *Noctuites gersdorfi* from the lacustrine deposits at Willershausen, Germany (Kernbach, 1967).

Chapter 3

A world catalog of fossil Lepidoptera

Duplicated from Sohn et al., 2012 (Zootaxa 3286: 1–132)

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An annotated catalog of fossil and subfossil Lepidoptera (Insecta: Holometabola) of the world

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Abstract

In this catalog, we attempt to assemble all fossil records of Lepidoptera described formally or informally in the world literature. A total of 667 records dealing with at least 4,568 specimens have been compiled. They include descriptions of 131 fossil genera and 229 fossil species, as well as 72 extant genera and 21 extant species to which some of these fossils supposedly belong or show superficial similarity. Replacement names of two fossil genera are proposed to avoid homonymy: *Baltopsyche* Sohn, **gen. nov.** for *Palaeopsyche* Sobczyk and Kobbert, 2009 and *Netoxena* Sohn, **gen. nov.** for *Xena* Martins-Neto, 1999. New generic combinations are proposed for: *Tortrix*? *destructus* Cockerell, 1916, *Tortrix florissantanus* Cockerell, 1907, and *Tortrix* sp. sensu Gravenhorst (1835), all three to *Tortricites* Kozlov, 1988; *Pterophorus oligocenicus* Bigot, Nel and Nel, 1986, to *Merrifieldia* Tutt, 1905; *Aporia* sp. *sensu* Branscheid (1969) to *Pierites* Heer, 1849; *Noctua* spp. *sensu* Hope (1836) and Lomnicki (1894), both to *Noctuites* Heer, 1849. Eleven names improperly proposed for lepidopteran fossils are invalidated: *Baltonides roeselliformis* Skalski in Kosmowska-Ceranowicz and Popiolek, 1981; *Baltodines* Kupryjanowicz, 2001; *Barbarothea* Scudder, 1890; *Lepidopterites* Piton, 1936; *Palaeozygaena* Reiss, 1936; *Psamateia calipsa* Martins-Neto, 2002; *Saxibatinca meyi* Skalski in Kristensen and Skalski, 1998; *Spatalistiforma submerga* Skalski, 1976; *Thanatites juvenalis* Scudder, 1875; *Tortricibaltia diakonoffi* Skalski, 1976; and *Zygaenites* Reiss, 1936. An unnecessary subsequent type designation for *Pierites* Heer, 1849, is discussed. A total of 129 records include lepidopteran fossils which cannot be placed in any taxonomic rank. There also exist at least 25 fossil records which lack any evidence of the supposed lepidopteran association. Misidentified specimens, including 18 fossil genera, 29 fossil species and 12 unnamed fossils, are excluded from Lepidoptera. All the known lepidopteran fossils are annotated by fossil type, specimen deposition, excavation locality, association with plants when present, and geological age. A bibliographic list of lepidopteran fossils is provided.

Key words: Nomenclature, paleobiodiversity, paleontology, plant-insect interactions, taxonomy.

Introduction

Fossils provide the most direct window on ancestral lineages and their morphological character states (Hermsen and Hendricks 2007; Cobbett *et al.* 2007) and play an especially important role in tracing the evolutionary history of organisms not represented in the extant fauna. As molecular dating analyses have become common in the last decade (Drummond *et al.* 2006), the value of fossils in evolutionary studies has increased measurably, attributable to their role of providing calibration points for estimating divergence times. Confident dating requires multiple fossils (the more the better; see Pyron 2010) which are securely identified and of appropriate age. However, the availability of such fossils is strongly taxon-dependent.

While the Lepidoptera are one of the so-called “Big Four” insect orders in extant species diversity (Grimaldi and Engel 2005), their fossil record is proportionally very sparse (Kapoor 1981; Labandeira and Sepkoski 1993). Kristensen and Skalski (1998) estimated that only 600–700 total fossil specimens of lepidopterans are known. Taphonomic simulations with extant species suggest that the fragility and buoyancy of the body and wings of Lepidoptera make them especially unlikely to be preserved in lacustrine fossil beds (Duncan 1997), compared to other insect groups. Probably for this reason, amber inclusions and trace fossils such as leaf mines constitute the majority of fossil evidence for Lepidoptera (Skalski 1976a; Kristensen and Skalski 1998; Grimaldi and Engel

2005). Even with amber and trace fossils included, the total fossil record of lepidopterans appears to be much poorer than those of other major insect orders (Labandeira and Sepkoski 1993; Kristensen *et al.* 2007).

Lepidopteran fossils are especially scarce in Mesozoic strata and are known mainly from the Cenozoic (de Jong 2007). This bias was initially taken to mean that Lepidoptera had a more recent history than other groups (Heer 1876). The current consensus is that the Lepidoptera originated during the Early Mesozoic, but that the radiations leading to their modern mega-diversity essentially did not occur until the Paleogene Period (Riek 1970; Kapoor 1981; Ollerton 1999; Grimaldi and Engel 2005). Another widely accepted generalization about the lepidopteran fossil record has been “almost zero extinction” at the family level (Kapoor 1981; Carpenter 1992), as only three families described as fossils are seemingly extinct. Confidence in both of these assertions is undermined, however, by the fact that the lepidopteran fossil record, in addition to being sparse, has been minimally studied. Most lepidopteran fossils have only superficial original descriptions, have never been critically re-examined, and hence have very uncertain taxonomic assignments at present. Many additional fossils remain undescribed in collections. Much of what is known about lepidopteran fossils resides in difficult-to-access publications or unpublished sources. The purpose of the catalog presented here is to make this information more accessible and thereby facilitate expanded study of the lepidopteran fossil record.

Previous efforts to catalog the lepidopteran fossil record have been sporadic. Scudder (1891) and Handlirsch (1907) compiled all fossils which were known at the time. In the most comprehensive but not exhaustive review to date, Kozlov (1988) included all types of lepidopteran fossils, organized in a modern classification. Genus or family-level reviews were provided by Laurentiaux (1953), Danilevsky and Martynova (1962) and Carpenter (1992). Kozlov *et al.* (2002) and Grimaldi and Engel (2005) treated the fossil record of Lepidoptera in the context of evolutionary history. Ross and Jarzembowski (1993) and Labandeira (1994) reviewed the first fossil occurrences of the lepidopteran families. Other surveys have been restricted in time or space or by taxon. Lepidoptera of the Mesozoic were reviewed by Whalley (1986); those of the South American Cenozoic were listed by Petrulevicius and Martins-Neto (2000). Leestmans (1983) summarized the lepidopteran fossils found in France; Meyer (2003) treated the insect fossils of Florissant; Scudder (1875) reviewed butterfly fossils; van Schepdeal (1974) reviewed Palearctic macrolepidopteran fossils; Skalski (1990a) reviewed fossils of primitive Lepidoptera. In comparison to other types of fossils, amber inclusions have been more rigorously cataloged and revised (Kusnezov 1941; Bachofen-Echt 1949; Andrée 1951; Skalski 1976b; Keilbach 1982; Spahr 1989; Poinar 1992). Museum specimen inventories, such as Rasnitsyn and Ross (2000) and Kupryjanowicz (2001), are additional valuable sources and often uncover hidden, unstudied fossils of Lepidoptera.

This catalog attempts to compile all the lepidopteran fossils described or mentioned in the world literature. It also includes as many records as we could find from informal publications such as conference abstracts and theses. Unlike the most extensive previous catalog (Kozlov 1988), it is annotated with specimen data for each fossil, including fossil type, current depository, excavation locality and fossil bed age. The present catalog is a revised and expanded version of an on-line database posted as a part of the Assembling Tree of Life for Lepidoptera project (http://www.leptree.net/fossil). We do not attempt to revise fossil identifications, though we include citations of all the published evaluations of those identifications that we could find. Our primary purpose is to provide in one place as much of the raw information about known lepidopteran fossils as possible, in order to encourage and facilitate further study.

Methods and conventions

Sources and categories. The primary source for references in this catalog is the comprehensive collection of fossil insect literature maintained by one of us (C.C.L.). From this collection we examined publications of all types, in any language, which mention lepidopteran fossils, retrieving as much raw information as possible. In general, only original descriptions were compiled. Subsequent citations also were included when they provided new taxonomic insights or photographs. Data missing from primary sources were added, if possible, using other sources. Ambiguities in the raw data were checked and if possible, corrected. Non-English references were translated by generous colleagues (see Acknowledgments) or using Google Translate (http://translate.google.com).

The name-bearing taxa included here comprise those which are fully described or at least tentatively defined, and for which at least a genus-level association is known. In addition to formally published taxa, we also include informal records from theses, conference abstracts and newsletters, unless they treat new taxa which are invalid according to the ICZN 4th edition (Article 9). In contrast to previous catalogs, we also compiled undescribed specimens and/or collections of lepidopteran fossils whenever such information was available to us. A number of such specimens were found during inventories of the lepidopteran fossil holdings at several major collections undertaken by the first author during visits in 2009 and 2011.

Whenever possible, we checked the identification of each fossil proposed in the literature against the diagnoses of modern classifications from all the reviews in Kristensen (1998). However, most lepidopteran fossils are incomplete and preserve few diagnostic characteristics. We retained the original taxonomic position of a fossil, even when tentative or suspected to be problematic, unless there was reasonable evidence for a new position. In previous catalogs, such ambiguous fossils have typically been relegated to the category 'Lepidoptera *incertae sedis*.' We see no advantage to this practice, which discards nearly all characteristics observed on such fossils. Instead, we treated ambiguous fossils as "questionably placed" within the subfamily, family or superfamily to which it had originally been assigned. It should be noted, however, that the uncertainty of placement for these fossils can be great. For example, *Phalaenites crenata* Heer, 1849, here designated as questionably placed in Geometridae, may not even belong to Geometroidea or to any currently-recognized macrolepidopteran group.

Our "Lepidoptera *incertae sedis*" section includes only fossils which show no diagnostic characteristics or for which taxonomic affinity was regarded as ambiguous by the describing author, such as when two families were given as possible placements. Fossils never subjected to taxonomic study are also placed in this section. Fossils whose assignment even to Lepidoptera is tentative, suspect or ambiguously stated are placed in the "Putative Lepidoptera" section of this catalog. Last, we include a section entitled "excluded from Lepidoptera" for fossils which were assigned to Lepidoptera at some point but currently are excluded.

Within each section, name-bearing fossils are presented in alphabetical order. Unnamed fossils or collective descriptions thereof are arranged alphabetically by first author of the original record. When sets of different types of fossils were collectively described by the same author, they are listed as separate accounts. Each fossil account accompanies bibliographic citations and, in parentheses, the genus combination or taxonomic interpretation suggested by the author. Our own interpretations and annotations are given in brackets. It is often impossible to determine whether fossil specimens or collections mentioned in multiple papers are mutually exclusive. Hence, some fossils may be doubly counted in our catalog. We tried to minimize such redundancy by checking the institutional catalog numbers of the fossils. When such identifiers are unavailable, we simply point out the possibility of overlap.

Annotation entries. Each account listed in this catalog is annotated as to fossil type, specimen deposition, fossil locality and geological age, in that order, with fields separated by slashes (/). Fields with missing data are described as "unknown" or simply left blank. The formats for each field are as follows:

i) Fossil type. Fossils are classified into ten modes of deposition: amber (AM), asphaltum (AS), compression/impression (CI), copal (CO), gut contents or coprolite of insectivore (GC), peat or lignite (PE), salt deposit (SA), silica permineralization (SI), sieved residue (SR), and trace fossil (T). For extended discussion of the modes of preservation in the insect fossil record, see Labandeira (1999). The categories are not mutually exclusive. For example, leaf-mine fossils are designated as both compression/impression and trace fossil. In such cases, both abbreviations are shown. Subfossils and fossils were not distinguished because these categories are often difficult to separate in literature descriptions and are variably defined, such as Holocene-only occurrences, or older material that has not undergone appreciable fossilization. Following the fossil type, the fossil contents are given in parenthesis, namely, life stage (egg, larva, pupa, and adult) and completeness of preservation (e.g., whole body or fragmentary material).

ii) Specimen deposition. For each fossil we specify the confirmed or best-estimate current location. Acronyms, given below, are used for institutional specimen depositories. For clarity, the names of private collectors are given in full. In the absence of more recent information, the collection name stated by the original author is provided if possible; otherwise the field is left vacant. When the specimen is suspected by previous authors of being lost, we follow their opinion. The following information is given in parentheses. Type status of specimen(s), if any, is reported, using abbreviations listed below. If the specimens are not types, we report only the number of specimens (= exemplars), abbreviated as 'ex.' The type designation or number of specimens is followed, separated by a colon, by the institutional catalog number(s), if these exist. The institutional catalog numbers are cited with the numbers assigned by the original authors.

iii) Excavation locality. The source country is given first, followed by successively more specific locality information. Non-English locality names are provided together with English names when the latter exist. The formal stratigraphic unit, when known, is listed in parentheses and followed by “Fm. (= formation)” if appropriate. The source for the lithostratigraphic age assignment is either taken from the original publication or extrapolated from other geological sources based on the site where the fossil was initially discovered. In some instances formal designation of the formation was not provided in the original fossil description or in related sources. In such cases we recorded a lithological characterization of the sedimentary unit from which the fossil was retrieved without attribution to a particular formation; an example is “East African Copal.”

iv) Geological age. The age of the fossil bed is given as geological stage followed by period, using the terminology of Gradstein *et al.* (2004) which presents the internationally accepted standard for geologic time nomenclature. If no age assignment was given by the author or the age of the fossil bed is controversial, we consulted other sources and chose the most persuasive or conservative date.

When possible, records of trace fossils of leaf mines, galls and wood borings include recorded plant hosts. We follow the plant identification given in the original papers, often including the species, genus, and family. Family-level assignments of fossil plant hosts are based on Mabberley (1993).

Occasionally we include a comment field at the end of an account, for example, when there is uncertainty in the original description; an obvious nomenclatural change is inevitable; the author(s) assigned a taxonomic placement to an unnamed fossil; or overlap in content between separate accounts is suspected.

Taxonomy and nomenclature. For most fossils we followed the taxonomic interpretation of the original author or subsequent reviewer. In some cases, we modernized outdated classifications, while in others we had to choose among conflicting classifications advanced by different authors. In the latter instances, we listed all the differing opinions in parentheses and provided bibliographic citations. Clade names and arrangements above the family level follow Nieukerken *et al.* (2011), while the subfamily classification, where applicable, follows Appendix 1 of Kristensen (2003). For some butterflies and bombycoids, the fossils are classified to tribal level as defined in the original descriptions. Taxon names proposed primarily for extant species are given without further details of the original description. We mostly exclude ichnotaxon names, but do use collective generic names (ICZN 4th edition, Article 42) which include ichnospecies, for example, *Stigmellites* Kernbach, 1967.

Extant taxon names often have been used to describe trace fossils by analogy, whether or not the fossil seems likely to belong to the extant taxon. Usage of such analogies varies widely among authors. Some authors state that no taxonomic connection between extant and fossil taxa is implied by the analogy. In such cases, we disregarded the extant analogs as identifiers of the records. We used recent analog names as indicating relationship only when the authors unambiguously state that this is their intention.

We followed the latest version of the code (ICZN 4th edition, effective from 2000) entirely, especially the rules for fossil taxa (Article 20 and 42). We use ‘nomen nudum’ to denote invalid names, and ‘nomen conditionalis’ in cases where the author actually meant ‘fossil state.’ Only the former are invalid under the code (ICZN 4th edition, Glossary).

Collective generic names ending with ‘-ites’ are commonly used for species whose taxonomic placement is not entirely convincing or for which only family-level association is assured (Kozlov 1988). Such names are valid according to the code (ICZN 4th edition, Articles 20, 23.7 and 42.2.1) and are subject to the rules for genus-group nomenclature, except that type designation is not obligatory. Despite this exemption, type species have been designated by subsequent researchers for some collective genera. These secondary type designations can be problematic. For example, Hemming (1967) redesignated *Pierites freyeri* Heer as the type species of *Pierites* Heer, 1849, based on the fact that Heer included only one species. However, *freyeri* was subsequently moved to *Pontia* by Scudder (1875b). As a result, *Pierites* becomes a synonym of *Pontia* and an alternative collective name is required for pierids of uncertain association. We avoided such complicated and seemingly pointless exercises by simply disregarding the subsequent type designation. Finally, when a fossil taxon retains an incorrect species name ending after a change of taxonomic position, we adjust the name as required by the code (ICZN 4th edition, Article 30.1.3).

Abbreviations used. For taphonomy:
AM = amber
AS = asphaltum and tar sands
CI = compression or impression

CO = copal
GC = gut contents or coprolite of insectivorous animals
PE = peat or lignite
SA = salt deposits
SI = silica or other permineralization
SR = sieved residue
T = trace fossil (larval case; mine or other feeding damage)

For type status:
CHT = counterpart of HT
HT = holotype
NT = neotype
PT = paratype
SY = syntype

Institutional specimen depositories, by continent:

[Africa]

BPUW	Bernard Price Institute, University of the Witwatersrand, Johannesburg, South Africa, including recently transferred collections from the South African National Botanical Institute at Pretoria.

[Asia]

CNUB	College of Life Sciences, Capital Normal University, Beijing, China
IEUH	Institute of Evolution, University of Haifa, Israel
KCMK	Kumamoto City Museum, Kumamoto, Japan
LBMS	Lake Biwa Museum, Kusatsu, Shiga, Japan
NIGP	Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China
NSMT	Department of Paleontology, National Science Museum, Tokyo, Japan
OMNH	Osaka Prefectural Museum of Natural History, Osaka, Japan
PFDL	Paleontological Fossil Depository, Lingu Prov., Shandong, China
SFML	Shanwang Fossil Museum, Lingu Prov., Shandong, China
SJCA	St. John’s College, Agra, Uttar Pradesh, India

[Australia and New Zealand]

GCUA	Geological Collection, University of Auckland, Auckland, New Zealand
GDVU	Geology Department of Victoria University, Wellington, Australia
GMUQ	Geographical Museum, University of Queensland, Queensland, Australia
IGNS	Institute of Geological and Nuclear Science, Gracefield Research Centre, Lower Hutt, New Zealand
MVVA	National Museum of Victoria, Victoria, Australia
QMSB	Queensland Museum, South Brisbane, Australia

[Europe]

AMKR	Amber Museum in Kaliningrad, Russia
ANZM	Arabako Natur Zientzien Museoa, Natural Sciences Museum of Álava (= Museo de Ciencias Naturales de Álava), Vitoria-Gasteiz, Spain
BGRG	Federal Institute for Geosciences and Natural Resources (= Bundesanstalt für Geowissenschaften und Rohstoffe), Hannover, Germany
BMNH	Department of Paleontology, Natural History Museum, London, United Kingdom
BPGM	Bavarian State Collection for Paleontology and Geology (= Bayerische Staatssammlung für Palaeontologie und Geologie), Munich, Bavaria, Germany
BTVU	School of Biosciences and Process Technology, Linnaeus University (= Linnéuniversitetet or Växjö University), Småland, Sweden
CMNH	Coburg Museum of Natural History (= Naturkunde-Museum Coburg), Coburg, Germany
DBRD	German Amber Museum (= Deutsches Bernsteinmuseum), Ribnitz-Damgarten, Germany

EMUG	Institute of Geography and Geology, Ernst Moritz Arndt University (= Institut für Geographie und Geologie, Ernst-Moritz-Arndt-Universität), Greifswald, Germany
ENSM	Mines Paris Tech (= École Nationale Supérieure des Mines de Paris or École des Mines de Paris), Paris, France
EPGM	Department of Stratigraphy, Paleontology and Marine Geoscience, University of Barcelona (= Departament d'Estratigrafia, Paleontologia i Geociéncies Marines, Universitat de Barcelona), Barcelona, Spain
FMND	Fur Museum, Nederby, Denmark
FMUH	Paleontological Collection, Geological Museum of Finnish Museum of Natural History (= Luonnontieteellinen Keskusmuseo), University of Helsinki, Helsinki, Finland
FNSF	Forschungsinstitut, Nature Museum Senckenberg (= Naturmuseum Senckenberg), Senckenberganlage, Frankfurt, Germany
GBCU	Department of General Botany, N. Copernicus University (= Zakład Botaniki Ogólnej, Uniwersytetu M. Kopernika), Torun, Poland
GBNM	Heerlen Branch of the Geological Survey, the Netherlands Mining District (= Geologisch Bureau voor het Nederlandse Mijngebied), Heerlen, Netherlands
GMUH	Geological and Paleontological Institute and Museum, University of Hamburg (= Geologisch-Paläontologisches Institut und Museum der Universität Hamburg), Hamburg, Germany
GPTUC	Institute of Geology and Paleontology, Clausthal University of Technology (= Institute für Geologie und Paläontologie, Technische Universität Clausthal), Clausthal-Zellerfeld, Germany
GPUF	Geological and Paleontological Institute, Goethe University Frankfurt (= Geologisch-Paläontologisches Institut, Johann Wolfgang Goethe Universität), Frankfurt, Germany
GPUG	Geological-Paleontological Institute, University of Göttingen (= Geologisch-Paläontologisches Institut, Universität Göttingen), Göttingen, Germany
GPUT	Institute and Museum for Geology and Paleontology, University of Tübingen (= Institut und Museum für Geologie und Paläontologie, Universität Tübingen), Tübingen, Germany
GSAV	Geological Survey of Austria (= Geologische Bundesanstalt), Vienna, Austria
HLDG	Museum Wiesbaden (= Hessischen Landesmuseums), Darmstadt, Germany
HNHM	Mineral Collection, Hungarian Natural History Museum (= Magyar Természettudományi Múzeum), Budapest, Hungary
IGGB	National Institute of Geology and Geophysics (= Institutul Geological Romaniei), Bucharest, Romania
IGMF	Center for Geology and Geophysics of Montpellier (= Centre Géologique et Géophysique de Montpellier or l'Institut de Géologie de Montpellier), Montpellier, France
IPEG	Institute for Plant Protection Research (= Institut für Pflanzenschutzforschung), Eberswalde, Germany
IPUS	Institute for Geology and Paleontology, University of Stuttgart (= Institut für Geologie und Paläontologie, Universität Stuttgart), Stuttgart, Germany
LFUF	Agriculture and Forestry Zoological Institute of the University of Helsinki (= Agrikultur-forstvetenskapliga fakulteten, Helsingfors Universitet), Helsinki, Finland
LGUL	Laboratory of Geology, University of Lyon (= Laboratoire de Géologie de l'Université de Lyon), Lyon, France
LNHM	Lvov Natural History Museum, Lvov, Ukraine
MCFE	Civic Museum of Archaeology and Natural Science, "Federico Eusebio" (= Museo Civico Archeologico e di Scienze Naturali Federico Eusebio), Alba, Piedmont, Italy
MCNV	Museum of Natural Science in Valencia (= Museo de Ciencias Naturales de Valencia), Valencia, Spain
MEPA	Polish Academy of Sciences' Earth Museum (= Muzeum Ziemi Polskiej Akademii Nauk w Warszawie), Warsaw, Poland
MHMM	Henrik Madsen Collection, Morsland Historical Museum (= Morslands Historiske Museum), Mors, Denmark
MMAG	A.A. Mitchell Collection, Maidstone Museum and Bentlif Art Gallery, Maidstone, England
MNCN	National Museum of Natural Science (= Museo Nacional de Ciencias Naturales), Madrid, Spain

MNHN	Institute of Paleontology, National Museum of Natural History in Paris (= Institut de Paleontologie, Muséum National d'Histoire Narurelle de Paris), Paris, France
MNHU	Berlin Museum of Natural History (= Museum für Naturkunde Berlin or Museum für Naturkunde Humboldt-Universität), Berlin, Germany
MPMV	Municipal Museum of Paleontology in Valencia (= Museo Paleontológico Municipal de Valencia), Valencia, Spain
MPUG	Museum of Amber Inclusions, Department of Invertebrate Zoology, University of Gdańsk (= Muzeum Inkluzji w Bursztynie, Universytet Gdańsk), Gdańsk, Poland
MTRE	Territory Museum in Riccione (= Museo del Territorio, Riccione), Emilia, Italy.
MVMF	Natural History Museum of Marseille (= Musée de la Ville de Marseille, France or Museum d'Histoire Naturelle de Marseille), Marseille, France
NASU	National Academy of Sciences of Ukraine (Natsional’na Akademiya Nauk Ukrayiny), Kiev, Ukraine
NHMB	Natural History Museum in Basel (= Naturhistorisches Museum Basel), Basel, Switzerland
NHMD	Geological Museum, Natural History Museum of Denmark, University of Copenhagen (= Geologisk Museum, Statens Naturhistoriske Museum, Københavns Universitet), Copenhagen, Denmark
NHMG	Natural History Museum of Graz (= Naturkundemuseum, Universalmuseums Joanneum), Graz, Austria
NHMW	Museum of Natural History Vienna (= Naturhistorisches Museum Wien), Vienna, Austria
NHUW	Museum of Natural History at University of Wroclaw (= Muzeum Przyrodnicze we Wrocławiu), Wroclaw, Poland
NMLN	Natural History Museum of Mainz and Rheinland-Pfalz State Collection for Natural History (= Naturhistorischen Museum Mainz/Landessammlung für Naturkunde Rheinland-Pfalz), Mainz, Germany
NMPC	National Museum (= Národní Muzeum or Musei Nationalis Pragae), Prague, Czech Republic
OUNH	Oxford University Museum of Natural History, Oxford, United Kingdom
PAML	Palanga Amber Museum (= Palangos Gintaro Muziejus), Palanga, Lithuania
PIFU	Paleontological Institute, Free University of Berlin (= Wissenschaftliche Einrichtung Paläontologie and Paläontologisches Institut der Freie Universität Berlin), Berlin, Germany
PIRAS	Paleontological Institute, Russian Academy of Sciences, Moscow, Russia
PLUW	Paleozoological Laboratory, University of Warszawa (= Uniwersytet Warszawski), Warszawa, Poland
PMUZ	Paleontological Institute and Museum, University of Zurich (= Paläontologisches Institut und Museum, Universität Zürich), Zurich, Switzerland
PNRL	Paleontological collection, Regional Natural Park in Luberon (= Parc Naturel Régional du Lubéron), Lubéron, France
RMOD	Amber Museum in Oksbol (= Ravmuseet i Oksbøl), Oksbøl, Denmark
RPMH	Roemer and Pelizaeus Museum (= Roemer- und Pelizaeus-Museum), Hildesheim, Germany
SMMG	State Museum for Mineralogy and Geology in Dresden (= Staatliches Museum für Mineralogie und Geologie zu Dresden), Dresden, Germany
SMNS	Stuttgart State Museum of Natural History (= Staatliches Museum für Naturkunde Stuttgart or Württemberg Royal Natural Cabinet), Stuttgart, Germany
TUBF	Faculty of Geosciences, Freiberg Mining Academy, University of Technology (= Sektion Geowissenschaften, Technische Universität Bergakademie Freiberg), Freiberg, Germany
WSIB	W. Szafer Institute of Botany, Polish Academy of Sciences (= Polska Akademia Nauk Instytut Botaniki im Władysława Szafera), Kraków, Poland
ZMCD	Zoological Museum, Natural History Museum of Denmark, University of Copenhagen (= Zoologisk Museum, Statens Naturhistoriske Museum, Københavns Universitet), Copenhagen, Denmark

[North America]

AIOSU	Amber Institute, Oregon State University, Corvallis, Oregon, U.S.A.
ANSP	Department of Entomology, Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.
BHM	Black Hills Institute of Geological Research (= Black Hills Minerals), Hill City, South Dakota, U.S.A.
CSUM	St. Cloud State University in St. Cloud, Minnesota, U.S.A.

DMNH	Denver Museum of Nature and Science, Denver, Colorado, U.S.A.
FFNM	Florissant Fossil Beds National Monument, Teller Co., Colorado, U.S.A.
FMNH	Field Museum of Natural History, Chicago, Illinois, U.S.A.
FMUF	Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A
GSCBO	Geological Survey of Canada Branch, Dept. of Mines and Technical Surveys, Ottawa, Ontario, Canada
GBIU	Department of Geological Sciences and Biology, Indiana University, Bloomington, Indiana, U.S.A.
KNHM	Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, U.S.A.
MCZH	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
NHLA	Natural History Museum of Los Angeles County (= Los Angeles County Museum), Los Angeles, California, U.S.A.
PLME	Prehistoric Life Museum, Evanston, Illinois, U.S.A.
PMNH	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.
PSWC	Paul R. Stewart Museum, Waynesburg College, Waynesburg, Pennsylvania, U.S.A.
ROMUT	Royal Ontario Museum, University of Toronto, Toronto, Canada
TBMM	Thomas Burke Memorial Museum, University of Washington, Seattle, Washington, U.S.A.
UAME	University of Alberta Museums, Edmonton, Aberta, Canada
UCMP	University of California Museum of Paleontology, Berkeley and Davis, California, U.S.A.
UCNH	University of Colorado Museum of Natural History, Boulder, Colorado, U.S.A.
UIMM	University of Idaho College of Mines Museum, Moscow, Idaho, U.S.A.
USNM	United States National Museum of Natural History, Washington, DC, U.S.A.

[South America]

AOFT	Apex (Trinidad) Oilfields, Ltd., near Fyzabad, Trinidad
DGUFC	Department of Geology, Federal University of Ceará (= Departamento de Geologia da Universidade Federal do Ceará), Fortaleza, Ceará, Brazil
DGUG	Department of Geoscience, University of Guarulhos (= Departamento de Geociências, Universidade de Guarulhos), São Paulo, Brazil
IGEO	National Museum and Institute of Geoscience, Federal University of Rio de Janeiro (= Museu Nacional et Instituto de Geociências da Universidade Federal), Rio de Janeiro, Brazil
IGUSP	Institute of Geoscience, University of São Paulo (= Instituto de Geociências, Universidade de São Paulo), São Paulo, Brazil
LPUSP	Laboratory of Paleontology, Biology Department, FFCL, University of São Paulo campus de Ribeirão Preto (= FFCL/USP campo Ribeirão Preto), Ribeirão, São Paulo, Brazil
MPEF	Egidio Feruglio Paleontologic Museum (= Museo Paleontólogico Egidio Feruglio), Trelew, Chubut, Argentina

Other abbreviations:
auct = ‘sensu the author’ (Latin “of authors”)
cf = ‘close to’ (Latin “compare”)
ex = ‘number of exemplars’ (Latin “copy”)
nec = ‘not the author’ (Latin “and not”)
sic = ‘misspelling’ (Latin “thus”)

A catalog of lepidopteran fossils

Note: The annotation at the end of each species account consists of: fossil type/specimen deposition/excavation locality/geological age.

1. Fossils securely placed in Lepidoptera

Order Lepidoptera

Lepidopteran lineages in the polyphyletic Necrotauliidae stock

Comment: Necrotauliidae was proposed by Handlirsch (1906) as a trichopteran family. Since the original description lacked unambiguous definition, the family was later used as a collective group to accommodate “primitive” Trichoptera-like Mesozoic insects (Ansorge 2002). However, stem group Trichoptera are very difficult to distinguish from stem group Lepidoptera. This ambiguity has augmented the heterogeneity of the Necrotauliidae. Ansorge (2002) modernized the definition of the family, restricting it to the genera *Necrotaulius* Handlirsch, 1906 and *Mesotrichopteridium* Handlirsch, 1906. He also redefined *Necrotaulius*, the type genus of Necrotauliidae, to include only the type species, *N. dobbertinensis* Handlirsch, 1906. According to this new definition, the family Necrotauliidae accommodates only stem amphiesmenopterans, that is, those which lived prior to the divergence between Trichoptera and Lepidoptera. Ansorge (2002) found that at least seven genera previously included in Necrotauliidae are indeed lepidopteran lineages. Their placement in the phylogeny of Lepidoptera, however, remains unknown. Since his revision did not cover all necrotauliids in the former broad sense, future studies could reveal additional early lepidopterans within this paraphyletic assemblage.

ARCHIPTILIA Handlirsch, 1939: 97 (Trichoptera); Ansorge, 2002: 71 (Lepidoptera).
Type species: *Archiptilia ovata* Handlirsch, 1939.

ovata Handlirsch, 1939: 97, pl. 9: 168 (*Archiptilia*).
CI (adult: forewing)/EMUG (HT: 123/162)/Germany: Lower Saxony, Mecklenburg, Schwinz near Dobbertin (Posidonia Shale)/early Toarcian, Early Jurassic.

EPIDIDONTUS Handlirsch, 1939: 98 (Trichoptera); Ansorge, 2002: 71 (Lepidoptera).
Type species *Epididontus geinitzianus* Handlirsch, 1939.

geinitzianus Handlirsch, 1939: 98, pl. 9: 170 (*Epididontus*).
CI (adult: forewing)/MNHU (HT: 61.1)/Germany: Lower Saxony, Mecklenburg, Schwinz near Dobbertin (Posidonia Shale)/early Toarcian, Early Jurassic.

METARCHITAULIUS Handlirsch, 1939: 96 (Trichoptera); Ansorge, 2002: 71 (Lepidoptera).
Type species: *Metarchitaulius longus* Handlirsch, 1939.

longus Handlirsch, 1939: 96, pl. 9: 166 (*Metarchitaulius*).
CI (adult: forewing)/EMUG (HT: 123/85)/Germany: Lower Saxony, Mecklenburg, Schwinz near Dobbertin (Posidonia Shale)/early Toarcian, Early Jurassic.

NANNOTRICHOPTERON Handlirsch, 1906: 486 (Trichoptera); Ansorge, 2002: 71 (Lepidoptera).
Type species: *Nannotrichopteron gracile* Handlirsch, 1906.

gracile Handlirsch, 1906: 486, pl. 42: 41 (*Nannotrichopteron*).
CI (adult: forewing)/EMUG (HT: 122/78)/Germany: Lower Saxony, Mecklenburg, Schwinz near Dobbertin (Posidonia Shale)/early Toarcian, Early Jurassic.

NECROTAULIUS auct Ivanov, 2002: 290 (Lepidoptera) (nec Handlirsch, 1906 [Trichoptera]).

tener Sukatsheva, 1990: 97, fig. 96, pl. 8: 10 (*Necrotaulius*); Ivanov, 2002: 290, fig. 3.
CI (adult: whole body)/PIRAS (HT: No. 3015/819)/Russia: Chita Province, Shelopugino District, Unda River at Zhidka (Baleyan Fm.)/Aptian–Albian, Early Cretaceous.
Comment: This fossil was originally assigned to Trichoptera. Later, Ivanov (2002) found it to possess some, though not all, of the apomorphies for Lepidoptera. The definition of *Necrotaulius* is currently restricted to the type

species, *N. dobbertinensis* Handlirsch, 1906 (Ansorge 2002). Therefore, a generic revision for all the remaining tentative "*Necrotaulius*," including *N. tener,* is needed.

PALAEOTAULIUS Handlirsch, 1939: 95 (Trichoptera); Ansorge, 2002: 71 (Lepidoptera).
Type species: *Palaeotaulius vicinus* Handlirsch, 1939.

vicinus Handlirsch, 1939: 95, pl. 9: 164 (*Palaeotaulius*).
CI (adult: forewing)/EMUG (HT: 123/87)/Germany: Lower Saxony, Mecklenburg, Schwinz near Dobbertin (Posidonia Shale)/early Toarcian, Early Jurassic.

PARARCHITAULIUS Handlirsch, 1939: 95 (Trichoptera); Ansorge, 2002: 71 (Lepidoptera).
[Type species: *Pararchitaulius ovalis* Handlirsch, 1939]

ovalis Handlirsch, 1939: 95, pl. 9: 165 (*Pararchitaulius*).
CI (adult: forewing)/EMUG (HT: 123/86)/Germany: Lower Saxony, Mecklenburg, Schwinz near Dobbertin (Posidonia Shale)/early Toarcian, Early Jurassic.

PARATAULIUS Handlirsch, 1939: 96 (Trichoptera); Ansorge, 2002: 71 (Lepidoptera).
Type species: *Parataulius jurassicus* Handlirsch, 1939.

jurassicus Handlirsch, 1939: 97, pl. 9: 167 (*Parataulius*).
CI (adult: forewing)/EMUG (HT: 123/78)/Germany: Lower Saxony, Mecklenburg, Schwinz near Dobbertin (Posidonia Shale)/early Toarcian, Early Jurassic.

PARATRICHOPTERIDIUM auct Ansorge, 2002: 71 (Lepidoptera) (nec Handlirsch, 1906 [Trichoptera]).

efossum Handlirsch, 1939: 100, pl. 10: 175 (?*Paratrichopteridium*).
CI (adult: hindwing)/EMUG (HT: 123/83)/Germany: Lower Saxony, Mecklenburg, Schwinz near Dobbertin (Posidonia Shale)/early Toarcian, Early Jurassic.

costale Handlirsch, 1939: 100, pl. 10: 176 (?*Paratrichopteridium*).
CI (adult: forewing?)/EMUG (HT: 123/84)/Germany: Lower Saxony, Mecklenburg, Schwinz near Dobbertin (Posidonia Shale)/early Toarcian, Early Jurassic.

PSEUDORTHOPHLEBIA Handlirsch, 1906: 485 (Trichoptera); Ansorge, 2002: 71 (Lepidoptera).
Type species: *Pseudorthophlebia platyptera* Handlirsch, 1906.

platyptera Handlirsch, 1906: 485, pl. 42: 40 (*Pseudorthophlebia*).
CI (adult: forewing)/EMUG (HT: 122/76)/Germany: Lower Saxony, Mecklenburg, Schwinz near Dobbertin (Posidonia Shale)/early Toarcian, Early Jurassic.

Suborder *incertae sedis*

Family ARCHAEOLEPIIDAE Whalley, 1985: 159

ARCHAEOLEPIS Whalley, 1985: 159 (Archaeolepiidae); Skalski, 1990a: 125 (?Eolepidopterigidae).
Type species: *Archaeolepis mane* Whalley, 1985.

mane Whalley, 1985: 160, figs. 58–60 (*Archaeolepis*).
CI (adult: wings)/BMNH (HT: In.59397)/United Kingdom: England, Dorset, Charmouth, Black Ven (calcareous flatstone, Turneri Zone, probably Bed 75a)/Sinemurian, Early Jurassic.
Comment: Kristensen and Skalski (1998: 16) regard this as "the oldest known fossil which can with great certainty be referred to the Lepidoptera."

Family MESOKRISTENSENIIDAE Huang, Nel and Minet, 2010: 875

MESOKRISTENSENIA Huang, Nel and Minet, 2010: 875.
Type species: *Mesokristensenia latipenna* Huang, Nel and Minet, 2010.

angustipenna Huang, Nel and Minet, 2010: 879, figs. 4, 5, 8 (*Mesokristensenia*).
CI (adult: whole body)/NIGP (HT: no. 150463)/China: Inner Mongolia, Ningcheng Co., Wuhua township, near Daohugou (Jiulongshan Fm.)/Bathonian–Callovian, Middle Jurassic.

latipenna Huang, Nel and Minet, 2010: 876, figs. 1, 6a–c (*Mesokristensenia*).
CI (adult: whole body)/NIGP (HT: no. 150460)/China: Inner Mongolia, Ningcheng Co., Wuhua township, near Daohugou (Jiulongshan Fm.)/Bathonian–Callovian, Middle Jurassic.

sinica Huang, Nel and Minet, 2010: 877, figs. 3, 7 (*Mesokristensenia*).
CI (adult: whole body)/NIGP (HT: no. 150462)/China: Inner Mongolia, Ningcheng Co., Wuhua township, near Daohugou (Jiulongshan Fm.)/Bathonian–Callovian, Middle Jurassic.

—Huang, Nel and Minet, 2010: 877, figs. 2, 6d (*Mesokristensenia*).
CI (adult: forewing)/NIGP (HT: no. 150461)/China: Inner Mongolia, Ningcheng Co., Wuhua township, near Daohugou (Jiulongshan Fm.)/Bathonian–Callovian, Middle Jurassic.

FAMILY *incertae sedis*

KARATAUNIA Kozlov, 1989: 42.
Type species: *Karataunia lapidaria* Kozlov, 1989.

lapidaria Kozlov, 1989: 42, fig. 1f (*Karataunia*).
CI (adult: whole body)/PIRAS (HT: PIN 2066/3461and3453)/Kazakhstan: Chimkent Oblast, Chayan district, Aulie close to the village of Mikhailovka (Karabastau Fm.)/Oxfordian–Kimmeridgian, Late Jurassic.

GENUS *incertae sedis*

—Grimaldi and Engel, 2005: 562, fig. 13: 16 (basal lepidopteran).
CI (adult: whole body)/AMNH (1 ex: SF46441)/Brazil: Ceará State, ca. 4 km from Santana do Cairiri, Nova Olinda (Crato Fm.)/late Aptian, Early Cretaceous.

Suborder Eolepidopterigina Rasnitsyn, 1983: 468

= Zeugloptera (nec Chapman, 1917); Carpenter, 1992: 372 [part]
= Dacnonypha (nec Hinton, 1946); Kozlov, 1988: 28

Superfamily EOLEPIDOPTERIGOIDEA Rasnitsyn, 1983: 470

Family EOLEPIDOPTERIGIDAE Rasnitsyn, 1983: 470

= Micropterigidae (nec Herrich-Schäffer, 1855); Skalski, 1979a: 92 [for *Undopterix*]
= Undopterigidae Kozlov, 1988: 28 [under Dacnonypha]

Note: Kristensen and Skalski (1998: 16) questioned the monophyly of Eolepidopterigidae which lacks convincing support. Assignment of all taxa other than *Eolepidopterix* to Eolepidopterigidae is tentative. We exclude *Psamateia calipsa* Martins-Neto, 2002, **nomen nudum**, an alleged eolepidopterigid, described from an unpublished thesis. The taxon name was introduced again in Martins-Neto (2005) without description. In fact, the descriptions of *Psamateia* and its type *P. calipsa* have never been published and thus, the taxon names are invalid (ICZN 4th edition, Article 8).

EOLEPIDOPTERIX Rasnitsyn, 1983: 470.
Type species: *Eolepidopterix jurassica* Rasnitsyn, 1983.

jurassica Rasnitsyn, 1983: 470, fig. 1 (*Eolepidopterix*).
CI (adult: whole body)/PIRAS (HT: PIN 3053/416)/Russia: Siberia, Transbaikalia, Chita district, Uda (Udinskaya Fm.)/?Oxfordian, Late Jurassic.

Questionably placed in Eolepidopterigidae

DAIOPTERIX Skalski, 1984: 389.
Type species: *Daiopterix rasnitsyni* Skalski, 1984.

olgae Kozlov, 1989: 38, fig. 1b (*Daiopterix*); Grimaldi and Engel, 2005: 562, fig. 13: 15.
CI (adult: whole body)/PIRAS (HT: PIN 3063/741)/Russia: Tshitinsk region, Shelopugitz district, left bank of the Daia River, 2km above the mouth of the Shiviya River Valley; central Siberia, Chitinsk Oblast (Glushkovo Fm.)/Tithonian–Berriasian, Late Jurassic–Early Cretaceous boundary.

rasnitsyni Skalski, 1984: 390, figs. 1–5 (*Daiopterix*).
CI (adult: whole body)/PIRAS (HT: PIN 3063/922=LEP.FOSS.389 IPM/AWS)/Russia: Tshitinsk region, Shelopugitz district, left bank of the Daia River (Glushkovo Fm.)/Tithonian–Berriasian, Late Jurassic–Early Cretaceous boundary.

GRACILEPTERYX Martins-Neto and Vulcano, 1989: 463.
Type species: *Gracilepterix pulchra* Martins-Neto and Vulcano, 1989.

pulchra Martins-Neto and Vulcano, 1989: 463, figs. 2a–d (*Gracilepterix*).
CI (adult: whole body)/private collection, Maria A. Vulcano, São Paulo, Brazil (HT: CV-1476)/Brazil: Ceará State, ca. 4 km from Santana do Cairiri, Nova Olinda (Crato Fm.)/Late Aptian, Early Cretaceous.

PALAEOLEPIDOPTERIX Kozlov, 1989: 37.
Type species: *Palaeolepidopterix aurea* Kozlov, 1989.
aurea Kozlov, 1989: 38, fig. 1a (*Palaeolepidopterix*).

CI (adult: whole body)/PIRAS (HT: PIN 2239/607)/Kazakhstan: Chimkent Oblast, Chayan district, Aulie close to the village of Mikhailovka (Karabastau Fm.)/Oxfordian–Kimmeridgian, Late Jurassic.

UNDOPTERIX Skalski, 1979a: 92.
Type species: *Undopterix sukatshevae* Skalski, 1979.

cariensis Martins-Neto and Vulcano, 1989: 463, fig. 2f (*Undopterix*).
CI (adult: forewing)/IGUSP (HT: GP/1T-1635)/Brazil: Ceará State, ca. 4 km from Santana do Cairiri, Nova Olinda (Crato Fm.)/Late Aptian, Early Cretaceous.

sukatshevae Skalski, 1979a: 94, figs. 4–6, pl. 9: 1, pl. 10: 1 (*Undopterix*).
CI (adult: whole body)/PIRAS (HT: PIN 3015/815=LEP.FOSS.290/IPM/AWS)/Russia: Chita Province, Shelopugino district, Unda River at Zhidka (Baleyan Fm.)/Aptian–Albian, Early Cretaceous.

NETOXENA Sohn, **gen. nov.** A replacement name for *Xena* Martins-Neto, 1999.
= *Xena* Martins-Neto, 1999: 533. A junior homonym of *Xena* Nartshuk, 1964 [Diptera: Chloropidae].
Type species: *Xena nana* Martins-Neto, 1999.

nana Martins-Neto, 1999: 533, figs. 2–3 (*Xena*). **comb. nov.**
CI (adult: whole body)/LPUSP (HT: RGMN-T030)/Brazil: Ceará State, ca. 4 km from Santana do Cairiri, Nova Olinda (Crato Fm.)/Late Aptian, Early Cretaceous.

GENUS *incertae sedis*

—Skalski, 1990a: 126 (undescribed Eolepidopterigina).
CI (not stated)/not stated/not stated/Late Jurassic–Early Cretaceous.

Suborder Zeugloptera Chapman, 1917 [extant]

= Micropterigina Herrich-Schäffer, 1855

Superfamily MICROPTERIGOIDEA Herrich-Schäffer, 1855 [extant]

Family MICROPTERIGIDAE Herrich-Schäffer, 1855 [extant]

BALTIMARTYRIA Skalski, 1995: 27.
Type species: *Micropteryx* [sic] *proavittella* Rebel, 1936.
= *Paragrionympha*; Skalski, 1976c: 223. Nomen nudum (see Kristensen and Nielsen, 1979: 141).

proavittella Rebel, 1936: 185, fig. 17 (*Micropteryx* [sic]); Whalley, 1977: 526 (*Sabatinca*); Skalski, 1995: 28, figs. 1, 2, 5, 6 (*Baltimartyria*).
= *Micropteryx* [sic] *proavitella* [sic]; Kusnezov, 1941: 69.
AM (adult: whole body)/GPUT (HT: no. 1450/1=LEP.SUCC. 238 IGPT/AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

rasnitsyni Mey, 2011: 333, figs. 1-11 (*Baltimartyria*).
AM (adult: whole body)/MNHU (HT: MB.I 5950)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

MICROPTERIX Hübner, 1825 [extant]
= *Electrocrania* Kusnezov, 1941: 19.
Type species: *Electrocrania immensipalpa* Kusnezov, 1941.
Comment: Kristensen and Skalski (1998: 17) questioned the synonymy of *Electrocrania* with *Micropterix* suggested by Kozlov (1988). They were uncertain whether *Electrocrania* was homoneurous or glossatan.

angelica Jarzembowski, 1980: 263, fig. 49 (*Micropterix*).
CI (adult: partial forewing)/BMNH (HT: In.17411)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/Late Priabonian, Late Eocene.

gertraudae Kurz and Kurz, 2010: electronic source (*Micropterix*).
AM (adult: whole body)/private collection, Michael Kurz, Hallein-Rif, Austria (HT: MK-14295)/Russia: Kaliningrad, Yantarny (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

immensipalpa Kusnezov, 1941: 20, figs. 1–3 (*Electrocrania*); Kozlov, 1988: 26 , fig. 2 (*Micropterix*).
AM (adult: whole body)/PIRAS (HT: no. 8)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Kupryjanowicz, 2001: 62, fig. 80 (*Micropterix*).
AM (adult: whole body)/MEPA (1 ex: no. 15510)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.
Comment: The author stated that this record was based on an identification by Skalski. It could be one of the specimens in Skalski's papers.

—Skalski, 1976b: 199 (*Micropterix*); Skalski, 1990a: 126 [multiple species]; Skalski in Kristensen and Skalski, 1998: 24.
AM (not stated)/not stated (> 2 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

MOLEROPTERIX Engel and Kinzelbach, 2008: 1444.
Type species: *Moleropterix kalbei* Engel and Kinzelbach, 2008.

kalbei Engel and Kinzelbach, 2008: 1445, figs. 1, 2 (*Moleropterix*).
CI (adult: forewing)/KNHM (HT: KU-NHM-ENT FFD-002)/Denmark: Fur Island, Stolleklint Clay (Fur Fm.)/late Thanetian, Late Paleocene.

PALAEOSABATINCA Kozlov, 1988: 26.
Type species: *Palaeosabatinca zherichini* Kozlov, 1988.

zherichini Kozlov, 1988: 27, fig. 3 (*Palaeosabatinca*).
CI (adult: whole body)/PIRAS (HT: PIN 3064/515)/Russia: Transbaikalia, Baisa, left bank of Vitim River (Zaza Fm.)/Hauterivian, Early Cretaceous.

PARASABATINCA Whalley, 1978: 73.
Type species: *Parasabatinca aftimacrai* Whalley, 1978.

aftimacrai Whalley, 1978: 73, pl. 11: 1–3, pl. 12: 1–3, pl. 13: 1, pl. 14: 1 (*Parasabatinca*).
AM (adult: whole body)/BMNH (HT: "embedded in plastic"; PT: 2 ex)/Lebanon: Hammana, Mdeyrij (Lebanese Amber, Grès de Basa Fm. or lateral equivalents)/Hauterivian–Aptian, Early Cretaceous.
Comment: Kristensen and Skalski (1998: 17) confirmed placement of this fossil in the so-called *Sabatinca* group, based on two apomorphies. It is the earliest definitive Micropterigidae.

caldasae Martins-Neto and Vulcano, 1989: 460, figs. 1a–e (*Parasabatinca*).
CI (adult: whole body)/private collection, Maria A. Vulcano, São Paulo, Brazil (HT: CV-146); IGUSP (PT: CD-129, GP/1T-1630); DGUFC (PT: AMA-I-01)/Brazil: Ceará State, ca. 4 km from Santana do Cairiri, Nova Olinda (Crato Fm.)/late Aptian, Early Cretaceous.

SABATINCA Walker, 1863 [extant]

perveta Cockerell, 1919: 23 (*Micropteryx* [sic]); Rebel, 1936: 165 (*Mnesarchaea*); Kusnezov, 1941: 69 (*Dyseriocrania*); Skalski, 1973c: 650 (*Mnemonica*); Whalley, 1977: 526 (*Sabatinca*); Ross and York, 2000: 14, fig. 6.
AM (adult: whole body)/BMNH (HT: In.19135)/Myanmar: Kachin Prov., Hukawang Valley (Burmese Amber, "channel facies" of an unnamed formation)/late Aptian, Early Cretaceous.

—Skalski, 1990a: 126 (*Sabatinca* group) [multiple species].
= *Saxibatinca meyi* Skalski in Kristensen and Skalski, 1998: 24. Nomen nudum [manuscript name].
AM (not stated)/not stated (several specimens)/Germany: Tagebau Goitsche, Bitterfeld Coal Mine (Saxonian Amber, Cottbus Fm.)/Lutetian, Middle Eocene.

—Skalski in Kristensen and Skalski, 1998: 24 (sabatincoid-like micropterigid)
AM (not stated)/not stated (1 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

GENUS *incertae sedis*

—Ansorge, 2002: 72, fig. 15 (two Lepidoptera related to Micropterigidae).
CI (adult: forewing)/MNHU (2 ex: LGA 1500; LGA 2017)/Germany: Mecklenburg, Grimmen (Grüne Serie)/early Toarcian, Early Jurassic.

—Azar *et al.*, 2010: 286, 288, fig. 36c (micropterigid moth).
AM (adult: whole body)/not stated/Lebanon: Hammana, Mdeyrij (Lebanese Amber, Grès de Basa Fm. or lateral equivalents)/Hauterivian–Aptian, Early Cretaceous.

—Grimaldi *et al.*, 2002: 11, fig. 42c (Micropterigidae); Grimaldi and Engel, 2005: 562, fig. 13: 17.
AM (adult: whole body)/AMNH (1 ex: Bu701)/Myanmar: Kachin Prov., Hukawang Valley (Burmese Amber, "channel facies" of an unnamed formation)/late Aptian, Early Cretaceous.

—Martínez-Delclós *et al.*, 1999: 14 (Micropterigidae).
AM (adult: whole body)/?MCNV/Spain: Basque County, Álava, Peñacerrada (Nograro Fm.)/Aptian, Early Cretaceous.
Comment: The author compared wing venation in this fossil to *Parasabatinca* and *Undopterix*. It is possibly the same fossil referred to as "Lepidoptera" by Alonso *et al.* (2000).

—Rasnitsyn and Ross, 2000: 24 (Micropterigidae) [multiple species].
AM (adult: whole body)/BMNH (3 ex: In.20167; In.20168; In.20204)/Myanmar: Kachin Prov., Hukawang Valley (Burmese Amber, "channel facies" of an unnamed formation)/late Aptian, Early Cretaceous.

Questionably placed in Micropterigidae

AULIEPTERIX Kozlov, 1989: 40.
Type species: *Auliepterix mirabilis* Kozlov, 1989
Comment: Kristensen and Skalski (1998: 17) questioned the micropterigid association of this genus due to the lack of apomorphies supporting the relationship.

minima Kozlov, 1989: 40, fig. 1c (*Auliepterix*).
CI (adult: whole body)/PIRAS (HT: PIN 4307/39)/Mongolia: Ara-Khangayskiy Aymak, 6km west of Khotont Somon, the northern part of Ukha (Arkhangai Fm.)/Tithonian–Berriasian, Late Jurassic–Early Cretaceous boundary (Lukashevich, 1996).

mirabilis Kozlov, 1989: 40, fig. 1d (*Auliepterix*).
CI (adult: whole body)/PIRAS (HT: PIN 2997/858,891)/Kazakhstan: Chimkent Oblast, Chayan district, Aulie close to the village of Mikhailovka (Karabastau Fm.)/Oxfordian–Kimmeridgian, Late Jurassic.

GENUS *incertae sedis*

—Kühne *et al.*, 1973: 63, fig. 1 (*Micropterix*); Kozlov, 1988: 54 (uncertain).
AM (adult: 3 types of wing scales)/PIFU (150 ex)/France: Sarthe, Quarry 2.5km S of Durtal (Aquitanian Amber)/ Albian–Cenomanian, Early–Late Cretaceous boundary.

—Richter, 1988: 122, fig. 8 (Micropterigidae).
GC (adult: cuticular fragments and wing scales)/FNSF/Germany: Hesse, S Frankfurt, near Darmstadt, Messel oil shale-layers (Messel Fm.)/early Lutetian, Middle Eocene.

—Schlüter, 1974: 254, figs. 1–2 (Micropterigidae); Schlüter, 1975: 157, fig. 5.
AM (adult: wing scales)/?PIFU/France: Durtal, Angouleme Fouras, Rochefort (Aquitanian Amber)/ Albian–Cenomanian, Early–Late Cretaceous boundary.

Suborder Glossata Fabricius, 1775

SUPERFAMILY *incertae sedis*

PROTOLEPIS Kozlov, 1989: 41.
Type species: *Protolepis cuprealata* Kozlov, 1989.

cuprealata Kozlov, 1989: 41, fig. 1e (*Protolepis*).
CI (adult: whole body)/PIRAS (HT: PIN 2066/3564)/Kazakhstan: Chimkent Oblast, Chayan district, Aulie close to the village of Mikhailovka (Karabastau Fm.)/Oxfordian–Kimmeridgian, Late Jurassic.
Comment: Kristensen and Skalski (1998: 16) cited this as one of the earliest Glossata but also raised the possibility that its re-examination might not confirm its glossatan relationship.

GENUS *incertae sedis*

—Grimaldi and Engel, 2005: 564, fig. 13: 21 (glossatan moth).
AM (larva: whole body)/AMNH (1 ex: JG 19/70)/Lebanon: Hammana, Mdeyrij (Lebanese Amber, Grès de Basa Fm. or lateral equivalents)/Hauterivian–Aptian, Early Cretaceous.

—Grimaldi and Engel, 2005: 564, fig. 13: 22 (glossatan moth).
AM (adult)/AMNH (1 ex: NJ)/USA: New Jersey, Middlesex Co., Sayreville (New Jersey Amber, Raritan Fm.)/ Turonian, Late Cretaceous.

—Grimaldi and Engel, 2005: 568, fig. 13: 28 (glossatan moth).
AM (adult: whole body)/AMNH (1 ex: NJ-638)/USA: New Jersey, Middlesex Co., Sayreville (New Jersey Amber, Raritan Fm.)/Turonian, Late Cretaceous.

—Grimaldi *et al.*, 2002: 11, fig. 42d (Glossata).
AM (adult: whole body)/AMNH (1 ex: Bu187)/Myanmar: Kachin Prov., Hukawang Valley (Burmese Amber, "channel facies" of an unnamed formation)/late Aptian, Early Cretaceous.

—Rust, 1999: 347 (glossatan moth).
CI (adult: various)/MHMM (3 ex: MM 11-A2083; 6M-2127; 14M-5226)/Denmark: Mors Island (Fur Fm.)/late Thanetian, Late Paleocene.

—Wedmann, 2000: 107–108, fig. 46 (glossatan moth) [two species].
CI (pupa)/NMLN (2 ex: no. 5404; no. 8831)/Germany: Rhineland–Palatinate, Westerwald (Enspel Fm.)/Chattian, Late Oligocene.

Superfamily ERIOCRANIOIDEA Rebel, 1901 [extant]

Family ERIOCRANIIDAE Rebel, 1901 [extant]

cf. *ERIOCRANIELLA* Viette, 1949 [extant]

—Opler, 1973: 1321, fig. 1b (cf. *Eriocraniella*).
CI and T (leaf mine)/UCMP/USA: Idaho, Thorn Creek (Payette Fm.)/Tortonian, Late Miocene.
Fossil plant host: Fagaceae —*Quercus simulata* Knowlt.

Questionably placed in Eriocraniidae

ERIOCRANITES Kernbach, 1967: 104 (Eriocraniidae); Kozlov, 1988: 54 (uncertain).
Type species: *Eriocranites hercynicus* Kernbach, 1967. A subsequent designation by Clark *et al.* (1971: 582).

hercynicus Kernbach, 1967: 104, fig. 2 (*Eriocranites*).
CI (adult: wings)/GPUG (HT: 596-1=16283)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

GENUS *incertae sedis*

—Kozlov *et al.*, 2002: 225, fig. 300 (Suborder Eriocraniina).
CI (adult: whole body)/PIRAS (1 ex: PIN 2784/1933)/Kazakhstan: Karatau (Karabastau Fm.)/Oxfordian–Kimmeridgian, Late Jurassic.

—Skalski, 1990c: 164 [in table] (Eriocraniidae).
AM (not stated)/not stated/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Skalski, 1990c: 164 [in table] (Eriocraniidae).
AM (not stated)/not stated/Myanmar: Kachin Prov., Hukawang Valley (Burmese Amber, "channel facies" of an unnamed formation)/late Aptian, Early Cretaceous.

Superfamily LOPHOCORONOIDEA Common, 1990 [extant]

Family LOPHOCORONIDAE Common, 1973 [extant]

Questionably placed in Lophocoronidae

GENUS *incertae sedis*

—Skalski, 1979c: 63, fig. 1 (Lophocoronidae).
AM (adult: whole body)/not stated/Russia: Siberia, E Taimyr, Taimyr Autonomous Okrug, Chatanga (Taimyr Amber, Kheta Fm.)/Coniacian, Late Cretaceous.
Comment: Nielsen and Kristensen (1996) criticized the assignment of this fossil to Lophocoronidae.

Infraorder Exoporia Dugdale, 1974 [extant]

Superfamily MNESARCHAEOIDEA Eyer, 1924 [extant]

Family MNESARCHAEIDAE Eyer, 1924 [extant]

Questionably placed in Mnesarchaeidae

GENUS *incertae sedis*

—Zherikhin and Sukacheva, 1973: 20 [in table] (Mnesarchaeidae); Rohdendorf and Zherikhin, 1974: 83, fig. 1 [left upper]; Skalski, 1979c: 63.
AM (adult: forewing)/not stated [?PIRAS] (1ex)/Russia: Siberia, E Taimyr, Taimyr Autonomous Okrug, Chatanga (Taimyr Amber, Kheta Fm.)/Coniacian, Late Cretaceous.
Comment: Kristensen and Skalski (1998) doubted the assignment of this fossil to Mnesarchaeidae.

Superfamily HEPIALOIDEA Stephens, 1829 [extant]

Family HEPIALIDAE Stephens, 1829 [extant]

OIOPHASSUS Zhang, 1989: 93.
Type species: *Oiophassus nycterus* Zhang, 1989.

nycterus Zhang, 1989: 94, fig. 75, pl. 20: 4 (*Oiophassus*).
CI (adult: wings)/SFML (HT: s82702)/China: Shandong Prov., Lingu, Shanwang (Shanwang Fm.)/Langhian, Middle Miocene.

OXYCANUS Walker, 1855 [extant]

cf. *antipoda* Herrich-Schäffer, [1853] (*Epiolus*) [extant]; Keble, 1947: 49 (cf. *fuscomaculatus*) [fossil].
SI (larva: whole body)/MVVA (2 ex: P16153; P16154)/Australia: Victoria, Pejark Marsh (unconsolidated sediments)/Late Holocene.

PROTOHEPIALUS Pierce, 1945: 5.
Type species *Protohepialus comstocki* Pierce, 1945.

comstocki Pierce, 1945: 5, pl. 3 and 4 (*Protohepialus*).
= *Protohepialus incertus* (nec Piton, 1940); Skalski, 1990a: 126.
CI (adult: partial wing)/NHLA (HT: no. 3072)/USA: California, Los Angeles Co., SE Puente (Puente Fm.)/Late Miocene.

Questionably placed in Hepialidae

PROHEPIALUS Piton, 1940: 217 (Hepialidae); Carpenter, 1992: 380 (uncertain).
Type species: *Prohepialus incertus* Piton, 1940.

incertus Piton, 1940: 217, pl. 17: 1 (*Prohepialus*).
CI (adult: whole body)/MNHN (HT: no. 426)/France: Cantal, Menat, Puy-de-Dôme (spongio-diatomite beds)/ Selandrian, Middle Paleocene (Wappler *et al.* 2009).

—Jarzembowski, 1976: 13 (*Prohepialus*); Jarzembowski, 1980: 265, figs. 38, 47, 59.
CI (adult: partial forewing or partial hindwing)/BMNH (3 ex: In.17464; In.64528; In.64538)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/Late Priabonian, Late Eocene.

GENUS *incertae sedis*

—Evans, 1931: 99, pl. 12 (Hepialidae).
CI (adult: wing scales)/?GCUA/New Zealand: North Island, Waikato, near Huntly, Glen Afton mine (Waikato Coal Measures)/Priabonian, Late Eocene (Harris, 1984).
Comment: Evans (1931) mentioned that Dr. R. J. Tillyard examined the scales and thought they resembled those of the extant *Wiseana signata* [Hepialidae].

Infraorder Heteroneura Tillyard, 1918

SUPERFAMILY *incertae sedis*

—Rust, 1999: 347, pl. 28: b (Heteroneura gen. et sp. indet.); Rust, 2000b: 579, fig. 1.
CI (adult: whole or partial body)/MHMM (ca. 110 ex: MM 6M-2127; 14M-A2198; 14M-B2249; 14M-B2921; 14M-B2971; 14M-B4328; 14M-2337; I239; I 272; I357; I495; I613; I665; I2315; I3930; VSK2246; 5-3973; 6-3314) and private collection, Erwin Rettig, Nykøbing, Mors, Limfjord, Denmark [now NHMD?] (6 ex: ERK SA97 K28; SA96 O23; KL96 O63; KL94 B51; KL97 R6; SK94 K51)/Denmark: Jutland, Mors Island (Fur Fm.)/late Thanetian, Late Paleocene.

Superfamily NEPTICULOIDEA Stainton, 1859 [extant]

Family NEPTICULIDAE Stainton, 1859 [extant]

ACALYPTRIS Meyrick, 1921 [extant]

—Skalski, 1990a: 127 (*Niepeltia*); Skalski, 1990b: 144 (*Acalyptris*).
CO (adult: whole body)/not stated/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/Late Pleistocene.

ECTOEDEMIA Busck, 1907 [extant]

—Labandeira *et al.*, 1994: 12279, figs. 1a–d (*Ectoedemia*) [multiple species].
CI and T (leaf mine)/FMUF (> 2 ex: UF12701; UF7255 etc.)/USA: Kansas and Nebraska, Braun Ranch, Hoisington and other localities (Dakota Fm.)/late Albian, Early Cretaceous.
Fossil plant host: Undescribed platanoids.
Comment: Kristensen and Skalski (1998) cited this record as the earliest fossil evidence of Nepticulidae and also of the extant genus *Ectoedemia*.

—Skalski, 1976b: 199 (*Ectoedemia*).
AM (adult: whole body)/not stated (1 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

JOHANSSONIELLA Koçak, 1981 [extant], a replacement name for *Johanssonia* Borkowski, 1972.

—Skalski, 1976b: 199 (*Johanssonia*).
CO (not stated)/not stated (1 ex)/not stated/not stated.

cf. *STIGMELLA* Schrank, 1802 [extant]

almeidae Martins-Neto, 1989: 381, pl. 1: c (?*Nepticula*).
CI and T (leaf mine)/IGUSP (HT: GP/1T-1644)/Brazil: São Paulo, Tremembé, along the road that connects Rodovia Presidente Dutra with Campos do Jordão (Tremembé Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.
Fossil plant host: Symplocaceae —*Symplocos* sp.

ulmivora Fologne, 1860 (*Nepticula*) [extant]; Kernbach, 1967: 106, fig. 5 [fossil].
CI and T (leaf mine)/GPUG (1 ex: 596-4=9111)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).
Fossil plant host: not stated [?Ulmaceae].

—Donner and Wilkinson, 1989: 9 (cf. *Stigmella*).
CI and T (leaf mine)/private collection, Christopher Wilkinson, Botswana/Kazakhstan: no details/Turonian, Late Cretaceous.

—Kinzelbach, 1970: 94, 96, fig. 1 (*Stigmella*).
CI and T (leaf mine)/HLDG (1 ex: Me7408)/Germany: Hesse, S Frankfurt, near Darmstadt, Messel oil shale-layers (Messel Fm.)/early Lutetian, Middle Eocene.
Fossil plant host: Moraceae.

—Kuroko, 1987: 119, fig. 1 (*Stigmella*).
CI and T (leaf mine)/private collection, Tachu Koshimizu, Nagano, Japan (1 ex)/Japan: central Honshu, the border between Nagano and Gumma Prefectures (Kabutoiwa Plant Bed)/?Tortonian–Messinian, Late Miocene.
Fossil plant host: Betulaceae —cf. *Betula grossa* Sieb. et Zucc.

—Labandeira, 1998a: 110, figs. 3d–e (*Stigmella*) [2 spp.].
CI and T (leaf mine)/FMUF (2 ex: UF7252; UF16173)/USA: Kansas, Cloud Co., Braun's Ranch (Dakota Fm.)/late Albian, Early Cretaceous.
Fossil plant host: Laurales —*Pabiana kvacekii* Upchurch et Dilcher; an unidentified angiosperm.
Comment: Kristensen and Skalski (1998) cited this record as the earliest fossil evidence of Nepticulidae and also of the extant genus *Stigmella*.

—Labandeira, 2002a: 45, figs. 4a–b (*Stigmella*).
CI and T (leaf mine)/TBMM (1 ex: no. 57293a)/USA: Washington, Whatcom Co., near Bellingham (Chuckanut Fm.)/Lutetian, Middle Eocene.

—Labandeira, 2002a: 45, figs. 4e–g (*Stigmella*).
CI and T (leaf mine)/TBMM (1 ex: no. 76477)/USA: Washington State, Ferry Co., Republic (Klondike Mountain Fm.)/Lutetian, Middle Eocene.
Fossil plant host: Rosaceae —cf. *Sorbus*.
Comment: The author stated that the fossil mine is particularly similar to those made by the extant *Stigmella nylandriella* Tengström and *S. magdalenae* Klimesch.

—Labandeira *et al.*, 1994: 12279, 12280, figs. 1e–h (*Stigmella*) [multiple species].
CI and T (leaf mine)/FMUF (3 ex: UF12712; UF4811; UF12718 etc.)/USA: Kansas and Nebraska, Rose Creek, Hoishington and other localities (Dakota Fm.)/late Albian, Early Cretaceous.
Fossil plant host: Laurales —*Pandemophyllum kvacekii* Upchurch et Dilcher.

—Labandeira *et al.*, 2002b: 2062, fig. 1h (*Stigmella*).
CI and T (leaf mine)/PMNH (1 ex: no. 6367a)/USA: SW North Dakota, Williston Basin, near Marmarth (Hell Creek Fm.)/latest Maastrichtian, Late Cretaceous.
Fossil plant host: Rosaceae —cf. *Rubus*.

—Liebhold *et al.*, 1982: 456, figs. 1–2 (*Stigmella*).
CI and T (leaf mine)/UCMP (1 ex: no. 8437)/USA: Southern Idaho (Trapper Creek Fm.)/early Langhian, Middle Miocene.
Fossil plant host: Berberidaceae —*Mahonia reticulata* (MacGinitie) Brown.

—Opler, 1973: 1321, fig. 1a (*Nepticula*).
CI and T (leaf mine)/UCMP/USA: California, San Luis Obispo Co., Temblor Range (Temblor Fm.)/Middle Miocene.
Fossil plant host: Fagaceae —cf. *Quercus virginiana* Mill.

—Opler, 1973: 1321 (*Nepticula*).
CI and T (leaf mine)/UCMP/USA: Nevada, Nye Co., Cedar Mountains, Upper Goldyke (Esmeralda Fm.)/Serravallian, Middle Miocene.
Fossil plant host: Fagaceae —*Quercus hanibalii* Dorf.

—Opler, 1973: 1321 (*Nepticula*) [2 spp.?].
CI and T (leaf mine)/UCMP (2 ex)/USA: Idaho, Thorn Creek (Payette Fm.)/Middle to Late Miocene.
Fossil plant host: Fagaceae —*Quercus simulata* Knowlt.; *Lithocarpus* sp.

—Opler, 1973: 1321 (*Nepticula*).
CI and T (leaf mine)/UCMP/USA: Nevada, Churchill Co., Buffalo Canyon (Buffalo Canyon Fm.)/Langhian, Middle Miocene.
Fossil plant host: Fagaceae —*Quercus hanibalii* Dorf.

—Opler, 1973: 1321 (*Nepticula*).
CI and T (leaf mine)/UCMP/USA: Nevada, Lyon Co., near Yerington (Aldritch Station Fm.)/Zanclean, Early Pliocene.
Fossil plant host: Fagaceae —*Quercus hanibalii* Dorf.

—Opler, 1973: 1321 (*Nepticula*); Opler, 1974: 74, pl. 7.
CI and T (leaf mine)/UCMP/USA: Nevada, Storey Co., Dead Camel Range (Chloropagus Fm.)/Serravallian, Middle Miocene.
Fossil plant host: Fagaceae —*Quercus wislizenoides* Axelrod.
Comment: The author stated that it is indistinguishable from mines made by living *Nepticula variella* Braun.

—Opler, 1973: 1321 (?*Nepticula*).
CI and T (leaf mine)/UCMP/USA: Oregon, Columbia Plateau, Blue Mountains, Stinking Water (Mascall Fm.)/Serravallian, Middle Miocene.
Fossil plant host: Fagaceae —*Quercus pseudolyrata* (Lesq.).

—Stephenson, 1991: 168, 170 (Mine type TLm1, TLm2a, TLm2b, TLm3); Stephenson and Scott, 1992: 547, figs. 5: b, d, e, f, h, figs. 6: d, e; Lang *et al.*, 1995: 159–162, 165–168, 170, figs. 3a, 3b, 3d, 3g, 3h, 4a–g, 4i–k, 4m, 4n, pl. 2: 2, 3, 7, 9, pl. 3: 1–3, 5, 6 [multiple species].

CI and T (leaf mine)/BMNH (13 ex: V.45868; V.48524; V.48798; V.49808; V.49905; V.50089; V.50460; V.50622; V.50698; V.50731; V.50733; V.50904; V.50952)/United Kingdom: Hampshire, East Dorset, Bournemouth (Branksome Sand Fm.)/Lutetian, Middle Eocene (McElwaine, 1998).

Comment: The authors used analogies to recent leaf mines to characterize the fossils, but it is not clear that they intended to link various fossil taxa with extant species (see Lang *et al.* 1995 for the analog).

—Wilf *et al*., 2005: 8944 (*Stigmella*).

CI and T (leaf mine)/MPEF/Argentina: Patagonia, Chubut, Laguna del Hunco (Tufolitas Laguna del Hunco)/Ypresian, Early Eocene (Genise and Petrulevicius, 2001).

STIGMELLITES Kernbach, 1967: 104.

Type species: *Stigmellites heringi* Kernbach, 1967. A subsequent designation by Clark *et al.* (1971: 582).

araliae Fritsch, 1882: 6, pl. 2: 7 (*Tinea*); Zherikhin, 1978: 74 (Eriocranioidea); Kozlov, 1988: 30 (*Stigmellites*).

CI and T (leaf mine)/not stated [lost?]/Czech Republic: Bohemia, Perucher-Schichten, Vyšerovic; Bohemia, Perucher-Schichten, Lipenz (Perucher Fm.)/Cenomanian, Late Cretaceous.

Fossil plant host: Araliaceae.

balticus Kozlov, 1988: 30, fig. 4 (*Stigmellites*); Skalski, 1990b: 144 (uncertain).

AM (adult: whole body)/private collection, K. M. Sadilenko, Moscow, Russia (HT: no. 15-1-4)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

carpiniorientalis Straus, 1977: 60, fig. 62 (*Stigmellites*).

CI and T (leaf mine)/GPUG (HT: 22763; PT: 22134)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

Fossil plant host: Betulaceae —*Carpinus orientalis* Mill. [extant].

centennis Jarzembowski, 1989: 448 (?*Stigmellites*).

= Mine type 2; Crane and Jarzembowski, 1980: 633, fig. 4, 9.

CI and T (leaf mine)/BMNH (HT: In.64549)/United Kingdom: S England, Berkshire, Newbury, Cold Ash (Reading Fm.)/Thanetian, Late Paleocene.

Fossil plant host: ?Fabaceae.

fossilis Heyden, 1862: 77, pl. 10: 2 (*Nepticula*); Opler, 1973: 1321 (dipterous mine); Kozlov, 1988: 31 (*Stigmellites*).

CI and T (leaf mine)/originally collection of the Senckenberg Nature-Study Society, Frankfurt [not found, probably lost]/Germany: Rhineland, Wetterau and Röhn, Niederrhein, Siebengebirge (Rott Fm.)/Chattian, Late Oligocene.

Fossil plant host: Juglandaceae —*Juglans acuminata* Braun.

gossi Jarzembowski, 1989: 448 (?*Stigmellites*).

= Mine type 1; Crane and Jarzembowski, 1980: 632, figs. 6, 8.

CI and T (leaf mine)/BMNH (HT: In.64547; PT: In.64548)/United Kingdom: S England, Berkshire, Newbury, Cold Ash (Reading Fm.)/Thanetian, Late Paleocene.

Comment: Crane and Jarzembowski (1980) stated that this mine is similar to an unidentified species of *Stigmella* on *Quercus cerris* L.

heringi Kernbach, 1967: 104, fig. 3 (*Stigmellites*).

CI and T (leaf mine)/GPUG (HT: 596-2=11137)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2002).

kzyldzharicus Kozlov, 1988: 32, fig. 5, pl. 2: 1 (*Stigmellites*); Grimaldi and Engel, 2005: 572, fig. 13: 32.
= Eriocraniidae mine; Zherikhin, 1978: 79.
= Nepticulidae mine; Skalski, 1979c: 64.
CI and T (leaf mine)/PIRAS (HT: PIN 2383/206; PT: PIN 2383/214)/Kazakhstan: Kzyl-Ordinsky Region, Chilinsky, northwest spur of Karatau mountain range, Kzyl-Dzhar (Beleuty Fm.)/Turonian, Late Cretaceous.
Fossil plant host: Platanaceae —*Platanus ambicula* Vachr.; *Platanus* sp.

messelensis Straus, 1976: 446 (*Stigmellites*).
= "worm or larva": Bornhardt, 1975: 471.
CI and T (leaf mine)/not stated (in unspecified private collector's possession)/Germany: Hesse, S Frankfurt, near Darmstadt, Messel oil shale-layers (Messel Fm.)/early Lutetian, Middle Eocene.

pliotityrellus Kernbach, 1967: 106, fig. 4 (*Stigmella*); Kozlov, 1988: 32 (*Stigmellites*).
CI and T (leaf mine)/GPUG (HT: 596-3=3050)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).
Fossil plant host: Fagaceae —*Fagus* sp.

samsonovi Kozlov, 1988: 33, pl. 2: 3 (*Stigmellites*).
CI and T (leaf mine)/PIRAS (HT: PIN 2383/209)/Kazakhstan: Kzyl-Ordinsky Region, Chilinsky, northwest spur of Karatau mountain range, Kzyl-Dzhar (Beleuty Fm.)/Turonian, Late Cretaceous.
Fossil plant host: Cercidiphyllaceae —*Trochodendroides arctica* (Heer) Berry.

serpentina Kozlov, 1988: 32, pl. 2: 2 (*Stigmellites*).
CI and T (leaf mine)/PIRAS (HT: PIN 2383/205)/Kazakhstan: Kzyl-Ordinsky Region, Chilinsky, northwest spur of Karatau mountain range, Kzyl-Dzhar (Beleuty Fm.)/Turonian, Late Cretaceous.
Fossil plant host: Cercidiphyllaceae —*Trochodendroides arctica* (Heer) Berry.

sharovi Kozlov, 1988: 33, pl. 2: 4 (*Stigmellites*).
CI and T (leaf mine)/PIRAS (HT: PIN 2383/208)/Kazakhstan: Kzyl-Ordinsky Region, Chilinsky, northwest spur of Karatau mountain range, Kzyl-Dzhar (Beleuty Fm.)/Turonian, Late Cretaceous.
Fossil plant host: Cercidiphyllaceae —*Trochodendroides arctica* (Heer) Berry.

tyshchenkoi Kozlov, 1988: 33, pl. 2: 5 (*Stigmellites*).
CI and T (leaf mine)/PIRAS (HT: PIN 2383/211)/Kzyl-Ordinsky Region, Chilinsky, northwest spur of Karatau mountain range, Kzyl-Dzhar (Beleuty Fm.)/Turonian, Late Cretaceous.
Fossil plant host: Platanaceae —*Platanus latior* Knowlt.

zelkovae Straus, 1977: 61, fig. 14 (*Stigmellites*).
CI and T (leaf mine)/GPUG (HT: no. 23973)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).
Fossil plant host: Ulmaceae —*Zelkova* sp.
Comment: Straus (1977) attributed this fossil to *Stigmellites* because of its similarity to extant nepticulid leaf mines.

—Jarzembowski, 1995: 146 (*Stigmellites*).
CI and T (leaf mine)/BMNH/United Kingdom: Hampshire, East Dorset, Bournemouth (Branksome Sand Fm.)/Lutetian, Middle Eocene (McElwaine, 1998).

—Jarzembowski, 1980: 270, fig. 50 (species A); Kozlov, 1988: 32 (*Stigmellites*).
CI (adult: whole body)/BMNH (1 ex: I.9492)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.
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—Jarzembowski, 1980: 271 (species B); Kozlov, 1988: 32 (*Stigmellites*).

CI (adult: whole body)/BMNH (1 ex: In.64540)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

GENUS *incertae sedis*

—Opler, 1973: 1321 (nepticulid mine).
= “galleries”; Berry, 1916: 32, pl. 23: 3, pl. 31: 1, 3, pl. 38: 4, pl. 39, pl. 92.
= “healed wounds on leaf”; Brooks, 1955: 4, 6, pl. 1: 5.
CI and T (leaf mine)/USNM/USA: Tennessee, Henry Co., SW of Puryear, Wilcox deposits (Claiborne Fm.)/late Ypresian, Early Eocene.
Fossil plant host: ?Proteaceae —*Proteoides wilcoxensis* Berry.

—Donner and Wilkinson, 1989: 9 (Nepticulidae) [multiple species?].
CI and T (leaf mine)/GDVU/not stated/Middle Miocene.

—Donner and Wilkinson, 1989: 9 (Nepticulidae) [multiple species?].
CI and T (leaf mine)/not stated (2 ex)/North America: no details/Middle Miocene.

—Labandeira, 2002b: 49, 252, fig. 2.10e (Nepticulidae).
CI and T (leaf mine)/USNM /USA: Wyoming, Washakie Co., Big Cedar Ridge (Meeteetsee Fm.) /early Maastrichtian, Late Cretaceous.
Fossil plant host: Cercidiphyllaceae —*Cercidiphyllum* sp.

—Peñalver and Delclòs, 2004: 82, fig. 6: 2. pl. 2: 2 (Nepticulidae).
= “leaf-mine”; Peñalver and Delclòs, 1997: 150, fig. 1.
CI and T (leaf mine)/MCNV (1 ex: MPV RIB-242)/Spain: Castellón Prov., near Ribesalbes, “La Rinconada” site (bituminous rhythmites)/Aquitanian, Early Miocene.
Fossil plant host: Lauraceae —*Laurophyllum* sp.

—Skalski, 1979c: 64 (Nepticulidae); Boucot, 1990: 108, fig. 102.
CI and T (leaf mine)/?PIRAS/Kazakhstan: Karatau (Karabastau Fm.)/Oxfordian–Kimmeridgian, Early Jurassic.
Fossil plant host: Cercidiphyllaceae —*Trochodendroides arctica* (Heer) Berry.

—Stephenson, 1991: 154–156, 163 (Mine type KLmla, KLm1b, KLm1c, KLm2, KLm3, KLm11) [multiple species].
CI and T (leaf mine)/GBIU (32 ex: IU15706-4811; IU15706-7525; IU15706-7528; IU15709-4818; IU15709-7531; IU15709-7535; IU15706-4539; IU15706-7521; IU15706-7525; IU15706-7527; IU15706-4810; IU15703-3856; IU15703-7523a; IU15706-7255; IU15706-7256; IU15709-3950; IU15709-4819; IU15713-4696; IU15713-4834; IU15713-4936; IU15713-7242; IU15713-7243; IU15713-7244; IU15713-7245; IU15713-7246; IU15723-7247; IU15713-7248; IU15713-7249; IU15713-7324; IU15706-4536; IU15706-7113; IU15714-7250)/USA: Kansas and Nebraska, Braun Ranch, Hoisington and other localities (Dakota Fm.)/late Albian, Early Cretaceous.
Comment: The author suggested that recent analogs of these fossils are leaf mines caused by various species of *Stigmella* and other nepticulid moth larvae.

Questionably placed in Nepticulidae

—Rozefelds, 1988a: 4, figs. 3a–c (Nepticulidae) [multiple species].
CI and T (leaf mine)/MVVA (1 ex: NMVP183064)/Australia: Victoria, Alcoa Anglesea Coal Mine, S38°25´ E144°11´ (Eastern View Fm.)/Priabonian, Late Eocene.

Fossil plant host: Lauraceae.

—Rozefelds, 1988b: 77, fig. 2 (Nepticulidae); Labandeira *et al.* 1994: 12281 (?Nepticulidae).
CI and T (leaf mine)/QMSB (1 ex: QMF15346)/Australia: North Queensland, Cape York Peninsula, Cape Melville, Clack Island (Battle Camp Fm.)/Tithonian–Berriasian, Late Jurassic–Early Cretaceous boundary.
Fossil plant host: Umkomasiaceae —*Pachyteris crassa* (Halle) Townrow.
Comment: If this mine indeed is a nepticulid lepidopteran, it would establish the clade on a preangiospermous seed-fern lineage, the Umkomasiaceae (Corystospermales).

Clade Eulepidoptera Börner, 1939 [extant]

Clade Incurvariina Börner, 1939 [extant]

Superfamily ADELOIDEA Bruand, 1850 [extant]

Family HELIOZELIDAE Heineman and Wocke, 1876 [extant]

cf. *ANTISPILA* Hübner, 1825 [extant]

—Labandeira, 2002a: 45, figs. 4l–n (cf. *Antispila*).
CI and T (leaf mine)/TBMM (1 ex: no. 36831)/USA: Washington State, Ferry Co., Republic (Klondike Mountain Fm.)/early Lutetian, Middle Eocene.
Fossil plant host: Myricaceae —*Comptonia columbiana* Dawson.

GENUS *incertae sedis*

—Skalski, 1976b: 199 (Heliozelidae).
AM (not stated)/not stated (1 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Family ADELIDAE Bruand, 1850 [extant]

***ADELA* Latreille,** 1796 [extant]

kuznetzovi Kozlov, 1987: 59, fig. 1a (*Adela*).
AM (adult: whole body)/PAML (HT: Ap-1484)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

similis Kozlov, 1987: 60, fig. 1b (*Adela*).
AM (adult: whole body)/PAML (HT: Eo-14160/Ap-3466)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

ADELITES Rebel, 1934a: 373.
Type species: *Adelites electreella* Rebel, 1934.

acutitarsellus Rebel, 1936: 168, fig. 2 (*Prophalonia*); Skalski, 1976b: 201 (?*Prophalonia*); Kozlov, 1988: 29 (*Adelites*).
= *Adelites scutitarsella* [sic]; Keilbach, 1982: 313.

AM (adult: whole body)/MNHU (HT: MB-L5)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

electreellus Rebel, 1934a: 15 (*Adelites*).
= "*Adelites*"; Rebel, 1934b: 373 [no description].
= *Adelites electrella* [sic]; Keilbach, 1982: 313.
AM (adult: whole body)/BPGM (HT: L-3)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

purpurascens Rebel, 1936: 184 (*Adelites*); Kusnezov, 1941: 68 (?*Adelites*).
AM (adult: whole body)/BPGM (HT: no. 179)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

serraticornellus Rebel, 1936: 183, fig. 16 (*Adelites*).
AM (adult: whole body)/GPUT (HT: 3B662)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

GENUS *incertae sedis*

—Skalski, 1990a: 127 (Adelidae) [multiple species].
AM (not stated)/not stated/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Family INCURVARIIDAE Spuler, 1898 [extant]

INCURVARIA Haworth, 1828 [extant]

cf. *oehlmanniella* Hübner, 1796 (*Tinea*) [extant]; Straus, 1977: 59, fig. 44 [fossil].
CI and T (leaf mine)/GPUG (1 ex: no. 15427)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).
Fossil plant host: ?Ericaceae —cf. *Vaccinium*.

—Hering, 1957 (*Incurvaria* sp.) [extant]; Straus, 1977: 59–60, fig. 55 [fossil].
CI and T (leaf mine)/GPUG (1 ex: no. 21313)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).
Fossil plant host: Berberidaceae —*Berberis* sp.

—Skalski, 1990a: 127 (*Incurvaria*).
CI and T (leaf mine)/not stated/not stated/Pliocene.

PROPHALONIA Rebel, 1936: 167 (Tortricidae); Skalski, 1973b: 342 (Tineoidea); Skalski, 1976b: 200 (Incurvariidae).
Type species: *Prophalonia gigas* Rebel, 1936.

gigas Rebel, 1936: 167, fig. 1 (*Prophalonia*).
AM (adult: whole body)/MNHU (HT: MB-L4)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

GENUS *incertae sedis*

—Kupryjanowicz, 2001: 62 (Incurvariidae).
AM (adult: whole body)/MEPA (1 ex: no. 17864)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.
Comment: The author stated that this record was based on an identification by Skalski.

—Labandeira, 1998b: 20, fig. 2d (Incurvariidae).
CI and T (leaf mine)/USNM/USA: Utah, Uintah Co., Bonanza locality (Green River Fm.)/Ypresian, Middle Eocene.
Fossil plant host: Platanaceae —*Macginitiea wyomingensis* (Knowlton et Cockerell) Manchester.
Comment: The author stated that this fossil is similar to feeding damage by the extant genus *Paraclemensia*.

—Labandeira, 2002a: 46, figs. 4h–i (aff. *Incurvaria*).
CI and T (leaf mine)/TBMM (1 ex: no. 71371)/USA: Washington State, Ferry Co., Republic (Klondike Mountain Fm.)/early Lutetian, Middle Eocene.
Fossil plant host: Cornaceae —*Aucuba* sp.

—Labandeira, 2002a: 46 (probably incurvariid damage).
= holes made by a fungus; Schaarschmidt, 1992: fig. 34.
CI and T (leaf mine)/not stated/Germany: Hesse, S Frankfurt, near Darmstadt, Messel oil shale-layers (Messel Fm.)/early Lutetian, Middle Eocene.
Fossil plant host: Lauraceae —*Laurophyllum*.

—Skalski, 1979c: 63 (Incurvariidae).
AM (adult: whole body)/not stated/Russia: Siberia, E Taimyr, Taimyr Autonomous Okrug, Chatanga (Taimyr Amber, Kheta Fm.)/Coniacian, Late Cretaceous.

Questionably placed in Incurvariidae

INCURVARITES Rebel, 1934a: 14 (Incurvariidae); Skalski, 1976b: 200 (?Incurvariidae).
Type species: *Incurvarites alienella* Rebel, 1934.
= *Incurvariites* [sic]; Whalley, 1986: 260 [in figure legend].

alienellus Rebel, 1934a: 14, fig. 6 (*Incurvarites*).
= "*Incurvarites*"; Rebel, 1934b: 373 [no description].
AM (adult: whole body)/BPGM (HT: L-10)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

GENUS *incertae sedis*

—Whalley, 1978: 77, pl. 13: 3–4 (Incurvariidae); Kozlov, 1988: 54 (uncertain).
AM (adult: wing scales)/BMNH/Lebanon: Hammana, Mdeyrij (Lebanese Amber, Grès de Basa Fm. or lateral equivalents)/Hauterivian–Aptian, Early Cretaceous.

FAMILY *incertae sedis*

—Krassilov and Shuklina, 2008: 243, fig. 3if (incurvarioid case construction holes).
CI and T (leaf damage)/IEUH (>1 ex: IG1-739; etc.)/Israel: Negev Desert, central Negev, Makhtesh Ramon (Upper Hatira Fm.); Negev Desert, southern Negev, Arava Valley, Gerofit (Ora Fm.)/Turonian, Late Cretaceous.
Fossil plant host: Cercidiphyllaceae —*Eocercidiphyllites glandulosus* Krassilov.

Clade Etimonotrysia Minet, 1984 [extant]

Superfamily TISCHERIOIDEA Spuler, 1898 [extant]

Family TISCHERIIDAE Spuler, 1898 [extant]

Questionably placed in Tischeriidae

GENUS *incertae sedis*

—Stephenson, 1991: 166 (Mine type KLm14).
CI and T (leaf mine)/GBIU (1 ex: IU15808-7545)/USA: Tennessee, Carroll Co., Vale, Cooper Pit (Ripley Fm.)/Maastrichtian, Late Cretaceous.
Comment: The author suggested that recent analogs of these fossils are leaf mines caused by extant *Tischeria* sp.

Clade Ditrysia Börner, 1825 [extant]

Superfamily TINEOIDEA Latreille, 1810 [extant]

Family TINEIDAE Latreille, 1810 [extant]

Subfamily ACROLOPHINAE Busck, 1912 [extant]

ACROLOPHUS Poey, 1832 [extant]

—Grimaldi and Engel, 2005: fig. 13: 36 (*Acrolophus*).
AM (adult: whole body)/AMNH (1 ex)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

GENUS *incertae sedis*

—Kristensen and Skalski, 1998: 18, 25 (Acrolophidae).
AM (unknown)/not stated/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

Subfamily DRYADAULINAE Bradley, 1966 [extant]

cf. ***DRYADAULA*** Meyrick, 1893 [extant]

—Kristensen and Skalski, 1998: 18 (cf. *Choropleca*).
AM (unknown)/not stated/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

Subfamily HIEROXESTINAE Meyrick, 1893 [extant]

cf. *OPOGONA* Zeller, 1853 [extant]

—Kristensen and Skalski, 1998: 18 (cf. *Opogona*).
AM (unknown)/not stated/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

Subfamily MEESSIINAE Capuse, 1966 [extant]

ELECTROMEESIA Kozlov, 1987: 63; Kozlov, 1988: 36 (Meessiinae).
Type species: *Electromeessia zaguljaevi* Kozlov, 1987.

zaguljaevi Kozlov, 1987: 63, fig. 2d (*Electromeessia*).
AM (adult: whole body)/PIRAS (HT: PIN 363/77)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

PALAEOINFURCITINEA Kozlov, 1987: 62; Kozlov, 1988: 36 (Meessiinae).
Type species: *Palaeoinfurcitinea rohdendorfi* Kozlov, 1987.

rohdendorfi Kozlov, 1987: 62, fig. 2c (*Palaeoinfurcitinea*).
AM (adult: whole body)/PIRAS (HT: PIN 964/661)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

PARATRIAXOMASIA Jarzembowski, 1980: 267; Kozlov, 1988: 36 (Meessiinae).
Type species: *Paratriaxomasia solentensis* Jarzembowski, 1980.

solentenis Jarzembowski, 1980: 267, fig. 53 (*Paratriaxomasia*).
CI (adult: whole body)/BMNH (HT: In.9166)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

SIMULOTENIA Skalski, 1977: 16; Kozlov, 1988: 36 (Meessiinae).
Type species: *Simulotenia intermedia* Skalski, 1977.

intermedia Skalski, 1977: 16, figs. 10–11, pl. 1: 1, pl. 2: 1 (*Simulotenia*).
AM (adult: whole body)/MEPA (HT: 49/3 G/9 no. 1535/8, 3 MZ/AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

TINEOLAMIMA Rebel, 1934a: 13; Kozlov, 1988: 36 (Meessiinae).
Type species: *Tineolamima aurella* Rebel, 1934.
= *Tineolamina* [sic]; Keilbach, 1982: 314.

aurella Rebel, 1934a: 13, pl. 1: 5 (*Tineolamima*); Kusnezov, 1941: 69 (?*Tineolamima*).
= Tineidae (s. l.); Rebel, 1934b: 373 (part).
AM (adult: whole body)/originally BPGM (HT: L-1)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

EUDARCIA Clemens, 1860 [extant]

—Sobczyk and Kobbert, 2009: 18, fig. 2 (*Eudarcia*)
AM and T (larval case)/private collection, Max J. Kobbert, Münster, Germany (1 ex: T069)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Subfamily MYRMECOZELINAE Zagulajev, 1968 [extant]

MARTYNEA Kusnezov, 1941: 24; Kozlov, 1988: 36 (Myrmecozelinae).
Type species: *Martynea rebeli* Kusnezov, 1941.

rebeli Kusnezov, 1941: 27, figs. 9–10 (*Martynea*).
AM (adult: whole body)/PIRAS (HT: no. 14)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

PSEUDOCEPHITINEA Kozlov, 1987: 62; Kozlov, 1988: 36 (Myrmecozelinae).
Type species: *Pseudocephitinea svetlanae* Kozlov, 1987.

svetlanae Kozlov, 1987: 62, fig. 2b (*Pseudocephitinea*).
AM (adult: whole body)/PIRAS (HT: PIN 367/78)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Subfamily SCARDIINAE Eyer, 1924 [extant]

GLESSOSCARDIA Kusnezov, 1941: 39; Kozlov, 1988: 35 (Scardiinae).
Type species: *Glessoscardia gerasimovi* Kusnezov, 1941.

gerasimovi Kusnezov, 1941: 43, figs. 27–28 (*Glessoscardia*).
AM (larva: whole body)/PIRAS (HT: no. 16)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

PALAEOSCARDITES Kusnezov, 1941: 36; Kozlov, 1988: 35 (Scardiinae).
Type species: *Palaeoscardiites mordvilkoi* Kusnezov, 1941.

mordvilkoi Kusnezov, 1941: 37, figs. 20–24 (*Palaeoscardiites*).
AM (adult: whole body)/PIRAS (HT: no. 7)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

PROSCARDITES Kusnezov, 1941: 33; Kozlov, 1988: 35 (Scardiinae).
Type species: *Proscardiites martynovi* Kuznezov, 1941.

martynovi Kusnezov, 1941: 34, figs. 16–19 (*Proscardiites*).
AM (adult: whole body)/PIRAS (HT: no. 5)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

SCARDITES Kusnezov, 1941: 30; Kozlov, 1988: 35 (Scardiinae).
Type species: *Scardiites meyricki* Kusnezov, 1941.

meyricki Kusnezov, 1941: 32, figs. 13–15 (*Scardiites*).
AM (adult: whole body)/PIRAS (HT: no. 2)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Subfamily TINEINAE Latreille, 1810 [extant]

cf. ***CERATOPHAGA*** Petersen, 1957 [extant]

—Hill, 1987: 543, fig. B2 (cf. *Ceratophaga*).
SI and T (larval feeding damage)/not stated [private collection, Mary Leakey?] (>1 ex: LAET 75 958 7E; etc.)/Tanzania: Laetoli, Upper Laetoli Beds (Laetoli Fm.); Olduvai Gorge, site FLK (Olduvai Fm.) and Ethiopia: Omo Basin (Shungura Fm.)/?Piacenzian, Late Pliocene–Early Pleistocene boundary.
Comment: These fossils are larval feeding damage on bovid horn cores.

MONOPIBALTIA Skalski, 1974: 98; Kozlov, 1988: 35 (Tineinae).
Type species: *Monopibaltia ignitella* Skalski, 1974.

ignitella Skalski, 1974: 98, figs. 7–10 (*Monopibaltia*).
AM (adult: whole body)/IPEG (HT: LEP.SUCC.11 DEI/AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

PALAEOTINEA Kozlov, 1987: 60; Kozlov, 1988: 35 (Tineinae).
Type species: *Palaeotinea rasnitsyni* Kozlov, 1987.

rasnitsyni Kozlov, 1987: 61, fig. 2a (*Palaeotinea*).
AM (adult: whole body)/private collection, K. M. Sadilenko, Moscow, Russia (HT: 2-1-9)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Subfamily TILLYARDINEINAE Kozlov, 1988: 37

DYSMASIITES Kusnezov, 1941: 28; Kozlov, 1988: 37 (Tillyardineinae).
Type species: *Dysmasiites carpenteri* Kusnezov, 1941.

carpenteri Kusnezov, 1941: 29, figs. 11–12 (*Dysmasiites*).
AM (adult: whole body)/PIRAS (HT: no. 3)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

TILLYARDINEA Kusnezov, 1941: 22; Kozlov, 1988: 37 (Tillyardineinae).
Type species: *Tillyardinea eocaenica* Kusnezov, 1941.

eocaenica Kusnezov, 1941: 23, figs. 5–8 (*Tillyardinea*).
AM (adult: whole body)/PIRAS (HT: no. 1)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

TINEOSEMOPSIS Skalski, 1974: 97 (Nemapogoninae); Kozlov, 1988: 37 (Tillyardineinae).
Type species: *Tineosemopsis decurtatus* Skalski, 1974.

decurtatus Skalski, 1974: 97, figs. 1–6 (*Tineosemopsis*).
AM (adult: whole body)/private collection, Oehlke Eberswalde, Germany (HT: LEP.SUCC.10 AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

SUBFAMILY *incertae sedis*

ARCHITINEA Rebel, 1934a: 10.
Type species: *Architinea balticella* Rebel, 1834.

balticella Rebel, 1934a: 10, fig. 4 (*Architinea*).
= Tineidae (s.l.); Rebel, 1934b: 373 (part).
AM (whole body)/BPGM (HT: L-8)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

TINEITELLA Fletcher, 1940: 18, a replacement name for *Tineites*.
= *Tineites* Kawall, 1876: 171. A junior homonym of *Tineites* Germar, 1842 [Ephemeroptera].
Type species: *Tineites crystalli* Kawall, 1876.

crystalli Kawall, 1876: 171 (*Tineites*); Kozlov, 1988: 55 (?*Tineites*).
SI (larva)/not stated (6 ex)/Russia: Siberia, Central Ural Mountains, Ufalei/Cenozoic.
Comment: Kozlov (1988) doubted its association with Tineidae.

sepositellus Rebel, 1934a: 12, fig. 5 (*Architinea*); Kusnezov, 1941: 68 (?*Architinea*); Kozlov, 1988: 37 (*Tineites*); Fletcher, 1940: 18 (*Tineitella*).
= Tineidae (s.l.); Rebel, 1934b: 373 (part).
AM (adult: whole body)/BPGM (HT: L-9)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

sucinacius Kozlov, 1987: 63, fig. 3 (*Tineites*).
AM (adult: whole body)/private collection, K. M. Sadilenko, Moscow, Russia (HT: 5-2-1)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Handschin, 1944: 8, pl. 3: 7–10, 13 (Tineidarum gen. indet.); Kozlov, 1988: 38 (*Tineites*) [multiple species?].
SI (larva and pupa)/NHMB/France: Lot Prov., Quercy (Phosphorites Fm.)/Rupelian, Early Oligocene.

GENUS *incertae sedis*

—Grimaldi and Engel, 2005: 575, fig. 13: 35 (Tineidae).
AM and T (larval case)/AMNH (1 ex: DR11-14)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Grimaldi and Nascimbene, 2010: 180 (Tineidae) [multiple species].
AM (adult: whole body)/?AMNH/USA: New Jersey, Middlesex Co., Sayreville (New Jersey Amber, Raritan Fm.)/Turonian, Late Cretaceous.
Comment: The authors mentioned these amber inclusions as “definitive representatives of the recent family Tineidae.”

—Jarzembowski, 1980: 269, fig. 55 (Tineidae).
CI (adult: whole body)/BMNH (1 ex: In.9614)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

—Kupryjanowicz, 2001: 62, fig. 81 (Tineidae).
AM (adult: whole body)/MEPA (1 ex: no. 16212)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.
Comment: The author stated that this record was based on an identification by Skalski.

—Menge, 1856: 28–29 (Tineidae) [multiple species].
AM (adult and larva)/not stated (67 ex: [lost?])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Menge, 1856: 28–29 (Tineidae) [multiple species].
AM and T (larval case)/not stated (2 ex: [lost?])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Poinar, 1992: 162, 282 (Tineidae).
AM (not stated)/?UCMP/Mexico: Chiapas, Simojovel (Mexican Amber, Simojovel Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

—Poinar *et al.*, 1991: 210, figs. 1–2 (Tineidae).
AM (adult: whole body)/AIOSU (1 ex: S-1-23)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Rosenkjaer, 1906: 96, 107, 115, 120, 132 (Møl-coconer [= moth cocoon]); Henriksen, 1933: 214 (Tineidae spp.).
SR (cocoon)/not stated/Denmark: Jutland, Grundudgravninger (unconsolidated sediments)/Holocene.
Comment: These fossils may represent the larval cases. Henriksen (1933) considered them to have been made by the extant *Tinea pellionella* and/or *Tineola bisselliella*.

—Skalski, 1976b: 199 (Tineidae).
AM (not stated)/not stated/Mexico: Chiapas, Simojovel (Mexican Amber, Simojovel Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

—Weitschat, 2009: 253, fig. 43 (Tineidae).
AM (larva and larval case)/DBRD/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Weitschat and Wichard, 1998: 198, pl. 79: a–c (Tineidae) [multiple species].
AM (larva and larval case)/RMOD (> 3 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Questionably placed in Tineidae

GENUS *incertae sedis*

—Skalski, 1973a: 157, fig. 3, pl. 36 (?Tineidae)
AM (adult: whole body)/PLUW (HT: no. 174, 9 IGUW/AWS)/Lithuania: Klaipedos, Palanga (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Family PSYCHIDAE Boisduval, 1829 [extant]

Subfamily OIKETICINAE Herrich-Schäffer, 1855 [extant]

—Sobczyk and Kobbert, 2009: 18, figs. 3, 5 (Oiketicinae) [multiple species].
AM and T (larval case)/private collection, Max J. Kobbert, Münster, Germany (2 ex: T279; T609)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Sobczyk and Kobbert, 2009: 18, fig. 4 (Oiketicinae).
AM (larval case with larva)/private collection, Max J. Kobbert, Münster, Germany (1 ex: T314)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Subfamily PSYCHINAE Boisduval, 1829 [extant]

PROUTIA Tutt, 1899 [extant]

—Sobczyk and Kobbert, 2009: 18, fig. 6 (*Proutia*).
AM and T (larval case)/private collection, Max J. Kobbert, Münster, Germany (1 ex: T338)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Subfamily EPICHNOPTERIGINAE Tutt, 1900 [extant]

REBELIA Heylaerts, 1900 [extant]

—Sobczyk and Kobbert, 2009: 13 [in abstract], 16 (*Rebelia*).
AM and T (larval case)/not stated/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Subfamily NARYCIINAE Tutt, 1900 [extant]

DAHLICA Enderlein, 1912 [extant]

triquetrella Hübner, 1813 (*Tinea*) [extant]; Sobczyk and Kobbert, 2009: 17, 19, figs. 9, 10 [fossil].
AM and T (larval case)/private collection, Max J. Kobbert, Münster, Germany (2 ex: T663; T729)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Subfamily TYPHONIINAE Lederer, 1853 [extant]

GENUS *incertae sedis*

—Sobczyk and Kobbert, 2009: 19, figs. 7, 8 (Typhoniinae).
AM and T (larval case)/private collection, Max J. Kobbert, Münster, Germany (1 ex: T338)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

SUBFAMILY *incertae sedis*

ADELOPSYCHE Cockerell, 1926: 17 (Cossidae); Kozlov, 1988: 34 (Psychidae).
Type species: *Adelopsyche frustrans* Cockerell, 1926.

frustrans Cockerell, 1926: 18, fig. 1 (*Adelopsyche*).
CI (adult: whole body)/UCNH (HT)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

PSYCHITES Kozlov, 1988: 34.
Type species: not designated.

pineellus Heer, 1849: 184 (*Psyche*); Kozlov, 1988: 34 (*Psychites*).
= *Psyche pincella* [sic]; Giebel, 1856: 189.
= *Psyche pioneela* [sic]; Scudder, 1891: 679.
CI and T (larval case)/private collection, “Herrn [Mr.] Lavater” [lost or now possibly in PMUZ]/Switzerland: Neuchâtel Canton, Oeningen (“Molasseformatien”)/Messinian, Late Miocene.

pristinellus Rebel, 1934a: 10, pl. 1: 4 (?*Sterrhopteryx*); Kozlov, 1988: 34 (*Psychites*); Sobczyk and Kobbert, 2009: 18, fig. 1 (“*Sterrhopteryx*”).
= “Psychiden-Sädke”; Rebel, 1934b: 373.

AM (larva and larval case)/BPGM (HT: H-8); private collection, Max J. Kobbert, Münster, Germany (1 ex: T144)/ Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Kozlov, 1988: 34, fig. 6 (*Psychites*).
AM and T (larval case)/PIRAS (1 ex: PIN 363/79)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

BALTOPSYCHE Sohn, **gen. nov.** A replacement name for *Palaeopsyche* Sobczyk and Kobbert, 2009.
= *PALAEOPSYCHE* Sobczyk and Kobbert, 2009: 17. A junior homonym of *Palaeopsyche* Perkins, 1905 [Lepidoptera: Epipyropidae].
Type species: *Palaeopsyche secundum* Sobczyk and Kobbert, 2009.

secundum Sobczyk and Kobbert, 2009: 17, fig. 11 (*Palaeopsyche*). **comb. nov.**
AM and T (larval case)/private collection, Max J. Kobbert, Münster, Germany (HT: T666; PT: T349; T618; T557); private collection, Thomas Sobczyk, Hoyerswerda, Germany (PT: ST15)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

transversum Sobczyk and Kobbert, 2009: 20, fig. 12 (*Palaeopsyche*). **comb. nov.**
AM and T (larval case)/private collection, Max J. Kobbert, Münster, Germany (HT: T316; PT: T710); private collection, Thomas Sobczyk, Hoyerswerda, Germany (PT: 021TS)/Baltic Region (Baltic Amber, Prussian Fm.)/ Lutetian, Middle Eocene.

GENUS *incertae sedis*

—Bachofen-Echt, 1949: 147, fig 133–137 (Psychidae) [multiple species].
= Tineidae (s. l.); Rebel, 1934b: 373 (part)
AM and T (larva and larval case)/BPGM (> 1 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Menge, 1856: 27–28 (Psychidae, 7 species).
AM and T (larval case)/not stated (15 ex: [lost?])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Nuorteva and Kinnunen, 2008: 117, fig. 9 (Psychidae).
AM and T (larval case)/FMUH (1 ex: no. 5640)/Lithuania: Klaipedos, Palanga (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Perkovsky *et al.*, 2003: 427, fig. 3 (Psychidae) [multiple species].
AM and T (larva and larval case)/NASU/Ukraine: northern Rovno and Zhitomir Regions, Klesov locality (Rovno Amber, Obukhov Fm.)/Priabonian, Late Eocene.

—Sobczyk and Kobbert, 2009: 15 (Psychidae) [multiple species].
AM and T (larval case)/private collection, Max J. Kobbert, Münster, Germany (56 ex: T103; T183; T195; T197; T211; T219; T221; T231; T232; T269; T322; T339; T376; T389; T416; T430; T439; T452; T482; T491; T517; T518; T519; T529; T531; T543; T602; T603; T604; T605; T606; T608; T610; T611; T612; T648; T650; T651; T664; T667; T669; T670; T697; T703; T704; T705; T706; T707; T708; T709; T722; T723; T724; T725; T726; T727); private collection, Thomas Sobczyk, Hoyerswerda, Germany (13 ex: 004TS; 006TS; 008TS; 009TS; 014TS; 015TS; 016TS; 022TS; 023TS; 024TS; 026TS; 027TS; 041TS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Weitschat, 2009: 253, figs. 41, 44 (Psychidae) [multiple species].
AM and T (larval case)/DBRD/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Weitschat and Wichard, 1998: 198, pl. 79: f–h (Psychidae) [multiple species].
AM and T (larva or larval case)/RMOD (> 3 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Questionably placed in Psychidae

—Lewis, 1976: 345, fig. 1a (Psychidae).
CI and T (feeding mark)/CSUM/USA: SW Montana, Madison County, Ruby River Basin between Peterson and Mormon Creeks (Renova Fm.)/Chattian, Late Oligocene.
Fossil plant host: Fagaceae —*Quercus convexa* Lesq. [extant].

FAMILY *incertae sedis*

GENUS *incertae sedis*

—Hurd *et al.*, 1962: 110 (Tineoidea).
AM (adult: whole body)/?UCMP/Mexico: Chiapas, Simojovel (Mexican Amber, Simojovel Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

—Perkovsky *et al.*, 2003: 427 (Tineoidea) [multiple species].
AM (adult: whole body)/NASU/Ukraine: northern Rovno and Zhitomir Regions, Klesov locality (Rovno Amber, Obukhov Fm.)/Priabonian, Late Eocene.

Superfamily GRACILLARIOIDEA Stainton, 1854 [extant]

Family BUCCULATRICIDAE Fracker, 1915 [extant]

BUCCULATRIX Zeller, 1839 [extant]

platani Kozlov, 1988: 39, pl. 2: 6 (*Bucculatrix*).
CI and T (leaf mine)/PIRAS (HT: PIN 2383/213)/Kazakhstan: Kzyl-Ordinsky Region, Chilinsky, northwest spur of Karatau mountain range, Kzyl-Dzhar (Beleuty Fm.)/Turonian, Late Cretaceous.
Fossil plant host: Platanaceae —*Platanus cuneifolia* Bronn.

thoracella Thunberg, 1794 (*Tinea*) [extant]; Straus, 1977: 58, fig. 61 [fossil].
CI and T (leaf mine)/GPUG (1 ex: no. 18422)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).
Fossil plant host: Malvaceae —*Tilia* sp.
Comment: Straus (1977) suggested that this mine is identical to leaf mines on *Tilia* made by the extant species *Bucculatrix thoracella*.

—Opler, 1973: 1321, fig. 1c (*Bucculatrix*).
CI and T (leaf mine)/UCMP/USA: Nevada, Buffalo Canyon (Buffalo Canyon Fm.)/Langhian, Middle Miocene.
Fossil plant host: Fagaceae —*Quercus hanibalii* Dorf.

—Opler, 1982: 145 (*Bucculatrix*).
CI and T (leaf mine)/not stated [?UCMP]/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.
Fossil plant host: Fagaceae —*Quercus drymeja* Unger [reported as “*Zelkova*” *drymeja* by Opler (1982)]

Family GRACILLARIIDAE Stainton, 1854 [extant]

Subfamily PHYLLOCNISTINAE Herrich-Schäffer, 1857 [extant]

cf. *PHYLLOCNISTIS* Zeller, 1848 [extant]

cf. *liriodendronella* Clemens, 1863 (*Phyllocnistis*) [extant]; Chambers, 1882: 529 [fossil].
= tineid or tortricid leaf mines; Hagen, 1882: 265.
CI and T (leaf mine)/MCZH/USA: central Kansas (Dakota Fm.)/late Albian, Early Cretaceous.
Fossil plant host: ?Magnoliaceae.

cf. *liquidambarisella* Chambers, 1875 (*Phyllocnistis*) [extant]; Chambers, 1882: 529 [fossil].
= tineid or tortricid leaf mines; Hagen, 1882: 265.
CI and T (leaf mine)/MCZH/USA: central Kansas (Dakota Fm.)/late Albian, Early Cretaceous.
Fossil plant host: ?Altingiaceae.
Comment: Chambers (1882) linked this fossil with the extant species solely by the host association.

—Jarzembowski, 1995: 146 (*Phyllocnistis*).
CI and T (leaf mine)/BMNH/United Kingdom: Hampshire, East Dorset, Bournemouth (Branksome Sand Fm.)/Lutetian, Middle Eocene (McElwaine, 1998).

—Knowlton, 1917: 80, pl. 33: 5 (*Phyllocnistis*).
CI and T (leaf mine)/USNM [not found in an inventory by J.-C. Sohn at USNM]/USA: Wyoming, Lincoln County, Cumberland (Frontier Fm.)/Turonian, Late Cretaceous.
Fossil plant host: ?Staphyleaceae —?*Staphylea fremonti* Knowlt.
Comment: This record was based on identification by Busck.

—Labandeira, 2002a: 47, figs. 4c–d (phyllocnistine).
CI and T (leaf mine)/TBMM (1 ex: no. 94055a)/Canada: British Columbia, McAbee/Lutetian, Middle Eocene.

—Labandeira *et al.*, 1994: 12279, figs. 1i–l (*Phyllocnistis*).
CI and T (leaf mine)/FMUF (2 ex: UF4818; UF15709-7351)/USA: Kansas, Cloud Co., Braun's Ranch (Dakota Fm.)/Albian–Cenomanian, Late Cretaceous.
Fossil plant host: Chloranthaceae —*Densinervum* sp. and *Crassidenticulum decurrens* Upchurch and Dilcher; Lauraceae —*Pabiana variloba* Upchurch and Dilcher.
Comment: Kristensen and Skalski (1998: 16) regard these mines as “the earliest convincing evidence for the existence of the Ditrysia.”; also see Davis (1994).

—Stephenson, 1991: 168 (*Phyllocnistis*); Stephenson and Scott, 1992: 547, fig. 5: a; Lang *et al.*, 1995: 158, fig. 3c, pl. 2: 1.
CI and T (leaf mine)/BMNH (1 ex: V.50974)/United Kingdom: Hampshire, East Dorset, Bournemouth (Branksome Sand Fm.)/Lutetian, Middle Eocene (McElwaine, 1998).
Comment: The authors used similarity to recent leaf mines to characterize this fossil. It is not clear that they intended to link the fossil taxonomically with extant species (see Lang *et al.* 1995 for the analog).

Subfamily GRACILLARIINAE Stainton, 1854 [extant]

cf. *ACROCERCOPS* Wallengren, 1881 [extant]

—Opler, 1973: 1321 (cf. *Acrocercops*).
CI and T (leaf mine)/UCMP/USA: Oregon, Harney Co. (Trout Creek Fm.)/Serravallian, Middle Miocene.
Fossil plant host: Fagaceae —*Quercus consimilis* Newb.

cf. *CALOPTILIA* Hübner, 1825 [extant]

cf. *alchimiella* Scopoli, 1763 (*Palaena*) [extant]; Straus, 1977: 58 [fossil].
CI and T (leaf mine)/GPUG (1 ex: no. 22788)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene.
Fossil plant host: Fagaceae —*Fagus* cf. *orientalis* Lipsky.
Comment: Straus (1977) associated this fossil with the leaf mine made by the extant *Caloptilia alchimiella*.

cf. *roscipennella* Hübner, 1796 (*Tinea*) [extant]; Straus, 1977: 58, fig. 76 [fossil]; Givulescu, 1984: 6, pl. 3: 4 [fossil].
CI and T (leaf mine)/GPUG (1 ex: no. 22440); IGGB (1 ex: no. P.25789)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene.
Fossil plant host: Betulaceae; Juglandaceae —*Juglans* sp.
Comment: Straus' (1977) identification was based on similarity to the extant species in leaf mine shape and host association. Givulescu (1984) reported a leaf mine fossil which he considered to be same as cf. *Caloptilia roscipennella*, identified by Straus (1977).

cf. *sassafrasella* Chambers, 1876 (*Gracilaria*) [extant]; Chambers, 1882: 529 [fossil].
= tineid or tortricid leaf mines; Hagen, 1882: 265.
CI and T (leaf mine)/MCZH/USA: central Kansas (Dakota Fm.)/late Albian, Early Cretaceous.
Fossil plant host: Lauraceae —"*Sassafras*" *cretaceum* Newbe.
Comment: Chambers (1882) linked this fossil with the extant species solely by host association.

—Lewis, 1969: 1210 (Nepticulidae); Opler, 1973: 1322 (*Caloptilia*).
CI and T (leaf mine)/CSUM/USA: E Washington State, Spokane, Brickyard (Latah Fm.)/Serravalian, Middle Miocene.
Fossil plant host: ?Fagaceae —?*Quercus*.

—Straus, 1977: 58, fig. 60 (*Coriscium* [a synonym of *Caloptilia*]).
CI and T (leaf mine)/GPUG (1 ex: no. 30838)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).
Fossil plant host: Magnoliaceae —*Magnolia*; or Oleaceae —*Syringa*.
Comment: The author's identification was based on similarity to the extant fauna in leaf mine shape.

GRACILLARIITES Kozlov, 1987: 67.
Type species: not designated.

lithuanicus Kozlov, 1987: 68, fig. 5a (*Gracillariites*).
AM (adult: whole body)/PAML (HT: Ap-9983)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

mixtus Kozlov, 1987: 68, figs. 5b, 5c (*Gracillariites*).
AM (adult: whole body)/private collection, K. M. Sadilenko, Moscow, Russia (HT: 6-1-1)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Jarzembowski, 1980: 274, fig. 64 (uncertain, species H); Kozlov, 1988: 40 (*Gracillariites*).
CI (adult: partial body and wings)/BMNH (1 ex: I.8809)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

cf. *PARORNIX* Spuler, 1910 [extant]

—Straus, 1977: 59, fig. 49 (cf. *Parornix*).
CI and T (leaf mine)/GPUG (1 ex: no. 15876/a)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).
Fossil plant host: Rosaceae —*Amelanchier* sp.
Comment: The author's identification was based on similarity to extant species in leaf mine shape and host association.

Subfamily LITHOCOLLETINAE Stainton, 1854 [extant]

cf. *CAMERARIA* Chapman, 1902 [extant]

cf. *aceriella* Clemens, 1859 (*Lithocolletis*) [extant]; Chambers, 1882: 529 [fossil].
= tineid or tortricid leaf mines; Hagen, 1882: 265.
CI and T (leaf mine)/MCZH/USA: central Kansas (Dakota Fm.)/late Albian, Early Cretaceous.
Fossil plant host: Sapindaceae —*Acer* sp.
Comment: Chambers (1882) linked this fossil with the extant species solely on the basis of host association.

—Opler, 1973: 1321 (cf. *Cameraria*).
CI and T (leaf mine)/UCMP/USA: Idaho, Thorn Creek (Payette Fm.)/Tortonian, Late Miocene.
Fossil plant host: Fagaceae —*Quercus simulata* Knowlt and ?*Lithocarpus* sp.

cf. *PHYLLONORYCTER* Hübner, 1822 [extant]

maestingella Müller, 1764 (*Phalaena Tinea*) [extant]; Straus, 1977: 59, fig. 59 (*Lithocolletis*) [fossil].
CI and T (leaf mine)/GPUG (2 ex: no. 30057; no. 15026)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).
Fossil plant host: Fagaceae —*Fagus* sp.
Comment: Straus (1977) assigned these fossil mines to the extant species *Phyllonorycter maestingella*, based on similarity in leaf mine shape and host association.

oliveirae Martins-Neto, 1989: 381, pl. 1: d (*Phyllonorycter*).
CI and T (leaf mine)/IGUSP (HT: GP/1T-1645)/Brazil: São Paulo, Taubaté, Estiva District, Argila Vírgllio, Mineraçáo Company (Tremembé Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.
Fossil plant host: Symplocaceae —*Symplocos* sp.

—Freeman, 1965: 1069, fig. 1 (*Lithocolletis*).
CI and T (leaf mine)/GSCBO/Canada: British Columbia, White Lake Basin/Priabonian, Late Eocene.

—Krassilov and Shuklina, 2008: 243, fig. 3i (lithocolletiform mines).
CI and T (leaf mine)/IEUH (>1 ex: IG1-644; etc.)/Israel: Negev Desert, central Negev, Makhtesh Ramon (Upper Hatira Fm.); Negev Desert, southern Negev, Arava Valley, Gerofit (Ora Fm.)/Turonian, Late Cretaceous.
Fossil plant host: Myrtales —*Dewalquea gerofitica* (Dobruskina) Krassilov.

—Lewis, 1985: 257, fig. 21 (?*Lithocolletis*).
CI and T (leaf mine)/UIMM (1 ex: T-0069)/USA: northern Idaho, Clarkia locality P-33 (Latah Fm.)/Serravalian, Middle Miocene.
Fossil plant host: Fagaceae —*Quercus* sp.

—Opler, 1973: 1321, fig. 1d (*Lithocolletis*).

CI and T (leaf mine)/UCMP/USA: Nevada, Nye Co., Cedar Mountains, Upper Goldyke (Esmeralda Fm.)/Serravallian, Middle Miocene.

Fossil plant host: Fagaceae —*Quercus hanibalii* Dorf.

—Opler, 1973: 1321 (*Lithocolletis*).

CI and T (leaf mine)/UMCP/USA: Nevada, SW Mineral County, Hawthorn, Stewart Valley Fossil Beds (Savage Canyon Fm.)/Serravalian, Middle Miocene (Perkins *et al.* 1998).

Fossil plant host: Salicaceae —*Populus trichocarpa* var. *ingrata* (Jeps.) Parish.

—Stephenson, 1991: 171 (Mine Type TLm5); Lang *et al.*, 1995: 155, fig. 2b, pl. 1: 1–2 (?*Lithocolletis*).

CI and T (leaf mine)/BMNH (1 ex: V.49146)/United Kingdom: Hampshire, East Dorset, Bournemouth (Branksome Sand Fm.)/Lutetian, Middle Eocene (McElwaine, 1998).

Comment: The authors used similarity to various recent leaf mines to characterize this fossil. It is not clear that they intended to link the fossil taxonomically with extant species (see Lang *et al.* 1995 for the modern analog cited).

SUBFAMILY *incertae sedis*

GENUS *incertae sedis*

—Labandeira *et al.*, 2002a: 315, fig. 12 (a gracillariid leaf mine).

CI and T (leaf mine)/DMNH (6 ex: no. 7199; no. 7263; no. 7313; no. 7325; no. 7498; no. 20023)/USA: SW North Dakota, Williston Basin (Hell Creek Fm.)/latest Maastrichtian, Late Cretaceous.

Fossil plant host: Laurales (cf. Lauraceae) —*Marmarthia pearsonii* Johnson.

—Poinar and Brown, 2002: 131, fig. 12 (Gracillariidae).

AM and T (leaf mine)/AIOSU (1 ex; Sd-9-125)/Mexico: Chiapas, Simojovel (Mexican Amber, Simojovel Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

Fossil plant host: Fabaceae —*Hymenaea mexicana* Poinar and Brown.

—Poinar *et al.*, 1991: 210, figs. 3–5 (Gracillariidae).

AM (adult: whole body)/AIOSU (1 ex: S-1-24)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Ross *et al.*, 2010: 234 (Gracillariidae).

AM (not stated)/not stated/Myanmar: Kachin Prov., Hukawang Valley (Burmese Amber, “channel facies” of an unnamed formation)/late Aptian, Early Cretaceous.

Questionably placed in Gracillariidae

—Hickey and Hodges, 1975: 718–719, fig. 2a (?*Phyllocnistis*); Kozlov, 1988: 55 (uncertain).

CI and T (leaf mine)/USNM (1 ex: 208538)/USA: Wyoming, Sheridan Pass area southwest of Dubois (Wind River Fm.)/late Ypresian, Early Eocene.

Fossil plant host: Meliaceae —*Cedrela* sp.

—Wilf *et al.*, 2005: 8945, fig. 1 (?gracillariid mines).

CI and T (leaf mine)/MPEF (1 ex: Pb 983)/Argentina: Patagonia, Chubut, Laguna del Hunco (Tufolitas Laguna del Hunco)/Ypresian, Early Eocene (Genise and Petrulevicius, 2001).

Fossil plant host: Sapindaceae —“*Cupania*” *grosse-serrata* (Engelh.) Berry.

Superfamily YPONOMEUTOIDEA Stephens, 1829 [extant]

Family ARGYRESTHIIDAE Bruand, 1850 [extant]

Questionably placed in Argyresthiidae

ARGYRESTHITES Rebel, 1934a (Argyresthiidae): 5; Skalski, 1976b: 201 (?Argyresthiidae); Keilbach, 1982: 314 (?Yponomeutidae); Kozlov, 1988: 53 (uncertain).
Type species: *Argyresthites succinella* Rebel, 1934.

balticellus Rebel, 1936: 175, fig. 8 (*Argyresthites*); Skalski, 1976b: 201 (?*Argyresthites*).
AM (adult: whole body)/MNHU (HT: [not found in an inventory by J.-C. Sohn at MNHU])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

succinellus Rebel, 1934a: 5, fig. 2 (*Argyresthites*).
= Hyponomeutidae; Rebel, 1934b: 373.
AM (adult: whole body)/BPGM (HT: L-2)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Family PRAYDIDAE Moriuti, 1977 [extant]

Questionably placed in Praydidae

cf. *PRAYS* Hübner, 1826 [extant]

—Lang *et al.*, 1995: 154–155, fig. 2a, pl. 1: 7 (cf. *Prays*).
CI and T (leaf mine)/BMNH (1 ex: V.50937)/United Kingdom: Hampshire, East Dorset, Bournemouth (Branksome Sand Fm.)/Lutetian, Middle Eocene (McElwaine, 1998).
Comment: The authors used similarity to recent leaf mines to characterize this fossil. It is not clear they intended to link the fossil taxonomically with extant species (see Lang *et al.* 1995 for the putative modern analog).

GENUS *incertae sedis*

—Stephenson, 1991: 159 (Mine Type KLm4b).
CI and T (leaf mine)/GBIU (1 ex: IU15706-4609)/USA: Kansas and Nebraska, Braun Ranch, Hoisington and other localities [not specified] (Dakota Fm.)/late Albian, Early Cretaceous.
Comment: The author suggested that the fossil is similar to leaf mines made by *Prays oleae* larvae.

Family YPONOMEUTIDAE Stephens, 1829 [extant]

Questionably placed in Yponomeutidae

GENUS *incertae sedis*

—Skalski, 1976c: 228, fig. 22 (Yponomeutidae).
CO (adult: whole body)/not stated/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/Late Pleistocene.

Family PLUTELLIDAE Guenée, 1845 [extant]

PLUTELLITES Kozlov, 1988: 38.
Type species: not designated.

acutipenellus Rebel, 1936: 174, fig. 6 (*Epinomeuta*); Kusnezov, 1941: 68 (?*Epinomeuta*); Kozlov, 1988: 38 (*Plutellites*).
AM (adult: whole body)/MNHU (HT: MB-N.5 [not found in an inventory by J.-C. Sohn at MNHU])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

inversellus Rebel, 1936: 173, fig. 5 (*Epinomeuta*); Kusnezov, 1941: 68 (?*Epinomeuta*); Kozlov, 1988: 38 (*Plutellites*).
= *Epinomeuta universella* [sic]; Skalski, 1976b: 201.
AM (adult: whole body)/MNHU (HT: MB-L6)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

minorellus Rebel, 1936: 174, fig. 7 (*Epinomeuta*); Kusnezov, 1941: 68 (?*Epinomeuta*); Kozlov, 1988: 38 (*Plutellites*).
AM (adult: whole body)/MNHU (HT: MB-L8)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

tenebricus Kozlov, 1988: 39, fig. 7 (*Plutellites*).
AM (adult: whole body)/PIRAS (HT: PIN 363/80)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—MacKay, 1969: 1173, figs. 1, 2, 5a (?Plutellidae); Kozlov, 1988: 38 (*Plutellites*).
AM (larva: whole body)/ZMCD (1 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—MacKay, 1969: 1178, figs. 4, 5c (?Plutellidae); Kozlov, 1988: 38 (*Plutellites*).
AM (1st instar larva: whole body)/ZMCD (1 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Questionably placed in Plutellidae

EPINOMEUTA Rebel, 1936: 172 (Yponomeutidae); Kozlov, 1988: 38 (Plutellidae); Carpenter, 1992: 380 (?Tineidae).
Type species: *Epinomeuta truncatipennella* Rebel, 1936.

truncatipennella Rebel, 1936: 172, fig. 4 (*Epinomeuta*).
AM (adult: whole body)/MNHU (HT: MB-L7)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

SCYTHROPITES Rebel, 1936: 169 (Yponomeutidae); Keilbach, 1982: 315 (Scythriidae [sic?]); Kozlov, 1988: 39 (Plutellidae).
Type species: *Scythropites balticella* Rebel, 1936.

balticellus Rebel, 1936: 169, fig. 3 (*Scythropites*).
AM (adult: whole body)/GPUT (HT: n 3B 660)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

GENUS *incertae sedis*

—Jarzembowski, 1980: 275, fig. 58 (species K).
CI (adult: partial body and wings)/BMNH (1 ex: In.25219)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

—Skalski, 1976b: 201 (?Plutellidae).
AM (not stated)/not stated/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Skalski, 1977: 20, pl. 8: 1, 2 (inclusion 2).
AM (adult: whole body)/MEPA (1 ex: G/19 No. 1927/45, 6 MZ/AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Family HELIODINIDAE Heinemann and Wocke, 1876 [extant]

Questionably placed in Heliodinidae

GENUS *incertae sedis*

—Skalski, 1990c: 164 [in table] (Heliodinidae).
AM (not stated)/not stated/Italy: Sicily, a beach on the Simeto River (Sicilian Amber)/Rupelian, Early Oligocene (Skalski and Veggiani, 1990).

Family LYONETIIDAE Stainton, 1854 [extant]
= Prolyonetiidae Kusnezov, 1941: 45

Subfamily CEMIOSTOMINAE Spuler, 1898 [extant]

PROLYONETIA Kusnezov, 1941: 43 (Lyonetiidae); Kozlov, 1988: 39 (Leucopterinae [= Cemiostominae]).
Type species: *Prolyonetia cockerelli* Kusnezov, 1941.

cockerelli Kusnezov, 1941: 45, figs. 30–32 (*Prolyonetia*).
= *Prolyonetia zeckerelli* [sic]; Larsson, 1978: 122.
AM (adult: whole body)/PIRAS (HT: no. 12)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.
Comment: The author likened this fossil to the extant *Bucculatrix* and *Oenophila,* both no longer placed in Lyonetiidae.

Questionably placed in Lyonetiidae

cf. *LYONETIA* Hübner, 1825 [extant]
—Stephenson, 1991: 170 (Mine Type TLm4); Lang *et al.*, 1995: 152, fig. 1e, pl. 1: 3, 5.
CI and T (leaf mine)/BMNH (1 ex: V.48272)/United Kingdom: Hampshire, East Dorset, Bournemouth (Branksome Sand Fm.)/Lutetian, Middle Eocene (McElwaine, 1998).
Comment: Stephenson (1991) pointed to *Incurvaria pectinea* Haworth as a recent analog of this leaf mine fossil. Lang *et al.* (1995) noted *Lyonetia prunifoliella* Hübner as a candidate recent analog.

GENUS *incertae sedis*

—Jarzembowski, 1980: 271, fig. 57 (species C).
CI (adult: whole body)/BMNH (2 ex: In.25512/25252; In.17142)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.
Comment: Jarzembowski (1980) noted its resemblance to the extant *Leucoptera* and *Bedellia*. The latter is no longer considered a lyonetiid.

—Opler, 1973: 1322 (Lyonetiidae).
CI (cocoon)/UCMP/western North America (no specific locality)/Middle Cenozoic (no specific age).

—Rebel, 1934a: 16 (Coleophoridae); Larson, 1978: 123 (?Coleophoridae); Keilbach, 1982: 314 (Lyonetiidae).
AM and T (larval case)/BPGM (no. 173 [not found in an inventory by J.-C. Sohn at BPGM])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Clade Apoditrysia Minet, 1983

Superfamily GELECHIOIDEA Stainton, 1854 [extant]

Family AUTOSTICHIDAE Le Marchand, 1947 [extant]

Subfamily SYMMOCINAE Gozmany, 1957 [extant]

MICROSYMMOCITES Skalski, 1977: 18.
Type species: *Microsymmocites kuznetzovi* Skalski, 1977.
= *Microsymmocytes* [sic]; Keilbach, 1982: 316.

kuznetzovi Skalski, 1977: 19, figs. 16–17, pl. 6: 1, pl. 7: 1 (*Microsymmocites*).
AM (adult: whole body)/MEPA (HT: 114/34 G/44 No. 2015/1, 2 MZ/AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Questionably placed in Autostichidae

SYMMOCITES Kusnezov, 1941: 54 (Gelechiidae); Carpenter, 1992: 380 (uncertain).
Type species: *Symmocites rohdendorfi* Kusnezov, 1941.
= *Symmocytes* [sic]; Keilbach, 1982: 316.

rohdendorfi Kusnezov, 1941: 56, figs. 39–44 (*Symmocites*).
AM (adult: whole body)/PIRAS (SY: no. 9; no. 13)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

OEGOCONIITES Kusnezov, 1941: 51 (Gelechiidae); Skalski, 1976b: 203 (Oecophoridae); Kozlov, 1988: 42 (Xyloryctidae); Poinar, 1992: 162–163 (Symmocidae).
Type species: *Oegoconiites borisjaki* Kusnezov, 1941.

borisjaki Kusnezov, 1941: 53, figs. 37–38 (*Oegoconiites*).
AM (adult: whole body)/PIRAS (HT: no. 4)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Family COLEOPHORIDAE Bruand, 1850 [extant]

Subfamily COLEOPHORINAE Bruand, 1850 [extant]

cf. *COLEOPHORA* Hübner, 1822 [extant]

—Givulescu, 1984: 131 (cf. ?*Coleophora* sp.).
CI and T (leaf mine)/not stated [?IGGB]/Romania: Maramures Co., Chiuzbaia, "F" site/Late Miocene.

—Krassilov, 2007: 17, fig. 2 (feeding damage typical of coleophorid miners).
CI and T (leaf mine)/IEUH (> 1 ex: IG1-847; etc.)/Israel: Negev Desert, central Negev, Makhtesh Ramon (Upper Hatira Fm.); Negev Desert, southern Negev, Arava Valley (Ora Fm.)/Albian–Turonian, Late Cretaceous.
Fossil plant host: Myrtales —*Dewalquea gerofitica* (Dobruskina) Krassilov.

—Labandeira, 2002a: 47, figs. 6e–f (cf. *Coleophora*).
CI and T (leaf mine)/TBMM (1 ex: no. 77608)/USA: Washington State, Ferry Co., Republic (Klondike Mountain Fm.)/Lutetian, Middle Eocene.

—Straus, 1977: 58, fig. 56 (cf. *Coleophora*) [multiple species].
CI and T (leaf mine)/GPUG (7 ex: no. 21040; no. 21695/a; no. 22549/a; no. 22858; no. 22907; no. 22996/a; no. 30809)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene.
Fossil plant host: Tiliaceae —*Tilia* sp.
Comment: The author tentatively identified these as the leaf mines made by various species of *Coleophora*.

Family COSMOPTERIGIDAE Heinemann and Wocke, [1876] [extant]

Subfamily CHRYSOPELEIINAE Mosher, 1916 [extant]

Questionably placed in Chrysopeleiinae

—Skalski, 1976b: 199 (?Walshiidae [= Chrysopeleiinae]).
AM (not stated)/not stated/Mexico: Chiapas, Simojovel (Mexican Amber, Simojovel Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

SUBFAMILY *incertae sedis*

—Poinar, 1992: 163 (Cosmopterigidae) [multiple species].
AM (not stated)/?UCMP/Mexico: Chiapas, Simojovel (Mexican Amber, Simojovel Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

—Poinar, 1992: 163, 287 (Cosmopterigidae) [multiple species].
AM (not stated)/not stated/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Skalski, 1976b: 199 (Cosmopterigidae).
AM (not stated)/not stated/Mexico: Chiapas, Simojovel (Mexican Amber, Simojovel Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.
Comment: It is not clear whether or not Skalski (1976b) and Poinar (1992) were referring to the same fossil specimens.

Family BLASTOBASIIDAE Meyrick, 1894 [extant]

GENUS *incertae sedis*

—Poinar, 1992: 163, 287 (Blastobasiidae) [multiple species].
AM (not stated)/not stated/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

Family ELACHISTIDAE Bruand, 1850 [extant]

Subfamily DEPRESSARIINAE Meyrick, 1883 [extant]

DEPRESSARITES Rebel, 1936: 175.
Type species: *Depressarites levipalpella* Rebel, 1936.
= *Depressariites* [sic]; Kozlov, 1988: 44.

blastuliferellus Rebel, 1936: 177 (*Depressarites*); Skalski, 1976b: 202 (?*Depressarites*).
AM (adult: whole body)/MNHU (HT: no number; 1 ex: N 24 [both not found in an inventory by J.-C. Sohn at MNHU])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

levipalpellus Rebel, 1936: 175, fig. 9 (*Depressarites*).
AM (adult: whole body)/GPUT (not stated)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

PALAEODEPRESSARIA Skalski, 1979b: 101.
Type species: *Palaeodepressaria hannemanni* Skalski, 1979.

hannemanni Skalski, 1979b: 101, figs. 1–5, pl. 1–2 (*Palaeodepressaria*).
AM (adult: whole body)/MNHU (HT: MB L/11=LEP.SUCC.134 MB/AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Questionably placed in Depressarinae

GENUS *incertae sedis*

—Stephenson, 1991: 165 (Mine Type KLm13).
CI and T (leaf mine)/GBIU (1 ex: IU15708-1519)/USA: Kansas and Nebraska, Braun Ranch, Hoisington and other localities [unspecified] (Dakota Fm.)/late Albian, Early Cretaceous.
Comment: The author suggested as recent analogs of these fossils the leaf mines made by *Agonopterix senecionsis* larvae.

Subfamily ELACHISTINAE Bruand, 1850 [extant]

ELACHISTITES Kozlov, 1987: 64.
Type species: not designated.

inclusus Kozlov, 1987: 64, fig. 4a (*Elachistites*).
AM (adult: whole body)/private collection, K. M. Sadilenko, Moscow, Russia (HT: 4-3-3)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

sukatshevae Kozlov, 1987: 66. figs. 4b, 4c (*Elachistites*).
AM (adult: whole body)/private collection, K. M. Sadilenko, Moscow, Russia (HT: 12-5/6-6)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

MICROPERITTIA Kozlov, 1987: 66.
Type species: *Microperittia probosciphera* Kozlov, 1987.
= *Baltonides* [sic] Skalski in Kosmowska-Ceranowicz and Popiolek, 1981: 10–11. Nomen nudum [no description].
= *Baltodines* Kupryjanowicz, 2001: 62. Nomen nudum [unnecessary emendation].

probosciphera Kozlov, 1987: 66, figs. 4d, 4e (*Microperittia*).
AM (adult: whole body)/private collection, K. M. Sadilenko, Moscow, Russia (HT: 15-2-5)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Skalski, 1976b: 205, fig. 13 (Heliodinidae); Skalski, 1977: 13, fig. 7; Kozlov, 1988: 42 (Elachistidae: *Microperittia*) [multiple species]; Skalski, 1990c: 163 (Heliodinidae); Poinar, 1992: 163 (Chrysoesthiidae).
= *Baltonides* [sic] *roeselliformis* Skalski in Kosmowska-Ceranowicz and Popiolek, 1981: 10–11, fig. 10. Nomen nudum [no description].
AM (adult: whole body)/MEPA (2 ex: no. 16523; no. 18778); not stated (ca. 20 samples)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

PALAEOELACHISTA Kozlov, 1987: 67.
Type species: *Palaeoelachista traugottolseni* Kozlov, 1987.

traugottolseni Kozlov, 1987: 67, fig. 4f (*Palaeoelachista*).
AM (adult: whole body)/private collection, K. M. Sadilenko, Moscow, Russia (HT: 2-1-8)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

PRAEMENDESIA Kozlov, 1987: 67.
Type species: *Praemendesia minima* Kozlov, 1987.

minima Kozlov, 1987: 67, fig. 4g (*Praemendesia*).
AM (adult: whole body)/private collection, K. M. Sadilenko, Moscow, Russia (HT: 14-2-6)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Subfamily ETHMIINAE Busck, 1909 [extant]

Questionably placed in Ethmiinae

GENUS *incertae sedis*

—Skalski, 1976b: 199 (Ethmiidae).
AM (not stated)/not stated/Mexico: Chiapas, Simojovel (Mexican Amber, Simojovel Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

Subfamily STENOMATINAE Meyrick, 1906 [extant]

HEXERITES Cockerell, 1933: 480 (Thyrididae); Kozlov, 1988: 54 (uncertain); Skalski, 1990b: 144 (Elachistidae, Stenomatinae).
Type species: *Hexerites primalis* Cockerell, 1933.
primalis Cockerell, 1933: 480 (*Hexerites*).
CI (adult: whole body)/UCNH/USA: Colorado, Rio Blanco Co., Piceance Creek Basin (Green River Fm.)/early Lutetian, Middle Eocene.

cf. *ETHMIA* Hübner, 1819 [extant]

mortuella Scudder, 1890: 603, pl. 15: 12, 17 (*Psecadia*); Kozlov, 1988: 54 (*incertae sedis*); Meyer, 2003: 224 (*Ethmia*).
CI (adult: whole body)/MCZH (HT: no. 8460/9630)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

Family MOMPHIDAE Herrich-Schäffer, 1857 [extant]

Questionably placed in Momphidae

cf. *ANYBIA* Stainton, 1854 [extant]; Kozlov, 1988: 53 (uncertain).

cuprella Rebel, 1934a: 9 (?*Anybia*); Kusnezov, 1941: 68 (Tineoderum gen.).
= Elachistidae; Rebel, 1934b: 373.
AM (adult: whole body)/BPGM (HT: [not found in an inventory by J.-C. Sohn at BPGM])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

GENUS *incertae sedis*

—Stephenson, 1991: 159 (Mine type KLm4a).
CI and T (leaf mine)/GBIU (1 ex: IU15703-4424)/USA: Kansas and Nebraska, Braun Ranch, Hoisington and other localities [unspecified] (Dakota Fm.)/late Albian, Early Cretaceous.
Comment: The author suggested leaf mines of *Mompha raschkiella* larvae as a recent analog of these fossils.

Family GELECHIIDAE Stainton, 1854 [extant]

cf. *EVIPPE* Chambers, 1873 [extant]

—Opler, 1973: 1321, 1322 (cf. *Evippe*).
CI and T (leaf mine)/UCMP/USA: Nevada, Lyon Co., near Yearington (Aldritch Station Fm.)/Zanclean, Early Pliocene.
Fossil plant host: Fagaceae —*Quercus hanibalii* Dorf.

cf. *RECURVARIA* Haworth, 1828 [extant]

cf. *nanella* [Denis and Schiffermüller], 1775 (*Tinea*) [extant]; Straus, 1977: 60, fig. 51 [fossil].
CI and T (leaf mine)/GPUG (1 ex: no. 12724/a)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).
Fossil plant host: Rosaceae —*Sorbus torminalis* L. [extant].
Comment: Straus (1977) stated that "the overall shape of the mine corresponds to ones caused by the extant species *Recurvaria nanella* but also possibly represents a closely related species."

GENUS *incertae sedis*

—Poinar, 1992: 287 (Gelechiidae).
AM (not stated)/not stated/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Ross *et al.*, 2010: 234 (Gelechiidae).
AM (not stated)/not stated/Myanmar: Kachin Prov., Hukawang Valley (Burmese Amber, "channel facies" of an unnamed formation)/late Aptian, Early Cretaceous.

—Skalski, 1976b: 203 (Gelechiidae).
AM (not stated)/not stated/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Skalski, 1976b: 199 (Gelechiidae).
AM (not stated)/not stated/Mexico: Chiapas, Simojovel (Mexican Amber, Simojovel Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

Family OECOPHORIDAE Bruand, 1849 [extant]

Subfamily OECOPHORINAE Bruand, 1849 [extant]

BORKHAUSENITES Rebel, 1934a: 6.
Type species: *Borkhausenites bachofeni* Rebel, 1934.

bachofeni Rebel, 1934a: 6, fig. 3, pl. 1: 2 (*Borkhausenites*).
AM (adult: whole body)/BPGM (HT: L-6)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

EPIBORKHAUSENITES Skalski, 1973a: 153.
Type species: *Epiborkhausenites obscurotrimaculatus* Skalski, 1973.

obscurotrimaculatus Skalski, 1973a: 154, fig. 1, 2, pl. 33–35 (*Epiborkhausenites*).
AM (adult: whole body)/PLUW (HT: no.16, 8 IGUW/AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

GLESSEUMEYRICKIA Kusnezov, 1941: 47.
Type species: *Glesseumeyrickia henrikseni* Kusnezov, 1941.

henrikseni Kusnezov, 1941: 48, figs. 33–34 (*Glesseumeyrickia*).
AM (adult: whole body)/PIRAS (HT: no. 10)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

cf. *HOFMANNOPHILA* Spuler, 1910 [extant]
= *Hophmannophila* [sic]; Skalski, 1976b: 202, 221.

—Skalski, 1976b: 202 (*Hophmannophila* [sic]).
AM (not stated)/not stated/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

NEOBORKHAUSENITES Skalski, 1977: 20.
Type species: *Borkhausenites incertella* Rebel, 1936.

incertellus Rebel, 1936: 178, fig. 10 (*Borkhausenites*)/Skalski, 1977: 20, fig. 3 (*Neoborkhausenites*).
AM (adult: whole body)/GPUT (HT: 3 B 665, No. 1388/1, 23 IGPT/AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

OECOPHORINITES Kozlov, 1988: 43.
Type species: not designated.

angustipennellus Rebel, 1936: 179, fig. 11 (*Borkhausenites*); Skalski, 1976b: 202 (?*Borkhausenites*); Kozlov, 1988: 43 (*Oecophorinites*).
AM (adult: whole body)/MNHU (HT: [not found in an inventory by J.-C. Sohn at MNHU])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

crassellus Rebel, 1936: 182, fig. 15 (*Borkhausenites*); Skalski, 1976b: 202 (?*Borkhausenites*); Kozlov, 1988: 43 (*Oecophorinites*).
AM (adult: whole body)/MNHU (HT: MB-L2)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

implicatellus Rebel, 1936: 181, fig. 13 (*Borkhausenites*); Skalski, 1976b: 202 (?*Borkhausenites*); Kozlov, 1988: 43 (*Oecophorinites*).
AM (adult: whole body)/MNHU (HT [not found in an inventory by J.-C. Sohn at MNHU])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

incolumnellus Rebel, 1934a: 8, pl. 1: 3 (*Borkhausenites*); Skalski, 1976b: 202 (?*Borkhausenites*); Kozlov, 1988: 43 (*Oecophorinites*).
= Oecophoridae; Rebel, 1934b: 373.
AM (adult: whole body)/BPGM (HT: L-7; 1 ex: L-4)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

ingentellus Rebel, 1936: 182 (*Borkhausenites*); Skalski, 1976b: 202 (?*Borkhausenites*); Kozlov, 1988: 43 (*Oecophorinites*).
AM (adult: whole body)/MNHU (HT: MB-L3)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

innominatus Kusnezov, 1941: 50, figs. 35–36; Kozlov, 1988: 43 (*Oecophorites*).
AM (adult: whole body)/PIRAS (HT: no. 11)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

vulneratellus Rebel, 1936: 180, fig. 12 (*Borkhausenites*); Skalski, 1976b: 202 (?*Borkhausenites*); Kozlov, 1988: 43 (*Oecophorinites*).
AM (adult: whole body)/BPGM (HT: L–5)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

PARABORKHAUSENITES Kusnezov, 1941: 49.
Type species: *Borkhausenites vicinella* Rebel, 1936.

vicinellus Rebel, 1936: 181, fig. 14 (*Borkhausenites*); Kusnezov,1941: 49 (*Paraborkhausenites*).
AM (adult: whole body)/MNHU (HT: MB-L1)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

SCHIFFERMUELLERIA Hübner, 1825 [extant]

jantharica Skalski, 1977: 17, figs. 12–14, pl. 3: 1, pl. 4: 1, pl. 5: 1 (*Schiffermuelleria*).
AM (adult: whole body)/MEPA (HT: 49/28 G/10 No. 1831/14, 1 MZ/AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

SUBFAMILY *incertae sedis*

GENUS *incertae sedis*

—Grimaldi and Engel, 2005: 577, fig. 13: 40 (Oecophoridae).
AM (adult: whole body)/AMNH/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Hurd *et al.*, 1962: 110 (Oecophoridae).
AM (not stated)/?UCMP/Mexico: Chiapas, Simojovel (Mexican Amber, Simojovel Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

—Kupryjanowicz, 2001: 62, fig. 82 (Oecophoridae) [multiple species].
AM (adult: whole body)/MEPA (3 ex: no. 17444; no. 17863; no. 19167)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.
Comment: The author stated that this record was based on an identification by Skalski.

—MacKay, 1969: 1176, figs. 3, 5b (?Oecophoridae).
AM (larva: whole body)/ZMCD/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Rebel, 1934a: 3, fig. 1, pl. 1: 1 (Tortricidae); Kusnezov, 1941: 69 (Oecophoridae).
AM (larva: whole body)/BPGM (1 ex: H-3)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Skalski, 1990c: 164 [in table] (Oecophoridae).
AM (not stated)/not stated/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

FAMILY *incertae sedis*

—Grimaldi and Engel, 2005: 577, fig. 13: 39 (gelechioid moth).
AM (adult: whole body)/AMNH (1 ex: DR14-278)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Kusnezov, 1941: 59, fig. 47 (Gelechiodeorum gen. et sp. no. 1, ?Oecophoridae); Kozlov, 1988: 54 (?Coleophomorpha).
AM (adult: whole body)/PIRAS (1 ex: no. 6)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Kusnezov, 1941: 60, figs. 48–49 (Gelechiodeorum gen. et sp. no. 2, ?Oecophoridae); Kozlov, 1988: 54 (?Coleophomorpha).
AM (adult: whole body)/PIRAS (1 ex: no. 17)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Jarzembowski, 1980: 269, fig. 56 (Gelechioidea).
AM (adult: partial body and wings)/BMNH (1 ex: In.9042)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

—Peñalver and Grimaldi, 2006: 3 (Gelechioidea).
AM (adult: whole body)/AMNH (1 ex: DR-18-1)/Dominican Republic: Cordillera Septentorial between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.
Comment: This moth is from the same piece of amber in which *Voltinia dramba* (Riodinidae) is included.

—Perkovsky *et al.*, 2003: 429 (Gelechioidea) [multiple species].

AM (adult)/NASU/Ukraine: northern Rovno and Zhitomir Regions, Klesov locality (Rovno Amber, Obukhov Fm.)/Priabonian, Late Eocene.

Questionably placed in Gelechioidea

YPSOLOPHUS auct Germar, 1837: [23] (Tineidae) (nec Fabricius, 1798 [extant]); Kozlov, 1988: 55 (Coleophoromorpha).

insignis Germar, 1837: [23], pl. 20 (*Ypsolophus*).
CI (adult: whole body)/not stated [lost?]/Germany: former Rhine Province, vicinity of Bonn/?Aquitanian, Early Miocene.

GENUS *incertae sedis*

—Skalski, 1977: 20, pl. 4: 2 (inclusion 2).
AM (adult: head)/MEPA (1 ex: G/22 No. 2001/5, 5 MZ/AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Superfamily ZYGAENOIDEA Latreille, 1809 [extant]

Family LIMACODIDAE Duponchel, 1845 [extant]

GENUS *incertae sedis*

—Blair, 1927: 140 (cf. *Limacodes*).
AS (adult: wings)/originally AOFT [not traced]/Trinidad: oil-bearing sand (Kerogen-rich sandstone)/?Gelasian, ?Late Pliocene.
Comment: The author suggested that it is allied to the extant genus *Limacodes*.

Family ZYGAENIDAE Latreille, 1809 [extant]

Subfamily PROCRIDINAE Boisduval, 1828 [extant]

—McNamara *et al.*, 2011: 2 (forester moths).
CI (adult: whole body)/FNSF (2 ex)/Germany: Hesse, S Frankfurt, near Darmstadt, Messel oil shale-layers (Messel Fm.)/early Lutetian, Middle Eocene.

Subfamily ZYGAENINAE Latreille, 1809 [extant]

cf. *NEUROSYMPLOCA* Wallengren, 1858 [extant]

oligocenica Fernández-Rubio and Nel, 2000: 8, figs. 1–5 (?*Neurosymploca*).
CI (adult: whole body)/MNHN (HT: MNHN-LP-R 55185 = no. 3754), private collection, Francine Papier, near Strasbourg, France (1 ex)/ France: Alpes-de-Haute-Provence, Céreste (Calcaires de Montfuron Fm. or Calcaites de Vachères Fm.)/Rupelian (= Stampien), Early Oligocene (Heie and Lutz, 2002).

cf. *ZYGAENA* Fabricius, 1775 [extant]
= *Zygaenites* (nec Burgeff, 1951); Reiss, 1936: 556. Nomen nudum [no description].
= *Palaeozygaena* Reiss, 1936: 556. Nomen nudum [no description].

miocaenica Reiss, 1936: 556, pl. 7 (?*Zygaena*).
CI (adult: whole body)/SMNS (HT: Nr. 22342)/Germany: Baden–Württemberg, Esslingen, Randecker Maar ("dysodile beds")/Burdigalian, Early Miocene.

turolensis Fernández-Rubio *et al.*, 1991: 80, figs. 2–13, 15: 3 (?*Zygaena*); Fernández-Rubio and Peñalver, 1994: 40, figs. 2–6.
CI (adult: whole body)/MNCN (HT: I-16888), MPMV (1295a-RM; 1295b-RM)/Spain: Teruel, Rubielos de Mora ("bituminous rhythmites")/Burdigalian, Early Miocene (Peñalver and Engel, 2006).

ZYGAENITES Burgeff, 1951: 3.
Type species: *Zygaenites controversus* Burgeff, 1951.

controversus Burgeff, 1951: 2–3, figs. 1c, 1d (*Zygaenites*).
CI (adult: whole body)/SMNS (HT and CHT)/Germany: Baden–Württemberg, Esslingen, Randecker Maar ("dysodile beds")/Burdigalian, Early Miocene.

GENUS *incertae sedis*

—Leestmans, 1983: 73, fig. 14 (Zygaenidae).
CI (adult: whole body)/ENSM (lost)/France: Bouches-du-Rhone, Aix-en-Provence ("laminites lacustres")/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).
Comment: Only a photo taken by Théobald in 1935 is extant.

Questionably placed in Zygaenidae

—de Serres, 1829: 230 (*Zygaena* [*s. l.*]).
= *Zyganena* [sic] sp.; Théobald, 1937: [in table 11].
CI (adult: not stated)/originally IGMF [lost?]/France: Bouches-du-Rhone, Aix-en-Provence ("laminites lacustres")/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).
Comment: Leestmans (1983) mentioned the possibility that the specimen in de Serres (1829) is the same as one of the fossils photographed by Théobald. The latter specimen is also missing.

Superfamily COSSOIDEA Leach, 1815 [extant]

Family COSSIDAE Leach, 1815 [extant]

KLEOPATHRA Martins-Neto, 1998a: 75.
Type species: *Kleopathra noctodiva* Martins-Neto, 1998.

nemogypsia Martins-Neto, 1998a: 76, fig. 1b (*Kleopathra*).
CI (adult: forewing)/DGUG (HT: UnG/IT-034)/Brazil: São Paulo, Tremembé City, near Padre Eternal, Fazenda Santa Fé (Tremembé Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

noctodiva Martins-Neto, 1998a: 76, fig. 1a (*Kleopathra*).
CI (adult: forewing)/DGUG (HT: UnG/IT-033)/Brazil: São Paulo, Tremembé City, near Padre Eternal, Fazenda Santa Fé (Tremembé Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

Questionably placed in Cossidae

GURNETIA Cockerell, 1921: 472 (Cossidae); Jarzembowski, 1980: 275 (?Cossidae); Carpenter, 1992: 380 (uncertain).
Type species: *Gurnetia durranti* Cockerell, 1921.

durranti Cockerell, 1921: 473, fig. 38 (*Gurnetia*); Jarzembowski, 1980: 275, figs. 60, 66.
CI (adult: partial forewing)/BMNH (HT: In.24324)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

GENUS *incertae sedis*

—Richter and Storch, 1980: 365, fig. 14 (Cossidae).
GC (adult: cuticular fragments)/FNSF/Germany: Hesse, S Frankfurt, near Darmstadt, Messel oil shale-layers (Messel Fm.)/early Lutetian, Middle Eocene.

Family CASTNIIDAE Boisduval, 1828 [extant]

DOMINICKUS Tindale, 1985: 35.
Type species: *Dominickus castinoides* Tindale, 1985.

castinoides Tindale, 1985: 35, figs. 1–3 (*Dominickus*).
CI (adult: forewings)/FMNH (HT: P.22949)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

Family SESIIDAE Boisduval, 1828 [extant]

Questionably placed in Sesiidae

cf. *Sesia* auct de Serres, 1829: 230 (nec Fabricius, 1775 [extant]).

—de Serres, 1829: 230 (?*Sesia*).
CI (adult: not stated)/originally IGMF [lost?]/France: Bouches-du-Rhone, Aix-en-Provence (“laminites lacustres”)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).

—Hope, 1836: 146 (?*Sesia*).
AM (not stated)/not stated/not stated/not stated.
Comment: It is unclear whether this is the same fossil noted by de Serres (1829). Hope (1836) asserted that he was the “authority” of this fossil specimen.

Superfamily TORTRICOIDEA Latreille, 1802 [extant]

Family TORTRICIDAE Latreille, 1802 [extant]

Subfamily CHLIDANOTINAE Meyrick, 1906 [extant]

POLYVENA Poinar and Brown, 1993: 25.
Type species: *Polyvena horatis* Poinar and Brown, 1993.

horatis Poinar and Brown, 1993: 26, 28, figs. 1–3 (*Polyvena*).
AM (adult: whole body)/originally UCMP [now ?AIOSU] (HT: L-3-24)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/ Burdigalian, Early Miocene.

Subfamily OLETHREUTINAE Walsingham, 1895 [extant]

ELECTRESIA Kusnezov, 1941: 62.
Type species: *Electresia zalesskii* Kusnezov, 1941.

zalesskii Kusnezov, 1941: 63, figs. 50–52 (*Electresia*).
AM (adult: whole body)/private collection, B. V. Miloradovitsch, Russia (HT: no. 20)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

TORTRICIBALTIA Skalski, 1992: 140.
Type species: *Tortricibaltia diakonoffi* Skalski, 1992.
= *Tortricibaltia* Skalski, 1976b: 203. Nomen nudum [no description].

diakonoffi Skalski, 1992: 140, figs. 1–5 (*Tortricibaltia*).
= *Tortricibaltia diakonoffi* Skalski, 1976b: 203. Nomen nudum [no description].
AM (adult: whole body)/FMNH (HT: LEP.SUCC.49 NHMC/AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/ Lutetian, Middle Eocene.

TORTRICIDROSIS Skalski, 1973b: 339.
Type species: *Tortricidrosis inclusa* Skalski, 1973.

inclusa Skalski, 1973b: 339, figs. 1–5 (*Tortricidrosis*).
AM (adult: whole body)/MNHU (HT: MB L-10=LEP.SUCC.133/AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

cf. *RETINIA* Guenée, 1845 [extant]

cf. *resinella* Linnaeus, 1758 (*Paleana Tortrix*) [extant]; Koponen and Nuorteva, 1973: 21, 34, 60, fig. 24 (*Evetria*) [fossil].
PE and T (larval feeding damage)/LFUF (1 ex: 1000J, R 16)/Finland: Umgebung, Piionsuo Moors (peat deposits)/ Pleistocene.
Fossil plant host: Pinaceae —*Pinus* sp. [stem].

RHOPOBOTA Lederer, 1859 [extant]
—Skalski, 1976b: 203 (*Rhopobota*).
CO (not stated)/not stated/not stated [?East African Copal]/not stated.

Questionably placed in Olethreutinae

GENUS *incertae sedis*

—Skalski, 1992: 144, fig. 7 (?Olethreutinae).

AM (adult: partial body)/FMNH (1 ex: LEP.SUCC.35 NHMC/AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/ Lutetian, Middle Eocene.

Subfamily TORTRICINAE Latreille, 1802 [extant]

SPATALISTIFORMA Skalski, 1992: 142.
Type species: *Spatalistiforma submerga* Skalski, 1992.
= *Spatalistiforma* Skalski, 1976b: 203. Nomen nudum [no description].

submerga Skalski, 1992: 142, fig. 6 (*Spatalistiforma*).
= *Spatalistiforma submerga* Skalski, 1976b: 203. Nomen nudum [no description].
AM (adult: whole body)/ZMCD (HT: 12-4/1957=LEP.SUCC.88 UZMC/AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

SUBFAMILY *incertae sedis*

TORTRICITES Kozlov, 1988: 40.
Type species: not designated.

destructus Cockerell, 1916: 98 (?*Tortrix*); Skalski, 1992: 137 (uncertain). **comb. nov.**
CI (adult: whole body)/USNM (HT: no. 61998 [not found in an inventory by J.-C. Sohn at USNM])/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.
Comment: In the original description, the author noted that he was unsure of the generic position of this fossil. Therefore, the genus name *Tortrix* (?) as used in the original description most likely refers to tortricid-like fossils now synonymous with *Tortricites*. To avoid any confusion with the extant genus *Tortrix* Linnaeus, 1758, we combine this fossil into *Tortricites*.

florissantanus Cockerell, 1907c: 416 (*Tortrix*); Skalski, 1992: 137 (uncertain); Meyer, 2003: 224, fig. 194. **comb. nov.**
CI (adult: whole body)/UCNH (HT: no. 8579)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.
Comment: The name *Tortrix* in Cockerell's usage, i.e. "*Tortrix* (*sensu lato*)", encompassed nearly all tortricids, and thus is not equivalent to the extant valid genus *Tortrix* Linnaeus, 1758. Since there is no difference between *Tortrix* sensu Cockerell (1907c) and the currently valid genus, *Tortricites*, we place this fossil in *Tortricites*.

sadilenkoi Kozlov, 1988: 41, fig. 8 (*Tortricites*).
AM (adult: head, thorax and partial forewing)/private collection, K. M. Sadilenko, Moscow, Russia (HT: no. 4)/ Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

skalskii Kozlov, 1988: 41, fig. 9 (*Tortricites*).
AM (adult: head, partial body and wings)/PIRAS (HT: PIN 964/659; PT: PIN 964/660)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Gravenhorst, 1835: 92 (*Tortrix*). **comb. nov.**
AM (adult)/not stated (part of ca. 40 ex: [lost?])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.
Comment: The author likened this fossil to several extant Tortricidae, including *Ptycholoma lecheana* (= *Tortrix lecheana*), *Olethreutes arcuellla* (= *Tortrix arcuana*), *Orthotaenia undulana* (= *Tortrix urticana*), and *Ancylis unguicella* (= *Tortrix falcana*). *Tortrix* in this former sense was essentially equal to Tortricidae, not *Tortrix* as currently circumscribed. We therefore place this fossil in *Tortricites*, which was designated specifically to accommodate tortricid-like fossils which cannot be assigned to any tortricid subgroup.

GENUS *incertae sedis*

—Grimaldi and Engel, 2005: 580, fig. 13: 47 (Tortricidae).
AM (adult: whole body)/AMNH (1 ex: DR8-43)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Menge, 1856: 29–30 (Tortricidae) [multiple species].
AM (adult, larva or pupa)/not stated (26 ex: [lost?])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Poinar, 1992: 287 (Tortricidae).
AM (not stated)/not stated/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Skalski, 1973b: 342 (Tortricidae).
AM (not stated)/not stated (1 ex)/Mexico: Chiapas, Simojovel (Mexican Amber, Simojovel Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

Superfamily PTEROPHOROIDEA Latreille, 1802 [extant]

Family PTEROPHORIDAE Latreille, 1802 [extant]

MERRIFIELDIA Tutt, 1905 [extant]

oligocenicus Bigot, Nel and Nel, 1986: 283, figs. 1–4, 5e (*Pterophorus*). **comb. nov.**
CI (adult: whole body)/MNHN (HT: B47277)/France: Bouches-du-Rhone, Aix-en-Provence (“laminites lacustres”)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).
Comment: The authors associated this fossil with the extant *tridactyla-spicidactylus* (= now *malacodactylus*) group, currently placed in *Merrifieldia* following the division of *Pterophorus s. l.* by Gielis (1996). We therefore move it to *Merrifieldia*.

Questionably placed in Pterophoridae

GENUS *incertae sedis*

—Haase, 1890: 26 (*Pterophorus*); Handlirsch, 1908: 628.
CI (not stated)/originally collection of Dr. A. Assmann [now ?NHUW]/not stated/not stated.
Comment: No description or illustration is available for this fossil. Haase (1890) mentioned it based on the drawing provided by Dr. A. Assmann who did not state the depository of this fossil.

—Piton, 1936: 17, 23, fig. 61 (*Lepidopterites*, nomen nudum).
CI (adult: forewing, thorax and abdomen fragments)/MNHN (1 ex: no. 61)/France: Cantal, Puy-de-Dôme, Lac Chambon (“cinerites”)/Pliocene.
Comment: It is not clear whether the author intended to propose *Lepidopterites* as a generic name. Although he mentioned that the fossil is close to Pterophoridae, *Lepidopterites* was used to represent its lepidopteran association, not a specific association with any family or genus. In this case, the taxon name *Lepidopterites* is actually a collective name for an order and thus cannot be used as a generic name. Moreover, Piton’s description, since it was published after 1930, should meet the requirements of ICZN article 13.1. Since *Lepidopterites* was not accompanied by any description and its definition was not given unambiguously, the name is invalid and rejected.

Superfamily CARPOSINOIDEA Walsingham, 1897

Family COPROMORPHIDAE Meyrick, 1905 [extant]

COPROMORPHA Meyrick, 1886 [extant]

fossilis Jarzembowski, 1980: 270, fig. 52 (*Copromorpha*).
CI (adult: whole body)/BMNH (HT: In.25766)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

GENUS *incertae sedis*

—Skalski, 1990c: 164 [in table] (Copromorphidae).
AM (not stated)/not stated/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Clade Obtectomera Minet, 1986 [extant]

Superfamily THYRIDOIDEA Herrich-Schäffer, 1846 [extant]

Family THYRIDIDAE Herrich-Schäffer, 1846 [extant]

Subfamily SICULODINAE Meyrick, 1884 [extant]

GENUS *incertae sedis*

—Skalski, 1985: 208 (cf. *Rhodoneura*); Skalski, 1990b: 144(Thyrididae).
AM (adult: whole body)/not stated/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.
Comment: Skalski (1985) mentioned that this fossil is similar to the extant *Rhodoneura*.

Superfamily PYRALOIDEA Latreille, 1809 [extant]

Family PYRALIDAE Latreille, 1809 [extant]

Subfamily CHRYSAUGINAE Lederer, 1863 [extant]

PETISCA Martins-Neto, 1998b: 63.
Type species: *Petisca dryellina* Martins-Neto, 1998.

dryellina Martins-Neto, 1998b: 63, fig. 2d (*Petisca*).
CI (adult: forewing)/DGUG (HT: UnG/1T-83)/Brazil: São Paulo, Tremembé City, near Padre Eternal, Fazenda Santa Fé (Tremembé Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

Subfamily PYRALINAE Latreille, 1809 [extant]

GLENDOTRICHA Kusnezov, 1941: 64.
Type species: *Glendotricha olgae* Kusnezov, 1941.

olgae Kusnezov, 1941: 66, figs. 54–57 (*Glendotricha*).
AM (adult: whole body)/private collection, B. V. Miloradovitsch, Russia (HT: no. 20)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Questionably placed in Pyralidae

GALLERITES Kernbach, 1967: 106 (Galleriidae); Carpenter, 1992: 380 (uncertain).
Type species: *Gallerites keleri* Kernbach, 1967. A subsequent designation by Clark *et al.* (1971: 582).

keleri Kernbach, 1967: 106, fig. 6 (*Gallerites*).
CI (adult: whole body)/GPUG (HT: 596-5=13547)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

FAMILY *incertae sedis*

PYRALITES Heer, 1856: 30.
Type species: *Pyralites obscurus* Heer, 1856. A subsequent designation by Jarzembowski (1980: 276).
Comment: The genus *Pyralites* was originally proposed to accommodate Pyralidae with an unknown generic affiliation. At the time, Pyralidae was the sole family in the superfamily Pyraloidea. Current division of Pyralidae into two separate families, Pyralidae and Crambidae, necessitates emendation of the definition of *Pyralites*. It should now constitute a collective generic name for species of Pyraloidea, which cannot be assigned to any subgroups thereof.

preecei Jarzembowski, 1980: 276, fig. 69 (*Pyralites*).
CI (adult: partial body and wings)/BMNH (HT: I.8640)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

obscurus Heer, 1856: 30, pl. 2: 6 (*Pyralites*); Kozlov, 1988: 55 (uncertain).
CI (adult: partial body and wings)/PMUZ (HT)/France: Bouches-du-Rhone, Aix-en-Provence (“laminites lacustres”)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).

GENUS *incertae sedis*

—Bonde *et al.*, 2008: 143 (Pyralidae).
CI (adult: whole body)/MHMM (1 ex: DK 188)/Denmark: Jutland, Mors Island, Ejerslev Molergrav (Fur Fm.)/late Thanetian, Late Paleocene–Early Eocene.

—Grimaldi and Engel, 2005: 580, fig. 13: 48 (Pyralidae).
AM (larva: whole body)/AMNH/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Questionably placed in Pyraloidea

—Hiura and Miyatake, 1974: 389 (Pyralidae).
CO (adult: whole body)/?OMNH (1 ex: 133B)/Japan: Gifu Pref., Mizunami (Mizunami Amber)/late Pleiostocene.

—Zeuner, 1931: 313–315, pl. 9: 6, 11: 3, 4 (?Pyralidae).
CI (larva: whole body)/SMNS (3 ex: Nr. 11; Nr. 15; Nr. 68)/Germany: Baden–Württemberg, Esslingen, Randecker Maar (“dysodile beds”)/Burdigalian, Early Miocene.

Superfamily PAPILIONOIDEA Latreille, 1802 [extant]

Family HESPERIIDAE Latreille, 1809 [extant]

PAMPHILITES Scudder, 1875b: 66.
Type species: *Pamphilites abditus* Scudder, 1875.

abditus Scudder, 1875b: 68, pl. 3: 14, 17, 18 (*Pamphilites*); Nel and Nel, 1986: 343, pl. 1: 1.
CI (adult: forewing)/MVMF (HT: lost); MNHN (NT: IPM B-24308)/France: Bouches-du-Rhone, Aix-en-Provence ("laminites lacustres")/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).
Comment: Scudder (1875b) compared this fossil to South American hesperiids. The South American affinity of this fossil species was, however, disputed by de Jong (2007: 330).

THANATITES Scudder, 1875b: 62.
Type species: *Vanessa vetula* Heyden, 1859.

vetulus Heyden, 1859: 12, pl. 1: 10 (*Vanessa*); Kirby, 1871: 179 (*Araschnia*); Scudder, 1875b: 63, pl. 3: 12, 16 (*Thanatites*).
= *Thanatites juvenalis* Scudder, 1875b: pl. 3: figs. 12, 16. Nomen nudum [print error].
= *Thanatites vetulinus* [sic]; Kozlov, 1988: 49.
CI (adult: whole body)/BMNH (HT: [not found, possibly destroyed])/Germany: Rhineland, Wetterau and Röhn, Niederrhein, Siebengebirge (Rott Fm.)/Chattian, Late Oligocene.

ANDRONYMUS Holland, 1896 [extant]
= *Androgynus* [sic]; Skalski, 1976b: 199.

neander Plötz, 1884 (*Andronymus*) [extant]; Skalski, 1976b: 199 [fossil].
CO (adult: whole body)/BMNH (1 ex: no. 58522)/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/Late Pleistocene.

GENUS *incertae sedis*

–Andersen and Andersen, 1996: 427, fig. 30 (Hesperiidae); Rust, 1998b: 138; Kristensen and Skalski, 1998: 19, fig. 2.6; Bonde *et al.*, 2008: 144.
CI (adult: whole body)/MHMM (1 ex: DK 136)/Denmark: Jutland, Fur Island, Stolleklint Clay (Fur Fm.)/late Thanetian, Late Paleocene.
Comment: Kristensen and Skalski (1998: 19) referred this to "the oldest butterfly fossil so far known."

—Zeuner, 1960: 310 (Hesperiidae).
CO? (not stated)/not stated/not stated/Pleistocene.
Comment: This is one of two Hesperiidae fossils which Zeuner (1960) judged to belong to recent species.

Family RIODINIDAE Grote, 1895 [extant]

Subfamily RIODININAE Grote, 1895 [extant]

Tribe MESOSEMIINI Bates, 1859 [extant]

VOLTINIA Stichel, 1910 [extant]

dramba Hall *et al.*, 2004: 797, fig 1a–i (*Voltinia*); Grimaldi and Engel, 2005: fig. 13.69.
= Riodinidae fossil; Grimaldi, 1996: 88.

= Nymphalidae fossil; Grimaldi and Engel, 2005: fig. 13.68.

AM (adult: whole body)/USNM (HT); M. Murata collection, Kyoto, Japan (PT); E. Morone collection, Torino, Italy (PT); AMNH (1 ex: DR-18-1)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

Tribe NYMPHIDIINI Bates, 1859 [extant]

THEOPE Doubleday, 1847 [extant]

—DeVries and Poinar, 1997: 1138, fig. 1 (*Theope*).

AM (larva: whole body)/AIOSU (1 ex)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

Questionably placed in Riodinidae

RIODINELLA Durden and Rose, 1978: 15 (Riodinidae); Hall *et al.*, 2004: 797 (uncertain).

Type species: *Riodinella nympha* Durden and Rose, 1978.

nympha Durden and Rose, 1978: 17, figs. 4, 5, 6e, 6f (*Riodinella*).

CI (adult: whole body)/PLME (HT: no. 3a) and BHM (CHT: no. 3b)/USA: Colorado, Rio Blanco Co., Piceance Creek Basin, Ray Fome (Green River Fm.)/early Lutetian, Middle Eocene.

Family LYCAENIDAE Leach, [1815] [extant]

Subfamily LYCAENINAE Leach, [1815] [extant]

cf. *THECLA* Fabricius, 1807 [extant]

—Benassi, 1896: 318 (cf. *Thecla*).

CI (larva)/not stated [lost?]/Italy: Centovalli, Val Vigezzo (“argille sabbiose”)/Pleistocene or Holocene.

SUBFAMILY incertae sedis

AQUISEXTANA Théobald, 1937: 160.

Type species: *Aquisextana irenaei* Théobald, 1937.

irenaei Théobald, 1937: 160, figs. 2, 3, pl. 1: 1, pl. 2: 1 (*Aquisextana*).

= a fossil *Polyommatus*?; Scudder, 1875b: 85.

CI (adult: whole body)/IGMF (HT: MA 1)/France: Bouches-du-Rhone, Aix-en-Provence (“laminites lacustres”)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).

Questionably placed in Lycaenidae

LITHOPSYCHE Butler, 1889: 294 (Euchemidae, Geometroidea); Jarzembowski, 1980: 283 (Riodinidae); Hall *et al.*, 2004: 799 (uncertain).

Type species: *Lithopsyche antiqua* Butler, 1889.

= *Calospilites* van Schepdael, 1974: 9, 15, 18. An unnecessary replacement name.

Type species: *Lithopsyche antiqua* Butler, 1889.

antiqua Butler, 1889: 294, pl. 31: 3, 6 (*Lithopsyche*); Jarzembowski, 1980: 283, figs. 74, 77.
CI (adult: whole body)/BMNH (HT: I.19984)/United Kingdom: England, Isle of Wight, Gurnet Bay (Bouldnor Fm.)/Late Priabonian, Late Eocene.

LYCAENITES Rebel, 1898: 742 (Lycaenidae); Carpenter, 1992: 380 (uncertain).
Type species: *Lycaenites gabbroensis* Rebel, 1898.

gabbroensis Rebel, 1898: 742, pl. 1: 5, 7 (*Lycaenites*).
CI (adult: whole body)/NHMW (HT: 1898/0013/0005; CHT: 1898/0013/0006)/Italy: Tuscany, Gabbro/Messinian, Late Miocene (Baciu *et al.* 2005).

—Bachofen-Echt, 1949: 150 (*Lycaenites*).
AM (not stated)/not stated [?BPGM, not found in an inventory by J.-C. Sohn at BPGM])/not stated/not stated.
Comment: It is unclear whether the author was referring to Gravenhorst's (1835) record or to an undescribed fossil. He assigned this record to *Lycaenites* without giving any explanation.

GENUS *incertae sedis*

—Gravenhorst, 1835: 93 (*Papilio*); Giebel, 1856: 187 (undescribed butterfly); Scudder, 1875b: 87 (*Thecla*, unconfirmed).
AM (larva)/not stated (part of ca. 40 ex: [lost?])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.
Comment: The author compared these specimens to an extant lycaenid, *Satyrium w-album* (= *Papilio w. album* auct), which is why we place it here.

Family NYMPHALIDAE Swainson, 1827 [extant]

Subfamily BIBLIDINAE Boisduval, 1833 [extant]

DYNAMINE Hübner, 1819 [extant]

alexae Peñalver and Grimaldi, 2006: 7, figs. 2d, 3, 4, 5 (*Dynamine*).
AM (adult: partial forewing, whole hindwing and abdomen, mid- and hindleg)/AMNH (HT: DR-18-2)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

Subfamily DANAINAE Boisduval, 1833 [extant]

ARCHAEOLYCOREA Martins-Neto, 1989: 380.
Type species: *Archaeolycorea ferreirai* Martins-Neto, 1989.

ferreirai Martins-Neto, 1989: 380, fig. 4a (*Archaeolycorea*).
CI (adult: forewing)/IGEO (HT: 5618-I)/Brazil: São Paulo, near the municipality of Taubaté (Tremembé Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

—Martins-Neto, 1989: 380, pl. 1: e (*Archaeolycorea*).
CI (pupa)/IGUSP (1 ex: GP/T-1642)/Brazil: São Paulo, Tremembé, along the road that connects Rodovia Presi-

dente Dutra with Campos do Jordão (Tremembé Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

—Martins-Neto, 1989: 381 (*Archaeolycorea*).
CI (pupa)/IGUSP (1 ex: GP/T-1643)/Brazil: São Paulo, Taubaté, Estiva District, Argila Vírgllio, Mineração Company (Tremembé Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

GENUS *incertae sedis*

—Brito and Ribeiro, 1975: 109, pl. 1: 3, pl. 2 (Danaidae).
CI (adult: fore- and hindwing)/IGEO (1 ex: no. 311)/Brazil: São Paulo, Municipe de Tremembé, la Fazenda Santa Fe (Tremembé Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

Subfamily LIBYTHEINAE Boisduval, 1829 [extant]

LIBYTHEANA Michener, 1943 [extant]
= *Barbarothea* Scudder, 1890: 29. Nomen nudum [no description].
= *Barbarothea* Scudder, 1892: 21.
Type species: *Barbarothea florissanti* Scudder, 1892.
= *Prolibythea* Scudder, 1889: 461.
Type species: *Prolibythea vagabunda* Scudder, 1889.

florissanti Scudder, 1892: 23, figs. 1–5 (*Barbarothea*); Shields, 1985: 13, 18, 20 (*Libythea*); Kawahara, 2009: 273 (*Libytheana*).
CI (adult: whole body)/originally private collection, S. H. Long (not found according to Meyer, 2003)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

vagabunda Scudder, 1889: 465, pl. 53: 4–9 (*Prolibythea*); Shields, 1985: 13, 20 (*Libythea*); Kawahara, 2009: 273 (*Libytheana*).
CI (adult: whole body)/MCZH (HT: no. 16353)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

Subfamily SATYRINAE Boisduval, 1833 [extant]

cf. *LETHE* Hübner, 1819 [extant]

corbieri Nel, Nel and Balme, 1993: 21, figs. 1–3 (?*Lethe*); Pfretzschner, 1998: 59, figs. 1–3.
CI (adult: whole body; forewing)/PNRL (HT and CHT) and GPUT (1 ex)/France: Alpes-de-Haute-Provence, Céreste (Calcaires de Montfuron Fm. or Calcaites de Vachères Fm.)/Rupelian (= Stampien), Early Oligocene (Heie and Lutz, 2002).

LETHITES Scudder, 1875b: 34. A replacement name for *Satyrites* Scudder, 1872.
Type species: *Satyrites reynesii* Scudder, 1872.
= *Lethites* Scudder, 1875a: 265. Nomen nudum (see Hemming, 1967: 254).
= *Satyrites* Scudder, 1872: 66 [preoccupied by Blanchard and Brullé (1840)].
= *Latyrites* [sic]; Brodie, 1873: 17.

reynesii Scudder, 1872: 66, pl. 7 (*Satyrites*); Scudder, 1875b: 37, pl. 1: 2, 5 (*Lethites*).
= *Latyrites* [sic] *beynesii* [sic]; Brodie, 1873: 17.
CI (adult: whole body)/MVMF (HT)/France: Bouches-du-Rhone, Aix-en-Provence (“laminites lacustres”)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).

MYLOTHRITES Scudder, 1875b: 44.
Type species: *Vanessa pluto* Heer, 1849.

pluto Heer, 1849: 179, pl. 14: 4 (*Vanessa*); Edwards, 1868: 160 (*Argynnis*); Butler, 1873: 127, pl. 48: 7 (?*Junonia*); Scudder, 1875b: 44 (*Mylothrites*).
CI (adult: whole body)/NHMW (HT: 1940/0001/0011)/Croatia: Calicia, Radoboj (Brown Coal deposit, lignite)/Burdigalian, Early Miocene (Rasnitsyn and Zherikhin, 2002).

—Heer, 1849: 180, pl. 14: 5 (*Vanessa*); Scudder, 1875b: 49–50, fig. 1, pl. 2: 15 (*Mylothrites*).
= *Vanessa pluto* Heer, 1849: 180 (part).
CI (adult: hindwing)/NHMG (1 ex)/Croatia: Calicia, Radoboj (Brown Coal deposit, lignite)/Burdigalian, Early Miocene (Rasnitsyn and Zherikhin, 2002).

NEORINELLA Martins-Neto, Kucera-Santos, Vieira and Fragoso, 1993: 6.
Type species: *Neorinella garciae* Martines-Neto *et al.*, 1993.

garciae Martins-Neto, Kucera-Santos, Vieira and Fragoso, 1993: 7, figs. 2–3, pl. 1–2 (*Neorinella*).
CI (adult: whole body)/DGUG (HT)/Brazil: São Paulo, Bacia de Taubaté (Tremembé Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

NEORINOPIS Butler, 1873: 127.
Type species: *Cyllo sepulta* Boisduval, 1840.
= *Neorinopsis* [sic]; Théobald, 1937: [in table 11].

sepulta Boisduval, 1840: 371, pl. 8 (*Cyllo*); Kirby, 1871: 39 (?*Antirrhaea*); Butler, 1873: 127, pl. 48: 3 (*Neorinopis*); Nel and Nel, 1986: 346, pl. 1–2.
= *Papilio Satyrus* sp.; de Serres, 1829: 230.
= ?*Nymphale* sp.; Duponchel in Boisduval, 1838: 52.
= ?*Cyllo* sp.; Boisduval in Rambur, 1839: xi–xii.
= Vanessides; Lefebvre, 1851: 74.
= *Cullo* [sic] *sepulta*; Nel *et al.*, 1993: 31.
CI (adult: wing)/MNHN (HT: IPM B-24309)/France: Bouches-du-Rhone, Aix-en-Provence (“laminites lacustres”)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).

PSEUDONEORINA Nel and Descimon, 1994: 292.
Type species: *Pseudoneorina coulleti* Nel and Descimon, 1994.

coulleti Nel and Descimon, 1994: 292, figs. 1–5 (*Pseudoneorina*).
= butterfly; Henrotay, 1986: 272, 276 [in legend], pl. 2: 1.
CI (adult: whole body)/MNHN (HT: no. 2486); “Collection Coullet à Barrème” (PT); and private collection, Michel Henrotay/France: Alpes-de-Haute-Provence, Céreste (Calcaires de Montfuron Fm. or Calcaires de Vachères Fm.) and Dauphin (“laminites lacustres”)/Rupelian (= Stampien), Early Oligocene (Heie and Lutz, 2002).
Note: Dr. André Nel informed us that an undescribed butterfly fossil from Henrotay (1986) is actually conspecific with *Pseuconeorina coulleti* Nel and Descimon.

GENUS *incertae sedis*

—CoBabe *et al.*, 2002: 18, fig. 4c (Satyrinae).

CI (adult: forewing)/not stated/USA: Montana, Lewis and Clark Co., SE of Helena, western side of Canyon Ferry Reservoir/Chattian, Late Oligocene.

—Durden and Rose, 1978: 2 (Satyridae) [in footnote].
CI (not stated)/private collection, Lloyd Gunther, USA/USA: Colorado, Rio Blanco Co., Ray Dome (Green River Fm.)/early Lutetian, Middle Eocene.

—van Schepdael, 1974: 15, 20 (Satyridae).
= Tagfalter [= butterfly]; Wangrin, 1940: 193, fig.
CI (adult: whole body)/private collection, G. Wangrin, Szczecin, Poland (1 ex: [not traced])/Germany: Mecklenburg–West Pomerania, Stettin [now Szczecin] (mineral concretion)/Oligocene.

Subfamily NYMPHALINAE Swinson, 1827 [extant]

AGLAIS Dalman, 1816 [extant]

karaganica Nekrutenko, 1965a: 98 (*Vanessa*); Kozlov, 1988: 52 (*Aglais*).
CI (adult: hindwing)/PIRAS (HT: PIN 254/2936a)/Russia: N Caucasus, Stavropol Krai, Vishnevaya Balka (Karagan horizon)/Langhian, Middle Miocene.
Comment: Kristensen and Skalski (1998: 19) cited the view of R. de Jong that the assignment of this fossil to the extant genus *Aglais* is based on inadequate evidence.

APANTHESIS Scudder, 1889: 459.
Type species: *Apanthesis leuce* Scudder, 1889.

leuce Scudder, 1889: 461, pl. 52: 12, 13 (*Apanthesis*).
CI (adult: forewing)/MCZH (HT: no. 16354)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.
Comment: Comstock (1961) suggested that this species is very close to the extant Holarctic genus *Limenitis* in wing venation.

CHARAXES Ochsenheimer, 1816 [extant]

candiope Godart, 1824 (*Nymphalis*) [extant]; Skalski, 1976b: 198 [fossil].
CO (adult: whole body)/not stated/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/Late Pleistocene.

DOXOCOPA Hübner, 1819 [extant]

wilmattae Cockerell, 1907b: 361, pl. 10 (*Chloripp*e); Meyer, 2003: 224 (*Doxocopa*).
CI (adult: whole body)/MCZH (HT: B602) and USNM (1 ex: no. 58682)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

HESTINA Westwood, 1850 [extant]

japonica Felder et Felder, 1862 (*Apatura*) [extant]; Fujiyama, 1983b: 122, pl. 1: 1 [fossil].
CI (adult: partial forewing)/NSMT (1 ex: PA12228)/Japan: Tochigi Pref., Shiobara Fossil Lake (Miyajima Fm.)/Early or Middle Pleistocene.

cf. *JUNONIA* Hübner, 1819 [extant]

—Evers, 1907: 130, figs. 2, 3 (*Precis* [= *Junonia*] spp.); Kusnezov, 1941: 69 (Rhopalocera *incertae sedis*).
CO (adult: whole body)/originally private collection, J. von Evers, Hamburg, Germany [now ?GMUH] (2 ex)/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/Late Pleistocene.

JUPITELLIA Carpenter, 1985: 579. A replacement name for *Jupiteria* Scudder, 1889.
= *Jupiteria* Scudder, [1881] 1883: 290. Nomen nudum (see Scudder, 1891: 675).
= *Jupiteria* Scudder, 1889: 448.
Type species: *Jupiteria charon* Scudder, 1889. A homonym of *Jupiteria* Bellardi 1875 [Mollusca: Bivalvia].

charon Scudder, 1889: 450, pl. 52: 14–15 (*Jupiteria*); Carpenter, 1985: 579 (*Jupitellia*).
CI (adult: whole body)/private collection, R. D. Lacoe, Pittston, Pennsylvania, USA (HT: no. 2100)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

LIMENITIS Fabricius, 1807 [extant]

—Branscheid, 1977: 87, figs. 3, 4 (*Limenitis*).
CI (adult: forewing and partial thorax)/GPUG (1 ex: no. 18558)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

LITHODRYAS Cockerell, 1909: 79. A replacement name for *Lithopsyche* Scudder, 1889.
= *Lithopsyche* Scudder, 1889: 454.
Type species: *Lithopsyche styx* Scudder, 1889. A homonym of *Lithopsyche* Butler, 1889 [Lepidoptera: ?Riodinidae].

styx Scudder, 1889: 454, pl. 53: 11, 16, 17 (*Lithopsyche*); Cockerell, 1909: 79 (*Lithodryas*).
CI (adult: whole body)/MCZH (HT)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

NYMPHALITES Scudder, 1889: 457.
Type species: *Nymphalites obscurum* Scudder, 1889.

atavus Charpentier, 1843: 408, pl. 22: 4, pl. 22: 4 (*Sphinx*); Kirby, 1872: 185 (?*Vanessa*), 648 (?*Nymphalis*); Scudder, 1875b: 41, pl. 1: 1, 3, 7 (*Eugonia*); Kozlov, 1988: 52 (*Nymphalites*).
= *Vanessa attavina*; Heer, 1849: 177, pl. 14: 3. Unjustified emendation.
= *Sphinx attavus* [sic]; Heer, 1849: 177.
= ?*Vanessa atovina*; Kirby, 1872: 185. Unjustified emendation.
= ?*Nymphalis atovina*; Kirby, 1872: 648. Unjustified emendation.
CI (adult: partial forewing)/not stated (lost)/Croatia: Calicia, Radoboj (Brown Coal deposit, lignite)/Burdigalian, Early Miocene (Rasnitsyn and Zherikhin, 2002).
Comment: Only illustrations are still extant. The specimen itself is said to be lost (Scudder, 1875b).

obscurus Scudder, 1889: 457, pl. 53: 10–13 (*Nymphalites*).
CI (adult: whole body)/MCZH (HT: no. 7768)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

scudderi Beutenmüller and Cockerell in Cockerell, 1908: 67, pl. 5: 6 (*Nymphalites*).
CI (adult: whole body)/AMNH (HT) and UCNH [CHT?]/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

zeuneri Jarzembowski, 1980: 279, figs. 72, 75, 76 (*Nymphalites*).
= *Lithosia* sp.; Smith in Woodward, 1878: 88.
= Butterfly: Scudder in Brodie, 1894a: 168.
= Butterfly: Scudder in Brodie, 1894b: 70.
= ?*Lithosia*: Handlirsch, 1907: 923.
= cf. *Euthalia*: Zeuner, 1960: 310.
CI (adult: fore- and hindwing)/BMNH (HT: I.10384; CHT)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

—Zeuner, 1931: 310–311, pl. 12: 2 (Apaturdi); Kozlov, 1988: 52 (*Nymphalites*).
CI (larva: whole body)/GPUT (1 ex: Nr. 38)/Germany: Baden–Württemberg, Esslingen, Randecker Maar (“dysodile beds”)/Burdigalian, Early Miocene.

—Zeuner, 1931: 309–310, pl. 6: 1a–b (?Nymphalidarum gen. et spec.); Kozlov, 1988: 52 (*Nymphalites*).
CI (larva: whole body)/SMNS (1 ex: Nr. 45)/Germany: Baden–Württemberg, Esslingen, Randecker Maar (“dysodile beds”)/Burdigalian, Early Miocene.

PRODRYAS Scudder, 1878: 520.
Type species: *Prodryas persephone* Scudder, 1878.

persephone Scudder, 1878: 524 (*Prodryas*); Scudder, 1889: 443, pl. 52: 1–10.
CI (adult: whole body)/MCZH (HT: MCZ-1=no. 394)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

VANESSA Fabricius, 1807 [extant]

amerindica Miller and Brown, 1989: 2, figs. 1–4 (*Vanessa*).
CI (adult: whole body)/FFNM (HT: FLFO-108) and FMUF (CHT: UF21999; PT: UF22000)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.
Comment: Miller and Brown (1989) assigned this fossil to the extant genus *Vanessa* and suggested an Old World affinity, based on similarities to extant *V. indica*. de Jong (2007: 331) challenged this argument, calling it premature and speculative.

—Nekrutenko, 1965b: 156, fig. 4 (*Pyrameis*); Kozlov, 1988: 52 (*Vanessa*).
= *Pyrameis fossilis* Nekrutenko, 1965b: 156, fig. 4. Nomen conditionalis (see Kozlov, 1988: 52).
CI (adult: hindwing)/PIRAS (HT: PIN 254/2753)/Russia: N Caucasus, Stavropol Krai, Vishnevaya Balka (Karagan horizon)/Langhian, Middle Miocene.

GENUS *incertae sedis*

—Hammond and Poinar, 1998: 275, figs. 1–3 (Nymphalidae).
AM (larva)/AIOSU/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

SUBFAMILY *incertae sedis*

GENUS *incertae sedis*

—Grote, 1901: 108; Kusnetzov, 1941: 69 (Rhopalocera).
CO (adult: whole body)/RPMH/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/Late Pleistocene.

Family PAPILIONIDAE Latreille, 1802 [extant]

Subfamily PARNASIINAE Duponchel, 1835 [extant]

Tribe LUEHDORFIINI Tutt, 1896 [extant]

DORITITES Rebel, 1898: 735 (Parnasiinae); Nazari *et al*., 2007: 152 (Luehdorfiini).
Type species: *Doritites bosniaskii* Rebel, 1898.
= *Luehdorfitis* Bryk, 1912: 53. An unnecessary replacement name for *Dorites* Rebel, 1898.
= *Dorititis* [sic]; Zeuner, 1960: 311.

bosniaskii Rebel, 1898: 740, pl. 1: 1–3 (*Doritites*); Bryk, 1912: 53 (*Luehdorfitis*); Bryk, 1913: 121 (*Luehdorfia*).
= *Luehdorfitis bosniackii* Bryk, 1912: 53. Unjustified emendation.
CI (adult: whole body)/NHMW (HT: 1898/0013/0001; CHT: 1898/0013/0002)/Italy: Tuscany, Gabbro/Messinian, Late Miocene (Baciu *et al.* 2005).

TRIBE *incertae sedis*

THAITES Scudder, 1875b: 57 (Parnasiinae); Bryk, 1916: 40 (?Papilionidae); Nazari *et al*., 2007: 152 (uncertain).
Type species: *Thaites ruminianus* Scudder, 1875.
= *Thaites* Heer, 1861: 153, 205. Nomen nudum (see Hemming, 1967: 436).
= *Thaites* de Saporta, 1872: 342. Nomen nudum (see Hemming, 1967: 436).
= *Thaitites* [sic]: Bryk, 1916: 42.

ruminianus Scudder, 1875b: 60, pl. 3: 1, 3, 6–10 (*Thaites*).
= *Thaites ruminiana* Heer, 1861: 153, 205. Nomen nudum (see Hemming, 1967: 436).
= *Thaites ruminiana* de Saporta, 1872: 342. Nomen nudum (see Hemming, 1967: 436).
CI (adult: whole body)/PMUZ (HT; 1 ex)/France: Bouches-du-Rhone, Aix-en-Provence ("laminites lacustres")/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).

GENUS *incertae sedis*

—Leestmans, 1983: 73, fig. 13 (Parnassinae).
CI (adult: whole body)/ENSM (lost)/France: Bouches-du-Rhone, Aix-en-Provence ("laminites lacustres")/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).
Comment: Only a photo taken by Théobald in 1935 is extant.

Subfamily PAPILIONINAE Latreille, 1802 [extant]

PAPILIO Linnaeus, 1758 [extant]

cf. ***maackii*** Ménétriés, 1859 (*Papilio*) [extant]; Fujiyama, 1968: 86, fig. 1, pl. 1: 1 [fossil].
CI (adult: partial forewing)/NSMT (1 ex: no. 7141)/Japan: Tochigi Pref., Shiobara Fossil Lake (Miyajima Fm.)/Early or Middle Pleistocene.

—Bachofen-Echt, 1949: 146 (*Papilio*).
AM (not stated)/not stated [?BPGM: not found in an inventory by J.-C. Sohn at BPGM])/not stated/not stated.
Comment: It is unclear whether Bachofen-Echt was referring to an undescribed amber inclusion or simply citing a previous record. The author pointed to an amber inclusion which can be assigned to "the family that *Papilio* belongs to."

Subfamily PRAEPAPILIONINAE Durden and Rose, 1978: 5

PRAEPAPILIO Durden and Rose, 1978: 5.
Type species: *Praepapilio colorado* Durden and Rose, 1978.
Comment: Kristensen and Skalski (1998: 19) regarded the two species of *Praepapilio* to be "the oldest named butterflies." de Jong (2007: 320) suggested that this genus belongs at the base of the Papilionidae.

colorado Durden and Rose, 1978: 6, figs. 1, 6a, 6b (*Praepapilio*).
CI (adult: whole body)/private collection, Hugh Rose, New Hampshire, USA (HT: no. 1)/USA: Colorado, Rio Blanco Co., Ray Dome (Green River Fm.)/early Lutetian, Middle Eocene.

gracilis Durden and Rose, 1978: 11, figs. 2, 3, 6c, 6d (*Praepapilio*).
CI (adult: whole body)/private collection, Hugh Rose, New Hampshire, USA (HT: no. 2a) and BHM (CHT: no. 2b)/USA: Colorado, Rio Blanco Co., Ray Dome (Green River Fm.)/early Lutetian, Middle Eocene.

Family PIERIDAE Duponchel, 1835 [extant]

Subfamily PIERINAE Duponchel, 1835 [extant]

BELENOIS Hübner, 1825 [extant]

crawshayi Butler, 1893 (*Belenois*) [extant]; Zeuner, 1942: 415 [fossil].
CO (adult: whole body)/BMNH (1 ex: I.3004)/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/Late Pleistocene.

COLIATES Scudder, 1875b: 51.
Type species: *Coliates proserpina* Scudder, 1875.

proserpina Scudder, 1875b: 52, pl. 2: 5 (*Coliates*).
CI (adult: forewing)/originally private collection, Count de Saporta [probably now MNHN]/France: Bouches-du-Rhone, Aix-en-Provence ("laminites lacustres")/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).

OLIGODONTA Brown, 1976: 2.
Type species: *Oligodonta florissantensis* Brown, 1976.

florissantensis Brown, 1976: 4, figs. 1–3 (*Oligodonta*).
CI (adult: whole body)/FFNM (HT); PSWC (CHT: WC-FL-1)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.
Comment: de Jong (2007: 322) criticized Brown's (1976) interpretation of this fossil and its family assignment.

PIERITES Heer, 1849: 182.

Type species: not designated.

Comment: Heer (1849) did not designate the type species of *Pierites*. Since Heer included only one species, *P. freyeri* Heer, 1849, Hemming (1967) interpreted the specimen as the type species of *Pierites*. This subsequent designation of the type species is problematic, since *P. freyeri* was transferred to the extant genus *Pontia* by Scudder (1875b). *Pierites* is currently used as a collective genus for fossils whose placement in Pieridae is uncertain (e.g. Kozlov 1988). For that reason, type species designation is not required (ICZN 4th edition, Article 13.3.2). We therefore disregard the subsequent designation of the type.

—Branscheid, 1968: 42, figs. 1–2 (*Aporia* cf. *crataegi*); Kozlov, 1988: 50 (*Pierites*).

CI (adult: forewing; hindwing)/GPUG (1 ex)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

—Branscheid, 1969: 102–103 (*Aporia*); Brauckmann *et al.*, 2001: 37, figs. 2–3 (?*Aporia*). **comb. nov.**

CI (adult: forewing and hindwing)/GPTUC (9 ex: 664-1[4588/a]; 646-2[9507/a]; 646-3[14264/a]; 646-4[17712/a]; 646-5[8472/a]; 646-6[8815]; 646-7[38/116a,b]; 646-8[8471/a]; 646-9[4828])/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

Comment: Following the example of Kozlov (1988) with regard to other alleged *Aporia* fossils, we treat these specimens as *Pierites* sp.

—Branscheid, 1977: 85, fig. 2 (*Aporia*). **comb. nov.**

CI (adult: hindwing)/originally private collection, A. Straus [now ?GPUG] (1 ex: no. 19563)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

Comment: Following the example of Kozlov (1988) with regard to other alleged *Aporia* fossils, we treat these specimens as *Pierites* sp.

—Kernbach, 1967: 108, fig. 12 (*Aporia*); Kozlov, 1988: 50 (*Pierites*).

= *Aporia crataegi* L. *fossilis* Kernbach, 1967: 108.

CI (adult: hindwing)/GPUG (1 ex: 596-12[13589])/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

PONTIA Fabricius, 1807 [extant]

freyeri Heer, 1849: 182, pl. 14: 6, pl. 14: 6 (*Pierites*); Scudder, 1875b: 54, pl. 2: 16, 18 (*Pontia*).

CI (adult: forewing)/originally stated as "k.k. montanistischen Sammlung zu Wien [possibly now GSAV]" (HT: [GSAV or lost?: not found in an inventory by J.-C. Sohn at GSAV])/Croatia: Calicia, Radoboj (Brown Coal deposit, lignite)/Burdigalian, Early Miocene (Rasnitsyn and Zherikhin, 2002).

STOLOPSYCHE Scudder, 1889: 467.

Type species: *Stolopsyche libytheoides* Scudder, 1889.

libytheoides Scudder, 1889: 468, pl. 53: 1–3 (*Stolopsyche*).

CI (adult: whole body)/MCZH (HT: no. 11077)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

Questionably placed in Pieridae

MIOPIERIS Zeuner, 1942: 409 (Pieridae); Carpenter, 1992: 380 (?Lycaenidae).

Type species: *Miopieris talboti* Zeuner, 1942.

talboti Zeuner, 1942: 409, fig. 1 (*Miopieris*).
CI (adult: whole body)/BMNH (HT)/Germany: Baden–Württemberg, Esslingen, Randecker Maar ("dysodile beds")/Burdigalian, Early Miocene.

GENUS *incertae sedis*

—Branscheid, 1977: 85, fig. 1 (Pieridae).
CI (adult: forewing)/GPUG (1 ex: no. 52-30 979)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

—Richter and Storch, 1980: 364, fig. 13 (Pieridae).
GC (adult: cuticular fragments)/FNSF/Germany: Hesse, S Frankfurt, near Darmstadt, Messel oil shale-layers (Messel Fm.)/early Lutetian, Middle Eocene.

FAMILY *incertae sedis*

GENUS *incertae sedis*

—Bachofen-Echt, 1949: 147 (Papilionidae).
AM (adult emerging from pupa)/originally private collection, Othenio Abel, Germany [lost?]/not stated/not stated.
Comment: The author referred to "one or two small papilionid butterflies" (147: lines 8 and 9).

—Benassi, 1896: 318 (butterfly).
CI (pupa)/not stated [lost?]/Italy: Centovalli, Val Vigezzo/Pleistocene or Holocene.

—Bonde *et al.*, 2008: 144 (Papilionoidea).
CI (adult: not stated)/NHMD/Denmark: Zutland, Fur Island, Stolleklint Clay (Fur Fm.)/late Thanetian, Late Paleocene.

—Durden and Rose, 1978: 1 (butterfly).
not stated/FFNM (1 ex)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

—Grote, 1901: 108 (Rhopalocera).
CO (adult: whole body)/RPMH/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/Late Pleistocene.

—Hope, 1836: 146 (*Papilio*); Scudder, 1875b: 87 (extant species).
CO and AM (not stated)/Strong collection [?OUNH: not found in an inventory by J.-C. Sohn at OUNH]/not stated/not stated.
Comment: For unknown reasons, Hope (1936) cited Brendt as the authority. Scudder (1875b) raised the possibility that the fossil is a forgery.

—Jarzembowski, 1980: 284, fig. 63 (Papilionoidea, genus indet.).
CI (adult: partial body and wings)/BMNH (1 ex: In.64545)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.
Comment: Jarzembowski (1980) noted a resemblance of this fossil to Lycaenidae and Nymphalidae.

—Kernbach, 1967: 108 (butterfly).
CI (adult)/GPUG (5 ex)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

—Larsson, 1975: 197, 204 (Rhopalocera) [multiple species].
CI (adult: wings)/NHMD and FMND (6 ex)/Denmark: NW Jutland, Limfjord area, Mo-clay (Fur and Olst Fms)/Late Paleocene–Early Eocene.

—Lemdahl, 2000: 307, fig. 5, tbl. 3 (larval jaws of butterflies).
SR (larva: mandibles)/BTVU/Switzerland: SW Alps, Hérémence (Late Glacial Maximum, unconsolidated sediments)/Younger Dryas, Holocene.

Clade Macroheterocera Chapman, 1893 [extant]

Superfamily BOMBYCOIDEA Latreille, 1802 [extant]

Family SATURNIIDAE Boisduval, 1837 [extant]

Subfamily AGLIINAE Packard, 1893 [extant]

AGLIA Ochsenheimer, 1810 [extant]

tau Linnaeus, 1758 (*Phalaena*) [extant]; Lindberg, 1900: 235 [fossil].
SR (larva: thoracic segments)/not stated/Finland: Lohja/Pleistocene.

Subfamily SATURNIINAE Boisduval, 1837 [extant]

Tribe ATTACINI Blanchard, 1840 [extant]

cf. *ROTHSCHILDIA* Grote, 1897 [extant]

fossilis Cockerell, 1914: 271, fig. 34 (?*Attacus*); Schüssler, 1933: 55 (*Rothschildia*).
CI (adult: partial forewing)/UCNH/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

Tribe BUNAEINI Packard, 1902 [extant]

cf. *CIRINA* Walker, 1855 [extant]

cf. *forda* Westwood, 1849 (*Saturnia*) [extant]; Kitching and Sadler, 2011: 551–552, figs. 20.1a–c, g–h [fossil].
SI (pupa: whole body)/not stated (1 ex: EP 352/03)/Tanzania: Laetoli, Upper Laetoli Beds (Laetoli Fm.)/?Gelasian, Late Pliocene.

SUBFAMILY *incertae sedis*

—Kunz, 2010: 43, 45, figs. (Saturniidae cocoons)
SI (cocoon)/various institutes (> 37 ex)/France: Alsace, North Middle Upper Rhine Graben, Bouxwiller quarry (Bouxwiller Fm.)/Lutetian, Middle Eocene.

Family SPHINGIDAE Latreille, 1802 [extant]

MIOCLANIS Zhang, Sun and Zhang, 1994: 82.

Type species: *Mioclanis shanwangiana* Zhang, Sun and Zhang, 1994.

shanwangiana Zhang, Sun and Zhang, 1994: 82, figs. 58, 59, pl. 10: 4 (*Mioclanis*).
CI (adult: whole body)/PFDL (HT: SK000361)/China: Shandong, Lingu, Shanwang (Shanwang Fm.)/Langhian, Middle Miocene.

GENUS *incertae sedis*

—Churcher, 1966: 990, fig. 15 (Sphingidae).
AS (adult: proboscis)/ROMUT/Peru: Piura, Talara (Lobitos Tablazo Fm.)/Late Pleistocene.

—Zhang, 1989: 94, pl. 20: 3 (Sphingidae).
CI (adult: whole body)/SFML (1 ex: no. 820157)/China: Shandong, Lingu, Shanwang (Shanwang Fm.)/Langhian, Middle Miocene.

Questionably placed in Sphingidae

SPHINGIDITES Kernbach, 1967: 108 (Sphingidae); Kozlov, 1988: 23, 55 (uncertain).
Type species: *Sphingidites weidneri* Kernbach, 1967. A subsequent designation by Clark *et al.* (1971: 582).
Comment: Brauckmann *et al.* (2001) held Kernbach's description of this genus to be invalid because of the lack of a diagnosis. It is not clear what Kernbach originally intended with this genus. We assume that it was designated to accommodate sphingid-like fossils whose association is not convincing. In this case, the collective genus does not need to have a type species or a diagnosis. The circumscription of the genus is not affected by the type species unnecessarily designated by Clark *et al.* (1971).

weidneri Kernbach, 1967: 108, fig. 11 (*Sphingidites*).
CI (larva: whole body)/GPUG (HT: 596-11=3435)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

GENUS *incertae sedis*

—Berendt, 1830: 37 (*Sphinx* [*s. l.*]); Kusnezov, 1941: 69 (Lepidoptera *incertae sedis*).
AM (?adult)/not stated/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Haase, 1890: 26 (*Sphinx*); Handlirsch, 1908: 628.
CI (not stated)/Dr. A. Assmann's collection [now ?NHUW]/not stated/not stated.
Comment: No description or illustration is available for this fossil. Haase (1890) mentioned the specimen based on a drawing provided by Dr. A. Assmann who did not state the depository of this fossil.

—Leakey, 1952: 624, fig. 1 (lepidopterous larva); Kitching and Sadler, 2011: 550 (probably Sphingidae).
SI (larva: whole body)/British-Kenya Miocene Expedition Collection, BMNH (1 ex)/Kenya: South Nyanza, Rusinga and M'fwangano Islands in Lake Victoria (Hiwegi Fm.)/Burdigalian, Early Miocene (van Couvering and Miller, 1969).

—Schöberlin, 1888: 69 (Sphingidae).
CI (larva: whole body)/originally Massmann Collection [private?]/Switzerland: Neuchâtel Canton, Oeningen ("Molasseformatien")/Messinian, Late Miocene.
Comment: The author likened this fossil to the larva of the extant *Hemaris fuciformis* in size.

—Zeuner, 1927: 321, figs. 1–3, 5 (“Sphingidenraupe”)
SI (larva: whole body)/GPUT (1 ex)/Germany: Baden–Württemberg, Esslingen, Randecker Maar (“dysodile beds”)/Burdigalian, Early Miocene.

Family BOMBYCIDAE Latreille, 1802 [extant]

Questionably placed in Bombycidae

BOMBYCITES Heer, 1849: 183; Handlirsch, 1908: 927 (uncertain).
Type species: *Bombycites oeningensis* Heer, 1849.

buechii Heer, 1865: 397, fig. 310 (*Bombycites*).
CI (larva: whole body)/not stated [maybe now PMUZ]/Switzerland: Neuchâtel Canton, Oeningen (“Molasseformatien”)/Messinian, Late Miocene.
Comment: The figure accompanying Heer’s original description is insufficient to show any affinity with any family of Lepidoptera (Kozlov 1988).
oeningensis Heer, 1849: 183, pl. 14: 7 (*Bombycites*).
CI (adult: partial body and wings)/PMUZ (HT)/Switzerland: Neuchâtel Canton, Oeningen (“Molasseformatien”)/Messinian, Late Miocene.
Comment: Handlirsch (1908) erroneously gave “pupa” as the stage of the fossil.

FAMILY *incertae sedis*

GENUS *incertae sedis*

—George, 1952: 88, fig. 55 (Sphingidae); Kozlov, 1988: 55 (uncertain).
CI (adult: wing scale)/SJCA (> 1 ex: slide no. 16)/Pakistan: Punjab, Salt Range, Warcha and Jankush Nulla Gorges (Saline Series dolomite)/Late Eocene (Lamba, 1944).

—Richter and Storch, 1980: 365, fig. 16 (?Sphingidae).
GC (adult: cuticular fragments)/FNSF/Germany: Hesse, S Frankfurt, near Darmstadt, Messel oil shale-layers (Messel Fm.)/early Lutetian, Middle Eocene.

Superfamily GEOMETROIDEA Leach, 1815 [extant]

Family GEOMETRIDAE Leach, 1815 [extant]

GEOMETRIDITES Kernbach, 1967: 107.
Type species: *Geometridites repens* Kernbach, 1967. A subsequent designation by Clark *et al.* (1971: 582).
Comment: Kernbach (1967) included two species when he proposed this genus but did not designate a type. Clark *et al.* (1971), recognizing this problem, made the genus name available by designating one species as the type. From this, Fletcher (1979) attributed the authorship of *Geometridites* to Clark *et al.* (1971). In the most recent code (ICZN 4th edition, Article 13.3.2), the requirement for type designation has been relaxed for collective fossil genera. Therefore, *Geometridites* is available even without a type species and authorship should be attributed to Kernbach (1967).

jordani Kernbach, 1967: 107, fig. 8 (*Geometridites*).
CI (adult: wings)/GPUG (HT: 596-7=10119 and 10119a)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

larentiiformis Jarzembowski, 1980: 278, fig. 71 (*Geometridites*).
CI (adult: partial forewing)/BMNH (HT: I.8866/8935)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

repens Kernbach, 1967: 107, fig. 7 (*Geometridites*).
CI (larva: whole body)/GPUG (HT: 596-6=11499/11499a)/Germany: Hesse, Brandenburg, Willershausen–Harz/ Piacenzian, Late Pliocene (Brauckmann *et al*. 2001).

—Heer, 1861: 153 (*Palaenites*); Kozlov, 1988: 45 (*Geometridites*).
= *Phalaenites proserpinae* Heer, 1861: 153. Nomen nudum (see Kozlov, 1988: 45).
= *Phalaena proserpinae*; van Schepdael, 1974: 14.
not stated (adult?)/not stated/France: Bouches-du-Rhone, Aix-en-Provence (“laminites lacustres”)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).

cf. *HYDRIOMENA* Hübner, 1825 [extant]

protrita Cockerell, 1922: 1, fig. 1 (?*Hydriomena*).
CI (adult: forewing)/AMNH (HT)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

HYPERYTHRA Guenée, 1857 [extant]

lutea Stoll, 1787 (*Phalaena Geometra*) [extant]; Evers, 1907: 130, fig. 1 [fossil]; Kozlov, 1988: 45 (*Geometridites* sp.).
CO (adult: whole body)/PJEH (1 ex)/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/ Late Pleistocene.

GENUS *incertae sedis*

—FIRGNE, 1990: 101, fig. 10.3.1 (pupa type I-A-1).
SR (pupa)/not stated [?OMNH] (1 ex: i-200)/Japan: Nagano Pref., Ikejiri-gawa Hollow, Hill Site excavation site (Nojiri-ko Fm.)/Late Pleistocene.

—Grimaldi and Engel, 2005: fig. 13: 24 (Geometridae).
AM (adult: whole body)/AMNH (1 ex: DR14-20)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Grimaldi and Engel, 2005: 586, fig. 13: 58 (Geometridae).
AM (larva: whole body)/private collection, E. Morone, Torino, Italy (1 ex: M0482)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Grimaldi and Engel, 2005: 586, fig. 13: 59 (Geometridae).
AM (adult: whole body)/AMNH/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Handlirsch, 1908: 1133 (Geometridae).
CO (not stated)/NHMW (2 ex)/Benin and Guinea/Pleistocene-Holocene.

—Lewis, 1992: 16 [in table] (Geometridae); Wilson, 1996: 226.

CI (not stated)/not stated [?TBMM or ?CSUM]/USA: Washington State, Ferry Co., Republic (Klondike Mountain Fm.)/Lutetian, Middle Eocene.

Questionably placed in Geometridae

ANGERONA auct Giebel, 1862: 317 (Geometridae) (nec Duponchel, 1829 [extant]); Kusnezov, 1941: 68 (Macrolepidoptera *incertae sedis*).

electrina Giebel, 1862: 317 (*Angerona*).
= *Angerona electrica* [sic]; Oppenheim, 1885: 347
CO (adult: whole body)/CMNH (1 ex: no. 4177)/not stated/possibly Holocene (after Bauer *et al.* 2005).

PHALAENITES Heer, 1849: 186; Kozlov, 1988: 55 (uncertain).
Type species: *Phalaenites crenata* Heer, 1849. A subsequent designation by Flecher (1979).

obsoletus Heer, 1849: 187, pl. 14: 12 (*Phalaenites*).
CI (adult: forewing)/originally stated as “k.k. montanistischen Sammlung zu Wien (possibly now GSAV)” (HT: [GSAV or lost?: not found in an inventory by J.-C. Sohn at GSAV])/Croatia: Calicia, Radoboj (Brown Coal deposit, lignite)/Burdigalian, Early Miocene (Rasnitsyn and Zherikhin, 2002).

crenatus Heer, 1849: 186, pl. 14: 11 (*Phalaenites*).
CI (adult: forewing)/originally stated as “k.k. montanistischen Sammlung zu Wien (possibly now GSAV)” (HT: [GSAV or lost?: not found in an inventory by J.-C. Sohn at GSAV])/Croatia: Calicia, Radoboj (Brown Coal deposit, lignite)/Burdigalian, Early Miocene (Rasnitsyn and Zherikhin, 2002).

PROBLONGOS Mérit and Mérit, 2008: 29, 31.
Type species: *Problongos baudiliensis* Mérit and Mérit, 2008.

baudiliensis Mérit and Mérit, 2008: 31, figs. 3, 4a (*Problongos*).
CI (adult: whole body)/private collection, Xavier Mérit, Palaiseau, France (HT)/France: Ardèche, Saint-Bauzile (diatomite)/Tortonian, Late Miocene.
Comment: The authors associated this fossil with the Geometridae, based solely on superficial similarity in wing shape. The evidence is weak, and we therefore treat this as a questionable geometrid fossil.

GENUS *incertae sedis*

—Harris and Raine, 2002: 461, fig. 1 (Geometridae).
SR (adult: saccular sclerite of male genitalia)/IGNS (1 ex: L10414/1)/New Zealand: Canterbury, Rakaia Gorge, north bank of Rakaia River (Broken River Fm.)/Albian–Turonian, Late Cretaceous.
Comment: The authors associated this fossil with the larentiine genus *Helastia*. It is not clear whether the supposed saccular sclerite is in fact a part of the male genitalia as opposed to something else. Even if the authors’ interpretation is correct, the fragment supports no diagnosis as to family. We therefore treat this as a questionable geometrid fossil.

Superfamily NOCTUOIDEA Latreille, 1809 [extant]

Family NOCTUIDAE Latreille, 1809 [extant]

Subfamily PLUSIINAE Boisduval, [1828] [extant]

GENUS *incertae sedis*

—FIRGNE, 1990: 101, fig.10.3.2 (pupa type II-D).
SR (pupa)/not stated [?OMNH] (1 ex: i-583)/Japan: Nagano Pref., Ikejiri-gawa Hollow, Hill Site excavation site (Nojiri-ko Fm.)/Late Pleistocene.

Subfamily NOCTUINAE Latreille, 1809 [extant]

EUROIS Hübner, 1821 [extant]

occulta Linnaeus, 1757 (*Noctua*) [extant]; Iversen, 1934: 343, 351, 354, 356 (*Agrotis*) [fossil].
SR (pupa: partial body)/NHMD? (65 ex)/Denmark: Greenland, Nordmånner-Siedlungen Østerbygden and Vesterbygden (Last Glacial Maximum, unconsolidated sediments)/Late Pleistocene.

Family EREBIDAE Leach, 1815 [extant]

Subfamily ARCTIINAE Leach, 1815 [extant]

Tribe SYNTOMINI Herrich-Schäffer, 1846 [extant]

OLIGAMATITES Kusnezov, 1928: 431.
Type species: *Oligamatites martynovi* Kusnezov, 1928.

martynovi Kusnezov, 1928: 431 (*Oligamatites*).
CI (adult: partial body, forewing and hindwing)/PIRAS (HT: PIN 2113 32/35)/Kazakhstan: Semipalatinsk Prov., Zaisan district, Mount Ashutas, Irtysh river, E of the sixth ravine/Oligocene.

PSEUDONACLIA Butler, 1876 [extant]

puella Boisduval, 1847 (*Naclia*) [extant]; Zeuner, 1943: 144, figs. 1–2 [fossil].
CO (adult: whole body)/BMNH (1 ex: In.17682)/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/Late Pleistocene.

Questionably assigned to Syntomini

CHARIDEA auct Dalman, 1826 (nec Dalman, 1816 [extant]).

metis Dalman, 1826: 497, pl. 5: 19 (*Charidea*); Hope, 1836: 146 (*Pavonia*); Walker, 1854: 277 (?*Euchromia*).
CO (adult: whole body)/originally in possession of J. W. Dalman [not traced]/origin uncertain (Dalman, 1826)/uncertain.

cf. *SYNTOMIS* Ochsenheimer, 1808 [extant]

—Hope, 1836: 146 (*Syntomis* spp.).
CO (not stated)/Hope and Strong collection [?OUNH: not found in an inventory by J.-C. Sohn at OUNH] (3 ex)/not stated/not stated.

Comment: Hope (1836) stated that there were several specimens belonging to this genus. He attributed the “authority” to Westwood, which possibly meant that Westwood would describe them. However, these specimens have never been described.

Tribe ARCTIINI Leach, 1815 [extant]

cf. *ARCTIA* Schrank, 1802 [extant]

—Klebs, 1890: 270 (*Arctia*).
AM (adult: not stated)/not stated [?AMKR] (1 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.
Comment: It is not clear that the author was specifically referring to the genus *Arctia* as currently defined. At the time, this genus name was applied to most large arctiine species. However, given that the specimen is stated to be “of a considerable size”, it would be very interesting to determine whether it is actually a large arctiine moth.

TRIBE *incertae sedis*

GENUS *incertae sedis*

—Joseph, 1986: cover page (a moth); Douglas and Stockey, 1996: 1151, fig. 16 (Arctiidae).
CI (adult: whole body)/TBMM (1 ex: no. 66000)/USA: Washington State, Ferry Co., Republic (Klondike Mountain Fm.)/Early Lutetian, Middle Eocene (Pearson and Obradovich, 1977).

—Kernbach, 1967: 107 (Arctiidae).
CI (adult: wings)/originally in Hering collection [lost?]/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).
Comment: This record was based on Dr. E. M. Hering's determination.

Questionably placed in Arctiinae

ARCTIITES Rebel, 1898: 732 (Arctiidae); Kozlov, 1988: 53 (uncertain).
Type species: *Arctiites deletus* Rebel, 1898.

deletus Rebel, 1898: 732, pl. 1: 6 (*Arctiites*).
CI (adult: body and partial forewing)/NHMW (HT: 1898/0013/0004; CHT: 1898/0013/0003)/Italy: Tuscany, Gabbro/Messinian, Late Miocene (Baciu *et al.* 2005).

STAUROPOLIA Skalski, 1988: 21.
Type species: *Stauropolia nekrutenkoi* Skalski, 1988.

nekrutenkoi Skalski, 1988: 22, figs. 1–2 (*Stauropolia*).
CI (adult: partial body and a forewing)/PIRAS (HT: no. 1102/2)/Russia: N Caucasus, near Stavropol Krai, Sengileyevskaya (Karagan horizon)/Langhian, Middle Miocene.

Subfamily LYMANTRIINAE Hampson, 1893 [extant]

cf. *EUPROCTIS* Hübner, 1819 [extant]

—Benassi, 1896: 318 (*Porthesia* [= *Euproctis*]); Handlirsch, 1908: 1133 (Bombycidae).
CI (adult: hindwing)/not stated [lost?]/Italy: Centovalli, Val Vigezzo/Pleistocene–Holocene.

GENUS *incertae sedis*

—Cavallo and Galletti, 1987: 174, pl. 12: 5 (Lymantriidae).
CI (adult: whole body)/MCFE (1 ex)/Italy: Piedmont, Alba, gypsiferous marls/Messinian, Late Miocene.
Comment: The authors did not describe this fossil, but included a drawing of it from an unpublished manuscript by Carlo Sturani.

Questionably placed in Lymantriinae

—Evers, 1907: 132 (Liparidae [= Lymantriinae] larva); Kusnezov, 1941: 69 (uncertain).
CO (larva: whole body)/GMUH (1 ex)/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/Late Pleistocene.

Subfamily CATOCALINAE Boisduval, 1828 [extant]

PHILODARCHIA Martins-Neto, 1998a: 77.
Type species *Philodarchia cigana* Martins-Neto, 1998.

cigana Martins-Neto, 1998a: 77, fig. 1c (*Philodarchia*).
CI (adult: whole body)/DGUG (HT: UnG/IT-058)/Brazil: São Paulo, Tremembé City, near Padre Eternal, Fazenda Santa Fé (Tremembé Fm.)/Late Oligocene–Early Miocene boundary.

Family NOTODONTIDAE Stephens, 1829 [extant]

GENUS *incertae sedis*

—Prokop, 2003: 335 [in table], 338 (Notodontidae).
CI (adult: forewing)/not stated [NMPC or private collection, Zdeněk Dvořák]/Czech Republic: Bohemia, Ústí Region, Bilina Mine (Most Fm.)/Aquitanian, Early Miocene.

Questionably placed in Notodontidae

CERURITES Kernbach, 1967: 107; Carpenter, 1992: 380 (uncertain).
Type species: *Cerurites wagneri* Kernbach, 1967. A subsequent designation by Clark *et al.* (1971: 582).

wagneri Kernbach, 1967: 107, fig. 10 (*Cerurites*).
CI (adult: whole body)/GPUG (HT: 596-10=12202)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

FAMILY *incertae sedis*

NOCTUITES Heer, 1849: 185.
Type species: *Noctuites haidingeri* Heer, 1849. A subsequent designation by Nye (1975).

= *Xyleutites* Kozhantchikov, 1957: 676 (Cossidae) [synonymized by Kozlov (1988: 45)].
Type species: *Xyleutites miocenicus* Kozhantchikov, 1957.

Comment: This genus was originally designated to accommodate noctuids of uncertain association. The family Noctuidae has now been restricted largely to the trifine subfamilies by Zahiri *et al.* (2010). This necessitates revision of the original concept of *Noctuites*. Most noctuoid fossils are incomplete, making them hard to place in a modern phylogeny of Noctuoidea. We suggest redefining the genus *Noctuites* to include noctuoids whose further association cannot be determined. Since our redefinition does not conflict with the subsequent type designation by Nye (1975), we retain *Noctuites haidingeri* Heer as the type species of the genus.

caucasicus Kozlov, 1988: 45, fig. 10, pl. 3: 1 (*Noctuites*).
CI (adult: forewing)/PIRAS (HT: PIN 254/175)/Russia: Stavropol Territory, 18 km to the west of Stavropol, Vishnevaya Balka, Cherry Ravine (Karagan horizon)/Langhian, Middle Miocene.

deperditus Heer, 1856: 30, pl. 2: 8 (*Noctuites*); Kozlov, 1988: 54 (*incertae sedis*).
CI (adult: whole body)/PMUZ (HT)/France: Bouches-du-Rhone, Aix-en-Provence (“laminites lacustres”)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).

effosus Heer, 1849: 185, pl. 14: 10 (*Noctuites*); Carpenter, 1992: 380 (*incertae sedis*).
= *Noctuites effossus* [sic]; Handlirsch, 1908: 924.
CI (adult: forewing)/originally stated as “k.k. montanistischen Sammlung zu Wien [possibly now GSAV]” (HT: [GSAV or lost?: not found in an inventory by J.-C. Sohn at GSAV])/Croatia: Calicia, Radoboj (Brown Coal deposit, lignite)/Burdigalian, Early Miocene (Rasnitsyn and Zherikhin, 2002).

gersdorfi Kernbach, 1967: 107, fig. 9 (*Noctuites*); Carpenter, 1992: 380 (*incertae sedis*).
CI (adult: wings)/GPUG (HT: 596-8; PT: 596-9)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

haidingeri Heer, 1849: 185, pl. 14: 9 (*Noctuites*).
CI (adult: forewing)/NHMG (HT: UMJG and P 77562)/Croatia: Calicia, Radoboj (Brown Coal deposit, lignite)/Burdigalian, Early Miocene (Rasnitsyn and Zherikhin, 2002).

incertissimus Oustalet, 1870: 158, pl. 1: 18 (*Noctuites*); Kozlov, 1988: 55 (*incertae sedis*).
CI (adult: whole body)/originally private collection, M. Lecoq [possibly at MNHN or lost]/France: Cantal, Puy-de-Dôme, ?Gergovia/Chattian, Late Oligocene.

kaspievi Kozlov, 1988: 46, fig. 11, pl. 3: 2 (*Noctuites*).
CI (adult: partial forewing)/PIRAS (HT: PIN 254/2057)/Russia: Stavropol Territory, 18 km west of Stavropol, Vishnevaya Balka, Cherry Ravine (Karagan horizon)/Langhian, Middle Miocene.

kozhantshikovi Kozlov, 1988: 47, fig. 13, pl. 3: 4–5 (*Noctuites*).
CI (adult: partial forewing)/PIRAS (HT: PIN 254/166)/Russia: Stavropol Territory, 18 km west of Stavropol, Vishnevaya Balka, Cherry Ravine (Chokraksky horizon)/Middle Miocene.

kusnezovi Kozlov, 1988: 47, fig. 12, pl. 3: 3 (*Noctuites*).
CI (adult: partial forewing)/PIRAS (HT: PIN 254/1912)/Russia: Stavropol Territory, 18 km west of Stavropol, Vishnevaya Balka, Cherry Ravine (Chokraksky horizon)/Middle Miocene.

maximus Kozlov, 1988: 47, fig. 14, pl. 4: 2–3 (*Noctuites*).
CI (adult: partial forewing)/PIRAS (HT: PIN 254/178)/Russia: Stavropol Territory, 18 km west of Stavropol, Vishnevaya Balka, Cherry Ravine (Chokraksky horizon)/Middle Miocene.

miocenicus Kozhanchikov, 1957: 676, fig. 2 (*Xyleutites*); Kozlov, 1988: 47, fig. 15, pl. 4: 1 (*Noctuites*).

CI (adult: forewing)/PIRAS (HT: 254/182)/Russia: Stavropol, Vishnevaya Balka, Cherry Ravine (unknown horizon)/Tortonian, Late Miocene.

radobojana Kozlov, 1988: 48 (*Noctuites*).
= (Noctuidae) *radobojana* Handlirsch, 1908: 924. Nomen nudum [non-binominal (Kozlov, 1988: 48)].
CI (adult: forewing)/originally stated as "Wiener Hofmuseum [now NHMW]" (HT: [NHMW or lost?: not found in an inventory by J.-C. Sohn at NHMW])/Croatia: Calicia, Radoboj (Brown Coal deposit, lignite)/Burdigalian, Early Miocene (Rasnitsyn and Zherikhin, 2002).

stavropolicus Kozlov, 1988: 48, fig. 16, pl. 4: 4 (*Noctuites*).
CI (adult: partial forewing)/PIRAS (HT: PIN 254/185)/Russia: Stavropol Territory, 18 km west of Stavropol, Temnolessky village (Chokraksky horizon)/Middle Miocene.

—Hope, 1836: 146 (*Noctua*). **comb. nov.**
AM (not stated)/not stated/not stated/not stated.
Comment: It is unlikely that the author was referring specifically to the genus *Noctua* as currently defined. Rather, he applied *Noctua* as a collective name for noctuids, making it equivalent to *Noctuites*. For this reason, we treat this fossil under *Noctuites*.

—Kozlov, 1988: 48, fig. 17, pl. 4: 5 (*Noctuites*).
CI (adult: body)/PIRAS (1 ex: PIN 254/201)/Russia: Stavropol Territory, 18 km to the west of Stavropol, Temnolessky village (Chokraksky horizon)/Middle Miocene.

—Lomnicki, 1894: 99, pl. 9: 81 (*Noctua*). **comb. nov.**
AS (adult: wing)/LNHM (1 ex)/Ukraine: L'viv, 1.5 miles SE of Drohobycz, Boryslawia [= Boryslav] (unconsolidated tar sands)/Pleistocene.
Comment: It is unlikely that the author was referring specifically to the genus *Noctua* as currently defined. Rather, Lomnicki applied *Noctua* as a collective name for noctuids, making it equivalent to *Noctuites*. For this reason, we treat this fossil under *Noctuites*.

GENUS *incertae sedis*

—Bonde *et al.*, 2008: 143 (Noctuidae).
CI (adult: whole body)/MHMM (1 ex: DK 172)/Denmark: Jutland, Mors Island, Ejerslev Molergrav (Fur Fm.)/late Thanetian, Late Paleocene.

—Curtis, 1829: 295 (?*Phalaena*); Handlirsch, 1908: 927 (uncertain).
CI (adult)/originally Murchison and Lyell's collection [lost?]/France: Bouches-du-Rhone, Aix-en-Provence ("laminites lacustres")/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).

—Douglas and Stockey, 1996:1151, fig. 33 (Noctuidae).
CI (adult: partial hindwing)/UAME (1 ex: no. 4579)/Canada: British Columbia, Quilchena Creek Valley (Allenby Fm.)/Lutetian, Middle Eocene (Mathewes and Brooke, 1971).

—Holst, 1908: 5 (Lepidoptera); Kolbe, 1932: 210; Henriksen, 1933: 213 (Noctuidae spp.)
SR (pupa)/not stated/Sweden: Lund, Toppeladugård, Allerødmuld Glacial (Last glacial interval, unconsolidated sediments)/Late Pleistocene.

—Poinar, 1992: 287 (Noctuidae).
AM (not stated)/not stated/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Reiss, 1936: 554 (Noctuidae).
CI (not stated)/SMNS (1 ex: Nr. 43951)/Germany: Baden–Württemberg, Esslingen, Randecker Maar ("dysodile beds")/Burdigalian, Early Miocene.

—Scudder, 1867: 117 (Noctuidae); Scudder, 1877: 765 (Diptera, *Eristalis lapideus*); Kozlov, 1988: 54 (Noctuidae).
CI (adult)/originally private collection, William Denton [now ?MCZH]/USA: Wyoming, Sweetwater Co., Green River (Green River Fm.)/early Lutetian, Middle Eocene.

—Théobald, 1937: 163, pl. 3: 20 (Noctuidae); Leestmans, 1983: 81, fig. 21.
CI (adult: whole body)/NHMB (1 ex: R. 827)/Germany: Baden–Württemberg, Kleinkems ("Plattiger Steinmergel")/late Chattian, Late Oligocene.

Questionably placed in Noctuoidea

Genus *incertae sedis*

—Bachofen-Echt, 1949: 150 (*Triphaena*); Skalski, 1990c: 164 [in table] (Noctuidae).
AM (not stated)/not stated [?BPGM: not found in an inventory by J.-C. Sohn at BPGM])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.
Comment: It is also possible that the author incorrectly cited Gervais (1877). Skalski (1990) simply listed Noctuidae from Baltic amber. It is likely that he cited Bachofen-Echt's record.

—Gall and Tiffney, 1983: 507, figs. 1a–c, f (Noctuidae); Whalley, 1986: 257 (?Noctuidae); Kozlov, 1988: 48 (*Noctuites*).
SI (egg)/PMNH/USA: Massachusetts, Martha's Vineyard, Gay Head (Magothy Fm.)/Campanian, Late Cretaceous.
Comment: If correctly identified, this fossil might be the earliest fossil evidence of Noctuoidea and the encompassing Macroheterocera. Kristensen and Skalski (1998: 20–21), however, strongly doubted the noctuid origin of the fossil eggs, which show only phenetic similarities, not diagnostic autapomorphies, with extant noctuid eggs.

—Gervais, 1877: 68 (maybe *Triphaena*); Kozlov, 1988: 57 (uncertain).
SI (pupa)/not stated [probably MNHN, if not lost]/France: Lot, Quercy (Phosphorites Fm.)/early Chattian, Late Oligocene (Wolsan and Lange-Berdé, 1996).

—Nuorteva and Kinnunen, 2008: 119, fig. 12 (Noctuidae).
AM and T (larval frass)/FMUH (1 ex: no. 5640)/Lithuania: Klaipedos, Palanga (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.
Comment: The authors likened the fossil to frass produced by the larvae of *Panolis flammea* (Noctuidae).

2. Lepidoptera *incertae sedis*

This section includes lepidopteran fossils whose taxonomic placement is uncertain due to their incomplete preservation or the lack of taxonomic study.

CHIONAEMOPSIS Cockerell and LeVeque, 1931: 354 (uncertain); Forbes, 1931: 479 (Attevidae); Kozlov, 1988: 53–54 (?Oecophoridae); Carpenter, 1992: 380 (?Yponomeutidae).
Type species: *Chionaemopsis quadrifasciatus* Cockerell and LeVeque, 1931.

quadrifasciatus Cockerell and LeVeque, 1931: 355 (*Chionaemopsis*).
CI (adult: partial forewing)/Henderson and Byram Collection [?UCNH]/USA: Colorado, Garfield Co., Piceance Creek Basin, Parachute Creek (Green River Fm.)/early Lutetian, Middle Eocene.

PHALAENA auct Bloch, 1776 (?Geometridae) (nec Linnaeus, 1758 [suppressed name]); Kozlov, 1988: 55 (uncertain).

geometra Bloch, 1776: 180 (*Phalaena*).
CO? (adult: whole body)/not traced (see Dunlop and Jekel, 2008 for details), only original drawing available/origin uncertain (see Dunlop and Jekel, 2008 for details)/uncertain.

PHYLLEDESTES Cockerell, 1907a: 188 (?Nymphalidae); Kozlov, 1988: 55 (uncertain); Meyer, 2003: 165 (?Noctuidae).
Type species: *Phylledestes vorax* Cockerell, 1907.

vorax Cockerell, 1907a: 188, fig. 9 (*Phylledeste*); Meyer, 2003: 165, fig. 198.
CI (larva: whole body)/UCNH (HT: no. 4608)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

cf. *TINEA* auct Presl, 1822 (nec Linnaeus, 1758 [extant]).

antiqua Presl, 1822: 199 (?*Tinea*).
AM (adult: whole body)/not traced (see Dunlop and Jekel, 2008)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.
Comment: The author likened this fossil to *Lithosia* [Erebiidae: Arctiinae] and *Tinea* [Tineidae], two very different moth genera. It is impossible to discern its true identity from the short original description. It is very unlikely to be related to *Tinea* as currently defined, given that at the time of the original description, *Tinea* encompassed most microlepidopterans.

GENUS *incertae sedis*

—Alonso *et al.*, 2000: 171, fig. 10: 5 (Lepidoptera).
AM (adult: whole body)/ANZM (1 ex: MCNA 8642)/Spain: Basque County, Álava, Peñacerrada (Nograro Fm.)/early Albian, Early Cretaceous.

—Ansorge, 1996: 69, pl. 13: 6–7 (Lepidoptera).
CI (adult: forewing)/MNHU (1ex: LGA 968)/Germany: Mecklenburg, Grimmen ("Grüne Serie")/early Toarcian, Early Jurassic.

—Ansorge and Kohring, 1995: 83, fig. 3 (Lepidoptera).
CI (pupa: whole body)/SMNH (1 ex)/Germany: Baden–Württemberg, Esslingen, Randecker Maar ("dysodile beds")/Burdigalian, Early Miocene.

—Archibald, 1995: fig. 3 (Lepidoptera).
CI (larva: whole body)/not stated/Canada: British Columbia, Okanagan Highlands, Horsefly River/Ypresian, Early Eocene (Archibald and Makarkin, 2006).

—Archibald, 1995: fig. 4 (Lepidoptera).
CI (adult: forewing)/not stated/Canada: British Columbia, Princeton Chert (Allenby Fm.)/Lutetian, Middle Eocene (Mathewes and Brooke, 1971).

—Bennike and Bøcher, 1990: 337 (gen. and sp. indet.).
SR (not stated)/NHMD/Denmark: Greenland, NE Peary Land (Kap København Fm.)/Gelasian, Late Pliocene–Early Pleistocene boundary.

—D'Abrera, 2001: 65 (moth in amber)
AM (adult: whole body)/not stated/not stated/not stated.

—Davis, 1989: 549 (Lepidoptera).
AM (not stated)/USNM/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.
—Evers, 1907: 129 (Lepidoptera) [multiple species].
CO (adult and larva: whole body)/PJEH (6 ex)/not stated/not stated.

—FIRGNE, 1990: 106, fig. 10.5 (Lepidoptera).
SR (pupa)/not stated [?OMNH] (197 ex)/Japan: Nagano Pref., Ikejiri-gawa Hollow, Hill Site excavation site (Nojiri-ko Fm.)/Late Pleistocene.

—Mueller, 1964: 22 (lepidopteran wing scales); Frey, 1964: 70.
SR (adult: wing scales)/not stated [?GBIU]/USA: Indiana, Kosciusko Co., Winona Lake and Wyland Lake; Marshall Co., Lawrence Lake (Last Glacial Maximum, unconsolidated sediments)/Late Pleistocene.

—Fujiyama, 1983a: 85 (Lepidoptera).
CI (not stated)/NSMT (1 ex)/Japan: Yamakata Pref., Kamiwada (Wada Fm.)/Late Miocene.

—Fujiyama, 1983a: 85 (Lepidoptera).
CI (not stated)/NSMT (1 ex)/Japan: Akita Pref., Sanzukawa/Late Miocene.

—Gelhaus and Johnson, 1996: 63 (Lepidoptera).
AM (not stated)/ANSP (1 ex)/USA: New Jersey, Middlesex Co., Sayreville (New Jersey Amber, Raritan Fm.)/Turonian, Late Cretaceous.

—Gentilini, 1991: 62 (Lepidoptera).
CI (adult: wings)/not stated [?MTRE]/Italy: Marche, Monte Castellaro ("Gessoso-Solfífera" Fm.)/early Messinian, Late Miocene.

—George, 1952: 100, fig. 56 (?microlepidoptera).
CI (pupa: antennal sheath)/SJCA (1 ex: slide no. 15)/India: Maharashtra, Nagpur, near Takli village, Seminary Hills (Takli Fm.)/Maastrichtian–Danian, Late Cretaceous–Early Paleocene interval (Sahni, 1984).

—Gravenhorst, 1835: 92 (*Tinea*).
AM (adult)/not stated (part of ca. 40 ex: [lost?])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.
Comment: The author likened the fossil to two extant species, *Chrysoteuchia culmella* (= *Tinea culmella*: Crambidae) and *Tinea pellionella* (Tineidae).

—Gravenhorst, 1835: 92 (Lepidoptera) [multiple species].
AM (adult?)/not stated (ca. 40 ex: [lost?])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Grimaldi and Engel, 2005: 52, fig. 2: 20 (Lepidoptera).
CI and T (leaf mine)/MVVA (1 ex: VM180365)/Australia: Victoria, Alcoa Anglesea Coal Mine, S38°25´ E144°11´ (Eastern View Fm.)/Priabonian, Late Eocene.

—Grimaldi and Nascimbene, 2010: 180, figs. 10d–f (Lepidoptera) [multiple species].
AM (adult: whole body)/not stated [?AMNH] (3 ex)/USA: New Jersey, Middlesex Co., Sayreville (New Jersey Amber, Raritan Fm.)/Turonian, Late Cretaceous.

—Grimaldi *et al*., 2000: 16, 26 [in table] (Lepidoptera) [multiple species].
AM (various)/AMNH (17 ex)/USA: New Jersey, Middlesex Co., Sayreville (New Jersey Amber, Raritan Fm.)/Turonian, Late Cretaceous.
Comment: Some of these fossils may be identical to ones depicted in Grimaldi and Engel (2005).

—Grimaldi *et al*., 2002: 11 (Lepidoptera) [multiple species].
AM (not stated)/AMNH (3 ex)/Myanmar: Kachin Prov., Hukawang Valley (Burmese Amber, "channel facies" of an unnamed formation)/late Aptian, Early Cretaceous.

—Grote, 1901: 108 (microlepidoptera); Kuznesov, 1941: 69 (*incertae sedis*).
CO (adult: not stated)/RPMH (1 ex)/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/Late Pleistocene.

—Grote, 1901: 108; Kusnezov, 1941: 69 (*incertae sedis*).
CO (pupa in cocoon)/RPMH (1 ex)/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/Late Pleistocene.

—Grote, 1901: 108 (Tineidae); Kusnezov, 1941: 69 (microlepidoptera).
CO (adult: whole body)/RPMH (1 ex)/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/Late Pleistocene.

—Haase, 1890: 26 ("Saniden"); Handlirsch, 1908: 628.
CI (not stated)/Dr. A. Assmann Collection [now ?NHUW]/not stated/not stated.

—Hand *et al*., 2010: 76 ("two moths").
AM (not stated)/not stated/Australia: northern Queensland, Cape York Peninsula (Cape York Amber, lignite)/stage unknown, probably Middle Miocene (Godthelp *et al.* 2010).

—Handschin, 1944: 8–9, figs. 10, 11, pl. 1: 8–10 (Tineidarum) [multiple species?].
SI (larva: partial body; pupa)/NHMB/France: Lot, Quercy (Phosphorites Fm.)/early Chattian, Late Oligocene (Wolsan and Lange-Berdé, 1996).

—Hayashi *et al*., 2002: 168 [in table 1] (Lepidoptera).
SR (pupa)/LBMS (4 ex)/Japan: Kyushu, Kagoshima Pref., Yoshimatsu-cho (Mizozono Fm.)/Late Pleistocene.

—Hayashi *et al*., 2004: 64 [in table 1] (Lepidoptera).
SR (pupa)/LBMS (1 ex)/Japan: Kyushu, Kumamoto Pref., Mashiki, Shimojin, Kanayama River (Tsumori Fm.)/Middle Pleistocene.

—Hayashi *et al*., 2005: 229 [in table 1] (Lepidoptera).
SR (pupa)/LBMS (1 ex)/Japan: Kyushu, Oita Pref., Kitsuki City, Beppu Bay (Hirabaru Fm.)/Middle Pleistocene.

—Hayashi *et al*., 2008: 91 [in table 1] (Lepidoptera).
SR (pupa)/LBMS (13 ex)/Japan: Honshu, southern Hiroshima Pref., Higashi-Hiroshima City, Saijo and Kurose Basins (Saijo Fm.)/Middle Pleistocene.

—Hayashi *et al*., 2009: 106 [in table 1] (Lepidoptera).
SR (pupa)/LBMS (6 ex)/Japan: Kyushu, Oita Pref., Kokonoe (Nogami Fm.)/Middle Pleistocene.

—Helm, 1899: 38 (microlepidoptera); Handlirsch, 1908: 928 (uncertain).
AM (not stated)/originally in Conwentz Collection (1 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Henriksen, 1922: 19 (Lepidoptera) [possibly one species].
CI (adult: not stated)/NHMD (4 ex)/Denmark: northern Jutland, western Limfjorden, Hanklit and Silstrup (Fur Fm.)/Thanetian, Late Paleocene–Early Eocene.

—Henrotay, 1986: 272 (Lepidoptera) [multiple species].
CI (not stated)/private collection, Michel Henrotay (7 ex)/France: Alpes-de-Haute-Provence, Dauphin ("laminites lacustres")/Rupelian, Early Oligocene.

—Hoffeins and Hoffeins, 2003: 385 [in table 3] (Lepidoptera) [multiple species].
AM (various)/private collection, Christel and Hans Werner Hoffeins, Hamburg, Germany (23 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Hoffeins and Hoffeins, 2003: 385 [in table 3] (Lepidoptera) [multiple species].
AM (various)/private collection, Christel and Hans Werner Hoffeins, Hamburg, Germany (70 ex)/Germany: Tagebau Goitsche, Bitterfeld Coal Mine (Saxonian Amber, Cottbus Fm.)/Lutetian, Middle Eocene.

—Hope, 1836: 146 ("*Tinea*," 4 spp.).
CO (not stated)/Hope collection [?OUNH: not found in an inventory by J.-C. Sohn at OUNH] (4 ex)/not stated/not stated.

—Hurd and Smith, 1957: 7 ("moths").
AM (not stated)/not stated/Mexico: Chiapas, Simojovel (Mexican Amber, Simojovel Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

—Jarzembowski, 1976: 12 ("small moth").
CI (not stated)/BMNH (1 ex)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.
Comment: This fossil could be one of the Lepidoptera later described by Jarzembowski (1980).

—Jarzembowski, 1980: 272 (species D).
CI (adult: abdomen and partial wings)/BMNH (1 ex: In.17392)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

—Jarzembowski, 1980: 272 (species E).
CI (adult: body and partial forewing)/BMNH (1 ex: In.25251)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

—Jarzembowski, 1980: 272 (species F).
CI (adult: partial body and wings)/BMNH (1 ex: In.9783)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

—Jarzembowski, 1980: 272, fig. 63 (species G).
CI (adult: body and partial forewing)/BMNH (1 ex: In.8917)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

—Jarzembowski, 1980: 274 (species I).
CI (adult: partial body and wings)/BMNH (1 ex: In.64541)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

—Jarzembowski, 1980: 274 (species J).
CI (adult: partial body and wings)/BMNH (1 ex: In.25157)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

—Jarzembowski, 1980: 275, fig. 65 (species L).

CI (adult: partial body and wings)/BMNH (1 ex: In.24506/64543)/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

—Joseph, 1986: 1 (Lepidoptera); Lewis, 1992: 15, 16 [multiple species].

CI (various)/TBMM or CSUM/USA: Washington State, Ferry Co., Republic (Klondike Mountain Fm.)/early Lutetian, Middle Eocene (Pearson and Obradovich, 1977).

—Kernbach, 1967: 103, fig. 1 (Lepidoptera) [multiple species].

CI (larva: whole body)/GPUG (16 ex: 596-13 etc.)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

—Kernbach, 1967: 103, 106 (Kleinschmetterlinge [= microlepidoptera]) [multiple species].

CI (adult)/GPUG (2 ex)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

—Kernbach, 1967: 103 (Großschmetterlinge [= macrolepidoptera]) [multiple species].

CI (adult)/GPUG (5 ex)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

Comment: The author initially mentioned 10 specimens of macrolepidopteran fossils, and subsequently mentioned five specimens of Rhopalocera fossils. We assume that the latter are a part of the ten, so count only five non-Rhopaloceran fossils here.

—Klebs, 1890: 270 (Lepidoptera) [multiple species].

AM (not stated)/?AMKR (ca. 1000 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Comment: The author mentioned that this collection includes almost 1000 specimens. It is very likely that some of these fossils have been described by subsequent researchers. It is, however, impossible to differentiate the described fossils. We therefore retain the stated original number of specimens.

—Knowlton, 1917: 80, pl. 35: 5 (Lepidoptera).

= "fruiting stage parasitic body [?fungus] or insect eggs"; Hall, 1845: 166, pl. 2: 5b, 5c.

CI (egg mass)/USNM [not found in an inventory by J.-C. Sohn at USNM]/USA: Wyoming, Lincoln County, Cumberland (Frontier Fm.)/Turonian, Late Cretaceous.

—Koponen and Nuorteva, 1973: 21, 34 (Lepidoptera) [multiple species].

PE (various)/LFUF/Finland: Hochmoor, Piionsuo Moor (peat deposits)/Pleistocene.

—Kosmowska-Ceranowicz, 1996: 59 ("larwa motyla").

AM (larva)/LNHM (1 ex: no. 194)/Poland: Lvov, Gdansk (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Kozlov, 1988: 22, pl. 1: 1, 2 (Larva *incertae sedis* no. 1 and 2) [multiple species].

CI (larva)/PIRAS (2 ex: PIN 3429/326; PIN 3429/328)/Russia: Primorsky Krai, Pozharsky District, Bol'shaya, upper reaches of Burachek River, near the Svetlovodnaya River ("lake diatomites")/?Late Oligocene (Rasnitsyn, 1986).

—Kozlov, 1988: 23, pl. 1: 3 (Lepidoptera).

CI (pupa)/PIRAS (1 ex: PIN 3122/1)/Kazakhstan: Chelkarsky District, Aktyubinsky Province, ravine at 3km E to the NE of Sandal/Oligocene.

—Krassilov, 2007: 15, fig.1; Krassilov and Shuklina, 2008: 243, fig. 5 (lepidopteran leaf mines) [multiple species]

CI and T (leaf mine)/IEUH (> 3 ex: IG1-1; IG1-45; IG1-139; etc.)/Israel: Negev Desert, central Negev, Makhtesh Ramon (Upper Hatira Fm.); Negev Desert, southern Negev, Arava Valley (Ora Fm.)/Albian–Turonian, Late Cretaceous.

Fossil plant host: Myrtales —*Paltydebeya papilionacea* Krassilov; etc.

—Kupryjanowicz, 2001: 62 (Lepidoptera) [multiple species].
AM (adult)/MEPA (19 ex: no. 4756; no. 5760; no. 11452; no. 14154; no. 14941; no. 15508; no. 15511; no. 15512; no. 15839; no. 17444; no. 17863; no. 18120; no. 18878; no. 19961; no. 20900; no. 20177; no. 5604 [lost]; no. 5765 [lost]; no. 15690 [lost])/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Kupryjanowicz, 2001: 62, fig. 79 (Lepidoptera).
AM (larva)/MEPA (1 ex: no. 13881)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Lancucka-Srodoniowa, 1964: 471–472, fig. 6 (lepidopteran coprolite).
= Order? Fruit; Reid and Reid, 1915: 124, pl 14: 31.
SI and T (coprolite)/GBNM (1 ex)/Netherlands: Limburg Prov., Reuver (Kieseloölite Fm.)/Gelasian, Late Pliocene–Early Pleistocene boundary (Kemna, 2008).

—Lancucka-Srodoniowa, 1964: 471–472, fig. 1 (lepidopteran coprolite).
= ?*Aralia racemosa* Fruit ; Reid and Reid, 1915: 124, pl. 14: 26.
SI and T (coprolite)/GBNM (1 ex)/Netherlands: Swalmen/Late Pliocene (Gregor, 1990).

—Lancucka-Srodoniowa, 1964: 471–472, figs. 13–14 (lepidopteran coprolite).
= *Carpolithus* sp. 1; Chandler, 1926: 44, pl. 7: 11a, b.
= *Carpolithus* sp., Fruit; Chandler, 1961: 155, pl. 30: 154–156.
SI and T (coprolite)/BMNH (4 ex: V42229; V42230; V42231; one specimen destroyed)/United Kingdom: S Hampshire, Isle of Wight, Headon Beds (Headon Hill Fm.)/Oligocene.

—Lancucka-Srodoniowa, 1964: 471, figs. 4–5 (lepidopteran coprolite).
= *Aralia* sp., Fruit; Szafer, 1947: 157, pl. 7: 21–22.
SI and T (coprolite)/WSIB (part of 22 ex)/Poland: Krościenko/Pliocene.

—Lancucka-Srodoniowa, 1964: 471, figs. 7–8 (lepidopteran coprolite).
= Araliaceae, Fruit; Szafer, 1954: 52, pl. 13: 21–22.
SI and T (coprolite)/WSIB (1 ex)/Poland: Krakow, Mizerna, Western Carpathians/Pliocene.

—Lancucka-Srodoniowa, 1964: 471, figs. 9–12 (lepidopteran coprolite).
= *Aralia* aff. *chinensis* L., Fruit; Szafer, 1961: 78, pl. 21: 1–3.
SI and T (coprolite)/WSIB (20 ex [in part?])/Poland: Upper Silesia, Stare Gliwice (Sarmatian deposit)/Messinian, Late Miocene (Worobiec, 2007).

—Lang *et al.*, 1995: 162, fig. 4a, pl. 3: 5 (lepidopteran mine).
CI and T (leaf mine)/BMNH (1 ex: V. 50089)/United Kingdom: Hampshire, East Dorset, Bournemouth (Branksome Sand Fm.)/Lutetian, Middle Eocene (McElwaine, 1998).
Comment: The authors stated that the fossil mine is similar to mines made by extant *Stigmella* or *Bedellia* larvae. It is not clear, however, that they intended to link the fossils taxonomically with any extant species (see Lang *et al.* 1995 for the analog modern taxa).

—Larsson, 1962: 324, 326 (Lepidoptera); Larsson, 1965: 140; Larsson, 1978: 187 [multiple species].
AM (adult and larva)/NHMD (58 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Leestmans, 1983: 72, fig. 17 (Lepidoptera).
CI (adult: whole body)/ENSM (lost)/France: Bouches-du-Rhone, Aix-en-Provence (“laminites lacustres”)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).
Comment: Only a photo taken by Théobald in 1935 is known for this specimen.

—Lemdahl, 2000: 307, fig. 2, tbl. 3 (Lepidoptera) [multiple species].
SR (not stated)/BTVU/Switzerland: Bern, Gerzensee (Late Glacial Maximum, unconsolidated sediments)/Younger Dryas, Early Holocene.

—Lewis, 1989: 5–6 (Lepidoptera).
CI (not stated)/not stated/USA: Nevada, SW Mineral County, Hawthorn, Stewart Valley Fossil Beds (Savage Canyon Fm.)/Serravalian, Middle Miocene (Perkins *et al.*, 1998).

—Martínez-Delclós *et al.*, 2004: fig. 3g
CO (adult: whole body)/EPGM (1 ex)/Madagascar (copal stalactite)/Holocene.

—McCobb *et al.*, 1998: 555, fig. 3 (Lepidoptera) [multiple species].
CI (not stated)/MMAG/United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.)/late Priabonian, Late Eocene.

—Miki, 1937: 305, Fig. 10p (caterpillar excrement); Lancucka-Srodoniowa, 1964: 471–472, figs. 17–19.
SI and T (coprolite)/not stated/Japan: Seto Naikai, Taniyagi-Higashiei (Stegodon Beds)/Pliocene.

—Minot, 1886: 46–47 (lepidopteran larvae).
CI (larva)/originally in Scudder's possession (2 ex: no. 16383 etc.)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.
Comment: This record was based on the author's personal communication with Scudder who identified the fossil.

—Moran and Matthews, 1983: 152 [in table] (Lepidoptera, undetermined).
SR (not stated)/UAME (not stated)/Canada: Northern Yukon Territory, Old Crow Basin, CRH-15 (77-51 lacustrine unit)/Middle–Late Pleistocene.

—Nel and Nel, 1985: 126, figs. 13–15 (undetermined larvae).
CI (larva: whole body)/private collection, André and Jacques Nel, á La Ciotat, France (3 ex)/France: Bouches-du-Rhone, Aix-en-Provence ("laminites lacustres")/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).

—Nel and Nel, 1985: 126, 128, figs. 16–17 (Lepidoptera).
CI (pupa)/private collection, André and Jacques Nel, á La Ciotat, France (1 ex: no. 343)/France: Eguilles Prov., Aix/Rupelian, Early Oligocene.

—Nel and Nel, 1985: 126, 128, figs. 18–19 (Lepidoptera).
CI (Pupa)/private collection, André and Jacques Nel, á La Ciotat, France (1 ex: no. 140)/France: Alpes-de-Haute-Provence, Céreste, Luberon ("Calcaires de Montfuron" or "Calcaires de Vachères")/Early Oligocene.

—Néraudeau *et al.*, 2002: 237, figs. 4–5 (Lepidoptera).
AM (not stated)/MNHN/France: Charente-Maritime, Archingeay (French Amber, Subunit Als 12 in "sandy, lignitic clay")/Late Albian, Early Cretaceous.

—Nudds and Selden, 2008: 249, fig. 273 (Lepidoptera).
AM (adult: whole body)/private collection with no detail (1 ex)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Peñalver, 1997: 32, fig. 3 (Lepidoptera) [multiple species].
CI and T (feeding mark)/MCNV (5 ex: 2234a-RM; 235a-RM; 2236a-RM; 2233a-RM; 2237-RM)/Spain: Teruel Prov., Rubielos de Mora, "Alto de la Venta" locality ("bituminous rhythmites")/Burdigalian, Early Miocene.

Fossil plant host: Myricaceae —*Myrica banksiaefolia* Unger; *Myrica* sp.; Salicaceae —*Salix cascadensis* Cockerell (= *tenera* Andersson).

—Peñalver and Delclòs, 2004: 80, 82, fig. 6: 1, pl. 2: 1 (Lepidoptera).
CI and T (leaf mine)/MPMV (1 ex: RIBES-81)/Spain: Castellón Prov., near Ribesalbes, "La Rinconada" locality (Izarra Fm.)/Burdigalian, Early Miocene.
Fossil plant host: ?Cannabaceae —?*Celtis*.

—Poinar and Poinar, 2005: 249, figs. 23–24 (lepidopteran caterpillar with tumors).
AM (larva: whole body)/AIOSU (1 ex)/Mexico: Chiapas, Simojovel (Mexican Amber, Simojovel Fm.)/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary.

—Pongrácz, 1928: 152 (Psychidae); Kozlov, 1988: 55 (uncertain).
CI (adult: whole body)/HNHM (1 ex)/Croatia: Calicia, Radoboj (Brown Coal deposit, lignite)/Burdigalian, Early Miocene (Rasnitsyn and Zherikhin, 2002).

—Procaccini, 1842: 449 (Lepidoptera); Handlirsch, 1908: 928 (uncertain).
CI (adult: whole body)/not stated/Italy: Sinigaglia/Late Miocene.
Comment: A short description by the original author states that the fossil has "scaled wings," which suggests that it is a lepidopteran.

—Prokop, 2003: 335 [in table] (Lepidoptera).
CI (adult: fragmentary body and wing)/SMMG/Czech Republic: Krusne hory Piedmont Basin, Ceske stredohori Mts. (Strezov Fm.)/Rupelian, Early Oligocene.

—Raffray, 1875: 126 (microlepidoptera).
CO (not stated)/not stated (1 ex)/Tanzania: Zanzibar Island (East African Copal, unconsolidated sediments)/Late Pleistocene.

—Rasnitsyn and Ross, 2000: 24 (Lepidoptera) [multiple species].
AM (adult: whole body)/BMNH (3 ex: In.19123; In.20151; In.20172)/Myanmar: Kachin Prov., Hukawang Valley (Burmese Amber, "channel facies")/late Aptian, Early Cretaceous.

—Rebel, 1934b: 372 (microlepidoptera).
AM (not stated)/originally in Klebs collection [?AMKR] (1 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Ross, 1998: 24, fig. 66 (Lepidoptera).
AM (larva: shed skin)/BMNH (1 ex)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Ross, 1998: 54, fig. 129 (Lepidoptera).
AM (adult: whole body)/BMNH (1 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Ross, 1998: 54, fig. 130 (Lepidoptera).
AM (larva: whole body)/MMAG (1 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Rozefelds, 1988a: 2, figs. 2a–d (lepidopteran mines) [multiple species].
CI and T (leaf mine)/MVVA (2 ex: MV P183063; MV P183064)/Australia: Victoria, Alcoa Anglesea Coal Mine, S38°25´ E144°11´ (Eastern View Fm.)/Priabonian, Late Eocene.

—Rust, 1998a: 54–57, figs. 9–10 (Lepidoptera) [multiple species].
CI (adult: whole body)/MHMM (3 ex: HM 14M-C2005; HM 14M-A2845; HM 14-B2673) and private collection, Bent Søe Mikkelsen, Denmark (BSM I 239)/Denmark: Jutland, Mors Island (Fur Fm.)/late Thanetian, Late Paleocene.

—Rust, 1998b:136, 138; 2000: 578, fig. 1 (Lepidoptera); Rust, 2000a: 530 [multiple species].

CI (adult)/not specified (ca. 1,750 ex)/Denmark: NW Jutland, western Limfjord area, Mo-clay (Fur and Olst Fms.)/late Thanetian, Late Paleocene.

—Rust, 1999: 351, pl. 28: c (Lepidoptera gen. et sp. indet. 1).

CI (adult: whole body)/MHMM (3 ex: MM 5-B2559; I311; I521) and private collection, Mr. Erwin Rettig, Nykøbing, Mors, Limfjord, Denmark (now ?NHMD, 1 ex: ERK FLA96 F13)/Denmark: Jutland, Mors Island (Fur Fm.)/late Thanetian, Late Paleocene.

—Rust, 1999: 351, pl. 28: d (Lepidoptera gen. et sp. indet. 2).

CI (adult: whole body)/MHMM (4 ex: MM 14M-B4034; I1877; I2838; I3542) and private collection, Mr. Erwin Rettig, Nykøbing, Mors, Limfjord, Denmark [now ?NHMD] (2 ex: ERK SA97 K10; KL94 E32)/Denmark: Jutland, Mors Island (Fur Fm.)/late Thanetian, Late Paleocene.

—Rust, 1999: 351, pl. 28: e (Lepidoptera gen. et sp. indet. 3).

CI (adult: whole body)/MHMM (4 ex: MM 12-C2753; 14M-A2975; 14M-C2600; 14M-3842) and private collection, Mr. Erwin Rettig, Nykøbing, Mors, Limfjord, Denmark [now ?NHMD] (1 ex: ERK SV 2A1)/Denmark: Jutland, Mors Island (Fur Fm.)/late Thanetian, Late Paleocene.

—Rust, 1999: 351, pl. 28: f (Lepidoptera gen. et sp. indet. 4).

CI (adult: forewing)/MHMM (4 ex: MM 11-A2465; 11-C3887; 14M-C3847; I1890); private collection, Mr. Erwin Rettig, Nykøbing, Mors, Limfjord, Denmark (now ?NHMD, 1 ex: ERK KL Y6); and GPUG (2 ex: GMUK 1954 95; 1954 543)/Denmark: Jutland, Mors Island (Fur Fm.)/late Thanetian, Late Paleocene.

—Rust, 1999: 351, pl. 29: a (Lepidoptera gen. et sp. indet. 5).

CI (adult: whole body)/GPUG (1 ex: GMUK 1998/24)/Denmark: NW Jutland, western Limfjord area, Mo-clay (Fur and Olst Fms.)/late Thanetian, Late Paleocene.

—Sanderson and Farr, 1960: 1313 (Lepidoptera).

AM (not stated)/not specified [3 institutes mentioned]/Dominican Republic: Palo Alto de la Cumbre, near Pedro Garcia, below Pico Diego de Ocampo/Burdigalian, Early Miocene.

—Scudder, 1881: 290 (Lepidoptera) [multiple species].

CI (adult)/not stated (ca. 12 ex)/USA: Colorado, Teller County, Florissant Beds National Monument (Florissant Fm.)/late Priabonian, Late Eocene.

Comment: The author stated that the collection included butterflies and moths. One fossil moth was identified as Pyralidae or Tortricidae. It is possible that some of these specimens have been described by subsequent researchers, but it is impossible to establish when, where or by whom.

—Sendelius, 1742: 80–90, pl. 2: 19–34, pl. 6: 33–35 (Lepidoptera) [multiple species]

AM (adult: whole body)/not stated [lost?]/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Comment: Only the illustrations are available. From the drawings it appears that at least some of the supposed lepidopteran inclusions are not Lepidoptera (Greven and Wichard 2010).

—de Serres, 1829: 230 (?*Bombyx* or ?*Cossus*); Swinton, 1881: 177, fig. 105 (?*Bombyx*).

CI (adult: head and wings)/MUMF (1 ex)/France: Bouches-du-Rhone, Aix-en-Provence ("laminites lacustres")/Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).

—Skalski, 1976a: 162 (Lepidoptera).

AM (pupa)/IPUS/Lebanon: Hammana, Mdeyrij (Lebanese Amber, Grès de Basa Fm. or lateral equivalents)/Hauterivian–Aptian, Early Cretaceous.

Comment: This record originated from the author's personal communication with Dr. Mickoleit.

—Skalski, 1977: 21, fig. 18, pl. 9: 1, pl. 10: 1 (inclusion 3 and 4, two species).
AM (wings and fragmentary legs)/MEPA (2 ex: 24/6 no. 1874/15, 7 MZ/AWS; 54/8 G/20 no. 1945/4, 4 MZ/AWS)/ Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Skalski, 1979a: 90 (Lepidoptera).
AM (adult)/not stated/Canada: Manitoba, Cedar Lake (Canadian amber, Foremost Fm.)/Campanian, Late Cretaceous.
Comment: This record originated from Skalski's personal communication with A. Mutuura.

—Skalski, 1979c: 63 (Lepidoptera).
AM (larva)/not stated/Russia: Siberia, E Taimyr, Taimyr Autonomous Okrug, Chatanga (Taimyr Amber, Kheta Fm.)/Coniacian, Late Cretaceous.

—Skalski, 1979c: 61 (Lepidoptera) [multiple species].
AM (adult: scales or whole body)/not stated/Lebanon: Hammana, Mdeyrij (Lebanese Amber, Grès de Basa Fm. or lateral equivalents)/Hauterivian–Aptian, Early Cretaceous.
Comment: This record originated from Skalski's personal communication with R. Dehm.

—Skalski, 1990c: 164 [in table] (undetermined Lepidoptera).
AM (not stated)/not stated/Romania: Carpathian Mountains (Romanian Amber)/Lutetian, Middle Eocene (Stout *et al.* 2000).

—Smith, 1874: 88 (butterflies) [multiple species].
CI (adult: wings)/not stated/United Kingdom: England, Isle of Wight, Gurnet Bay (Bouldnor Fm.)/late Priabonian, Late Eocene.

—Sohn *et al.*, 2011: 8 (lepidopterans).
CI (adult)/CNUB/China: Inner Mongolia, Ningcheng Co., Wuhua township, near Daohugou (Jiulongshan Fm.)/ Bathonian–Callovian, Middle Jurassic.

—Sohn *et al.*, 2011: 8 (lepidopterans).
AM (adult)/various institutes/Baltic Region (Baltic Amber, Prussian Fm.); Germany: Tagebau Goitsche, Bitterfeld Coal Mine (Saxonian Amber, Cottbus Fm.)/Lutetian, Middle Eocene.

—Sontag, 2003: 433 [in table 2], 437 [table 3a] (Lepidoptera) [multiple species].
AM (various)/MPUG (22 ex)/Lithuania: Klaipedos, Palanga (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Stark, 1925: 18 (lepidopteran scales); Frey, 1964: 70.
SR (adult: wing scales)/not stated/Germany: Baden–Württemberg, Wollmattingen, "Heidelmoos" (Last Glacial Maximum, unconsolidated sediments)/Late Pleistocene.

—Leestmans, 1983: 72, figs. 15–16 (Lepidoptera) [multiple species].
CI (adult: whole body)/LGUL (2 ex: lost)/France: Bouches-du-Rhone, Aix-en-Provence ("laminites lacustres")/ Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (Rasnitsyn and Zherikhin, 2002).
Comment: Only the photos taken by Théobald in 1935 are extant.

—Théobald, 1937: 132, pl. 1: 6 (Lepidoptera).
CI (adult: whole body)/MVMF (1ex: C42)/France: Gard, Ales, Célas ("lignites")/late Chattian, Late Oligocene.

—Théobald, 1937: 387 (Lepidoptera).
CI (larva)/not specified [3 institutes mentioned] (>10 ex)/France: Alpes-de-Haute-Provence, Céreste ("Calcaires de Montfuron" or "Calcaires de Vachères" Fm.)/Rupelian, Early Oligocene (Heie and Lutz, 2002).

—Weitschat, 2009: 253, fig. 42 (Lepidoptera).
AM (larva and larval case)/DBRD/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Weitschat and Wichard, 1998: 196, pl. 78: a–d (Lepidoptera) [multiple species].
AM (larva: whole body)/RMOD (>4 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Weitschat and Wichard, 1998: 196, pl. 78: e–h (Lepidoptera) [multiple species].
AM (adult: whole body)/RMOD (>4 ex)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Weitschat and Wichard, 1998: pl. 79: e (Lepidoptera).
AM (larva and larval case)/RMOD/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Wilf *et al.*, 2006: 1114, figs. 1c, 1d, 1g, 1h (Lepidoptera) [multiple species].
CI and T (leaf mine)/USNM (> 4 ex: no. 498156; no. 498157; no. 498160; no. 498161 etc.)/USA: SE Montana, Powder River Basin, Mexican Hat locality/Danian, Early Paleocene.
Fossil plant host: Cercidiphyllaceae —*Cercidiphyllum genetrix* (Newberry) Hickey; Juglandaceae —*Juglandiphyllites glabra* Manchester and Dilcher; Platanaceae —*Platanus raynoldsi* Newberry; Trochodendraceae —*Zizyphoides flabella* (Newberry) Crane, Manchester and Dilcher.

—Winkler *et al.*, 2010: 939 (lepidopteran mine).
= *Phytomyzites querci* Givulescu, 1984: 128, pl. 4: 3 (dipteran mine).
CI and T (leaf mine)/IGGB (1 ex: P.25800)/Romania: Maramures Co., Chiuzbaia/Messinian, Late Miocene.
Fossil plant host: Fagaceae —*Quercus* sp.

—Wu, 1997: 77, 191 (Lepidoptera) [multiple species].
AM (adult: whole body)/private collection, Rafael J. C. Wu, Dominica (3 ex: F-471; F-472; F-473)/Dominican Republic: Cordillera Septentrional between Santiago and Puerto Plata, La Toca group of mines (Dominican Amber, La Toca Fm.)/Burdigalian, Early Miocene.

—Zablocki, 1960: 47, fig. 2 (Lepidoptera-caused damage on pine cone); Kozlov, 1988: 24 (uncertain).
SA and T (feeding damage)/GBCU/Poland: Wieliczka, Wieliczka Salt Mine (“spiza” stratified salt deposits)/ Langhian–Serravallian, Middle Miocene.
Fossil plant host: Pinaceae —*Pinus kroli* Zablocki.

—Zeuner, 1931: 305, pl. 10: 1a–b (zwei Raupen, spec. indet.).
CI (larva: whole body)/private collection, W. Soergel, Wrocław, Poland (1 ex: Nr. 13/14)/Germany: Baden–Württemberg, Esslingen, Randecker Maar (“dysodile beds”)/Burdigalian, Early Miocene.

—Zeuner, 1931: 306–309, pl. 9: 6, 10: 2, 3, 11: 1, 2 (Raupe, spec. indet.).
CI (larva: whole body)/SMNS (5 ex: Nr. 12; Nr. 16; Nr. 17; Nr. 18; Nr. 48)/Germany: Baden–Württemberg, Esslingen, Randecker Maar (“dysodile beds”)/Burdigalian, Early Miocene.

—Zherikhin and Sukacheva, 1973: 38 [in table] (Lepidoptera); Skalski, 1976a: 162, fig. 6 (Homoneura); Skalski, 1979c: 63.
AM (adult: forewing)/not stated [?PIRAS] (1 ex)/Russia: Siberia, E Taimyr, Taimyr Autonomous Okrug, Chatanga (Taimyr Amber, Kheta Fm.)/Coniacian, Late Cretaceous.

3. Putative lepidopteran fossils

This section consists of fossils whose lepidopteran association is uncertain or ambiguously stated by the original authors.

—Ash and Hasiotis, 1996: 4; Ash, 1997: 243–244 (damage possibly by orthopterans, coleopterans or lepidopterans).
CI and T (feeding marks)/not stated/USA: Arizona, Navajo Co., Petrified Forest National Park (Chinle Fm.)/late Carnian–early Norian, Late Triassic.
Fossil plant host: Cynepteridaceae —*Cynepteris lasiophora* Ash; Bennetitales —*Zamites* sp.

—Brodie, 1873: 24 (?Lepidoptera).
CI (adult: wings)/not stated [lost?]/United Kingdom: England, Dorset, Purbeck Isle, Portland (Lower Purbeck Fm.)/Tithonian, Late Jurassic (Ensom *et al.* 2009).

—Bromell, 1729: 529 (*Insectorum ovula*); Scudder, 1875b: 1 (not confirmed).
CI (larva?)/not stated [lost?]/Sweden: "saxo foetido, Westrogothia" [near present-day Gothenburg]/?late Paleozoic.

—Bromell, 1729: 528 (*Papilionum majorum*); Scudder, 1875b: 1 (not confirmed).
CI (larva?)/not stated [lost?]/Sweden: "saxo foetido, Westrogothia" [near present-day Gothenburg]/?late Paleozoic.

—Bromell, 1729: 531 (*Papilionum minorum*); Scudder, 1875b: 1 (not confirmed).
CI (larva?)/not stated [lost?]/Sweden: "saxo foetido, Westrogothia" [near now Gothenburg]/?late Paleozoic.

—Kernbach, 1967: 103 (?Schmetterlingspuppen) [multiple species].
CI (pupa)/GPUG (3 ex)/Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene (Brauckmann *et al.* 2001).

—Müller, 1982: 13, pl. 3: 1–4, pl. 4: 4–5; Scott *et al.*, 1992: 141 (uncertain).
CI and T (leaf mine)/TUBF (1ex: FG 288/20)/Germany: Halle, Plötz/late Moscovian–Artinskian, Middle Pennsylvanian–Early Permian.
Fossil plant host: Callipteridiaceae —*Autunia conferta* (Sternberg) Kerp.
Comment: Labandeira (1998c) stated that these structures on a common, late Paleozoic peltasperm seed-fern are neither leaf mines nor lepidopteran in origin.

—Richter and Storch, 1988: 202 (Lepidoptera: Cossidae or Diptera: Culicidae).
GC (adult: cuticular fragments)/FNSF or GPUF/Germany: Hessen, Sieblos and Rhön (Sieblos Fm.)/Rupelian, Early Oligocene.

—Rohdendorf, 1939: 86 [in table] (?Lepidoptera).
CI (not stated)/PIRAS (2 ex)/Russia: near Voroshilovsk/Miocene.

—Rozefelds, 1985: 80, figs. B, C (lepidopteran or dipteran mines); Kristensen and Skalski, 1999: 16 (*incertae sedis*).
CI and T (leaf mine)/MVVA/Australia: Victoria, Alcoa Anglesea Coal Mine, S38°25´ E144°11´ (Eastern View Fm.)/Priabonian, Late Eocene.
Fossil plant host: Voltziaceae —*Heidiphyllum elongatum* (Morris) Retallack.
Comment: See Labandeira (1998c) for a discussion of these insect damage structures as nonlepidopteran in origin.

—Rozefelds, 1988a: 2, figs. 2e, 2f (lepidopteran or dipteran mines).
CI and T (leaf mine)/MVVA (1 ex: NMVP183065)/Australia: Victoria, Alcoa Anglesea Coal Mine, S38°25´ E144°11´ (Eastern View Fm.)/Priabonian, Late Eocene.
Fossil plant host: Elaeocarpaceae.

—Scudder, 1868: 627 (?Arctiidae).
SI (larva)/not stated/USA: Illinois, Will, Grundy and Kane Co., Morris Beds, Mazon Creek (Carbondale Fm.)/Moscovian, late Middle Pennsylvanian, Carboniferous.

—Sendelius, 1742: 169–171, pl. 5: 26–28, pl. 6: 1–4 (Lepidoptera) [multiple species].

AM (larva and pupa)/not stated (lost)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

Comment: Only the illustrations are available. To judge from the drawings, there could be some non-lepidopterans included in this collection.

—Skalski, 1974: 103, fig. 11 (Lepidoptera or Trichoptera).

AM (adult: whole body)/private collection, Oehlke Eberswalde, Germany (1 ex: LEP.SUCC.12 AWS)/Baltic Region (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene.

—Stephenson, 1991: 116 (Feeding Type KFa).

= *Phagophytichnus marginis-folii* Straus, 1977: 66 [part].

CI and T (feeding damage)/MNPC (1 ex: F1856); GBIU (1 ex: IU15706-7254); FMNH (6 ex: UP256; PP6203b; PP9404; PP10533; PP11519; PP11525)/USA: Kansas and Nebraska, Braun Ranch, Hoisington and other localities (Dakota Fm.); Tennessee, Carroll Co., Vale, Cooper Pit (Ripley Fm.)/late Albian, Early Cretaceous; early Maastrichtian, Late Cretaceous.

Comment: The author did not attempt to directly link these trace fossils to extant lineages, but pointed out similarities. In his thesis (Stephenson, 1991), feeding marks by the extant *Lymantria* (Erebidae: Lymantriinae) and *Phryganidia* (Notodontidae) were noted as possible analogs to the fossils.

—Stephenson, 1991: 117 (Feeding Type KFb).

= *Phagophytichnus marginis-folii* Straus, 1977: 66 [part].

CI and T (feeding damage)/GBIU (1 ex: IU15706-7539); FMNH (1 ex: PP6563)/USA: Kansas and Nebraska, Braun Ranch, Hoisington and other localities (Dakota Fm.); Tennessee, Carroll Co., Vale, Cooper Pit (Ripley Fm.)/late Albian, Early Cretaceous; early Maastrichtian, Late Cretaceous.

Comment: The author did not attempt to directly link these trace fossils with extant lineages, but pointed out similarities. In his paper, various Lepidoptera were mentioned as producing analogous feeding damage.

—Stephenson, 1991: 117 (Feeding Type KFc).

= *Phagophytichnus marginis-folii* Straus, 1977: 66 [part].

CI and T (feeding damage)/GBIU (1 ex: IU15706-7540)/USA: Kansas and Nebraska, Braun Ranch, Hoisington and other localities (Dakota Fm.)/late Albian, Early Cretaceous.

Comment: The author did not attempt to directly link these trace fossils with extant lineages, but pointed out similarities. He suggested that recent analogs to these trace fossils could be found in either Lepidoptera or Hymenoptera.

—Stephenson, 1991: 127 (Feeding Type TF2a).

= *Phagophytichnus marginis-folii* Straus, 1977: 66 [part].

CI and T (feeding damage)/GBIU (1 ex: IU15820-5931); FMNH (6 ex: PP5389; PP5512; PP5853; PP8060; PP8066; PP12107); BMNH (7 ex: v46705; v47524a; v24286; v48690a; v49503; v49728; v50059)/USA: Tennessee, Henry Co., Puryear, Puryear Clay Pit (Claiborne Fm.) and United Kingdom: Hampshire, East Dorset, Bournemouth (Branksome Sand Fm.)/Lutetian, Middle Eocene (McElwaine, 1998).

Comment: The author did not attempt to directly link these trace fossils with extant lineages, but pointed out similarities. He suggested that feeding marks by the extant *Urodus parvula* (Urodidae) are a possible analog to the trace fossils.

—Stephenson, 1991: 128 (Feeding Type TF3).

= *Phagophytichnus marginis-folii* Straus, 1977: 66 [part].

CI and T (feeding damage)/FMNH (8 ex: PP4882; PP5309; PP5634; PP5762; PP5994; PP9075; PP10261; PP10270); BMNH (7 ex: v48434; v49080; v49752; v50112; v50152; v50220; v50937)/USA: Tennessee, Henry Co., Puryear, Puryear Clay Pit (Claiborne Fm.) and United Kingdom: Hampshire, East Dorset, Bournemouth (Branksome Sand Fm.)/Lutetian, Middle Eocene (McElwaine, 1998).

Comment: The author did not attempt to directly link these trace fossils with extant lineages, but pointed out similarities. He suggested that damage by the extant *Nymphalis antiopa* (Nymphalidae) is a possible analog to the trace fossils.

—Stephenson, 1991: 135 (Feeding Type TF10a).
= *Phagophytichnus marginis-folii* Straus, 1977: 66 [part].
CI and T (feeding damage)/FMNH (1 ex: PP7745); BMNH (4 ex: v48215; v48404; v49925; v50020)/USA: Tennessee, Henry Co., Puryear, Puryear Clay Pit (Claiborne Fm.) and United Kingdom: Hampshire, East Dorset, Bournemouth (Branksome Sand Fm.)/Lutetian, Middle Eocene (McElwaine, 1998).
Comment: The author did not attempt to directly link these trace fossils with extant lineages, but pointed out similarities. He suggested feeding marks by the extant *Thyridopteryx ephemeraeformis* (Psychidae) as a possible analog to the trace fossils.

—Weyland *et al.*, 1960: 496 (probable eggs of insects, including Lepidoptera).
SR (egg)/FNSF/Germany: Upper Palatinate [= Oberpfalz]; Lower Rhine Bay, Embayment/Late Oligocene.

—Wilf *et al.*, 2005: 8944 (lepidopteran or coleopteran mines).
CI and T (leaf mine)/MPEF/Argentina: Chubut, Laguna del Hunco (Tufolitas Laguna de Hunco)/Ypresian, Early Eocene (Genise and Petrulevicius, 2001).
Fossil plant host: Araucariaceae —"*Zamia*" *tertiaria* Berry.
Comment: The plant host is a species of *Agathis*, rather than a cycad. The mine type resembles *Paraectopa* (Gracillariidae) or *Chrysorthenches* (Plutellidae) that occur on modern host species of *Agathis* (Wilf *et al.* 2005).

—Woodward, 1876: 64 (?Lepidoptera: *Tinea* sp.).
CI (not stated)/not stated/Coal Measures [possibly European part]/Late Carboniferous.
Comment: Woodward (1876) attributed the authorship of this record to "Fabricius." The original source cannot be found. Given the age of the fossil bed, it is very unlikely that the specimen actually represents a lepidopteran.

—Zherikhin and Sukacheva, 1973: 38 [in table] (?Lepidoptera).
AM (larva and pupa)/not stated [?PIRAS] (2 ex)/Russia: Siberia, E Taimyr, Taimyr Autonomous Okrug, Chatanga (Taimyr Amber, Kheta Fm.)/Coniacian, Late Cretaceous.

4. Fossils excluded from Lepidoptera

1) Name-bearing fossils

Archipsyche Handlirsch, 1906 [1907]: 624 (Lepidoptera), excluded by Carpenter (1932: 121) [Hemiptera: Palaeontinidae].

Beloptesis Handlirsch, 1906 [1907]: 625 (Lepidoptera), excluded by Hamilton (1992: 427) [Hemiptera: Palaeontinidae], a junior synonym of *Prolystra* Oppenheim, 1888.
Cyllonium Westwood, 1854: 395–396 (Lepidoptera); Handlirsch 1906 [1907]: 627, pl. 50: 14 (Lepidoptera *incertae sedis*), excluded by Scudder (1875b: 89) [Hemiptera].

benkerti Kuhn, 1951: 61, figs. 1–2 (*Geisfeldiella*), see *Geisfeldiella*.

boisduvalianum Westwood, 1854: 395, pl. 17: 17 (*Cyllonium*), see *Cyllonium*.

braueri Handlirsch, 1906 [1907]: 623–624, pl. 49: 17–18 (*Protopsyche*), a junior synonym of *Prolystra lithographica* Oppenheim, 1888, see *Protopsyche*.

compressa Oppenheim, 1885: 345, pl. 3: 11 (*Fabellovena*); Handlirsch, 1906: 576 (*Pseudosirex*); Maa, 1949: 17 (*Myrmicium*), see *Fabellovena*.

Curvicubitidae Hong, 1984: 782 (Lepidoptera), excluded by Whalley (1986: 267) [Neuroptera]; Kozlov (1988: 57) [Hemiptera].

Curvicubitus Hong, 1984: 782 (Lepidoptera: Curvicubitidae), excluded by Whalley (1986) [Neuroptera]; Kozlov (1988) [Hemiptera].

damesi Oppenheim, 1885: 333, pl. 1: 3 (*Phragmoecites*), see *Phragmoecites*.

eichstaettensis Handlirsch, 1906 [1907]: 624, pl. 50:1–2 (*Archipsyche*), see *Archipsyche*.

elegans Oppenheim, 1885: 345, pl. 3: 14 (*Fabellovena*); Handlirsch, 1906: 576 (*Pseudosirex*); Maa, 1949: 17 (*Myrmicium*), see *Fabellovena*.

Eocicada Oppenheim, 1888: 229 (Hemiptera); Handlirsch, 1906 [1907]: 626–7, pl. 50: 7–9 (Lepidoptera), excluded by Tillyard (1921: 282; 1933: 71) [Hemiptera: Palaeontinidae].

Eoses Tindale, 1945: 39 (Lepidoptera), excluded by Riek (1955: 660); Willmann (1984: 232) [Mecoptera], a junior synonym of *Mesochorista* Tillyard, 1916.

Eosetidae Tindale, 1945: 39 (Lepidoptera); Bourgogne, 1951: 365 (pathologic specimen), excluded by Willmann (1984: 232) [Mecoptera], a junior synonym of Permochoristidae Tillyard, 1917.

Fabellovena Oppenheim, 1885: 344 (Lepidoptera: Fabellovenae), excluded by Maa (1949: 17) [Hymenoptera: Myrmiciidae], a junior synonym of *Myrmicium* Westwood, 1854.

Fabellovenae Oppenheim, 1885: 344 (Lepidoptera), excluded by Maa (1949: 17) [Hymenoptera: Myrmiciidae].

Geisfeldiella Kuhn, 1951: 61 (Lepidoptera), excluded by Kluge (2004: 360) [Pterygota *incertae sedis*, possibly Odonata].

gigantea Weyenbergh, 1874: 101, pl. 3:4 (*Cicada*); Handlirsch, 1908 [1907]: 626, pl. 50:6 (Lepidoptera: *Beloptesis*? *gigantea*), excluded by Haase (1890: 20); Frickhinger (1994: 152) [Hemiptera: Palaeontinidae], a senior synonym of *Prolystra lithographica* Oppenheim, 1888.

gracilis Oppenheim, 1885: 344, pl. 2: 10 (*Rhipidorhabdus*); Handlirsch, 1906: 576 (*Pseudosirex*); Maa, 1949: 17 (*Myrmicium*), see *Rhipidorhabdus*.

hewitsonianum Westwood, 1854: 396, pl. 18: 27 (*Cyllonium*), see *Cyllonium*.

incertus Daudet, 1876: 415, pl. 17: 1–4 (*Satyrites*), excluded by Nel and Nel (1985: 129) [plant material].

jurassicus Oppenheim, 1885: 333, pl. 10: 4, 6 (*Palaeocossus*), see *Palaeocossus*.

karschi Oppenheim, 1885: 344, pl. 3: 13 (*Fabellovena*); Handlirsch, 1906: 576 (*Pseudosirex*); Maa, 1949: 17 (*Myrmicium*), see *Fabellovena*.

lameerei Handlirsch, 1906 [1907]: 627, pl. 50:10–12 (*Eocicada*), a junior synonym of *Eocicada microcephala* Oppenheim, 1888, see *Eocicada*.

Limacodites Handlirsch, 1906 [1907]: 622 (Lepidoptera: Limacodidae); van Schepdael, 1974: 4–5 (Lepidoptera: Limacodidae), excluded by Carpenter (1932: 120); Hamiltion (1992: 427) [Hemiptera: Palaeontinidae], a junior synonym of *Archipsyche* Handlirsch, 1906.

lithographica Oppenheim, 1888: 228–229, pl. 31: 1 (*Prolystra*), see *Prolystra*.

lithophilus Germar, 1842: 88 (*Tineites*), excluded by Haase (1890: 2); Demoulin (1955: 4) [Ephemeroptera].

macroceraticus Oppenheim, 1885: 347, pl. 12: 15 (*Ocnerites*), see *Ocnerites*.

magna Riek, 1976: 817, fig. 17, pl. 3: 4 (*Mesoses*), see *Mesoses*.

Mesoses Riek, 1976: 816 (Lepidoptera), excluded by Schlüter (1997: 309–310) [nonlepidopteran Paratrichoptera].

Mesosetidae Riek, 1976: 816 (Lepidoptera), excluded by Schlüter (1997: 309–310) [nonlepidopteran Paratrichoptera].

mesozonicus Handlirsch, 1906 [1907]: 622–623, pl. 49: 12–15 (*Limacodites*), a junior synonym of *Archipsyche eichstaettensis* Handlirsch, 1906, see *Limacodites*.

microcephala Oppenheim, 1888: 229, pl. 31: 30 (*Eocicada*), see *Eocicada*.

minimus Oppenheim, 1885: 344, pl. 2: 9 (*Rhipidorhabdus*); Handlirsch, 1906: 576 (*Pseudosirex*); Maa, 1949: 17 (*Myrmicium*), see *Rhipidorhabdus*.

Ocnerites Oppenheim, 1885: 347 (Lepidoptera: Lymantriidae), excluded by Haase (1890: 25) [Trichoptera].

oolitica Butler,1873: 126, pl. 48: 1–2 (*Palaeontina*), see *Palaeontina*.

oppenheimi Handlirsch, 1908 [1907]: 625–626, pl. 50:3–5 (*Beloptesis*), a junior synonym of *Prolystra lithographica* Oppenheim, 1888, see *Beloptesis*.

optata Riek, 1976: 816, fig. 16, pl. 3: 3 (*Mesoses*), see *Mesoses*.

Pachypsyche Handlirsch, 1906 [1907]: 623 (Lepidoptera), excluded by Meunier (1902: 10); Hamilton (1992: 427) [Hemiptera: Palaeontinidae].

Palaeocossus Oppenheim, 1885: 333 (Lepidoptera: Cossidae); Handlirsch, 1906 [1907]: 622, pl. 49: 10–11 (Lepidoptera: Palaeonitidae), excluded by Cockerell (1924: 135) [Hemiptera: Palaeontinidae].

Palaeontina Butler, 1873: 126 (Lepidoptera: Nymphalidae); Handlirsch, 1906 [1907]: 620, pl. 49: 1–7 (Lepidoptera: Palaeontinidae), excluded by Scudder (1875b: 89–95); Tillyard (1921: 281–282) [Hemiptera: Palaeontinidae].

Palaeontinidae Handlirsch, 1906 [1907]: 618 (Lepidoptera), excluded by Scudder (1875b: 89–95); Tillyard (1921: 281–282) [Hemiptera: Palaeontinidae].

Paratrichoptera Tillyard, 1919: 199 (Order nov.); Riek, 1976: 814 (Lepidoptera); excluded by Schlüter (1997: 307–310) [polyphyletic mecopteroid stock].

Phragmoecites Oppenheim, 1885: 333 (Lepidoptera: Cossidae); Handlirsch, 1908 [1907]: 621, pl. 49: 8–9 (Lepidoptera: Palaeonitidae), excluded by Haase (1890: 15–16); Cockerell (1924: 135) [Hemiptera: Palaeontinidae].

Prolystra Oppenheim, 1888: 228 (Hemiptera); Handlirsch, 1906 [1907]: 624–625, pl. 49: 20–23 (Lepidoptera), excluded by Haase (1890: 18–19); van Schepdael (1974: 4); Hamilton (1992: 427) [Hemiptera: Palaeontinidae].

Protopsyche Handlirsch, 1906 [1907]: 623 (Lepidoptera), excluded by van Schepdael (1974: 4); Hamilton (1992: 427) [Hemiptera: Palaeontinidae].

Rhipidorhabdi Oppenheim, 1885: 344 (Lepidoptera), excluded by Haase (1890: 27); Maa (1949: 17) [Hymenoptera: Myrmiciidae].

Rhipidorhabdus Oppenheim, 1885: 344 (Lepidoptera: Rhipidorhabdi), excluded by Haase (1890: 27); Maa (1949: 17) [Hymenoptera: Myrmiciidae], a junior synonym of *Myrmicium* Westwood, 1854.

schroeteri Germar, 1839: 193 (*Sphinx*); Hagen, 1862: 109 (*Belostoma*); Weyenbergh, 1869: 250, 272 (?*Hagenia*); Oppenheim, 1885: 344, pl. 2: 7 (*Rhipidorhabdus*); Deichmüller, 1886: 82 (*Pseudosirex*); Maa, 1949: 17 (*Myrmicium*), excluded by Deichmüller (1886: 82); Maa (1949: 17) [Hymenoptera: Myrmiciidae].

snelleni Weyenbergh, 1869: 261, pl. 34: 9 (*Sphinx*); Handlirsch, 1906: 575 (*Pseudosirex*), a junior synonym of *Sphinx schroeteri* Germar, 1839, see *schroeteri*.

triassica Tindale, 1945: 39, pl. 5 (*Eoses*); Riek, 1955: 660 (= *Mesochorista proavita*), see *Eoses*.

triassicus Hong, 1984: 783, fig. 1, pl. 1: 1 (*Curvicubitus*), see *Curvicubitus*.

vidali Meunier, 1902: 9, pl. 4: 3–5 (*Palaeontina*); Handlirsch, 1908 [1907]: 623–624, pl. 49: 19 (*Pachypsyche*), see *Pachypsyche*.

2) Unnamed fossils

—Anderson and Anderson, 1995: 36, tbl. 2; Anderson and Anderson, 1999: 77 [in table], fig. 26 (?Lepidoptera), see *Mesoses*.

Comment: For Lepidoptera, the authors originally counted 8 individuals belonging to 2 assemblages which exist in their collection (BWUP). Anderson and Anderson (1999) presented a drawing of one exemplar specimen which is obviously the same specimen as *Mesoses magna* described by Riek (1976). Likewise, three specimens described by Schlüter (1997) are possibly a part of Anderson and Anderson's collection. Considering the possibility for overlap, we reduce the original count to 4 specimens. It is likely that these four specimens belong to *Mesoses* as well.

—Barthel and Hetzer, 1982: 333 (Micropterigidae), excluded by Kozlov (1988: 57) [Trichoptera].

—Beringer and Hübner, 1726: 94 (*Papilionum* spp.); Scudder, 1875b: 1 (*incertae sedis*), excluded here [a fossil forgery (see Jahn and Wolff, 1963)].

—Bronn, 1837: 210, 481 (*Sphynx* [sic]), see *schroeteri* Germar, 1839.

—Brodie, 1845: xvii, pl. 1: 11 (caterpillar?), excluded here [unknown animal class].

—Guérin-Ménevilles, 1838: 170, excluded by Skalski (1977: 5) [Diptera: multiple species].

Comment: As Skalski (1977) indicated, the original author mistakenly listed the dipteran fossils under "Lepidoptera."

—Meyer, 2003: 162, fig. 193 (Lepidoptera or Trichoptera), excluded here [Trichoptera].

—Nel and Nel, 1985: 126, figs. 11, 12 (Sphingidae), excluded here [plant material].

Comment: Dr. André Nel carefully reexamined the specimen and some additional materials and found that these are actually flower petals of *Nymphaea* (pers. comm.).

—Schlotheim, 1820: 42 (*Sphinx*), see *schroeteri* Germar, 1839.

—Schröter, 1784: 411, pl. 3: 16 (*Sphinx*), see *schroeteri* Germar, 1839.

—Schlüter, 1997: 310, fig. 5a (Mesosetidae), see *Mesoses*.

—Scudder, 1867: 117 (?Limacodidae sp.), excluded by Scudder (1877: 741) [Diptera].

—Whalley, 1986: 269, fig. 17 (Amphiesmenoptera), excluded here [pre-lepidopteran Amphiesmenoptera].
Comment: Whalley stated that this fossil could be an ancestor of Antliophora and Amphiesmenoptera. However, the wing venation shows that it is related to the neuropteroid orders.

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References

Alonso, J., Arillo, A., Barrón, B., Corral, J.C., Grimalt, J., López, J.F., López, R., Martínez-Declòs, X., Otuño, V., Peñalver, E. & Trincão, P.R. (2000) A new fossil resin with biological inclusions in Lower Cretaceous deposits from Álava (northern Spain, Basque-Cantabrian Basin). *Journal of Paleontology*, 74(1), 158–178.

Andrée, K. (1951) *Der Bernstein, das Bernsteinland und Sein Leben*. Kosmos, Stuttgart, 95 pp.

Andersen, N.M. & Andersen, S. (1996) Kampemyrer og andre danekra fra Limfjordens askeserie–Studiet af en uddød insektfauna fra Danmarks Palaeogen. *Naturens Verden*, 11/12, 417–432.

Anderson, J.M. & Anderson, H.M. (1995) The Molteno Formation: window onto Late Triassic floral diversity. *Birbal Sahni Centenary*, 1995, 27–40.

Anderson, J.M. & Anderson, H.M. (1999) The Molteno Formation: the Triassic explosion and gymnosperm heyday. *In*: Anderson, J.M. (Ed.), *Towards Gondwana Alive: Promoting Biodiversity and Stemming the Sixth Extinction*. Gondwana Alive

Society, Pretoria, pp. 74–83.

Ansorge, J. (1996) Insekten aus dem oberen Lias von Grimmen (Vorpommern, Norddeutschland). *Neue Paläontologische Abhandlungen*, 2, 1–132.

Ansorge, J. (2002) Revision of the "Trichoptera" described by Geinitz and Handlirsch from the Lower Toarcian of Dobbertin (Germany) based on new material. *Proceedings of the 10th International Symposium on Trichoptera, Nova Supplementa Entomologica*, 15, 55–74.

Ansorge, J. & Kohring, R. (1995) Insekten aus dem Randecker Maar. *Fossilien*, 2, 80–90.

Archibald, B. (1995) *Some Eocene Insects from the Interior of British Columbia*. No. 1. The Vancouver Paleontological Society, Vancouver, 18 pp.

Archibald, S.B. & Makarkin, V.N. (2006) Tertiary giant lacewings (Neuroptera: Polystoechotidae): Revision and description of new taxa from western North America and Denmark. *Journal of Systematic Palaeontology*, 4(2), 119–155.

Ash, S. (1997) Evidence of arthropod-plant interactions in the Upper Triassic of the southwestern United States. *Lethaia*, 29, 237–248.

Ash, S. & Hasiotis, S.T. (1996) Upper Triassic arthropod–plant interactions in the American Southwest. *Abstracts of the Fifth Conference of the International Organisation of Palaeobotany*. Santa Barbara, California, p. 4.

Azar, D., Gèze, R. & Acra, F. (2010) Lebanese amber. *In*: Penny, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, pp. 271–298.

Bachofen-Echt, A. (1949) *Der Bernstein und Seine Einschlüsse*. Springer-Verlag, Vienna, 204 pp.

Baciu, D.-S., Bannikov, A.F. & Santini, F. (2005) A new species of Caproidae (Acanthomorpha, Teleostei) from the Messinian (upper Miocene) of Oran (Algeria). *Geodiversity*, 27(3), 381–390.

Barthel, M. & Hetzer, H. (1982) Bernstein-inklusen aus dem Miozän des Bitterfelder Raumes. *Zeitschrift für Angewandte Geologie*, 28(7), 314–336.

Bauer, A.M., Böhme, W. & Weitschat, W. (2005) An Early Eocene gecko from Baltic amber and its implications for the evolution of gecko adhesion. *Journal of the Zoological Society of London*, 265, 327–332.

Benassi, P. (1896) Piante ed insetti fossili di Re in Val Vigezzo. *Rivista Italiana di Paleontologia*, 2, 315–320.

Bennike, O. & Bøcher, J. (1990) Forest-tundra neighbouring the North Pole: plant and insect remains from the Plio–Pleistocene Kap København Formation, North Greenland. *Arctic*, 43(4), 331–338.

Berendt, G.C. (1830) *Die Insekten im Bernstein ein Beitrag zur Thiergeschichte der Vorwelt*. Nicolai, Danzig, 38 pp.

Beringer, J.B.A. & Hübner, G.L. (1726) *Lithographiae Wirceburgensis, Ducentis Lapidum Figuratorum, a Potiori Insectiformium, Prodigiosis Imaginibus Exornatae, Specimen Primum*. Würzburg, 96 pp+21 pls.

Berry, E.W. (1916) The Lower Eocene floras of southeastern North America. *U.S. Geological Survey, Professional Paper Series*, 91, 1–481.

Bigot, L., Nel, A. & Nel, J. (1986) Description de la première éspèce fossile connue de Ptérophore (Lepidoptera, Pterophoridae). *Alexanor*, 14(6), 283–288.

Blair, K.G. (1927) Insect remains from oil sand in Trinidad. *Transactions of the Entomological Society of London*, 75, 137–141.

Bloch, D. (1776) Beytrag zur Naturgeschichte des Kopals. *Beschäftigungen der Berlinischen Gesellschaft naturforschender Freunde*, 91–196.

Boisduval, M. (1838) Bulletin entomologique. *Annales de la Société Entomologique de France*, 7, xlix–lvi.

Boisduval, M. (1840) Sur une empreinte de Lepidoptére trouvée dans les marnes des environs d'Aix, en Provence, et commeniqée par M. de Saporta. *Annales de la Société Entomologique de France*, 9, 371–374.

Bonde, N., Andersen, S., Hald, N. & Jakobsen, S.L. (2008) *Danekra –Danmarks bedste fossiler*. Gyldendal, Copenhagen, 224 pp.

Boucot, A.J. (1990) *Evolutionary Paleobiology of Behavior and Coevolution*. Elsevier, Amsterdam, Oxford, New York & Tokyo, 725 pp.

Bourgogne, J. (1951) Order des Lepidopteres. *In*: Grasse, P.P. (Ed.), *Traité de Zoologie, Anatomie, Systematique, Biologie*, Vol. 10. Masson, Paris, pp. 174–448.

Branscheid, F. (1968) Ein weiterer Schmetterlingsflügel aus dem Pliozän von Willershausen. *Beihefte zu den Berichten der Naturhistorischen Gesellschaft zu Hannover*, 6, 41–42.

Branscheid, F. (1969) Funde von Tagfaltern (Rhopalocera, Lepidopt.) im Pliozän von Willershausen. *Berichte der Naturhistorischen Gesellschaft, Hannover*, 113, 101–106.

Branscheid, F. (1977) Fossile Schmetterlinge (Rhopalocera, Lepidopt.) aus dem Pliozän von Willershausen. *Beiträge zur Naturkunde Niedersachsens*, 30, 85–88.

Brauckmann, C., Brauckmann, B. & Gröning, E. (2001) Anmerkungen zu den bisher beschrieben Lepidopteren aus dem Jung-Tertiär (Pliozän) von Willershausen am Harz. *Jahresberichte des Naturwissenschaftlichen Vereins Wuppertal*, 54, 31–41.

Brito, I.M. & Ribeiro, F.A.M. (1975) Ocorrência de Lepidoptera nos folhelhos de Tremembé de algumas concideraçõs sobre a bacia geológica do Paraíba, Estado de São Paulo. *Anais da Academia Brasileira de Cièncias*, 47(1), 105–111.

Brodie, P.B. (1845) *A History of the Fossil Insects in the Secondary Rocks of England*. John van Voorst, London, 130 pp.

Brodie, P.B. (1873) The distribution and correction of fossil insects, and the supposed occurrence of Lepidoptera and Arachnidae in British and foreign strata, chiefly in the secondary rocks. *Warwickshire Natural History and Archaeological Society, Annual Report*, 37, 12–28.

Brodie, P.B. (1894a) Further remarks on the Tertiary (Eocene) insects from the Isle of Wight and on others from the Lias and

Coal Measures. *Geological Magazine*, (2)1, 167–169.

Brodie, P.B. (1894b) Notes on the Eocene Tertiary insects of the Isle of Wight. *Proceedings of the Warwickshire Natural History and Archaeological Field Club*, 1894, 67–70.

Bromell, M. (1729) Lithographia suecana, Section de lapidibus insectiferis scanicis et gothicis. *Acta Litteraria Sueciae*, 2, 493–497, 524–533.

Bronn, H.G. (1837) *Lethaea Geognostica oder Abbildungen und Beschreibungen der für die Gebirgs-Formationen bezeichnendsten Versteinerungen*, Vol. 1. E. Schweizerbart's Verlagshandlung, Stuttgart, 544 pp.

Brooks, H.K. (1955) Healed wounds and galls on fossil leaves from the Wilcox deposits (Eocene) of Western Tennessee. *Psyche*, 62(1), 1–9.

Brown, F.M. (1976) *Oligodonta florissantensis*, gen. n., sp. nov. (Lepidoptera: Pieridae). *Bulletin of the Allyn Museum*, 37, 1–4.

Bryk, F. (1912) “Parnassiana” V. Zur synopsis der asiatischen *Mnemosyne*. *Societas Entomologica*, 27, 52–53.

Bryk, F. (1913) Über eine neue Einteilung der Papilionidae unter Berücksichtigung des Flügelgeäders. *Archiv für Naturgeschichte A*, 79(2), 116–121.

Bryk, F. (1916) Über das Abändern der Rippenkonfiguration im Genus *Parnassius* Latr. *Archiv für Naturgeschichte A*, 82(5), 35–74.

Burgeff, H. (1951) Die Meeralpengrenze der Zygaenen (Lep.), eine mit Hilfe der Populationsanalyse der Arten der Gattung *Zygaena* (Lepidoptera) durchgeführte Untersuchung über die Lokalisation und die Bedeutung geographischer Rassen in ihrem Zusammenhang mit der Eiszeit. *Biologisches Zentralblatt*, 70(1/2), 1–23.

Butler, A.G. (1873) On fossil butterflies. *In*: Butler, A.G. (Ed.), *Lepidoptera Exotica*, Descriptions and illustrations of exotic Lepidoptera, Janson, E.W. (publ.), London, pp. 126–128, pl. 48.

Butler, A.G. (1889) Description of a new genus of fossil moths belonging to the geometrid family Euschemidae. *Proceedings of the Zoological Society of London*, 59, 292–297.

Carpenter, F.M. (1932) Jurassic insects from Solenhofen in the Carnegie Museum and the Museum of Comparative Zoölogy. *Annals of the Carnegie Museum*, 21, 97–129.

Carpenter, F.M. (1985) Substitute names for some extinct genera of fossil insects. *Psyche*, 92, 575–582.

Carpenter, F.M. (1992) Superclass Hexapoda. *In*: Kaesler, R.L., Brosius, E., Keim, J. & Priesner, J. (Eds.), *Treatise on Invertebrate Paleontology,* Part R (Arthropoda-4), 3 and 4 (Superclass Hexapoda). Geological Society of America and the University of Kansas, Boulder, Colorado and Lawrence, Kansas, pp. xxi+655.

Cavallo, O. & Galletti, P.A. (1987) Studi di Carlo Sturani su Odonati e altri insetti fossili del Messiniano albese (Piemonte) con descrizione di *Oryctodiplax gypsorum* n. gen. n. sp. (Odonata, Libellulidae). *Bollettino della Societá Paleontologica Italiana*, 26(1/2), 151–176.

Chambers, V.T. (1882) Burrowing larvae. *Nature*, 25(649), 529.

Chandler, M.E.J. (1926) The Upper Eocene Flora of Hardle, Hants. *Monograph of the Palaeontographical Society, London,* 78(361), 33–52.

Chandler, M.E.J. (1961) Flora of the Lower Headon beds of Hampshire and the Isle of Wight. *Bulletin of the British Museum (Natural History) Geology*, 5(5), 93–157.

Charpentier, T. (1843) Über Einige Fossile Insecten aus Radoboj in Croatien. *Verhandlungen der Kaiserlichen Leopoldinisch–Carolinischen Akademie der Naturforscher*, 12, 399–410, pl. 20–23.

Churcher, C.S. (1966) The insect fauna from the Talara tar seeps, Peru. *Canadian Journal of Zoology*, 44(6), 985–993.

Clark, J., Cole, R., Fawcett, S., Green, M., Howcroft, J., Niedbala, S., Rawkins, K., Théobald, O. & Tobias, M. (1971) *The Zoological Record* (1967). Vol. 104, 13. Insecta. The Zoological Society of London, London, 704 pp.

CoBabe, E.A., Chamberlain, K.R., Ivie, M.A. & Giersch, J.J. (2002) A new insect and plant Lagerstätte from a Tertiary lake deposit along the Canyon Ferry Reservoir, southwestern Montana. *Rocky Mountain Geology*, 37(1), 13–30.

Cobbett, A., Wilkinson, M. & Wills, M.A. (2007) Fossils impact as hard as living taxa in parsimony analyses of morphology. *Systematic Biology,* 56(5), 753–766.

Cockerell, T.D.A. (1907a) A fossil caterpillar. *The Canadian Entomologist*, 39, 187–188.

Cockerell, T.D.A. (1907b) A fossil butterfly of the genus *Chlorippe*. *The Canadian Entomologist*, 39, 361–362.

Cockerell, T.D.A. (1907c) A fossil tortricid moth. *The Canadian Entomologist*, 39, 416.

Cockerell, T.D.A. (1908) Fossil insects from Florissant, Colorado. *Bulletin of the American Museum of Natural History*, 24, 59–69, pl. 5.

Cockerell, T.D.A. (1909) A catalogue of the generic names based on American insects and arachnids from the Tertiary rocks, with indications of the type species. *Bulletin of the American Museum of Natural History*, 26, 77–86.

Cockerell, T.D.A. (1914) Fossil Saturniidae. *In*: Packard, A.S. & Cockerell, T.D.A. (Ed.), Monograph of the Bombycine Moths of North America, Part III. *Memoir of the National Academy of Science*, 12, 271.

Cockerell, T.D.A. (1916) Some American fossil insects. *Proceedings of the United States National Museum*, 51(2146), 89–106.

Cockerell, T.D.A. (1919) Two interesting insects in Burmese amber. *The Entomologist*, 52(676), 193–195.

Cockerell, T.D.A. (1921) Fossil arthropods in the British Museum —VI. Oligocene Insects from Gurnet Bay, Isle of Wright. *Annals and Magazine of Natural History,* (9)7, 453–480.

Cockerell, T.D.A. (1922) A fossil moth from Florissant, Colorado. *American Museum Novitates*, 34, 1–2.

Cockerell, T.D.A. (1924) Fossils in the Ondai Sair Formation, Mongolia. *Bulletin of the American Museum of Natural History*, 51, 129–144, pl. 1–2.

Cockerell, T.D.A. (1926) A new fossil moth from Florissant. *Psyche*, 33, 16–17.

Cockerell, T.D.A. (1933) A second moth from the Colorado Eocene. *The American Naturalist*, 67, 479–480.

Cockerell, T.D.A. & LeVeque, N. (1931) The antiquity of insect structures. *The American Naturalist*, 65, 351–359.

Comstock, W.P. (1961) *Butterflies of the American Tropics, The genus* Anaea, *Lepidoptera, Nymphalidae*. The American Museum of Natural History, New York, 214 pp.

Curtis, J. (1829) Observations upon a collection of fossil insects discovered near Aix in Provence, in the summer of 1828, by R. J. Murchison, esq. and Charles Lyell esq., jun. *Edinburgh New Philosophical Journal*, 7, 293–297.

D'Abrera, B. (2001) *The Concise Atlas of Butterflies of the World*. Hill House Publishers, Melbourne and London, 353 pp.

Dalman, J.W. (1826) Om Insekter inneslutne i Copal: jemte beskrifning på några deribland förekommande nya slägten och arter. *Kongliga Veternskaps-Akademiens Handlingar*, 1825(II), 375–410, pl. 5.

Danilevsky, A.S. & Martynova, O.M. (1962) Order Lepidoptera. Butterflies and moths. *In*: Rohdendorf, B.B. (Ed.), *Fundamentals of Paleontology*, Vol. 9. Arthropoda, Tracheata, Chelicerata. Akademiya Nauk SSSR Publishers, Moscow, pp. 437–444.

Daudet, H. (1876) Description d'une chenille fossile touvée dans calcaire d'Aix (Provence). *Revue et Magasin de Zoologie*, 415–424, pl. 17.

Davis, D.R. (1989) An exceptional fossil amber collection acquired by the Smithsonian Institution. *Proceedings of the Entomological Society of Washington*, 91(4), 545–550.

Davis, D.R. (1994) New leaf-mining moths from Chile, with remarks on the history and composition of Phyllocnistinae (Lepidoptera: Gracillariidae). *Neotropical Lepidoptera*, 5, 65–75.

de Jong, R. (2007) Estimating time and space in the evolution of the Lepidoptera. *Tijdschrift voor Entomologie*, 150, 319–346.

Deichmüller, V. (1886) Die Insekten aus dem lithographischen Schiefer im Dresdner Museum. *Mittheilungeil aus dem Königlische Mineralogisch-Geologischen und praehistorischen Museum in Dresden*, 7, 1–88

Demoulin, G. (1955) Contribution a l'étude morphologique systématique et phylogénique des Éphéméroptères Jurassiques d'Europe Centrale. *Koninklijk Belgisch Instituut voor Natuurwetenschappen, Mededelingen*, 31(39), 1–14.

de Saporta, G. (1872) Études sur la Végétation du Sud-Est de la France. A l'époque Tertiaire. *Annales des Sciences Naturelles*, (5)15, 277–351.

de Serres, M. (1829) *Géognosie des Terrains Tertiaires ou Tableau des Principaux Animaux Invertébrés des Terrains Marins Tertiaires, du midi de la France*. Romathio-Durville, Montpellier & Paris, 276 pp.

DeVries, P.J. & Poinar, Jr., G.O. (1997) Ancient butterfly-ant symbiosis: direct evidence from Dominican amber. *Proceedings of the Royal Society of London B*, 264, 1137–1140.

Donner, H. & Wilkinson, C. (1989) Nepticulidae (Insecta: Lepidoptera). *Fauna of New Zealand*, 16, 1–88.

Douglas, S.D. & Stockey, R.A. (1996) Insect fossils in middle Eocene deposits from British Columbia and Washington State: faunal diversity and geological range extensions. *Canadian Journal of Zoology*, 74(6), 1140–1157.

Drummond, A.J., Ho, S.Y.W., Phillips, M.J. & Rambaut, A. (2006) Relaxed phylogenetics and dating with confidence. *PLOS Biology*, 4(5), 699–710.

Duncan, I.J. (1997) *The Taphonomy of Insects*. Ph. D. thesis, Department of Geology, University of Bristol. Bristol, United Kingdom, xvi+328 pp.

Dunlop, J.A. & Jekel, D. (2008) The oldest available fossil arachnid name. *Palaeodiversity*, 1, 87–92.

Durden, C.J. & Rose, H. (1978) Butterflies from the Middle Eocene: the earliest occurrence of fossil Papilionoidea (Lepidoptera). *Pearce-Sellards Series, Texas Memorial Museum*, 29, 1–25.

Edwards, W.H. (1868) *The Butterflies of North America*, Volume 1. The American Entomological Society, Philadelphia, 450 pp.

Engel, M.S. & Kinzelbach, R.K. (2008) A primitive moth from the earliest Eocene Fur Formation ("Mo-clay") of Denmark (Lepidoptera: Micropterigidae). *Linzer biologische Beiträge*, 40(2), 1443–1448.

Evans, W.P. (1931) Traces of a lepidopterous insect from Middle Waikato Coal-Measures. *Transactions and Proceedings of the New Zealand Institute*, 62(1), 99–101.

Evers, J. (1907) Copal-Schmetterlinge. *Entomologisches Jahrbuch*, 1907, 129–132.

Fernández-Rubio, F. & Nel, A. (2000) *Neurosymploca*? *oligocenica* a new fossil species of Lepidoptera Zygaenoidea of the Oligocene of Céreste (Lubéron, France). *Boletin Sociedad Entomológica Aragonesa*, 27, 7–16.

Fernández-Rubio, F., Peñalver, E. & Martíez-Delclòs, X. (1991) *Zygaena*? *turolensis*, una nueva especie de Lepidoptera Zygaenidae del Mioceno de Rubielos de Mora (Teruel). Descripción y filogenia. *Estudios del Museo de Ciencias Naturales de Alava*, 6, 77–93.

Fernández-Rubio, F. & Peñalver, E. (1994) Un nuevo ejemplar fósil de *Zygaena*? *turolensis* Fernández-Rubio, Peñalver & Martínez-Delclòs, 1991 (Lepidoptera: Zygaenidae). *Estudios del Museo de Ciencias Naturales de Alava*, 9, 39–48.

Fletcher, T.B. (1940) New generic names for microlepidoptera. *Entomologist's Record*, 52, 17–19.

Fletcher, D.S. (1979) *Generic Names of Moths of the World.* Volume 3. Trustees of the British Museum (Natural History), London, xx+243 pp.

FIRGNE (Fossil Insect Research Group for Nojiri-ko Excavation) (1990) Fossil Insects obtained from the Nojiri-ko Formation during the 10th Nojiri-ko and the 5th Hill Site excavation. *Monograph of the Association for the Geological Collaboration in Japan*, 37, 93–110.

Forbes, T.M. (1931) The oldest moth. *The American Naturalist*, 65(700), 479–480.

Freeman, T.N. (1965) A lepidopterous leaf-mine from the Tertiary Period. *The Canadian Entomologist*, 97, 1069–1070.

Frey, D.G. (1964) Remains of animals in Quaternary lake and bog sediments and their interpretation. *Archiv für Hydrobiologie, Beihefte*, 2, 1–114.

Frickhinger, K.A. (1994) *The Fossils of Solnhofen*. Goldschneck-Verlag, Korb, 336 pp.

Fritsch, A. (1882) Fossile Arthropoden aus der Steinkohlen- und Kreideformation Böhmens. *Beiträge zur Paläontologie Österreich-Ungarns*, 2, 1–7, pl. 1–2.

Fujiyama, I. (1968) A Pleistocene fossil *Papilio* from Shiobara, Japan. *Bulletin of the National Science Museum*, Tokyo, 11(1), 85–95.

Fujiyama, I. (1983a) Neogene termites from northeastern districts of Japan, with references to the occurrence of fossil insects in the districts. *Memoirs of the National Science Museum*, 16, 83–98.

Fujiyama, I. (1983b) A Pleistocene nymphalid butterfly from Shiobara, Japan. *Bulletin of the National Science Museum (C)*, 9(4), 121–126.

Gall, L.F. & Tiffney, B.H. (1983) A fossil noctuid moth egg from the Late Cretaceous of eastern North America. *Science*, 219, 507–509.

Gelhaus, J.K. & Johnson, R. (1996) First record of crane flies (Tipulidae: Limoniinae) in Upper Cretaceous Amber from New Jersey, U.S.A. *Transactions of the American Entomological Society*, 122(1), 55–65.

Genise, J.F. & Petrulevicius, J.F. (2001) Caddisfly cases from the early Eocene of Chubut, Patagonia, Argentina. *Abstracts of the Second International International Congress on Paleoentomology*, Kraków, Poland, pp. 12–13.

Gentilini, G. (1991) Occurrence of the genus *Penthetria* Meigen, 1803, from the Lower Messinian of central Italy. *Bollettino della Società Entomologica Italiana*, 123(3), 62–66.

George, V.P. (1952) On some arthropod microfossils from India. *Agra University Journal of Research*, 1, 83–108.

Germar, E.F. (1837) *Fauna insectorum Europae*. Fasciculus 19. Insectorum protogaeae specimen sistens insecta carbonum fossilium. Kümmel, Halle, pl. 1–25

Germar, E.F. (1839) Die versteinerte Insecten Solenhofens. *Nova Acta Leopoldina*, 19, 187–222.

Germar, E.F. (1842) Beschreibung einiger neuen fossilen Insecten I., in dem lithographischen Schiefer Baierns, II. im Schieferthon des Steinkohlengebirges von Wetin. *Münster Beiträge, Petrefacten-Kunde*, 5, 79–90.

Gervais, M.P. (1877) Fossiles du Quercy. *Journal de Zoologie*, 6, 67–68.

Giebel, C.G. (1856) *Die Insecten und Spinnen der Vorwelt*. F.A. Brockhaus, Leipzig, 511 pp.

Giebel, C.G. (1862) Wirbelthier und Insektenreste im Bernstein. *Zeitschrift für die Gesammten Naturwissenschaften*, 20, 311–321.

Gielis, C. (1996) Pterophoridae. *In*: Huemer, P., Karsholt, O. & Lyneborg, L. (Eds.), *Microlepidoptera of Europe*, 1, 1–222.

Givulescu, R. (1984) Pathological elements on fossil leaves from Chiuzbaia (galls, mines and other insect traces). *Dãri de Seamã ale Şedinţelor, Institute of Geology and Geophysics*, 18(3), 123–133.

Godthelp, H., Hand, S., Archer, M., Creaser, P., Jones, A., Norris, B. & Wicks, D. (2010) Amber from Cape York Peninsula: Australia's first significant amber deposit. *Abstracts from the International Congress of Paleoentomology ("Fossils X3")*, Beijing, p. 131.

Gradstein, F.M., Ogg, J.G. & Smith, A.G. (2004) *A Geologic Time Scale 2004*. Cambridge University Press, Cambridge, 589 pp.

Gravenhorst, H. (1835) Bericht der entomologischen Sektion. *Schlesische Gesellschaft für Vaterländische Kultur Jahresbericht*, 1834, 88–95.

Gregor, H.-J. (1990) Contribution to the Late Neogene and Early Quaternary floral history of the Mediterranean. *Review of Palaeobotany and Palynology*, 62, 309–338.

Greven, H. & Wichard, W. (2010) Butterflies or caddisflies? Comments on the chapter "De Papilionibus" from the "Historia Succinorum" (1742) written by Nathanael Sendel. *Entomologie Heute*, 22, 107–150.

Grimaldi, D.A. (1996) *Amber, Widow to the Past*. Harry N. Abrams, Inc., New York, 216 pp.

Grimaldi, D.A. & Engel, M.S. (2005) *Evolution of the Insects*. Cambridge University Press, Cambridge, 755 pp.

Grimaldi, D.A. & Nascimbene, P.C. (2010) Raritan (New Jersey) amber. *In*: Penny, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, pp. 167–191.

Grimaldi, D.A., Engel, M.S. & Nascimbene, P.C. (2002) Fossiliferous Cretaceous amber from Myanmar (Burma): Its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates*, 3361, 1–71.

Grimaldi, D.A., Shedrinsky, A. & Wappler, T.P. (2000) A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. *In*: Grimaldi, D.A. (Ed.), *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*. Backhuys, Leiden, pp. 1–76.

Grote, A. R. (1901) Nachrichten aus dem Verein für Schmetterlingsfreunde in Hildesheim. *Inseckten-Börse*, 18, 108.

Guérin-Ménevilles, M. (1838) Note sur les insectes trouves dans l'ambre. *Revue Zoologique*, 1, 168–170.

Haase, E. (1890) Bemerkungen zur Palaeontologie der Insecten. *Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie*, 2, 1–33.

Hagen, H.A. (1862) Ueber die Neuropteren aus dem lithographischen Schiefer in Bayern. *Palaeontographica*, 10(2), 96–145

Hagen, H.A. (1882) Fossil insects of the Dakota group. *Nature*, 25(638), 265–266.

Hall, J. (1845) Report of the exploring expedition to the Rocky Mountains in the year 1842, and to Oregon and North California in the year 1843–44. *In*: Fremont, J.C., *Twenty-eighth Congress, 2nd Session*. House Executive Document, p. 166, pl. 2.

Hall, J.P.W., Robbins, R.K. & Harvey, D.J. (2004) Extinction and biogeography in the Caribbean: new evidence from a fossil riodinid butterfly in Dominican amber. *Proceedings of the Royal Society of London (B)*, 271, 797–801.

Hamilton, K.G.A. (1992) Lower Cretaceous Homoptera from the Koonwarra Fossil Bed in Australia, with a new superfamily and synopsis of Mesozoic Homoptera. *Annals of the Entomological Society of America*, 85(4), 423–430.

Hammond, P.C. & Poinar, Jr., G.O. (1998) A larval brush-footed butterfly (Lepidoptera: Nymphalidae) in Dominican amber, with a summary of fossil Nymphalidae. *Entomologica Scandinavica*, 29, 275–279.

Hand, S., Archer, M., Bickel, D., Creaser, P., Dettmann, M., Godthelp, H., Jones, A., Norris, B. & Wicks, D. (2010) Australian Cape York amber. *In*: Penny, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, pp. 69–79.

Handschin, E. (1944) Insekten aus den Phosphoriten des Quercy. *Schweizerische Palaeontologische Abhandlungen*, 64(4), 1–23.

Handlirsch, A. (1906) *Die Fossilen Insekten und die Phylogenie der Rezenten Formen*. Lieferung 4. Wilhelm Engelmann, Leipzig, pp. 481–640.

Handlirsch, A. (1907) *Die Fossilen Insekten und die Phylogenie der Rezenten Formen*. Lieferung 6. Wilhelm Engelmann, Leipzig, pp. 801–960.

Handlirsch, A. (1908) *Die Fossilen Insekten und die Phylogenie der Rezenten Formen*. Textband. Wilhelm Engelmann, Leipzig, 1430 pp.

Handlirsch, A. (1939) Neue Untersuchungen über die fossilen Insekten mit Ergänzungen und Nachträgen sowie Ausblicken auf phylogenetische, palaeogeographische und allgemein biologische Probleme, II. Teil. *Annalen des Naturhistorischen Museums in Wien*, 49, 1–240, pl. 1–16.

Harris, A.C. (1984) New Zealand pre-Pleistocene insect fossils. *New Zealand Entomologist*, 8, 47–49.

Harris, A.C. & Raine, J.I. (2002) A sclerite from a late Cretaceous moth (Insecta: Lepidoptera) from Raikaia Gorge, Canterbury, New Zealand. *Journal of the Royal Society of New Zealand*, 32(3), 457–462.

Hayashi, M., Yahiro, K. & Kitabayashi, E. (2005) Middle Pleistocene fossil insects from the Hirabaru Formation of Kitsuki City, Oita Prefecture, Kyushu, Japan. *Bulletin of the Mizunami Fossil Museum*, 32, 227–234.

Hayashi, M., Yahiro, K., Kitamura, N. & Kitabayashi, E. (2004) Middle Pleistocene fossil insects from the Tsumori Formation of Mashiki-machi, Mumamoto Prefecture Japan (Part 2). *Bulletin of the Mizunami Fossil Museum*, 31, 63–67.

Hayashi, M., Yashiro, K. & Kitabayashi, E. (2008) Middle Pleistocene fossil insects from the Saijo Formation of Higashi-Hiroshima City, Hiroshima Prefecture, Japan. *Bulletin of the Mizunami Fossil Museum*, 34, 89–93.

Hayashi, M., Yashiro, K. & Kitabayashi, E. (2009) Middle Pleistocene fossil insects from the Nogami Formation of Kokonoe, Oita Prefecture, Kyushu, Japan. *Bulletin of the Mizunami Fossil Museum*, 35, 105–110.

Heer, O. (1849) *Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien*, Vol. 2. Wilhelm Engelmann, Leipzig, 264 pp.

Heer, O. (1856) Ueber die fossilen Insekten von Aix in der Provence. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich*, 1, 1–40.

Heer, O. (1861) *Recherches sur le Climat et la Végétation du Pays Tertiaire*. Winterthur, Geneve & Paris, 220 pp.

Heer, O. (1865) *Die Urwelt der Schweiz*. Friedrich Schultheß, Zürich, 622 pp.

Heer, O. (1876) *The Primaeval World of Switzerland*, Vol. 2. Longmans, Green, and Co., London, 324 pp.

Heie, O.E. & Lutz, H. (2002) Fossile Aphiden aus den frühen Oligozän-Ablagerungen bei Céreste, Frankreich, mit Beschreibungen neuer Gattungen und Arten (Hemiptera: Sternorrhyncha: Aphidoidea). *Mainzer Naturwissenschaftliches Archiv*, 40, 113–122.

Helm, O. (1899) Insekteneinschlüsse in Gedanit. *Schriften der Naturforschenden Gesellschaft in Danzig*, 10, 38.

Hemming, F. (1967) Generic names of Butterflies of the World and their Type-species (Lepidoptera : Rhopalocera). *Bulletin of the British Museum of Natural History (Entomology) Supplement*, 9, 509 pp.

Henriksen, K.L. (1922) Eocene Insects from Denmark. *Danmarks geologiske Undersogelse* 2(37): 1–36.

Henriksen, K.L. (1933) Undersøgelser over Danmark-Skånes kvartaere Insektfauna. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, 96(2), 77–355, pl. 6–10.

Hentoray, M.-H. (1986) Decouverte d'un nouveau gisement de Lepidopteres, d'autres insectes et d'araignees fossiles a Dauphin (Hte Provence, France). *Linneana Belgica*, 10(6), 266–279.

Hermsen, E.J. & Hendricks, J.R. (2007) A method for constraining the age of origination of derived characters. *Cladistics*, 22, 1–11.

Heyden, C. (1862) Gliederthiere aus der Braunkohle des Niederrhein's, der Wetterau und der Röhn. *Palaeontographica*, 10, 62–82.

Hickey, L.J. & Hodges, R.W. (1975) Lepidopteran leaf mine from the Early Eocene Wind River Formation of northeastern Wyoming. *Science*, 189(4204), 718–720.

Heie, O.E. & Lutz, H. (2002) Fossile Aphiden aus den frühen Oligozän-Ablagerungen bei Céreste, Frankreich, mit Beschreibungen neuer Gattungen und Arten (Hemiptera: Sternorrhyncha: Aphidoidea). *Mainzer naturwissenschaftliches Archiv*, 40, 113–122.

Hiura, I. & Miyatake, Y. (1974) On the fossil Arthropoda in Mizunami amber from Gifu Prefecture (Pleistocene). *Bulletin of the Mizunami Fossil Museum*, (1), 385–392.

Hill, A. (1987) Damage to some fossil bones from Laetoli. *In*: Leakey, M.D. & Harris, J.M. (Eds.), *Laetoli. A Pliocene Site in*

Northern Tanzania. Clarendon Press, Oxford, pp. 543–545.

Hoffeins, C. & Hoffeins, H.W. (2003) Untersuchungen über die Häufigkeit von Inklusen in baltischen und bitterfelder Bernstein (Tertiär, Eozän) aus unselektierten Aufsammlungen unter besonderer Berücksichtigung der ordnung Diptera. *Studia Dipterologica*, 10(2), 381–392.

Holst, N.O. (1908) Efferskörd från de senglaciala lagren vid Toppeladugård. Sveriges Geologiska Underskötning. *Afhandlingar och Uppsatser C*, 210, 1–5.

Hong, Y.-C. (1984) Curvicubitidae fam. nov. (Lepidoptera? Insecta) from Middle Triassic of Shaanxi. *Acta Palaeontologica Sinica*, 23(6), 782–785.

Hope, F.W. (1836) Observations on Succinic Insects. *Transactions of the Entomological Society of London*, 1, 133–147.

Huang, D., Nel, A. & Minet, J. (2010) A new family of moths from the Middle Jurassic (Insecta: Lepidoptera). *Acta Geologica Sinica*, 84(4), 874–885.

Hurd, P.D.J. & Smith, R.F. (1957) The meaning of Mexico's amber. *Pacific Discovery*, 10(2), 6–7.

Hurd, P.D.J., Smith, R.F. & Durham, J.W. (1962) The fossiliferous amber of Chiapas, Mexico. *Ciencia*, 21(3), 108–118.

ICZN (International Commission on Zoological Nomenclature) (1999) *International Code of Zoological Nomenclature*, 4th ed. The International Trust for Zoological Nomenclature, London, 306 pp.

Iversen, J. (1934) Moorgeologische Untersuchungen auf Grönland. Ein Beitrag zur Beleuchtung der Ursachen des Unterganges der mittelalterlichen Nordmännerkultur. *Meddelelser fra Dansk Geologisk Forening*, 8, 341–358.

Jahn, M. & Woolf, D.J. (1963) *The Lying Stones of Dr. Johann Bartholomew Adam Beringer: Being his Lithographiæ Wirceburgensis*. University of California Press, Berkeley, 221 pp.

Jarzembowski, E.A. (1976) Report of Easter Field Meeting: the Lower Tertiaries of the Isle of Wight, 27–31.III.1975. *Tertiary Research*, 1(1), 11–16.

Jarzembowski, E.A. (1980) Fossil insects from the Bembridge Marls, Palaeogene of the Isle of Wight, southern England. *Bulletin of the British Museum of Natural History (Geology)*, 33(4), 237–293.

Jarzembowski, E.A. (1989) A century plus of fossil insects. *Proceedings of the Geologists' Association*, 100(4), 433–449.

Jarzembowski, E.A. (1995) Checklist of Tertiary insects from Dorset. *Proceedings of the Dorset Natural History and Archaeological Society*, 116, 145–146.

Joseph, N.C. (1986) Eocene flora and fauna unearthed at Republic. *Washington Geologic Newsletter*, 14(4), 3–5.

Kapoor, V.C. (1981) *Origin and Evolution of Insects*. Kalyani Publishers, New Delhi & Ludhiana, 144 pp.

Kawahara, A.Y. (2009) Phylogeny of snout butterflies (Lepidoptera: Nymphalidae: Libytheinae): combining evidence from the morphology of extant, fossil, and recently extinct taxa. *Cladistics*, 25, 263–278.

Kawall, J.H. (1876) Organische Einschlüsse im Bergkrystall. *Bulletin de la Société entomologique de Moscou*, 51, 170–173.

Keble, R.A. (1947) Notes on Australian Quaternary climates and migration. *Memoirs of the National Museum of Victoria Melbourne*, (15), 28–81.

Keilbach, R. (1982) Bibliographie und Liste der Arten tierischer Einschlüsse in fossilen Harzen sowie ihrer Aufbewahrungsorte. *Deutsche Entomologische Zeitschrift, N. F.*, 29(4/5), 301–491.

Kemna, H.A. (2008) A Revised Stratigraphy for the Pliocene and Lower Pleistocene Deposits of the Lower Rhine Embayment. *Netherlands Journal of Geosciences*, 87(1), 91–105.

Kernbach, K. (1967) Über die bisher im Pliozän von Willershausen gefundenen Schmetterlings- und Raupenreste. *Bericht der Naturhistorischen Gesellschaft zu Hannover*, 111, 103–108.

Kitching, I.J. & Sadler, S. (2011) Lepidoptera, Insecta. *In*: Harrison, T. (Ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context*, Vol. 2: Fossil Hominins and the Associated Fauna. Springer, Dordrecht, Heidelberg, London & New York, pp. 549–554.

Kinzelbach, R.K. (1970) Eine Gangmine aus dem eozänen Ölshiefer von Messel (Insecta: ?Lepidoptera). *Paläontologische Zeitschrift*, 44(1/2), 93–96.

Kirby, W.F. (1871) *A Synonymic Catalogue of Diurnal Lepidoptera*. J. Van Voorst, London, viii+690 pp.

Kirby, W.F. (1872) *A Synonymic Catalogue of Diurnal Lepidoptera*. Supplement. J. Van Voorst, London, pp. 691–882.

Klebs, R. (1890) Ueber die Fauna des Bernsteins. *Versammlung Deutscher Naturforscher und Ärzte in Heidelberg*, 18(23), 268–271.

Kluge, N.J. (2004) *The Phylogenetic System of Ephemeroptera*. Kluwer Academic Publishers, Dordrecht, 456 pp.

Knowlton, F.H. (1917) A fossil flora from the Frontier Formation of southwestern Wyoming. *United States Geological Survey Professional Paper*, 108, 73–95, pls. 1–39.

Kolbe, H. (1932) Fossile Coleopteren aus präglazialer Zeit Südschwedens. *Entomologiske Meddelelser*, 18, 208–214.

Koponen, M. & Nuorteva, M. (1973) Über subfossile Waldinsekten aus dem Moor Piionsuo in Südfinnland. *Acta Entomologica Fennica*, 29, 1–84.

Kosmowska-Ceranowicz, B. (1996) Zbiory bursztynu w Muzeum Przyrodniczym we Lwowie, dawnym Muzeum im. Dzieduszyckich. *Prace Muzeum Ziemi*, 44, 55–60.

Kosmowska-Ceranowicz, B. & Popiolek, J. (1981) On amber collections in Poland on the basis of unpublished Adam Chetnik's manuscripts from 1951–1958. *Prace Muzeum Ziemi*, 34, 1–29.

Kozhanchikov, I.V. (1957) Novyy Predstavitel' Sem. Cossidae Iz Miotsenovikh Otlozhenyy Kavkaza (Lepidoptera, Insecta). *Doklady Akademiya Nauk SSSR*, 113(3), 675–677.

Kozlov, M.V. (1987) Noviye Molevidniye Cheshuyekriliye iz Baltiiskogo Yantarya. *Paleontological Journal*, 1987(4), 59–67.

Kozlov, M.V. (1988) Paleontology of lepidopterans and problems of the phylogeny of the order Papilionida. *In*: Ponomarenko, A.G. (Ed.), *The Mesozoic–Cenozoic Crisis in the Evolution of Insects*. Academy of Sciences, Moscow, pp. 16–69.

Kozlov, M.V. (1989) New Upper Jurassic and Lower Cretaceous Lepidoptera (Papilionida). *Paleontological Journal*, 23(4), 34–39.

Kozlov, M.V., Ivanov, V.D. & Rasnitsyn, A.P. (2002) Order Lepidoptera Linné, 1758. The butterflies and moths (= Papilionida Laicharting, 1781). *In*: Rasnitsyn, A.P. & Quicke, D.L.J. (Ed.), *History of Insects*. Kluwer Academic Publishers, Dordrecht, Boston & London, pp. 220–227.

Krassilov, V.A. (2007) Mines and galls on fossil leaves from the Late Cretaceous of southern Negev, Israel. *African Invertebrates*, 48 (1), 13–22.

Krassilov, V. & Shuklina, S. (2008) Arthropod trace diversity on fossil leaves from the mid-Cretaceous of Negev, Israel. Alavesia, 2, 239–245.

Kristensen, N.P. (Ed.) (1998) Lepidoptera, Moths and Butterflies Vol. 1: Evolution, Systematics, and Biogeography. *Handbook of Zoology*, Vol. IV Arthropoda: Insecta, Part 35. Walter de Gruyter, Berlin & New York, 487 pp.

Kristensen, N.P. (2003) Appendices. *In*: Kristensen, N. P. (Ed.), Lepidoptera, Moths and Butterflies, Vol. 2: Morphology, Physiology, and Development. *Handbook of Zoology*, Vol. IV Arthropoda: Insecta, Part 36. Walter de Gruyter, Berlin, pp. 545–554.

Kristensen, N.P. & Nielsen, E.S. (1979) A new subfamily of micropterigid moths from South America. A contribution to the morphology and phylogeny of the Micropterigidae, with a generic catalogue of the family (Lepidoptera: Zeugloptera). *Steenstrupia*, 5(7), 69–147.

Kristensen, N.P. & Skalski, A.W. (1998) Phylogeny and palaeontology. *In*: Kristensen, N.P. (Ed.), Lepidoptera, Moths and Butterflies, Vol. 1: Evolution, Systematics, and Biogeography. *Handbook of Zoology*, Vol. IV Arthropoda: Insecta, Part 35. Walter de Gruyter, Berlin & New York, pp. 7–25.

Kristensen, N.P., Scoble, M. & Karsholt, O. (2007) Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. *Zootaxa*, 1668, 699–747.

Kuhn, O. (1951) Ein vermutlicher Schmetterling, *Geisfeldiella benkerti* n. g. n. sp. aus dem Lias ε_1 Nordfrankens. *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte*, 2, 58–61.

Kühne, W.G., Kubig, L. & Schlüter, T. (1973) Eine Micropterygide (Lepidoptera, Homoneura) aus mittelcretazischem Harz Westfrankreichs. *Mitteilungen der Deutschen Entomologischen Gesellschaft*, 32, 61–64.

Kunz, P. (2010) 30 ans déjà. *ASAM Bulletin*, 2010, 39–45.

Kupryjanowicz, J. (2001) Arthropods in Baltic amber and their photographic record. *In*: Kosmowska-Ceranowicz, B. (Ed.), The Amber Treasure Trove, Part I. The Tadeusz Giecewicz's collection at the Museum of the Earth, Polish Academy of Science, Warsaw. *Museum of the Earth Documentary Studies*, 18, 19–59.

Kuroko, H. (1987) A fossil leaf mine of Nepticulidae (Lepidoptera) from Japan. *Bulletin of the Sugadaira Montane Research Center*, 8, 119–121.

Kurz, M.A. & Kurz, M.E. (2010) *Micropterix gertraudae* Kurz M. A. & M. E. Kurz, 2010. Taxonomy Online. Available from http://www.nkis.info/nkis/extaustaxonshow.cgi?uid=guest&tax=161783&lang=e/ (accessed 13 August 2011).

Kusnezov, N. (1928) *Oligamatites martynovi*, gen. et sp. n., a fossil amatid lepidopteron from the Oligocene beds of Central Asia. *Doklady Akademiya Nauk SSSR*, 20(4), 431–436.

Kusnezov, N. (1941) *A Revision of Amber Lepidoptera*. Paleontological Institute, USSR Academy of Sciences, Moscow & Leningrad, 135 pp.

Labandeira, C.C. (1994) A compendium of fossil insect families. *Milwaukee Public Museum Contributions in Biology and Geology*, (88), 1–71.

Labandeira, C.C. (1998a) The role of insects in Late Jurassic to middle Cretaceous Ecosystems. Lower and Middle Cretaceous Terrestrial Ecosystems. *New Mexico Museum of Natural History and Science Bulletin*, 14, 105–124.

Labandeira, C.C. (1998b) Plant-Insect associations from the fossil record. *Geotimes*, 43, 18–24.

Labandeira, C.C. (1998c) Early history of arthropod and vascular plant associations. *Annual Review of Earth and Planetary Sciences*, 26, 329–377.

Labandeira, C.C. (1999) Insects and other hexapods. *In*: Singer, R. (Ed.), *Encyclopedia of Paleontology.* Fitzroy Dearborn, Chicago, pp. 603–624.

Labandeira, C.C. (2002a) Paleobiology of middle Eocene plant-insect associations from the Pacific Northwest: A preliminary report. *Rocky Mountain Geology*, 37(1), 31–59.

Labandeira, CC. (2002b) The history of associations between plants and animals. *In*: Herrera, C.M. & Pellmyr, O., (Eds.), *Plant–Animal Interactions: An Evolutionary Approach.* Blackwell Science, London, pp. 28–74, 248–261.

Labandeira, C.C., Dilcher, D.L., Davis, D.R. & Wagner, D.L. (1994) Ninety-seven million years of angiosperm-insect association: Paleobiological insights into the meaning of coevolution. *Proceedings of the National Academy of Sciences, USA*, 91, 12278–12282.

Labandeira, C.C., Johnson, K.R. & Lang, P.J. (2002a) Preliminary assessment of insect herbivory across the Cretaceous–Tertiary boundary: Major extinction and minimum rebound. *In*: Hartman, J.H., Johnson, K.R. & Nichols, D.J. (Eds.), The Hell Creek Formation and the Cretaceous–Tertiary Boundary in the Northern Great Plains. *Geological Society of America Special Paper*, 361, 297–327.

Labandeira, C.C., Johnson, K.R. & Wilf, P. (2002b) Impact of the terminal Cretaceous event on plant-insect associations. *Pro-*

ceedings of the National Acadmy of Sciences, USA, 99(4), 2061–2066.

Labandeira, C.C., & Sepkoski, J.J., Jr. (1993) Insect diversity in the fossil record. *Science*, 261, 310–315.

Lamba, B.S. (1944) A preliminary note on the age of the saline series in the Punjab Salt Range. *Current Science*, 13, 258.

Lancucka-Srodoniowa, M. (1964) Tertiary coprolites imitating fruits of the Araliaceae. *Acta Societatis Botanicorum Poloniae*, 33(2), 469–473.

Lang, P.J., Scott, A.C. & Stephenson, J. (1995) Evidence of plant-arthropod interactions from the Eocene Branksome Sand Formation, Bournemouth, England: Introduction and description of leaf mines. *Tertiary Research*, 15(4), 145–174.

Larsson, S.G. (1962) The Copenhagen collection of amber-fossils. *Entomologiske Meddelelser*, 31(4), 323–326.

Larsson, S.G. (1965) Reflections on the Baltic amber inclusions. *Entomologiske Meddelelser*, 34(2), 135–142.

Larsson, S.G. (1975) Paleobiology and mode of burial of the insects of the Lower Eocene Mo-clay of Denmark. *Bulletin of the Geological Society of Denmark*, 24, 193–209.

Larsson, S.G. (1978) Baltic Amber —a Palaeobiological Study. *Entomonograph*, Vol. 1. Scandinavian Science Press Ltd., Klampenborg, 187 pp.

Laurentiaux, D. (1953) Classe des Insectes. *In*: Piveteau, J. (Ed.), *Traité de Paléontologie*, Vol. 3. Masson et Cie, Paris, pp. 397–527.

Leakey, L.S.B. (1952) Lower Miocene invertebrates from Kenya. *Nature*, 169(4302), 624–625.

Leestmans, R. (1983) Les lépidoptères fossiles trouvés en France (Insecta Lepidoptera). *Linneana Belgica*, 9(1), 64–89.

Lefebvre, M.A. (1851) Relatives a l'empreinte d'un Lépidoptère fossile (*Cyllo Sepulta*) du Docteur Boisduval. *Annales de la Société Entomologique de France*, (2)9, 71–88, pl. 3.

Lemdahl, G. (2000) Late Glacial and Early Holocene insect assemblages from sites at different altitudes in the Swiss Alps —implications on climate and environment. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 159, 293–312.

Lewis, S.E. (1976) Lepidopterous feeding damage of live oak leaf (*Quercus convexa* Lesquereux) from the Ruby River Basin (Oligocene) of southwestern Montana. *Journal of Paleontology*, 50(2), 345–346.

Lewis, S.E. (1969) Lepidopterous larval-mining of an oak (?) leaf from the Latah Formation (Miocene) of eastern Washington. *Annals of the Entomological Society of America*, 62(5), 1210–1211.

Lewis, S.E. (1985) Miocene insects from the Clarkia deposits of northern Idaho. *In*: Smiley, C.J. (Ed.), *Late Cenozoic History of the Pacific Northwest*. American Association for the Advancement of Science, Pacific Division, pp. 245–264.

Lewis, S.E. (1989) Miocene insect localities in the United States. *Occasional Papers in Paleobiology, St. Cloud State University*, 3(4), 1–13.

Lewis, S.E. (1992) Insects of the Klondike Mountain Formation, Republic, Washington. *Washington Geology*, 20(3), 15–19.

Liebhold, A.M., Voney, W.J.A. & Schorn, H.E. (1982) An unidentified leaf mine in fossil *Mahonia reticulata* (Berberidaceae). *The Canadian Entomologist*, 114, 455–456.

Lindberg, H. (1900) Suomen turvesuot. *Suomen suoviljelysyhdistyksen vuosikirja*, 1900, 184–257.

Łomnicki, A.M. (1894) *Fauna Pleistocenica Insectorum Boryslaviensium*. Musaeum Dzieduszyckianum, Lvov, 116 pp.

Lukashevich, E.D. (1996) New chaoborids from the Mesozoic of Mongolia (Diptera: Chaoboridae). *Palaeontological Journal*, 30(5), 551–558.

Maa, T. (1949) A synopsis of Asiatic Siricoidea with notes on certain exotic and fossil forms (Hymenoptera Symphyta). *Notes d'Entomologie Chinoise* 13(2): 11–189.

Mabberley, D.J. (1993) *The Plant Book: A Portable Dictionary of the Higher Plants.* Cambridge University Press, Cambridge, xii+707 pp.

MacKay, M.R. (1969) Microlepidopterous larvae in Baltic amber. *Canadian Entomologist*, 101(11), 1173–1180.

Martínez-Delclós, X., Arillo, A., Ortuño, V. & Peñalver, E. (1999) El ámbar del Cretácico Inferior de Peñacerrada (Álava, España). *Temas Geológico-Mineros ITGE*, 26, 13–17.

Martínez-Delclós, X., Briggs, D.E.G. & Peñalver, E. (2004) Taphonomy of insects in carbonates and amber. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 203, 19–64.

Martins-Neto, R.G. (1989) Novos insetos Terciários do Estado de São Paulo. *Revista Brasileira de Geociências*, 19(3), 375–386.

Martins-Neto, R.G. (1998a) A paleontomofauna da Formação Tremembé (Bacia de Taubaté), Oligoceno do Estado de São Paulo: descrição de novos lepidópteros (Insecta). *Acta Geologica Leopoldensia*, 41(46/47), 75–82.

Martins-Neto, R.G. (1998b) A paleoentomofauna da Formação Tremembé (Bacia de Taubaté) Oligoceno do Estado de São Paulo: novos Hemiptera, Auchenorrhyncha, Hymenoptera, Coleoptera e Lepidoptera (Insecta). *Revista Universidade Guarulhos, Geociências*, 3(6), 58–70.

Martins-Neto, R.G. (1999) New genus and new species of Lepidoptera (Insecta, Eolepidopterigidae) from Santana Formation (Lower Cretaceous, northeast Brazil). *Boletim do 5th Simpósio sobre o Cretáceo do Brasil*, 1999, 531–535.

Martins-Neto, R.G. (2002) *Insetos Fósseis como Bioindicadores em Depósitos Sedimentares: um Estudo de Caso para o Mesozóico Sul-Americano*. Doctoral Thesis, Departamento de Geologia, Universidade do Vale do Rio dos Dinos, Porto Alegra, Brasil, 214 pp.

Martins-Neto, R.G. (2005) Estágio atual da Paleoartropodologia Brasileira: Hexápodes, Miriápodes, Crustáceos (Isopoda, Decapoda, Eucrustacea e Copepoda) e Quelicerados. *Arquivos do Museu Nacional, Rio de Janeiro*, 63(3), 471–494.

Martins-Neto, R.G. & Vulcano, M.A. (1989) Amphiesmenoptera (Trichoptera + Lepidoptera) na Formação Santana (Cretáceo Inferior) Bacia do Araripe, Nordeste do Brasil. I. Lepidoptera (Insecta). *Anais da Academia Brasileira de Ciências*, 61(4), 459–466.

Martins-Neto, R.G., Kucera-Santos, J.C., de Moraes Vieira, F.R. & de Campos Fragoso, L.M. (1993) Nova espécie de borboleta (Lepidoptera: Nymphalidae: Satirynae [sic]) da Formação Tremembé, Oligoceno do Estado de São Paulo. *Acta Geologica Leopoldensia*, 16, 5–16.

Mathewes, R.W. & Brooke, R.C. (1971) Fossil Taxodiaceae and new angiosperm macrofossils from Quilchena, British Columbia. *Syesis*, 4, 209–216.

McCobb, L.M.E., Duncan, I.J., Jarzembowski, E.A., Stankiewicz, B.A., Wills, M.A. & Briggs, D.E.G. (1998) Taphonomy of the insects from the Insect Bed (Bembridge Marls), late Eocene, Isle of Wight, England. *Geological Magazine*, 135(4), 553–563.

McElwaine, J.C. (1998) Do fossil plants signal palaeoatmospheric CO_2 concentration in the geological past? *Philosophical Transactions of the Royal Society B*, 353, 83–96.

McNamara, M., Briggs, D.E.G., Orr, P. J., Wedmann, S., Noh, H. & Cao, H. (2011) Fossilized biophotonic nanostructures reveal the original colors of 47-million-year-old moths. *PLoS Biology*, 9 (11), e1001200.

Menge, A. (1856) *Lebenszeichen Vorweltlicher, im Bernstein Eingeschlossener Thiere*. Programm der öffentlichen Prüfung der Schüler der Petrischule. A.W. Kafemann, Danzig, 32 pp.

Mérit, X. & Mérit, M. (2008) *Problongos baudiliensis* genus novus & species nova : un nouveau Lépidoptère fossile découvert dans la diatomite du miocène supérieur de Saint-Bauzile (Ardèche, F-07) (Lepidoptera, Geometridae, Ennominae). *Revue des Lépidoptéristes de France*, 17(39), 29–33.

Meunier, F. (1902) Una nueva Cicada del Kimeridgense en el Montsech Provincia de Lérida (Cataluña). *Memorias de la Real Academia de Ciencias y Artes de Barcelona*, 4(18), 9–14.

Mey, W. (2011) On the systematic position of *Baltimartyria* Skalski, 1995 and description of a new species from Baltic amber (Lepidoptera, Micropterigidae). *Zookeys*, 130, 331–342.

Meyer, H.W. (2003) *The Fossils of Florissant*. Smithsonian Books, Washington & London, 258 pp.

Miki, S. (1937) Plant fossils from the Stegodon Beds and the Elephas Beds near Akashi. *Japanese Journal of Botany*, 8(4), 303–341, pl. 8–9.

Miller, J.Y. & Brown, F.M. (1989) A new Oligocene fossil butterfly, *Vanessa amerindica* (Lepidoptera: Nymphalidae), from the Florissant Formation, Colorado. *Bulletin of the Allyn Museum*, 126, 1–9.

Minot, C.S. (1886) Zur Kentniss der Insektenhaut. *Archiv für Mikroskopische Anatomie*, 28, 37–47.

Morlan, R.H. & Matthews, J.V. (1983) Taphonomy and paleoecology of fossil insect assemblages from Old Crow River (CRH-15) Northern Yukon Territory, Canada. *Géographie physique et Quaternaire*, 37 (2), 147–157.

Müller, A.H. (1982) Über Hyponome fossiler und rezenter Insekten, erster Beitrag. *Freiberger Forschungshefte C*, 366, 7–27.

Mueller, W.P. (1964) The distribution of cladoceran remains in surficial sediments from three northern Indiana lakes. *Investigations of Indiana Lakes and Streams*, 6(1), 1–63.

Nekrutenko, Y.P. (1965a) A new Tertiary nymphalid (Lepidoptera, Rhopalocera). *Paleontologicheski Zhurnal*, 4, 97–99.

Nekrutenko, Y.P. (1965b) Tertiary nymphalid butterflies and some phylogenetic aspects of systematic lepidopterology. *Journal of Research on the Lepidoptera*, 4(3), 149–158.

Nel, A. & Descimon, H. (1994) Une nouvelle espèce de Lèpidoptère fossile du Stampien de Cèreste (04) (Lepidoptera–Satyridae). *Gèologie Mèditerranèenne*, 11(4), 287–293.

Nel, A. & Nel, J. (1985) A propos de chenilles et de chrysalides fossiles du Stampien en France. *Alexanor*, 14(3), 126–130.

Nel, A. & Nel, J. (1986) A propos de deux Lépidoptères fossiles du Stampien d'Aix-en-Provence (Lepidoptera, Hesperiidae et Nymphalidae Satyrinae). *Bulletin du Muséum National d'Histoire Naturelle, Paris*, (4), 8(3), 343–350.

Nel, A., Nel, J. & Balme, C. (1993) Un nouveau lépidoptère Satyrinae fossile de l'Oligocene du sud-est de la France (Insecta, Lepidoptera, Nymphalidae). *Linneana Belgica*, 14(1), 20–36.

Néraudeau, D., Perrichot, V., Dejax, J., Masure, E., Nel, A., Philippe, M., Moreau, P., Guillocheau, F. & Guyot, T. (2002) A new fossil locality with insects in amber and plants (likely uppermost Albian): Archingeay (Charente-Maritime, France). *Geobios*, 35, 233–240.

Nielsen, E.S. & Kristensen, N.P. (1996) The Australian moth family Lophocoronidae and the basal phylogeny of the Lepidoptera–Glossata. *Invertebrate Taxonomy*, 10, 1199–1302.

Nieukerken, E.J. van, 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.A., Brown, J.W., Bucheli, S.R., Davis, D.R., De Prins, J., De Prins, W., Epstein, M.E., Gentili-Poole, P., Gielis, C., Hattenschwiler, 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 Linnaeus, 1758. *In*: Zhang, Z.-Q. (Ed.), Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. *Zootaxa*, 3148, 212–221.

Nudds, J.R. & Selden, P.A. (2008) *Fossil Ecosystems of North America*. A Guide to the Sites and Their Extraordinary Biotas. University of Chicago Press, Chicago, 288 pp.

Nuorteva, M. & Kinnunen, K.A. (2008) Insect frass in Baltic amber. *Bulletin of the Geological Society of Finland*, 80, 105–124.

Nye, I.W.B. (1975) *The Generic Names of Moths of the World*, Vol. 1. Noctuoidea (part): Noctuidae, Agaristidae, and Nolidae.

Trustees of the British Museum (Natural History), London, 568 pp.

Ollerton, J. (1999) La evolución de las relaciones polinizador-planta en los artrópodos. *Boletin de la Sociedad Entomológica Aragonesa*, 26, 741–758.

Opler, P.A. (1973) Fossil lepidopterous leaf mines demonstrate the age of some insect-plant relationships. *Science*, 179, 1321–1323.

Opler, P.A. (1974) Biology, ecology, and host specificity of Microlepidoptera associated with *Quercus agrifolia* (Fagaceae). *University of California Publications in Entomology*, 75, 83 pp., 7 pls.

Opler, P.A. (1982) Fossil leaf-mines of *Bucculatrix* (Lyonetiidae) on *Zelkova* (Ulmaceae) from Florissant, Colorado. *Journal of the Lepidopterists' Society*, 36(2), 145–147.

Oppenheim, P. (1885) Die Ahnen unserer Schmetterlinge in der Sekundär- und Tertiärperiode. *Berliner Entomologische Zeitschrift*, 29(2), 331–349, pl. 10–12.

Oppenheim, P. (1888) Die Insectenwelt des lithographischen Schiefers in Bayern. *Palaeontographica*, 34, 215–247.

Oustalet, M.E. (1870) Recherches sur les Insectes Fossiles des Terrains Tertiaires de la France. *Annales des Sciences Géologiques*, 2, 1–175.

Pearson, R.C. & Obradovich, J.D. (1977) Eocene rocks in northeast Washington, Radiometric ages and correlations. *U.S. Geological Survey Bulletin*, 1433, 41 pp.

Peñalver, E. (1997) Hojas fósiles del Terciaro de Teruel con marcas de herbivorismo debidas a orugas. *Boletin de la Sociedad Entomologica Aragonesa*, 19, 29–33.

Peñalver, E. & Delclós, X. (2004) Insectos del Mioceno inferior de Ribesalbes (Castellón, España). Interacciones planta-insecto. *Treballs del Museu de Geologia de Barcelona*, 12, 69–95.

Peñalver, E. & Engel, M.S. (2006) Two wasp families rare in the fossil record (Hymenoptera): Perilampidae and Megaspilidae from the Miocene of Spain. *American Museum Novitates*, (3540), 12 pp.

Peñalver, E. & Grimaldi, D.A. (2006) New data on Miocene butterflies in Dominican amber (Lepidoptera: Riodinidae and Nymphalidae) with the description of a new nymphalid. *American Museum Novitates*, 3519, 1–17.

Perkins, M.E., Brown, F.H., Nash, W.P., McIntosh, W. & Williams, S.K. (1998) Sequence, age and source of silicic fallout tuffs in middle to late Miocene basins of the northern Basin and Range province. *Geological Society of America Bulletin*, 110, 344–360.

Perkovsky, E.E., Zosimovich, V.Y. & Vlaskin, A.Y. (2003) Rovno amber fauna: a preliminary report. *In*: Krzemińska, E. & Krzemiński, W. (Eds.), Proceedings of the Second Congress on Palaeoentomology "Fossil Insects". *Acta Zoological Cracoviensia*, 46(Supplement), 423–430.

Petrulevicius, J.F. & Martins-Neto, R.G. (2000) Checklist of South American Cenozoic insects. *Acta Geologica Hispanica*, 35(1/2), 135–147.

Pierce, W.D. (1945) Two new fossils from the Upper Miocene of the Puente Hills. *Bulletin, Southern California Academy of Sciences*, 44(1), 3–6.

Piton, L. (1936) Addition a la faune entomologique des cinerites du La Chambon (Puy-de -Dome). *Revue Scientifique du Bourbonnais et du Centre de la France*, 1936, 16–24.

Piton, L. (1940) *Paléontologie du Gisement Éocène de Menat (Puy-de-Dôme) (Flore et Faune)*. Imprimeries Paul Vallier, Clermont-Ferrand, 257 pp.

Poinar, Jr., G.O. (1992) *Life in Amber.* Stanford University Press, Stanford, 368 pp.

Poinar, Jr., G.O. & Brown, A.E. (2002) *Hymenaea mexicana* sp. nov. (Leguminosae: Caesalpinioideae) from Mexican amber indicates Old World connections. *Botanical Journal of the Linnean Society*, 139, 125–132.

Poinar, Jr., G.O. & Brown, J.W. (1993) A new fossil tortricid (Lepidoptera: Tortricidae) from Dominican amber. *Entomologica Scandinavica*, 23, 25–29.

Poinar, Jr., G.O. & Poinar, R. (2005) Fossil evidence of insect pathogens. *Journal of Invertebrate Pathology*, 89, 243–250.

Poinar, Jr., G.O., Treat, A.E. & Southcott, R.V. (1991) Mite parasitism of moths: Examples of palaeosymbiosis in Dominican amber. *Experientia*, 47, 210–212.

Pongrácz, A. (1928) Die fossilen Insekten von Ungarn, mit besonderer Berücksichtigung der Entwicklung der Europäischen Insekten-Fauna. *Annales Historico-Naturales Musei Nationalis Hungarici*, 25, 91–194.

Presl, J.S. (1822) Additamenta ad faunam protogaeam, sistens descriptiones aliquot animalium in succino inclusorum. *In*: Presl, J.S. & Presl, C.B. (Eds.), *Deliciae Pragensis, Historiam Naturalem Spectantes*. Calve, Prague, pp. 191–210.

Procaccini, V. (1842) Sugli entomoliti delle gessase Sinigagliesi. *Nuovi Annali delle Scienze Naturali*, 1842, 448–456.

Prokop, J. (2003) Remarks on palaeoenvironmental changes based on reviewed Tertiary insect associations from the Krušné hory piedmont basins and the České středhoří Mts in northwestern Bohemia (Czech Republic). *In*: Krzemińska, E. & Krzemiński, W. (Eds.), Proceedings of the Second Congress on Palaeoentomology "Fossil Insects". *Acta Zoological Cracoviensia*, 46(Supplement), 329–344.

Pyron, R.A. (2010) A likelihood method for assessing molecular divergence time estimates and the placement of fossil calibrations. *Systematic Biology*, 59, 185–194.

Raffray, M. (1875) "in Simon, M. E., Séance du 23 Juin 1875." *Annales de la Société Entomologique de France*, 5, 125–126.

Rambur, M. (1839) Bulletin entomologique. *Annales de la Société Entomologique de France*, 8, i–xviii.

Rasnitsyn, A.P. (1983) Pervaya nakhodka babochki yurskogo vozrasta. *Doklady Akademiya Nauk SSSR*, 269(2), 467–671.

Rasnitsyn, A.P. (1986) Review of the fossil Tiphiidae with description of a new species (Hymenoptera). *Psyche*, 93, 91–102.

Rasnitsyn, A.P. & Ross, A.J. (2000) A preliminary list of arthropod families present in the Burmese amber collection at the Natural History Museum, London. *Bulletin of the Natural History Museum, London (Geology)*, 56(1), 21–24.

Rasnitsyn, A.P. & Zherikhin, V.V. (2002) Appendix: Alphabetic list of selected insect fossil sites. Impression fossils. *In*: Rasnitsyn, A.P. & Quicke, D.L.J. (Ed.), *History of Insects*. Kluwer Academic Publishers, Dordrecht, Boston & London, pp. 437–444.

Rebel, H. (1898) Fossil Lepidopteren aus der Miocänformation von Gabbro. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften*, 107, 731–745.

Rebel, H. (1934a) Bernstein–Lepidopteren (aus der Sammlung Bachofen-Echt.). *Paleobiologica*, 6, 1–16, pl. 1.

Rebel, H. (1934b) Mikrolepidopteren aus dem baltischen Bernstein. *Forschungen und Fortschritte*, 10(80), 372–373.

Rebel, H. (1936) Mikrolepidopteren aus dem baltischen Bernstein. *Die Naturwissenschaften*, 24, 519–520.

Reid, C. & Reid, E.M. (1915) The Pliocene floras of the Dutch Prussian Border. *Mededeelingen van de Rijksopsporing van Delfstoffen*, (6), 1–178, pl. 1–20.

Reiss, H. (1936) Ein Zygaenenfund aus der Tertiärzeit. *Entomologische Rundschau*, 53(39), 554–556.

Richter, G. (1988) Problems in the analysis of stomach contents of Eocene mammals from the Messel oil shale-layers. *Courier Forschungsinstitut Senckenberg*, 107, 121–127.

Richter, G. & Storch, G. (1980) Beiträge zur Ernährungsbiologie eozäner Fledermäuse aus der “Grube Messel”. *Natur und Museum*, 110(12), 353–367.

Riek, E.F. (1955) Fossil insects from the Triassic beds at Mt. Crosby, Queensland. *Australian Journal of Zoology*, 3, 654–691.

Riek, E.F. (1970) Fossil history. *In*: CSIRO, *The Insects of Australia*. Melbourne University Press, Melbourne, pp. 168–186.

Riek, E.F. (1976) A new collection of insects from the Upper Triassic of South Africa. *Annals of the Natal Museum*, 22(3), 791–820.

Rohdendorf, B.B. (1939) O Miotsenovoy Faune Nasekomykh Okrestnostey g. Voroshilovska. *Priroda*, 12, 85–88.

Rohdendorf, B.B. & Zehrikhin, V.V. (1974) Paleontology and nature conservation. *Priroda*, 705(5), 82–91.

Ross, A.J. (1998) *Amber: The Natural Time Capsule*. Harvard University Press, Cambridge, 73 pp.

Ross, A.J. & Jarzembowski, E.A. (1993) Arthropoda (Hexapoda; Insecta). *In*: Benton, M.J. (Ed.), *The Fossil Record 2*. Chapman and Hall, London, pp. 363–426.

Ross, A.J., Mellish, C., York, P. & Crighton, B. (2010) Burmese amber. *In*: Penny, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, pp. 208–235.

Rosenkjaer, H.N. (1906) *Fra det Underjordiske København*. Geologiske og historiske Undersøgelser, København, 148 pp.

Rozefelds, A.C. (1985) The first records of fossil leaf mining from Australia. *Hornibrook Symposium, New Zealand Geological Survey Record*, 9, 80–81.

Rozefelds, A.C. (1988a) Insect leaf mines from the Eocene Anglesea locality, Victoria, Australia. *Alcheringa*, 12, 1–6.

Rozefelds, A.C. (1988b) Lepidoptera mines in *Pachypteris* leaves (Corystospermaceae: Pteridospermophyta) from the Upper Jurassic/Lower Cretaceous Battle Camp Formation, north Queensland. *Proceedings of the Royal Society of Queensland*, 99, 77–81.

Rust, J. (1998a) Biostratinomie von Insekten aus der Fur-Formation von Dänemark (Moler, oberes Paleozän/unteres Eozän. *Paläontologische Zeitschrift*, 71(1/2), 41–58.

Rust, J. (1998b) Fossil insects from the Fur and Olst Formations (“Mo Clay”) of Denmark (upper Paleocene/lowermost Eocene). *Proceedings of the First International Palaeoentomological Conference*, Moscow, AMBA Projects International, Bratislava, 135–139.

Rust, J. (1999) *Biologie der Insekten aus dem ältersten Tertiär Nordeuropas*. Unpublished Habilitation thesis, Biologische Fakultät der Georg-August, Universität Göttingen, 482 pp.

Rust, J. (2000a) Fossil record of mass moth migration. *Nature*, 405, 530–531.

Rust, J. (2000b) Massenflüge von Lepidopteren über die Nordsee im Alttertiär (Insecta, Lepidoptera). *Atalanta*, 31(3/4), 577–583.

Sahni, A. (1984) Cretaceous–Paleocene terrestrial faunas of India: Lack of endemism during drifting of the Indian Plate. *Science*, 226, 441–443.

Sanderson, M.W. & Farr, T.H. (1960) Amber with insect and plant inclusions from the Dominican Republic. *Science*, 131(3409), 1313.

Schlüter, T. (1974) Kritisches zum Nachweis von Schmetterings-schuppen aus einem fossilen Harz der mittleren Kreide Nordwestfrankreichs. *Entomologische Zeitschrift*, 84(23), 253–256.

Schlüter, T. (1975) Nachweis verschiedener Insecta-Ordines in einem mittelkretazischen Harz Nordwestfrankreichs. *Entomologica Germanica*, 1(2), 151–161.

Schlüter, T. (1997) Validity of the Paratrichoptera —an extinct insect order related to the Mecoptera, Diptera, Trichoptera or Lepidoptera? Suggestions based on discoveries in the Upper Triassic Molteno Formation of South Africa. *Berliner geowissenschaftliche Abhandlungen*, 25, 303–312.

Schlotheim, E.F. von (1820) *Die Petrfactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt erläutert*. Bekker’schen edit, Gotha, 457 pp.

Schöberlin, E. (1888) Der Oeninger Stinkschiefer und seine Insektenreste. *Societas Entomologica*, 3(9), 68–69.

Schröter, J.S. (1784) *Neue Litteratur und Beyträge zur Kenntniß der Naturgeschichte vorzüglich der Conchylien und Foßilien*, Vol. 1. Müller, Leipzig, 550 pp.

Schüssler, H. (1933) Saturniidae: 1. Subfam. Attacinae. *In*: Strand, E. (Ed.), *Lepidopterum Catalogus*. W. Junk, Berlin, 769 pp.

Scott, A.C., Stephenson, J. & Chaloner, W.G. (1992) Interaction and coevolution of plants and arthropods during the Palaeozoic and Mesozoic. *Philosophical Transactions of the Royal Society of London B*, 335, 129–165.

Scudder, S.H. (1867) Results of an examination of a small collection of fossil insects obtained by Prof. Wm. Denton in the Tertiary beds of Green River, Colorado. *Proceedings of the Boston Society of Natural History*, 11, 117–118.

Scudder, S.H. (1868) The insects of ancient America. *The American Naturalist*, 1(12), 625–631.

Scudder, S.H. (1872) Description d'un nouveau papillon fossile (*Satyrites reynesii*) trouve a Aix en Provence. *Revue et Magasin de Zoologie*, (2)23, 66–72.

Scudder, S.H. (1875a) Historical sketch of the generic names proposed for butterflies: A contribution to systematic nomenclature. *Proceedings of the American Academy of Arts and Sciences, New Series*, 2, 91–293.

Scudder, S.H. (1875b) Fossil butterflies. *Memoirs of the American Association for the Advancement of Science*, 1, 1–99.

Scudder, S.H. (1877) The first discovered traces of fossil insects in the American Tertiaries. *Bulletin of the United States Geological Survey of the Territories*, 3(4), 741–762.

Scudder, S.H. (1878) An account of some insects of unusual interest from the Tertiary rocks of Colorado and Wyoming. *Bulletin of the United States Geological Survey of the Territories*, 4(2), 519–543.

Scudder, S.H. (1881) The Tertiary lake-basin at Florissant, Colorado, between South and Hayden Parks. *Bulletin of the United States Geological Survey of the Territories*, 6, 279–300.

Scudder, S.H. (1889) The fossil butterflies of Florissant. *Annual Report of the United States Geological Survey*, 8, 433–474.

Scudder, S.H. (1890) The Tertiary Insects of North America. *Report of the United State Geological Survey of the Territories*, 13, 1–734, pl. 1–28.

Scudder, S.H. (1891) Index to the known fossil insects of the World including myriapods and arachnids. *Bulletin of the United States Geological Survey*, 71, 1–744.

Scudder, S.H. (1892) Some insects of special interest from Florissant, Colorado, and other points in the Tertiaries of Colorado and Utah. *Bulletin of the United States Geological Survey*, 93, 5–35.

Sendelius, N. (1742) *Historia Succinorum Corpora Aliena Involventium et Naturae Opere, Pictorum et Caelatorum ex Augustorum I et II Cimeliis Dresdae Conditis Aeri Insculptorum Conscripta*. Fridericum Gleditschium, Lipsiae, 328 pp., 13 pls.

Shields, O. (1985) Southeast Asian affinities in Colorado Oligocene Libytheidae. *Tokurana Special*, 1, 13–24.

Skalski, A.W. (1973a) Studies on the Lepidoptera from fossil resins. Part II. *Epiborkhausenites obscurotrimaculatus* gen. et. sp. nov. (Oecophoridae) and a tineid-moth discovered in the Baltic amber. *Acta Palaeontologica Polonica*, 28(1), 153–160.

Skalski, A.W. (1973b) Studies on the Lepidoptera from fossil resins. Part VI. *Tortricidrosis inclusa* gen. et spec. nov. from the Baltic amber (Lep., Tortricidae). *Deutsche Entomologische Zeitschrift, N. F.*, 20(4/5), 339–344.

Skalski, A.W. (1974) Zwei neue Gattungen und Arten der Familie Tineidae aus dem Baltischen Bernstein. *Beiträge zur Entomologie*, 24(1/4), 97–104.

Skalski, A.W. (1976a) Les lépidoptères fossiles de l'ambre, Etat actuel de nos connaissances. *Linneana Belgica*, 6(7), 154–169.

Skalski, A.W. (1976b) Les lépidoptères fossiles de l'ambre, Etat actuel de nos connaissances (2^{me} partie). *Linneana Belgica*, 6(8), 195–208.

Skalski, A.W. (1976c) Les lépidoptères fossiles de l'ambre, Etat actuel de nos connaissances (3^{me} partie et fin). *Linneana Belgica*, 6(9), 221–233.

Skalski, A.W. (1977) Studies on the Lepidoptera from fossil resins. Part 1. General remarks and descriptions of new genera and species of the families Tineidae and Oecophoridae from the Baltic amber. *Prace Muzeum Ziemi*, 26, 3–24.

Skalski, A.W. (1979a) A new member of the Family Micropterigidae (Lepidoptera) from the Lower Cretaceous of Transbaikalia. *Paleontological Journal*, 13(2), 206–214.

Skalski, A.W. (1979b) Study on the Lepidoptera from fossil resins. Part VII. *Palaeodepressaria hannemanni* gen. et spec. nov (Oecophoridae) from the Baltic amber. *Prace Muzeum Ziemi*, 32, 101–107.

Skalski, A.W. (1979c) Records of oldest Lepidoptera. *Nota Lepidopterologica*, 2(1/2), 61–66.

Skalski, A.W. (1984) A new lower Cretaceous Lepidoptera (Homoneura). *Bulletin of the Polish Academy of Science, Biological Sciences*, 32(11/12), 389–394.

Skalski, A.W. (1985) Motyle (Lepidoptera) w bursztynie baltyckim. *Wiadomosci Entomologiczne*, 6(3/4), 207–210.

Skalski, A.W. (1988) *Stauropolia nekrutenkoi* gen. et. sp. n. (Lepidoptera, Arctiidae)–a new fossil Tiger-moth from Miocene of the Caucasus. *Vestnik Zoologii*, 1988(4), 21–25.

Skalski, A.W. (1990a) An annotated review of all fossil records of Lower Lepidoptera. *Bulletin of the Sugadaira Montane Research Center*, 11, 125–128.

Skalski, A.W. (1990b) The families Nepticulidae and Thyrididae in Baltic amber (Lepidoptera). Proceedings of the Seventh Congress of the Societas Europaea Lepidopterologica, Lunz. *Nota Lepidopterologica Supplement*, 4, 144–145.

Skalski, A.W. (1990c) Lepidoptera in fossil resins with emphasis on new investigations. *Prace Muzeum Ziemi*, 41, 163–164.

Skalski, A.W. (1992) Studies on the Lepidoptera from fossil resins. Part III. Two new genera and species of Tortricidae from the Baltic Amber. *Annals of the Upper Silesian Museum, Entomology*, 3, 137–146.

Skalski, A.W. (1995) Study on the Lepidoptera from fossil resins. Part XI. *Baltimartyria*, a new genus for *Micropteryx proavittella* Rebel, 1936, with redescription of this species (Lepidoptera, Zeugloptera, Micropterigidae). *Amber & Fossils*, 1(1), 26–37.

Skalski, A.W. & Veggiani, A. (1990) Fossil resin in Sicily and the northern Apennines: geology and organic content. *Praze Muzeum Ziemi*, 41, 37–49.

Smith, E.J.A. (1874) Discovery of remains of plants and insects. *Nature*, 11, 88.

Sobczyk, T. & Kobbert, M.J. (2009) Die Psychidae des baltischen Bernsteins. *Nota lepidopterologica*, 32(1), 13–22.

Sohn, J.-C., Labandeira, C., Davis, D. & Mitter, C. (2011) Lepidopteran fossil record: an overview of the known fossils and recent discoveries. *Abstracts of the 60th Annual Meeting of the Lepidopterists' Society*, Yale University, New Haven, pp. 8–9.

Sontag, E. (2004) Zbiory inkluzji zwierzecych w Muzeum Inkluzji w bursztynie Uniwersytetu Gdanskiego. *Prace Muzeum Ziemi*, 47, 91–92.

Spahr, U. (1989) Ergänzungen und Berichtigungen zu R. Keilbachs Bibliographie und Liste der Bernsteinfossilien–Überordnung Mecopteroidea. *Stuttgarter Beiträge zur Naturkunde Series B (Geologie und Paläontologie)*, 87(157), 1–87.

Stark, P. (1925) Die Moore des badischen Bodenseegebiets. I. Die nähere Umgebung von Konstanz. *Berichte der Naturforschenden Gesellschaft zu Freiburg i. Br.*, 24, 1–123.

Stephenson, J. (1991) *Evidence of Plant/Insect Interactions in the Late Cretaceous and Early Tertiary.* Ph. D. Thesis, Department of Geology, University of London, 378 pp.

Stephenson, J. & Scott, A.C. (1992) The geological history of insect-related plant damage. *Terra Nova*, 4, 542–552.

Stout, E.C., Beck, C.W. & Anderson, K.B. (2000) Identification of rumanite (Romanian amber) as thermally altered succinite (Baltic amber). *Physics and Chemistry of Minerals*, 27(9), 665–678.

Straus, A. (1976) Eine Gangmine im Eocän von Messel. *Aufschluß*, 27, 445–446.

Straus, A. (1977) Gallen, Minen und andere Fraßspuren im Pliozän von Willershausen am Harz. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg*, 113, 43–80.

Swinton, A.H. (1881) A study of the variation of the Small Tortoiseshell Butterfly (*Vanessa urticae*). *Hardwicke's Science-Gossip*, 1881, 176–179.

Szafer, W. (1947) The Pliocene Flora of Krościenko in Poland II. Descriptive Part. *Rozprawy Wydzialu Matematyczno-Przyrodniczego Akademii Umiejetnos*, 72(2), 163–375, pl. 1–15.

Szafer, W. (1954) Pliocene flora from the vicinity of Czorsztyn (West Carpathians) and its relationship to the Pleistocene. *Instytut Geologiczny Prace*, 11, 1–238, 20 pls.

Szafer, W. (1961) Miocene flora from Stare Gliwice in Upper Silesia. *Instytut Geologiczny Prace*, 33, 1–205, 26 pls.

Théobald, N. (1937) *Les Insectes Fossiles des Terrains Oligocenes de France*. Imprimerie Georges Thomas, Nancy, 473 pp., 28 pls.

Tillyard, R.J. (1919) Mesozoic Insects of Queensland. No. 5. Mecoptera, the new order Paratrichoptera, and additions to Planipennia. *Proceedings of the Linnean Society of New South Wales*, 44, 194–212.

Tillyard, R.J. (1921) Mesozoic Insects of Queensland. No. 8. Hemiptera Homoptera (Contd.) The genus *Mesogereon*; with a discussion of its relationship with the Jurassic Palaeontinidae. *Proceedings of the Linnean Society of New South Wales*, 46, 270–284.

Tillyard, R.J. (1933) The Panorpoid complex in the British Rhaetic and Lias. *British Museum (Natural History) Fossil Insects*, 3, 1–79.

Tindale, N.B. (1945) Triassic insects of Queensland. 1. *Eoses*, a probable lepidopterous insect from the Triassic beds of Mt. Crosby, Queensland. *Proceedings of the Royal Society of Queensland*, 56(5), 37–46, pl. 5.

Tindale, N.B. (1985) A butterfly-moth (Lepidoptera, Castniidae) from the Oligocene shales of Florissant, Colorado. *Journal of Research on the Lepidoptera*, 24(1), 31–40.

van Couvering, J.A. & Miller, J.A. (1969) Miocene stratigraphy and age determinations, Rusinga Island, Kenya. *Nature*, 221, 628–632.

van Schepdeal, J. (1974) Macrolépidoptères fossiles du domaine Paléarctique, La paléontologie au service de l'écologie. *Les Naturalistes Belges*, 55(1), 3–37.

Walker, F. (1854) *List of the Specimens of Lepidopterous Insects in the Collection of the British Museum*, Part II. Lepidoptera Heterocera. British Museum, London, pp. 279–581.

Wangrin, G. von (1940) Tagfalter–Versteinerung in einer "Stettiner Kugel". *Entomologische Zeitschrift*, 53, 192–194.

Wappler, T., Currano, E.D., Wilf, P., Rust, J., & Labandeira, C.C. (2009) No post-Cretaceous ecosystem depression in European forests? Rich insect-feeding damage on diverse middle Palaeocene plants, Menat, France. *Proceedings of the Royal Society B*, 276, 4271–4277.

Wedmann, S. (2000) Die Insekten der oberoligozänen Fossillagerstätte Enspel (Westerwald, Deutschland). Systematik, Biostratinomie und Paläoökologie. *Mainzer Naturwissenschaftliches Archiv*, 23, 1–169.

Weitschat, W. (2009) Jäger, Gejagte, Parasiten und Blinde Passagiere-Momentaufnahmen aus dem Bernsteinwald. *Denisia 26, zugleich Kataloge der oberösterreichschen Landesmuseen Neue Serie*, 86, 243–256.

Weitschat, W. & Wichard, W. (1998) *Atlas der Pflanzen und Tiere im Baltischen Bernstein*. Friedrich Pfeil, Munich, 256 pp.

Westwood, J.O. (1854) Contributions to Fossil Entomology. *Quarterly Journal of Geological Society of London*, 10, 378–396, pl. 14–18.

Weyenbergh, Jr., H. (1869) Sur les insects fossils. Du Calcaire lithographique de la Bavière, qui se trouvent au Musée Teyler. *Archives du Musée Teyler*, 2, 247–294.

Weyenbergh, Jr., H. (1873) Notes sur quelques insects du calcaire jurassique de la Bavière. *Archives du Musée Teyler*, 3(3), 234–240.

Weyenbergh, Jr. H. (1874) Varia zoological et paleontológica. *Periodico Zoológico, Sociedad Entomológica Argentina*, 1, 77–111.

Weyland, H., Berendt, W. & Peters, I. (1960) Über einige bisher unbekannte Mikrofossilien aus der Braunkohle. *Senckenbergiana lethaea*, 41(1/6), 489–511.

Whalley, P.E.S. (1977) Lower Cretaceous Lepidoptera. *Nature*, 266, 526.

Whalley, P.E.S. (1978) New taxa of fossil and recent Micropterigidae with a discussion of their evolution and a comment on the evolution of Lepidoptera (Insecta). *Annals of the Transvaal Museum*, 31(8), 71–86.

Whalley, P.E.S. (1985) The systematics and biogeography of the Lower Jurassic insects of Dorset, England. *Bulletin of the British Museum of Natural History (Geology)*, 39(3), 107–189.

Whalley, P.E.S. (1986) A review of the current fossil evidence of Lepidoptera in the Mesozoic. *Biological Journal of the Linnean Society*, 28, 253–271.

Wilf, P., Labandeira, C.C. & Ellis, B. (2006) Decoupled plant and insect diversity after the end-Cretaceous extinction. *Science*, 313, 1112–1115.

Wilf, P., Labandeira, C.C., Johnson, K.R. & Cúneo, N.R. (2005) Richness of plant-insect associations in Eocene Patagonia: A legacy for South American biodiversity. *Proceedings of the National Academy of Sciences, USA*, 102(25), 8944–8948.

Willmann, R. (1984) Zur systematischen Stellung mesozoischer und tertiärer Mecopteran einschliesslich *Eoses triassica* Tindale (angeblich Lepidoptera) (Insecta, Holometabola). *Paläontologische Zeitschrift*, 58(3/4), 231–246.

Wilson, M.V.H. (1996) Insects near Eocene lakes of the interior. *In*: Ludvigsen, R. (Ed.), *Life in Stone: A Natural History of British Columbia's Fossils*. University of British Columbia Press, Vancouver, pp. 225–233.

Winkler, I.S., Labandeira, C.C., Wappler, T. and Wilf, P. (2010) Distinguishing Agromyzidae (Diptera) leaf mines in the fossil record: New taxa from the Paleogene of North America and Germany and their evolutionary implications. *Journal of Paleontology*, 84(5), 935–954.

Wolsan, M. & Lange-Badré, B. (1996) An arctomorph carnivoran skull from the Phosphorites du Quercy and the origin of procyonids. *Acta Palaeontologica Polonica*, 41(3), 277–298.

Woodward, H. (1876) On a remarkable fossil orthopterous insect from the Coal-Measures of Scotland. *Quarterly Journal of the Geological Society of London*, 32, 60–65.

Woodward, H. (1878) On the occurrence of *Branchipus* (or *Chirocephalus*) in a fossil state, associated with Archaeonicus and with numerous insect remains in the Eocene freshwater limestone of Gurnet Bay, Isle of Wight. *Geological Magazine*, (2)5, 88–89.

Worobiec, G. (2007) *Laurus abchasica* (Kolakovsky & Shakryl) Ferguson from the Neogene of the Bełchatów Lignite Mine (Central Poland). *Acta Palaeobotanica*, 47(1), 203–215.

Wu, R.J.C. (1997) *Secrets of a Lost World: Dominican Amber and Its Inclusions*. Privately published, Santo Domingo, 222 pp.

Zablocki, J. (1960) *Pinus Króli*, a new species of fossil pine from tertiary salt deposits in Wieliczka. *Studia Societatis Scientiarum Torunensis Sectio D (Botanica)*, 4(4), 43–48, pl. 1.

Zahiri, R., Kitching, I.J., Lafontaine, J.D., Mutanen, M., Kaila, L., Holloway, J.D. & Wahlberg, N. (2010) A new molecular phylogeny offers hope for a stable family level classification of the Noctuoidea (Lepidoptera). *Zoologica Scripta*, 40(2), 158–173.

Zeuner, F.E. (1927) Eine Sphingidenraupe aus dem Obermiozän von Böttingen. *Palaeontologische Zeitschrift*, 8, 321–326.

Zeuner, F.E. (1931) Die Insektenfauna des Böttinger Marmors. Eine systematische und paläobiologische Studie. *Fortschritte der Geologie und Palaeontologie*, 9(28), 1–406, pl. 1–19.

Zeuner, F.E. (1942) Two new fossil butterflies of the family Pieridae. *Annals and Magazine of Natural History*, 11, 409–416.

Zeuner, F.E. (1943) On recent and fossil *Pseudonaclia* Butler (Lep., Amatidae). *Annals and Magazine of Natural History,* 10, 140–144.

Zeuner, F.E. (1960) Notes on the evolution of the Rhopalocera (Lep.). *Verhandlungen: XI Internationaler Kongress für Entomologie*, 1, 310–313.

Zhang, J. (1989) *Fossil Insects from Shanwang, Shandong, China*. Shandong Science Technology Publishing House, Jinan, 459 pp.

Zhang, J., Sun, B. & Zhang, X. (1994) *Miocene Insects and Spiders from Shanwang*, Shandong. Science Press, Beijing, 298 pp., 42 pls.

Zherikhin, V.V. (1978) Development and changes of the Cretaceous and Cenozoic faunal assemblages (Tracheata and Chelicerata). *Trudy Paleontologischeskogo Instituta Akademii Nauk, SSSR*, 165, 1–198.

Zherikhin, V.V. & Sukacheva, I.D. (1973) On Cretaceous “ambers” (retinitis) with insects of North Siberia. *In*: Bei-Bienko, G.Y. (Ed.), *Doklady na XXIV Ezhegodnom Tshtenii Pamiati N. A. Cholodkovskogon*, 1971, 3–48.

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Corrections, additions, and nomenclatural notes to the recently published World catalog of fossil and subfossil Lepidoptera

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Sohn *et al.* (2012) recently published an annotated catalog of lepidopteran fossils, which was the first attempt to compile all the known fossil specimens, described or undescribed, from the world literature. This publication provided paleontological data such as fossil type, specimen deposition, excavation locality, fossil host plants, and geological age for at least 4,568 specimens, including 229 described fossil species. As originally intended, the catalog already elicited correspondence with various specialists who found errors that the authors were unaware of. We are confident that usefulness of the catalog increases with such feedback. In this article, we provide an update to correct the errors in the publication, together with new information found since the catalog was published, including one new synonym (*Baltopsyche* Sohn, 2012, **syn. nov.** = *Sucinopsyche* Sobczyk, 2011); the proposed change of the nominal *Zygaenites* to a collective group name; and the resurrection of *Satyrites* Scudder, 1872 over *Lethites* Scudder, 1875.

Corrections

In Sohn *et al.* (2012), there were a few erroneous page number or publication year citations of the original descriptions and also misspellings in taxon names. Corrections to these errors are shown in Table 1. In Sohn *et al.* (2012), the bibliographic references to Skalski (1973c) and Crane and Jarzembowski (1980) were unintentionally omitted; the bibliographic source of *Jupiteria* Scudder, 1881 and Rebel (1936) were incorrectly cited. For the corrections, see the reference section of this article.

TABLE 1. Corrections to Sohn *et al.* (2012).

page	it reads	it should read	remarks
27	***ADELITES*** Rebel, 1934a: 373	***ADELITES*** Rebel, 1934a: 15	wrong citation of page number
43	***ARGYRESTHITES*** Rebel, 1934a (Argyresthiidae): 5	***ARGYRESTHITES*** Rebel, 1934a: 5 (Argyresthiidae)	incorrect order of information
52	***innominatus*** Kusnezov, 1941: 50, figs. 35–36	***innominatus*** Kusnezov, 1941: 50, figs. 35–36 (*Paraborkhausenites*)	original generic combination missing
56	***castinoides*** Tindale	***castnioides*** Tindale	incorrect spelling of species name
65	*Satyrites* Scudder, 1872: 66	*Satyrites* Scudder, 1872: 71	wrong citation of page number
65	***reynesii*** Scudder, 1872: 66, pl. 7	***reynesii*** Scudder, 1872: 71, pl. 7	wrong citation of page number
66	***sepulta*** Boisduval, 1840: 371, pl. 8	***sepulta*** Boisduval, 1841: [273], pl. 8	wrong citation of publication year; the page number of the original description erroneously printed as '371' (actually '273')
66	***PSEUDONEORINA*** Nel and Descimon, 1994	***PSEUDONEORINA*** Nel and Descimon, 1986	wrong citation of publication year

......continued on the next page

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TABLE 1. (Continued)

page	it reads	it should read	remarks
66	***coulleti*** Nel and Descimon, 1994	***coulleti*** Nel and Descimon, 1986	wrong citation of publication year
68	= *Jupiteria* Scudder, [1881] 1883: 290.	= *Jupiteria* Scudder, [1881] 1883: 280.	wrong citation of page number
68	*Lithopsyche* Scudder, 1889: 454	*Lithopsyche* Scudder, 1889: 452	wrong citation of page number
68	***styx*** Scudder, 1889: 454, pl. 53: 11, 16, 17	***styx*** Scudder, 1889: 454, pl. 52: 11, 16, 17	wrong citation of plate number
71	cf. ***maackii*** Ménétriés, 1859	cf. ***maackii*** Ménétriés, 1858	wrong citation of publication year
71	***BELENOIS*** Hübner, 1825	***BELENOIS*** Hübner, 1819	wrong citation of publication year

Additions

1. Unidentified lepidopteran trace fossils in Currano *et al.* (2010) are missing in Sohn *et al.* (2012). This record needs to be added to the 'Lepidoptera *incertae sedis*' section of Sohn *et al.* (2012) as follows:

—Currano *et al.* 2010: 557-559 (lepidopteran leaf mines)
CI & T (leaf mine)/USNM (not stated)/ USA: Wyoming, southern Bighorn Basin (Willwood Fm.)/Ypresian, Early Eocene.

2. The generic name *Lithopsyche*, afterwards replaced by *Lithodryas* to avoid homonymy, appeared first in Scudder ([1881] 1883) and was described later (Scudder, 1889). According to the ICZN (1999), Scudder's 1881 record is unavailable as it lacks a description. This aspect is missing in Sohn *et al.* (2012: 68) and needs to be added as follows.

LITHODRYAS Cockerell, 1909: 79. A replacement name for *Lithopsyche* Scudder, 1889.
= *Lithopsyche* Scudder, [1881] 1883: 280. Invalid name.
= *Lithopsyche* Scudder, 1889: 452.
Type species: *Lithopsyche styx* Scudder, 1889. A junior homonym of *Lithopsyche* Butler, 1889 [Lepidoptera: ?Riodinidae].

Nomenclatural notes

1. Gender of generic names

For compound genus-group names ending in the suffix '-*ites*', Sohn *et al.* (2012) treated the gender of such genera as masculine, according to the ICZN (1999: Art. 30.1.4.4). The authors, however, neglected to notice the exceptions mentioned in the same article, namely the cases when the author of the compound genus-group name stated that it had another gender or treated it as feminine or neuter by combination with an adjective species name in that gender form. In those exceptional cases, the original spelling of the species name should be maintained. The genders of the following fossil genera were defined by the original authors with feminine or neuter species name endings which were unnecessarily changed by Sohn *et al.* (2012). The resulting corrections in species name endings are shown in brackets.

Adelites Rebel, 1934, defined as feminine [*acutitarsella* (nec *acutitarsellus*); *electreella* (nec *electreellus*); *serraticornella* (nec *serraticornellus*)].
Argyresthites Rebel, 1934, defined as feminine [*balticella* (nec *balticellus*); *succinella* (nec *succinellus*)].
Incurvarites Rebel, 1934, defined as feminine [*alienella* (nec *alienellus*)].
Noctuites Heer, 1849, defined as feminine [*effosa* (nec *effosus*); *caucasica* (nec *caucasicus*); *deperdita* (nec *deperditus*); *incertissima* (nec *incertissimus*); *maxima* (nec *maximus*); *miocenica* (nec *miocenicus*); *stavropolica* (nec *stavropolicus*)].
Note: Heer (1849) included two species, *haidingeri* and *effosa*, under *Noctuites* whose gender seems to be defined as feminine, given the ending of the latter species. Later when describing another species of *Noctuites*, he used a masculine ending (i.e. *deperditus*) which is emended here.

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Nymphalites Scudder, 1889, defined as neuter [*obscurum* (nec *obscurus*)].
Pamphilites Scudder, 1875, defined as feminine [*abdita* (nec *abditus*)].
Phalaenites Heer, 1849, defined as feminine [*obsoleta* (nec *obsoletus*); *crenata* (nec *crenatus*)].
Scythropites Rebel, 1936, defined as feminine [*balticella* (nec *balticellus*)].
Thanatites Scudder, 1875, defined as feminine [*vetula* (nec *vetulus*)].
Thaites Scudder, 1875, defined as feminine [*ruminiana* (nec *ruminianus*)].

The generic name *Tineitella* was proposed by Fletcher (1940) as a replacement for *Tineites* Kawall, 1876 which is a junior homonym of *Tineites* Germar, 1842. The gender of *Tineitella* was not specified by the author and is indeterminable from the endings of combined species names. It is, however, obviously feminine according to the gender of the suffix ‘-*ella*’. The change of the ending in *sepositella* to *sepositellus* as suggested by Sohn *et al.* (2012) is therefore unnecessary. Likewise the name *sucinacius* Kozlov, 1987 needs to be emended to ‘*sucinacia*’.

2. Status of generic names ending in ‘-*ites*’

The suffix ‘-*ites*’ is commonly, but not exclusively, used for collective-group names of fossils whose only taxonomic association can be determined above the genus level or for nominal fossil genera exhibiting similarity to an extant genus. The former names do not need type-species fixations to be available (ICZN, 1999: Articles 13.3.2; 42.3.1; and 67.14) but the latter do. In practice, however, it is often hard to tell one group of names from the other unless authors explicitly stated their intentions. For the generic names ending in ‘-*ites*’, Sohn *et al.* (2012) discussed only the possible collective-group names but not the nominal genus-group names. Collective-group names are discernable when the authors stated them explicitly as such; or when the name includes fossils which are diagnosable only at family level. At least 11 genera were very likely defined as collective-group names and they include: *Elachistite*s Kozlov, 1987; *Geometridites* Kernbach, 1967; *Gracillariites* Kozlov, 1988; *Noctuites* Heer, 1849; *Nymphalites* Scudder, 1889; *Oecophorinites* Kozlov, 1988; *Phalaenites* Heer, 1849; *Plutellites* Kozlov, 1988; *Psychites* Kozlov, 1988; *Sphingidites* Kernbach, 1967; and *Tortricites* Kozlov, 1988. *Stigmellites* Kernbach, 1967 was originally proposed as an ichnotaxon to accommodate trace fossils which show no generic affinity within Nepticulidae. The genus was later regarded as a collective-group name by Jarzembowski (1989) and Kozlov (1988). Of fossil genera ending in ‘-*ites*’, discerning them as nominal genus-group names is somewhat tricky. We regarded the fossil genera as nominal when the authors explicitly stated their diagnostic characters in comparison with other fossil or extant genera. Such diagnoses sometimes became available by the actions of subsequent researchers. Twenty seven genera fall into these criteria: *i.e. Adelites* Rebel, 1934; *Arctiites* Rebel, 1898; *Argyresthites* Rebel, 1934; *Borkhausenites* Rebel, 1934; *Cerurites* Kernbach, 1967; *Doritites* Rebel, 1898; *Depressarites* Rebel, 1936; *Dysmasiites* Kusnezov, 1941; *Epiborkhausenites* Skalski, 1973; *Eriocranites* Kernbach, 1967; *Gallerites* Kernbach, 1967; *Incurvarites* Rebel, 1934; *Lethites* Scudder, 1875; *Lycaenites* Rebel, 1898; *Microsymmocites* Skalski, 1977; *Mylothrites* Scudder, 1875; *Neoborkhausenites* Skalski, 1977; *Oegoconiites* Kusnezov, 1941; *Oligamatites* Kusnezov, 1928; *Palaeoscardites* Kusnezov, 1941; *Pamphilites* Scudder, 1875; *Proscardites* Kusnezov, 1941; *Pyralites* Heer, 1856; *Scythropites* Rebel, 1936; *Symmocites* Kusnezov, 1941; *Thaites* Scudder, 1875; and *Thanatites* Scudder, 1875. Three genera: *Bombycites* Heer, 1849, *Pierites* Heer, 1849; and *Tineites* Kawall, 1876 (preoccupied and replaced by *Tineitella* Fletcher, 1940), were originally proposed as nominal genus-group taxa but later changed to collective-group names with heterogeneous or non-diagnostic fossils subsequently incorporated (e.g., Heer, 1865 for *Bombycites*; Kozlov, 1988 for *Pierites* and *Tineites*). *Zygaenites* Burgeff, 1951 was proposed as a nominal genus-group name but is unavailable due to the lack of a description (ICZN, 1999: Article 13.3). We propose to make it available by changing it into a collective-group name indicating fossils which show some evidences of zygaenid association. Such a change is allowed by the ICZN (1999: Article 23.7.2).

3. Subsequent type designations

Several old works describing new fossil genera lacked statements about their type species in the original descriptions. Such genera require subsequent type species fixations to become available (ICZN, 1999: Articles 13.3 and 69), unless they are collective-group names. Sohn *et al.* (2012) briefly discussed this issue for some fossil genera but overlooked the unjustified subsequent type species fixations for six fossil genera: *Cerurites* Kernbach, 1967; *Eriocranites* Kernbach, 1967; *Gallerites* Kernbach, 1967; *Pyralites* Heer, 1856; *Sphingidites* Kernbach, 1967; and *Stigmellites* Kernbach, 1967. Each of these was established for a single species and thus their type species were automatically fixed by monotypy (ICZN, 1999: Article 68.3). Sohn *et al.* (2012) stated that the type species of *Pierites* Heer, 1849, was subsequently designated by Hemming (1967). This statement is inappropriate since Hemming (1967) did not propose a subsequent type designation for the genus. Heer (1849) established the genus by monotypy and thus

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the type species was already fixed. As Sohn *et al.* (2012) noted, the genus *Pierites* is now used as a collective-group name. The ICZN (1999: Article 67.14) establishes "If the name of a nominal genus-group taxon is subsequently applied to a collective group, the type species of that taxon is disregarded while the name is used as a collective-group name." From this provision, the type species of *Pierites* is disregarded. Likewise, the type species of the monotypic *Sphingidites* should also be disregarded. *Geometridites* and *Phalaenites* were originally defined as collective-group names and thus their subsequent type fixations are unnecessary.

The original description of *Depressarites* Rebel, 1936 was given as a form combined with the species description. Fixation of *Depressarites levipalpella* Rebel as the type species of the genus was first proposed by Nye & Fletcher (1991) who followed the third edition of the ICZN (1985). According to the fourth edition (ICZN, 1999: Article 13.4), the type species of *Depressarites* is automatically fixed with *Depressarites levipalpella* from the original description.

4. Availability of *Satyrites*

Satyrites was first established by Scudder in 1872 as a genus-group name, by implication with the genera *Debis* Doubleday, 1849 and *Cyllo* Boisduval, 1832 (= *Melanitis* Fabricius, 1807). The genus was later replaced with *Lethites* by Scudder (1875) who thought that his older genus was a junior homonym of Satyrites Blanchard & Brullé, 1840. This replacement, followed by Sohn *et al.* (2012), turned out to be erroneous. The supposed homonym Satyrites Blanchard & Brullé was actually proposed for a family-group taxon (see Hemming, 1967: 254, 402). Therefore, *Satyrites* Scudder, 1872, is an available and valid name. To reflect this aspect, the account of *Lethites* in Sohn *et al.* (2012) must be changed as follows:

SATYRITES Scudder, 1872: 66. **stat. rev.**
Type species: *Satyrites reynesii* Scudder, 1872.
= *Lethites* Scudder, 1875a: 265. Unnecessary replacement name (see Hemming, 1967: 254).
= *Lethites* Scudder, 1875b: 34. Subsequent citation.
= *Latyrites* [sic]; Brodie, 1873: 17.

5. New synonym

Baltopsyche was proposed by Sohn in Sohn *et al.* (2012) as a replacement name for *Palaeopsyche* Sobczyk and Kobbert, 2009 which is a junior homonym of *Palaeopsyche* Perkins, 1905. This proposal is however invalid as Sobczyk (2011) had already introduced a replacement name, *Sucinopsyche*, prior to Sohn *et al.* (2012) for the genus. Therefore, *Baltopsyche* becomes a junior objective synonym of *Sucinopsyche*. To accommodate this change, the account (Sohn *et al.* 2012: 37) regarding *Baltopsyche* needs to be updated as follows:

SUCINOPSYCHE Sobczyk, 2011: 309.
= *PALAEOPSYCHE* Sobczyk and Kobbert, 2009: 17. A junior homonym of *Palaeopsyche* Perkins, 1905 [Lepidoptera: Epipyropidae].
Type species: *Palaeopsyche secundum* Sobczyk and Kobbert, 2009.
= *BALTOPSYCHE* Sohn in Sohn *et al.*, 2012: 37. **syn. nov.** An unnecessary replacement name for *Palaeopsyche* Sobczyk and Kobbert, 2009.

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References

The references already cited in Sohn *et al.* (2012) are not shown to avoid redundancy, unless discussed in the text.

Crane, P.R. & Jarzembowski, E.A. (1980) Insect leaf mines from the Palaeocene of southern England. *Journal of Natural History*, 14, 629–636. http://dx.doi.org/10.1080/00222938000770531

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Currano, E.D., Labandeira, C.C. & Wilf, P. (2010) Fossil insect folivory tracks paleotemperature for six million years. *Ecological Monographs*, 80, 547–567. http://dx.doi.org/10.1890/09-2138.1

Heer, O. (1849) *Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien*, Vol. 2. Wilhelm Engelmann, Leipzig, 264 pp.

Hemming, F. (1967) Generic names of butterflies of the world and their type-species (Lepidoptera : Rhopalocera). *Bulletin of the British Museum of Natural History* (Entomology) Supplement, 9, 509 pp.

ICZN (International Commission on Zoological Nomenclature) (1985) *International Code of Zoological Nomenclature*, 3rd ed. The International Trust for Zoological Nomenclature, London, 338 pp.

ICZN (International Commission on Zoological Nomenclature) (1999) *International Code of Zoological Nomenclature*, 4th ed. The International Trust for Zoological Nomenclature, London, 306 pp.

Jarzembowski, E.A. (1989) A century plus of fossil insects. *Proceedings of the Geologists' Association*, 100(4), 433–449.

Kozlov, M.V. (1988) Paleontology of lepidopterans and problems of the phylogeny of the order Papilionida. *In*: Ponomarenko, A.G. (Ed.), *The Mesozoic–Cenozoic Crisis in the Evolution of Insects*. Academy of Sciences, Moscow, pp. 16–69.

Nye, I.W.B. & Fletcher, D.S. (1991) *Generic Names of Moths of the World*. Volume 6. Trustees of the British Museum (Natural History), London. xxix + 368 pp.

Rebel, H. (1936) Berstein-Lepidopteren. *Deutsche Entomologische Zeitschrift*, *Iris*, 49, 162–186.

Scudder, S.H. (1872) Description d'un nouveau papillon fossile (*Satyrites reynesii*) rouvé à Aix en Provence. *Revue et Magasin de Zoologie*, (2)23, 66–72.

Scudder, S.H. (1875) Fossil butterflies. *Memoirs of the American Association for the Advancement of Science*, 1, 1–99.

Scudder, S.H. ([1881] 1883) The Tertiary lake-basin at Florissant, Colorado, between South and Hayden Parks. *Annual Report of the United States Geological and Geographical Survey of the Territories*, 12, 271–293.

Scudder, S.H. (1889) The fossil butterflies of Florissant. *Annual Report of the United States Geological Survey*, 8, 433–474.

Skalski, A.W. (1973c) Uwagi o motylach z żywic kopalnych. *Polskie Pismo Entomologiczne*, 43, 647–654.

Sobczyk, T. (2011) *World Catalogue of Insects*, Vol. 10, Psychidae (Lepidoptera). Apollo Books, Stenstrup, 468 pp.

Sohn, J-C., Labandeira, C., Davis, D. & Mitter, C. (2012) An annotated catalog of fossil and subfossil Lepidoptera (Insecta: Holometabola) of the world. *Zootaxa*, 3286, 1–132.

Chapter 4

Taxonomy of New World Yponomeutoidea

- Revisions of *Eucalantica* and *Atemelia*

General Introduction

It is often said that the successful inference of phylogenetic relationships directly depends on good taxonomic resolution of the study group, which enables effective taxon-sampling for higher-level analyses (Wheeler, 2004). Most previous taxonomic work on Yponomeutoidea has focused on the Palearctic (Friese, 1960; Kyrki, 1990), leaving the New World fauna poorly characterized. Only 483 of the ca. 1900 described yponomeutoid species are from the Neararctic and Neotropical regions (Heppner, 1998). This bias has distorted our understanding of the world fauna and resulted in under-estimate of its morphological diversity. It may also have impeded phylogenetic studies by hindering the emergence of a universally agreed definition of Yponomeutoidea (Friese, 1960).

I contribute to taxonomic resolution of the yponomeutoids by completing revisionary work on two small, poorly studied, mainly New World groups. Each of these groups has been placed at some point in Yponomeutoidea, but the true affinities of each have been unclear. These groups are *Eucalantica* and *Atemelia*. My revisions reveal that the biodiversity of these groups has been underestimated and/or biased to the Palearctic fauna. The completed works have been published or is in submission. These are composed in this chapter.

4-1

A taxonomic review of *Eucalantica* Busck (Lepidoptera, Yponomeutidae) with descriptions of six new species

Reformatted from Sohn & Nishida, 2011 (ZooKeys 118: 75–96). doi: 10.3897/zookeys.118.956

Introduction

The genus *Eucalantica* was proposed by Busck (1904) to account for differences of the type species *Calantica polita* Walshingham, 1881, from other *Calantica* Zeller, 1847, a junior homonym of *Calantica* Gray, 1825, whose replacement name is *Niphonympha* Meyrick, 1914. Busck suggested that *Eucalantica* is distinguished from *Niphonympha* in having scale tufts on the 3rd segment of labial palpus, Rs_1 (=R_2) and Rs_2 (=R_3) stalked in the forewings, and CuA_2 arising near the middle of the cell in the hindwings. These characteristics are, however, homoplasious over the yponomeutoid lineages. Only their combination may help in distinguishing *Eucalantica* from other genera. The taxonomic position of the genus remains uncertain. Kyrki (1990) placed *Eucalantica* in Yponomeutidae without explanation. We follow this tentative placement. To establish which apomorphic characters define *Eucalantica,* a phylogenetic analysis of the Yponomeutoidea would be necessary but is beyond the scope of this work.

Eucalantica has been regarded as monobasic since the original description. Powell & Opler (2009) first challenged this status when mentioning the presence of species similar to *Eucalantica polita* from the high-elevation forests of Mexico and Costa Rica but they did not describe them. This discovery raised the possibility that the genus is more diverse and widely distributed than previously thought.

The purpose of this paper is to describe six new species of *Eucalantica*, five of which were from Costa Rica and one from southern USA and Mexico, to revise the definition of the genus and to present identification keys to adults based on external features and genitalia.

Materials and Methods

Pinned specimens from six institutional collections were examined. The abbreviations of these depositories are as follows:

BMNH – Natural History Museum (formerly British Museum of Natural History), London, UK;

EMEC – Essig Museum of Entomology, University of California, Berkeley, USA;

INBIO – Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica;

MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, USA;

UCR – Museo de Zoología, Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica;

USNM – National Museum of Natural History (formerly United States Museum of Natural History), Washington DC, USA.

Specimen label data are arranged by country, following in order of sex, state/province, specific locality, collecting date, collector and rearing records, if pertinent, and ending with specimen depository in parenthesis. The individuals whose sex cannot be determined are listed as ‘ex’.

Selected specimens were dissected for genitalia and abdominal structures, following Clarke (1941), except that chlorazol black was used for staining. Dissected genitalia were mounted on the microscope slides in Euparal resin (BioQuip Products Inc.). The genitalia slide numbers (GSN) are given for the dissected specimens with the suffix ‘USNM’ for USNM specimens, ‘EMEC-JCS’ for EMEC specimens and ‘SJC’ for INBIO specimens. Unmounted genitalia are stored in glycerin-filled, transparent envelopes which are attached with dissected specimens. Pinned specimens were examined under a Leica MZ APO stereoscope. Slide-mounted specimens were examined under a Leica LETTZ-DMRX microscope.

Terms for genitalia and wing venation follow Klots (1970) and Wootton (1979), respectively. The 7th, 8th, and 9th abdominal segments are abbreviated as A7, A8, A9 respectively in the descriptions; the 7th and 8th sternite of females as S7 and S8.

Taxonomic accounts

Genus *Eucalantica* Busck, 1904

Figs. 1-35

Eucalantica Busck, 1904: 750**.** Type species: *Calantica polita* Walsingham, 1881, by original designation and monotypy.

Diagnosis. This genus is superficially similar to *Thecobathra* Meyrick, 1922, which also has a silvery white body and forewings, but differs from the latter in having a dark brown costal streak in forewing. The male genitalia of *Eucalantica* are distinguished from those of *Thecobathra* in having three or four spines on socii (none or one spine in the latter) and a lack of dentiform projections on phallus (present in the latter). The female S8 is entirely or almost entirely sclerotized in *Eucalantica*, but not in *Thecobathra*. The female genitalia of those two genera are also different in the shape of the signum, if present: keel-like or discoid plate in *Eucalantica*, cruciform in *Thecobathra*.

Description. When resting, *Eucalantica* moths lay their body parallel to the substrate with their forelegs extended forward (Fig. 5).

Head (Fig. 1) – Vertex vestiture rough with white, piliform scales; frons dark brown. Antennae filiform, 3/5 as long as forewing; scape white, with brown pecten; pedicel and first two flagellomeres with two complete whorls of scales per segment, white dorsally, gray ventrally; the remaining flagellomeres with a dorsal cover of gray scales on anterior half, a complete whorl of gray scales on distal half. Labial palpus porrect, 1st segment pale brownish gray, 1/4 as long as 2nd; 2nd segment dark brown, with denser scales distad, as long as eye diameter; 3rd segment white except dark brown on ventrobasal area, with white scale tufts dorsally, as long as 2nd. Maxillary palpus 4 segmented. Proboscis devoid of scales, longer than labial palpus.

Thorax and abdomen – Tegula and mesonotum white. Foreleg lustrous dark brown dorsally, gray ventrally; epiphysis arising at middle. Midleg with coxa to tibia lustrous pale brown dorsally, silvery white ventrally; first tarsus dark brown dorsally, silvery white ventrally; the remaining tarsi brownish gray with dark brown ring on distal end. Hindleg silvery white, slightly tinged with pale brown ventrally. The forewings (Figs 6–14) white, elongate-triangular, costa straight, apex at anterior 1/3 of termen, obtuse-angled, termen oblique after apex; a black spot at the upper corner of discal cell; scattered black spots on the posterior 1/2 and distal 2/3; a brown or orange dorsal patch; however, the latter two are often reduced, depending on the individual. The forewing venation of *Eucalantica* (Fig. 2) with pterostigma 2/5 of costa before R; Rs_1 and Rs_2 stalked; Rs_4 below apex; M_2 and M_3 at base closer than M_1; CuA1 directed to tornus; CuA_2 ending at posterior margin. The hindwing slightly broader than forewing, pale gray, darkened to apex and anterior margin, termen broadly round, apex narrowly round; venation (Fig. 2) with $Sc+R_1$ ending at the middle of anterior margin; Rs directed to apex; M_1, M_2 and M_3 evenly spaced; CuP close to 1A+2A. Abdomen silvery white, slightly tinged with pale brown on basal half; pleural lobe silvery white.

Abdominal sternum II and terga (Fig. 3) – Apodeme slender, 1/5 as long as venula; venula slender, 4/5 as long as 2nd sternite; transverse ridge at posterior 1/6 of 2nd sternite. A pair of spiniform setal zones on tergum II~VII; in *polita*, paired zones expanded, fused with each other.

Male A8 (Fig. 4) – A pair of coremata twice as long as pleural lobes; tergite elliptical, with lanceolate caudal end; pleuron expanded posteriorly as lobate; sternite subtriangular, enlarged caudad, posterior margin concave.

Male genitalia (Figs 17–30) – Uncus linguiform, convex posteriorly, medially fused with tegumen; in four of the seven species, a pair of lateral humps present near apex; socii elongate, extended from ventrobasal area of uncus, with a row of 3–4 spines ventroterminally. Tuba analis with weakly sclerotized area ventrally (‘subscaphium’), continuous to gnathos; gnathos as a transverse bulge below tuba analis, with narrow, band-like sclerotization along apical edge. Valva obovate or rectangular, setose on the posterior half of the ventral side, with species-specific groove or projections above basal sacculus. Vinculum narrower to saccus; saccus elongate. Aedeagus straight or bent medially; cornuti absent or as a zone of minute spinules.

Female genitalia (Figs 31–35) – Papillae anales subtriangular. A pair of hairy humps on the distal margin of S8; interspace between the humps with dense, minute thorns, the thorny area extending above and below S8 humps. Segment S8 entirely or mostly sclerotized, sometimes posterolateral margins forming a semicircular fold (Figs 32 and 35, indicated by asterisk); depending on the species, with a pair of pits (Fig. 35a) or semicircular depression (Fig. 31b) near ostium.

Antrum digitate or bowl-shaped, with numerous minute thorns internally; thorny area extending caudally beyond ostium bursae. Ductus seminalis near a connection between ductus and corpus bursae; bulla seminalis as large as (in *polita*) or smaller than corpus or absent (in *costaricae*). Corpus bursae very fragile due to its thin wall; signum absent in two species, present in three species and shaped like a dentate keel or a small scobinate disk.

Species diversity. The distribution of *Eucalantica* as shown in this paper indicates a high diversity of the genus in the Central America. Three of the five Costa Rican species described in this paper were found in the high-elevation oak forests of Cerro de la Muerte region, indicating that multiple species can coexist in a single ecozone. Interestingly, there exists a different group of congeners in the high mountains of Heredia province. This pattern predicts more undescribed species of *Eucalantica* present along the montane systems of Costa Rica and other Central American countries.

Key to the adults of *Eucalantica* species including variants in forewing patterns

Note: External appearance is usually inadequate for species identification of *Eucalantica*. Whenever possible, examination of the genitalia is advised for reliable identifications of the species.

1. No patch and suffusion on dorsal area of forewing -------------------------------- 2

   Dorsal patch and/or suffusion on forewing present (Fig. 6) ---------------------- 3

2. Black spots scattered on forewing --------------------------------- *costaricae* sp. n.

Forewing almost immaculate (except discal spot) ------------------- *polita* (Fig. 8)

3. Dorsal patch on forewing without posterior suffusion ----------------------------- 4

Dorsal patch on forewing with posterior suffusion (Fig. 6) ----------------------- 6

4. Dorsal patch bar-like -- 5

Dorsal patch triangular --- *pumila* sp. n.

5. Terminal half of fringe pale grayish brown on forewing ------------ *polita* (Fig. 7)

Terminal 1/4 of fringe pale grayish brown on forewing ------------ *vaquero* sp. n.

6. Posterior suffusion extending along entire dorsal margin of forewing ---------- 7

Posterior suffusion only on basal 2/3 of dorsal margin of forewing ---------------

-- *ehecatlella* sp. n.

7. Posterior suffusion with apparent dorsal patch ------------------------------------ 8

Posterior suffusion with reduced dorsal patch ------------------------ *powelli* sp. n.

8. Black spots on forewing sparse and covering only distal third ---------------------

-- *icarusella* sp. n.

Black spots on forewing dense and scattered over entire surface -- *polita* (Fig. 9)

Key to *Eucalantica* species based on male genitalia

1. A pair of lateral lobes near uncus apex present ------------------------------------ 2

A pair of lateral lobes near uncus apex absent ------------------------------------- 5

2. Aedeagus with swelling at 3/5 (Figs 24e & 28e) ---------------------------------- 3

Aedeagus without swelling -- 4

3. Apex of uncus medially markedly convex (Fig. 27a) -------------- *vaquero* sp. n.

Apex of uncus medially nearly flat (Fig. 23a) --------------------- *icarusella* sp. n.

4. Valva with a triangular mound above subbasal saccular region (Fig. 17c) -------
--- *polita*

Valva without a mound above subbasal sacculus region (Fig. 25c) ----------------
-- *powelli* sp. n.

5. Valva obovate --- 6

Valva with costal and saccular margin parallel each other in most areas ---------
-- *pumila* sp. n.

6. Base of valva with two arched grooves (Fig. 21c) --------------- *ehecatlella* sp. n.

Base of valva with one arched groove (Fig. 19c) ----------------- *costaricae* sp. n.

Key to *Eucalantica* species based on female genitalia

(Note: the females of *E. ehecatlella* and *E. pumila* are unknown)

1. Signum present -- 2

Signum absent -- 4

2. Signum keel-shaped (Figs 34c & 35c) -- 3

Signum discoid (Fig. 33c) -- *costaricae* sp. n.

3. A pair of pits present on S8 around ostium bursae (Fig. 35a) --- *icarusella* sp. n.

S8 without pits -- *vaquero* sp. n.

4. S8 with a pair of semicircular folds posterolaterally (Fig. 32) ------ *powelli* sp. n.

S8 without semicircular fold --- *polita*

Eucalantica polita (Walsingham, 1881)

(Figures 1–2, 7–9, 17–18 & 31)

Calantica polita Walsingham, 1881: 302, pl. 35: 2.

Eucalantica polita; Busck, 1904: 750.

Types examined. Lectotype ♂ (here designated; Fig. 7) – USA: “Lectotype [on a round paper with cobalt blue border]”, “Lake Co./ CALIFORNIA/ 17-19 1871/ Wlsm. [on a rectangular paper]”, “Walsingham/ Collection/ 1910-427 [on a rectangular paper]”, “Calantica/ polita Wlsm/ P.Z.S.Lond.p.302.tf.35’2 1881/ TYPE ♂ [on a rectangular paper with black margins]”, BMNH. **Paralectotypes** 2♂ – USA: “Calantica polita Wl. Cala. [California], Pr.Z.S.1881.p302/ pl.35.f.2 [handwriting on a rectangular paper]”, “Type 14992 [in a red rectangular paper]”, “Wlsm. To Chamb. [handwriting on single line paper]”, MCZ. Walsingham (1881) did not state the exact type locality and the number of specimens for his description of *Calantica polita*. A male specimen from BMNH has a red-bordered round label written “Type”. Two type specimens of *C. polita* from MCZ are duplicates by Walsingham which were sent to Chambers (Miller and Hodges, 1990). Therefore, all three specimens from BMNH and MCZ which hold “Type” label must be syntypes as Miller and Hodges (1990) already indicated. We formally designate a lectotype of *C. polita* amongst these specimens.

Specimens examined. CANADA: 2♂, British Columbia, Vancouver, BC, 3 August 1902 (USNM); 1♂, British Columbia, Vancouver Isl., Wellington, 14 April 1902 (USNM); 3♂, ditto, February 1905, GW Taylor (USNM); 1♂, ditto, 27 April 1904, T Bryant (USNM); 1M, ditto, October 1905, GW Taylor (USNM); 3♂, ditto, November 1905, GW Taylor (USNM); 3♂, ditto, no date, GW Taylor

(USNM); 1♂, British Columbia, Vancouver Is., Duncans, 12 April 1892, Hanham (USNM); 1♂, ditto, June 1908, Hanham (USNM); 1♂, ditto, 5 October 1908, Hanham (USNM); 1♂, ditto, April 1909, Hanham (USNM); 1ex, ditto, no date, Hanham (USNM); 1♂1♀, British Columbia, Departure Bay, Bio Station, April 1909 (USNM); 1♂, British Columbia, Goldstream, 18 April 1921, EH Blackmore (USNM). USA: 1♂, Washington, Goldbar, 25 September 1983, DF Bray (USNM); 1♂, Washington, Long Beach, Clarke's Nursery, 24 July 1965, EP Breakey, "reared from *Vaccinium ovatum*", GSN [USNM-77947] (USNM); 1♂, Washington, Long Beach, 10 December 1964, EP Breakey & EG Tinius, "from larva boring rhododendron twig, emerged on 31 December 1964" (USNM); 2♂2♀, Washington, Tacoma, 20 May 1928, M Clarke (USNM); 1♂, Washington, Lake Crescent, June 1971, EC Zimmerman (USNM); 1ex, Washington, Tiago, 17 June 1918, HK Plank, "on huckberry [sic]/ winter" (USNM); 1♂, Washington, Seattle, 27 May 1901, GSN [USNM-91608] (USNM); 1♂, ditto, 12 October 1923, JFG Clarke (USNM); 1♂, ditto, 20 April 1931, WMW Baker, "leaf miner in rhododendron" (USNM); 1♂, Washington, Olympic Mts., 12 April 1892 (USNM); 6♂, Washington, Olympic Mts., Barnes Creek, 5–6 August 1936, AF Braun (USNM); 1♂, Washington, Olympic Mts., Hurricane Ridge, alt. 3000ft, 15 June 1955, JFG Clarke (USNM); 2♂, Washington, Harstine Island, 24 July 1960, EP Breakey, "from larvae (leaftiers) feeding in tips of huckleberry" (USNM); 1♀, Washington, Hoquiam, Burke Colr., 6 May 1904, Fivino (USNM); 3♂1♀, Washington, San Juan Co., Deer Harbor, Orcas Island, 14 July 2002, J Powell (EMEC); 1♂, Washington, Kitsap Co., Bainbridge Island, Venice District, 3–4

April 2001, J Powell (EMEC). 3♂1♀, Oregon, NW corner Douglas Co., Lake Tahkenitch, 26 August 1969, J Powell (EMEC); 1♂, ditto, [no date & collector info] (EMEC); 1♀, Oregon, Coos Co., Bullards Beach, 2 mi N from Bandon, 24–25 August 1969, J Powell (EMEC). 1♂♀, California, San Francisco, Big Basin, 18 June 1971, E Jäckh (USNM); 1♂, California, Del Norte Co., Redwoods, 23 August 1936, AF Braun (USNM); 1♂, California, Humboldt Co., Fieldbrook, 18 May 1903, HS Barber (USNM); 1♂, ditto, 26 May 1903, HS Barber (USNM); 1♂, California, Humboldt Co., 4 mi S from Fieldbrook, 29 June 1969, J Powell (EMEC); 11♂16♀, California, Humboldt Co., 11 mi NE from Blue Lake, Redwood Summit, 9 May 1961, J Powell (EMEC); 1♂, California, Monterey Co., Big Creek Reserve, 8–9 June 2001, J Powell (EMEC); 1♀, ditto, 21–22 July 1992, B Scaccia & R Zuniga (EMEC); 12♂28♀, California, Monterey Co., Big Creek Reserve, Devils Cr. Flat, alt. 120m, Redwood riparian, 23–25 April 1987, J Powell, "JAP no. 87D29: emerged in 16–21 May 1987, reared from *Vaccinium ovatum*" (EMEC); 6♂, California, Humboldt Co., Kneeland, 69 Prairie Lane, 12–14 March 2001, RS Wielgus, GSN [USNM96387] (USNM); 14♂11F, ditto, 18–20 March 2001, RS Wielgus (EMEC); 1♂, California, Humboldt Co., Arcata, 24 June 1969, J Powell (EMEC); 1♂, ditto, 28 June 1969, J Powell (EMEC); 1♀, California, Humboldt Co., Richardson Grove St. Park, 18 June 1962, CA Toschi (EMEC); 1♂, California, Marin Co., Inverness Ridge, 15 May 1970, J Powell (USNM); 3♂, ditto, alt. 100m, 21-24 May 1995, JA Powell (EMEC); 1♂2♀, ditto, alt. 40-250m, 20 October 1999, JA Powell (EMEC); 1♀, ditto, alt. 270m, 19 September 1998, JA Powell (EMEC); 1♂, ditto, alt. 250-300m, 19–20 May 1998, JA Powell (EMEC); 1♂, California, Marin Co., Inverness Park, alt. 150m, 26–30 September 1999, J Powell (EMEC); 1♂, ditto, 8-14 October 1999, J Powell (EMEC); 1♂1♀, ditto, 15-22 October 1999, J Powell (EMEC); 1♂, ditto, alt. 175m, 13–19 2003, J Powell (EMEC); 1♂, ditto, 20-26 October 2003, J Powell (EMEC); 2♂, California, Marin Co., 2mi SE Inverness Ridge, alt. 700-1100ft, 15–16 May 1970, RE Dietz (EMEC); 1♀, California, Marin Co., Mt. Vision, Inverness Ridge, 24 April 1982, JA Powell, "JAP no. 82D46: reared from *Vaccinium ovatum*" (EMEC);1♀, California, Marin Co., Palomarin, 7–8 May 1990, P Super (EMEC); 1♂2♀, California, Marin Co., Alpine Lake, alt. 250-350m, 11 April 1992, J Powell, "JAP no. 92D39.1: emerged on 8 May 1992, reared from *Vaccinium ovatum*" (EMEC); 3♂1♀, California, Tomales Bay, Marin Co., 21 January 1959, J Powell (EMEC); 1♂, ditto, 17 February 1961, J Powell (EMEC); 14♂10♀, California, San Mateo Co., San Bruno Mt., 13 April 1981, JA DeBenedictis, "JADeB no. 81103-A: emerged in 6–12 May 1981, reared from *Vaccinium ovatum*" (EMEC); 1♂, ditto, 16 May 1984, JB Whitfield & JA DeBenedictis, "JBW no. 84E31: emerged between 25 May & 4 June 1984, reared from *Vaccinium ovatum*" (EMEC); 1♂1♀, California, San Mateo Co., San Bruno Mt., Radio Tower Road, 16 May 1984, JA Powell, "JAP no. 84E31: emerged on 4 June 1984, reared from *Vaccinium ovatum*" (EMEC); 1♀, California, Sonoma Co., 10–25 May, AH Vachell (USNM); 1♂1♀, California, Sonoma Co., Salt Point St. Park, 20 July 1990, RJ Robertson (EMEC); 4♂5♀, California, Mendocino Co., 2 mi S from Rockport, 1 February 1962, J Powell (EMEC); 1♂1♀, California, Mendocino Co., 5 mi NW from Comptche, Pygmy Forest, 10 April 1981, JA

DeBenedictis, "JADeB no. 8100-A: emerged on 29 April & 4 May 1981, reared from *Vaccinium ovatum*" (EMEC); 4♂, California, Del Norte Co., 8 mi N from Klamath, Damnation Cr., 20 July 1969, DP Levin (EMEC); 1♂, California, Santa Barbara Co., Santa Cruz Is., Ridge N of Laguna Canyon, 28 April 1966 (EMEC); 1♀, California, Santa Barbara Co., Santa Cruz Is., Canada de la Cuesta, 15 March 1969, J Powell, "JAP no. 69C39: emerged on 4 April 1969, reared from *Vaccinium ovatum*" (EMEC); 1♀, California, Santa Barbara Co., Santa Cruz Is., Felton, 20–21 July 1991, J Powell (EMEC); 1♂, [no specific locality], 1882, Walsingham, GSN [USNM-91607] (USNM); 1♂, ditto, [no date], Fernald (USNM).

Diagnosis. This species externally resembles *Euceratia castella* Walsingham, 1881, among the described species of North America, but is easily distinguished from the latter in having a dorsal patch on forewings and by in lacking white annulations on the antennae.

Redescription (Figs 7-9). Forewing length 5.5–8mm (mean=7.19mm, n=58); basal 1/4 of costa dark brown; an oblique, bar-like, reddish brown patch on distal 1/3 of posterior margin, surrounded by black speckles; posterior suffusion reddish brown, as long as dorsal patch; posterior suffusion and/or dorsal patch lost and black specks peppering, depending on the individuals; a black spot at the end of discal cell; a black scale on each vein along termen; fringes white on basal half, grayish brown on distal half, or entirely white in some specimens. Hindwing anterior margin 2x longer than maximum width; fringe pale gray on basal half, white on distal half.

Male genitalia (Figs 17 & 18) (6 preparations examined) **–** Uncus (Fig. 17a) linguiform, convex posteriorly, with a pair of short, digitate tubercle posterolaterally; socii digitate, as long as saccus, with a row of 4 or 5 short ventral spines terminally, gradually smaller from basal to terminal spine (Fig. 17b). Tegumen parallel-sided; subscaphium (Fig. 17d) strongly bulged ventrad. Valva obovate, saccular margin evenly rounded, 2x longer than tegumen; costa curved at 1/4, narrowly sclerotized in basal 1/4; a small triangular mound above basal 2/5 of saccular margin (Fig. 17c). Saccus slender, as long as socius. Aedeagus (Fig. 18) slender, 3x length of saccus, weakly sinuate; cornutus absent.

Female genitalia (Fig. 31) (5 preparations examined) **–** S8 sclerotized, with a shallow bulge posterior to S8 humps; minute thorns on the bulge; semicircular depression anteriolaterally (Fig. 31b). Apophysis posterioris 2x longer than papillae anales, 2.5x longer than apophysis anteroris excluding basal Y-fork; longer branch of the Y-fork 1.2x longer than shorter branch or apophysis anterioris. Minute thorns on area between S8 humps and ostium bursae. Ductus bursae as long as apophysis posterioris; antrum in posterior 1/5 of ductus bursae, digitate, broadened at ostium, with minute thorns on internal wall (Fig. 31a); bulla seminalis as large as corpus bursae. Corpus bursae ovoid; signum absent.

Distribution (Fig. 15). Pacific side coastal regions of Canada (British Columbia) and United States (Washington, Oregon, California).

Host plant. The larvae feed on flowers and leaves of California Huckleberry, *Vaccinium ovatum* Pursh (Ericaceae) (Powell & Opler, 2009). In the USNM collection, there exist two specimens of *E. polita* reared from “rhododendron”, possibly *Rhododendron pacificum*. These records, however, need to be confirmed. The host record “huckberry” from USNM must be an error for “huckleberry”. The label data available from museum specimens indicate that the larvae are twig-borers, leaf-miners or leaf-tiers. The larvae of *E. polita* are primarily external feeders which web amongst inflorescences or young vegetative terminals of *Vaccinium ovatum* (Jerry Powell, personal communication). All records of the internal feeding larvae of *E. polita* are associated with “rhododendron”, a host which is yet unverified.

Remarks. *E. polita* shows continuous variations in forewing patterns between two extremes which are very reduced (Fig. 8) or maculate throughout (Fig. 9). Those variants coexist temporally and spatially, for which no taxonomic consideration is necessary. However, some of the variants can be confused with the new species described in this study. Walsingham (1881) illustrated an individual of *E. polita* whose forewings have only a dorsal patch and discal spot (Fig. 7). We found that this variant is predominant (ca. 87%) amongst the specimens examined in our study. The maculate variants were the rarest (ca. 0.7%).

***Eucalantica costaricae* Sohn & Nishida, sp. n.**

(Figures 3–4, 10, 19–20 & 33)

Type material. Holotype ♂ – COSTA RICA: Cartago, El Guarco, Macizo de la Muerte, Sector de la esperanza, 9˚46'14" N; 83˚47'59"W, alt. 2600m, February

2002, R Delgado, BN-INB0003434063, GSN [SJC 640] (INBIO). **Paratypes** (5♂2♀) – COSTA RICA: 2♂, San José, Cerro de la Muerte, Villa Mills, La Georgina, 9˚34'N; 83˚43'W, alt. 3000m, 20 February 1999, K Nishida (USNM & UCR); 1♀, San José, Cerro de la Muerte, Estación Biológica de la UCR, 9˚34'N; 83˚45'W, alt. 3050m, 2 February 1999, K. Nishida (BMNH). 1♂, Cartago, Cerro de la Muerte, Georgina, 9˚34'N; 83˚45'W, alt. 3000m, 23–25 May 1985, J Powell & PA Opler (INBIO); 1♂, ditto (EMEC); 1♂, ditto, 20 June 1988, J Brown & J Powell (EMEC); 1♀, Cartago, Villa Mills, 9˚34'N; 83˚43'W, alt. 3000m, 3–4 July 1999, J Powell (EMEC).

Diagnosis. This new species is superficially indistinguishable from some variants of *E. polita*. In such cases, examination of genitalia is necessary for reliable identification. *E. costaricae* differs from *E. polita* by the lack of lateral projections near the apex of the uncus in the male genitalia and in having a signum in the corpus bursae of the female genitalia.

Description (Fig. 10). Forewing length 6.5–8mm (mean=7.48mm, n=9); posterior suffusion and dorsal patch absent; in majority of individuals, black spots scattered on distal and posterior half; fringes entirely white. In some specimens, all forewing pattern elements are lost except a discal spot. Hindwing anterior margin 3x longer than the maxium width; fringes entirely white.

Male genitalia (Figs 19 & 20) (5 preparations examined) **–** Uncus (Fig. 19a) linguiform apically; socii lunate, as long as saccus, long hairy dorsally, with four terminal spines in a row, third spine from tip longest, followed by second, fourth, and first in order of length (Fig. 19b). Tegumen subtriangular, 1.5x broader than uncus; subscaphium (Fig. 19d) appressed to tegumen. Valva obovate, 2.5x longer than socii, costa slightly incurved at basal 1/3; arched setose area above saccular base (Fig. 19c). Saccus very slender, as long as socius. Aedeagus (Fig. 20) attenuate in distal half, as long as and slightly wider than saccus, bent medially; carina slender, triangular; a zone of minute spinulate cornuti in distal half of aedeagus.

Female genitalia (Fig. 33) (2 preparations examined) **–** S8 sclerotized; minute thorns on semicircular area above S8 humps. Apophysis posterioris 2.5x longer than apophysis anterioris excluding basal Y-fork; longer branch of Y-fork 5x longer than shorter branch. Ductus bursae as long as corpus bursae; antrum in posterior 1/7 of ductus bursae, cup-shaped, with minute thorns on internal wall (Fig. 33a); bulla seminalis 2/3 as large as corpus bursae. Corpus bursae ellipsoid; signum as a small, scobinate disc (Fig. 33c).

Distribution. Costa Rica (high elevations of Cerro de la Muerte of the Talamancan Mountain Range in Cartago and San José Provinces).

Habitat. The adult specimens have been collected exclusively from the high elevation forests of Cerro de la Muerte where oaks are dominant below 3,300m (Zuchowski, 2007). See Nishida *et al.* (2002) for more details about the habitats. The second author (KN) observed one individual of this species resting on the underside of a leaf of *Vaccinium floribundum* Kunth (Fig. 1). Given the host association of *E. polita* with another *Vaccinium*, this plant is likely the larval host of *E. costaricae*.

Etymology. The new species is named after Costa Rica, where the type locality is situated.

Eucalantica ehecatlella Sohn & Nishida, sp. n.

(Figures 6, 21 & 22)

Type material. Holotype ♂ – COSTA RICA: Heredia, Volcán Barva, 6 km ENE from Vara Blanca, 10˚10′34″N; 84˚06′41″W, alt. 1950–2050 m, 16 February 2002, BN-INB0003220413, GSN [SJC 642] (INBIO). **Paratype** ♂ – COSTA RICA: same locality as holotype, 21 March 2002, A Kawahara, BN-INB0003217116, abdomen missing (INBIO).

Diagnosis. This species is very close to *E. icarusella* in the shape of the dorsal patch of the forewing and in having entirely pale gray forewing fringes but differs from the latter by having most of the black dots sparsely scattered beyond the discal cell. *Eucalantica ehecatlella* is further distinguished from *E. icarusella* by the lack of projections near the apex of uncus in the male genitalia.

Description (Fig. 6). Forewing length 5.0–6.2 mm (n=2) with dark brown costal streak in basal 1/4; posterior suffusion on basal half of dorsal margin, reddish brown with an intermittent, black line along upper border; black spots sparsely scattered on distal 1/4; terminal line narrow, black, intermittent; fringes pale orange, paler on tornus. Hindwing anterior margin 2x longer than maximum width; fringes pale gray.

Male genitalia (Figs 21 & 22) (1 preparation examined) **–** Uncus (Fig. 21a) elongate, triangular, conical apically; socii bulged dorsally, sharp triangular in terminal 1/5, 1.5x longer than saccus, long-hairy dorsally, with four terminal spines in a row, third spine from tip longest, followed by second, fourth, and first in order of length (Fig. 21b). Tegumen parallel-sided; subscaphium (Fig. 21d) slightly bulged ventrad. Valva obovate, costal margin almost straight, apex broadly round; a semicircular emargination adjoining with a densely setose area and an oblique groove above saccular base (Fig. 21c); a subrectangular emargination near the middle of the base of valva ventrally (Fig. 21c). Saccus elongate, digitate, as long as uncus. Aedeagus (Fig. 22) of even width throughout, strongly curved medially, with a triangular carina terminally and a zone of minute-spinulate cornuti 1/3 as long as aedeagus.

Female – unknown.

Distribution. Costa Rica (Central Volcanic Range in Heredia Province).

Etymology. The specific epithet is derived from ‘Ehecatl’, a god of wind in Aztec mythology and refers to the windy habitat where the new species was collected.

Eucalantica icarusella Sohn & Nishida, sp. n.

(Figures 11, 23–24 & 35)

Type material. Holotype ♂ **–** COSTA RICA: San José, Cerro de la Muerte, Estación Biológica de la UCR, 9° 34' N; 83° 45' W, alt. 3050m, 20 February 1999

(K. Nishida), GSN [USNM96397], USNM. **Paratypes** (6♂4♀) – COSTA RICA: 1♂, San José, Cerro de la Muerte, Estación Biológica de la UCR, 9˚34'N; 83˚45'W, alt. 3100m, 20 December 1998, K Nishida (BMNH); 2♂, San José, Cerro de la Muerte, Estación Los Nimbolos, 9˚99'42.30″N; 83˚44'27.2″W, alt. 3150m, 24-27 July 2006, JB Sullivan (USNM). 2♀, Cartago, Cerro de Muerte, Pension La Georgina, 9˚34'N; 83˚45'W, alt. 3000m, 23–25 May 1985, J Powell, GSN [EMEC-JCS 003] (EMEC); 1♀, 7km SE El Canon, 9˚40'N; 83˚55'W, 28 May 1985 (J Powell), GSN [EMEC-JCS 001] (EMEC). 1♂1♀, Alajuela, Volcán Poás, 10˚11′00″N; 84˚12′30″W, alt. 2550m, 6-7 June 1988 (J Brown & JA Powell), GSN [EMEC-JCS 004 (♀)] (EMEC). 1♂, Heredia, Volcán Barva, 6 km ENE from Vara Blanca, 10˚10′34″N; 84˚06′41″W, alt. 1950–2050 m, 20 March 2002, K Nishida, abdomen missing (USNM); 1♂, ditto, 12 April 2002, K Nishida (UCR).

Diagnosis. This species is superficially similar to *E. costaricae*, but differs from the latter in having a posterior suffusion on the forewings and narrower hindwings. In the genitalia, *E. icarusella* is distinguished from *E. costaricae* in having projections (Fig. 23a) near the apex of the uncus in the males and having a pair of pits (Fig. 35a) near ostium bursae in the females.

Description (Fig. 11). Forewing length 5.3–7.9 mm (mean=7.07mm, n=9); costal streak dark brown, broadly spread basally; dorsal patch at the middle of posterior margin, dentiform, orange, with a black line on upper border; posterior suffusion on basal 1/2 of dorsal margin, orange, with an intermittent black line on upper border; black spots peppering in distal 3/4, denser to distal 1/3; fringes pale gray in basal 1/3, brownish gray in distal 2/3. Hindwing anterior margin 2.5x longer than maximum width; fringes pale gray.

Male genitalia (Figs 23 & 24) (3 preparations examined) **–** Uncus (Fig. 23a) linguiform, apex slightly protruded, lateral lobes digitate, with transverse edge apically; socii digitate, narrowly round apically, as long as saccus, long-hairy dorsally, with three terminal spines in a row, all almost same in length (Fig. 23b). Tegumen as long as uncus, subtriangular posteriorly, parallel laterally in anterior half, enlarged in posterior half; subscaphium (Fig. 23d) appressed to tegumen. Valva elongate, almost of even width throughout, rounded apically, 3.5x longer than saccus; costa slightly bulged at basal 1/5; a semicircular emargination above saccular base, adjoining with a small tubercle at upper end (Fig. 23c). Saccus digitate, robust, broadened to base, as long as socius. Aedeagus (Fig. 24) almost straight, slightly bulged medially (Fig. 24e), 2.5x longer than saccus; a zone of minute-spinulate cornuti 2/5 as long as aedeagus.

Female genitalia (Fig. 35) (4 preparation examined) **–** S8 sclerotized, quadrate, with a pair of semicircular, setose humps posteriorly; minute thorns on and posteriorn to S8 humps; semicircular, lateral pleats at the middle of S8 area (indicated with an asterisk in Fig. 35); a pair of pits adjacent to ostium (Fig. 35a). Apophysis posterioris 3.5x longer than apophysis anterioris excluding basal Y-fork; ventral branch of Y-fork fused with posterior margin of S8, dorsal branch 2x longer than apophysis anterioris, slightly sinuous. A zone of minute thorns extended from antrum to S8 pleats. Ductus bursae as long as corpus; antrum cylindrical, 1/6 as long as and 2x wider than ductus bursae, with minute thorns on internal wall (Fig. 35a); bulla seminalis 1/2 as long as ductus bursae. Corpus bursae oval, membranous, cervical area slightly protruding; signum keel-like with denticules on interior surface (Fig. 35c).

Distribution. Costa Rica (high elevations of Cartago, Heredia and San José).

Etymology. The new species is named after the Greek mythological character *Ikaros* (*Icarus* in Latin) and refers to the white forewing with scarlet dorsal suffusion resembling Icarus' waxy wings burnt down by sunlight.

Eucalantica powelli **Sohn, sp. n.**

(Figures 12, 25–26 & 32)

Type material. Holotype ♂ – COSTA RICA: Cartago, Cerro de la Muerte, La Georgina, 9˚34'N; 83˚45'W, alt. 3000 m, 23–25 June 1985, J Powell & PA Opler, GSN [EMEC-JCS 012] (EMEC). **Paratypes (**1♂4♀**)** – COSTA RICA: 1♀, San José, 4.6 km E from Villa Mills, Sendero al Mirador, Est. Cuericí, 9˚34'N; 83˚43'W, alt. 2640m, 17–22 March 1996, A Picado, GSN [SJC 806] (INBIO). 1♂, Cartago, 7 km SE El Cañón, 9˚40'N; 83˚55'W, alt. 2500 m, 28 May 1985, J Powell & JT Doyen (EMEC); 3♀, Cartago, Villa Mills, 9˚34'N; 83˚43'W, alt. 3000 m, 3–4 July 1999, J Powell, GSN [EMEC-JCS 002] (EMEC).

Diagnosis. This new species is similar to immaculate variants of *E. polita* (Fig. 8) but differs from the latter in having posterior suffusion on entire dorsal margin of forewings. They are also distinguished by the male genitalia, i.e. triangular projection on valva closer to sacculus in *E. powelli*, and also by the female genitalia, i.e. the presence of posterolateral semicircular pleats (indicated with an asterisk in Fig. 32) in *E. powelli*.

Description (Fig. 12). Forewing length 7.0–10.0 mm (mean=8.48mm, n=5); dorsal margin with a row of black dots from the base to the basal 1/3; posterior suffusion on distal 2/3 of dorsal margin, sinuate, orange, with an intermittent black line on upper boarder; terminal line on posterior half of termen, black, intermittent; fringes white in basal half, reddish brown in distal half.

Male genitalia (Figs 25 & 26) (2 preparations examined) **–** Uncus (Fig. 25a) elongate, subrectangular, as long as tegumen, with a pair of digitate lobes posterolaterally; socii digitate, as long as saccus, long-hairy dorsally, with four terminal spines in a row, third and fourth spines from top longest, followed by second, first in order of length (Fig. 25b). Tegumen parallel-sided; subscaphium (Fig. 25d) appressed to tegumen. Valva obovate; costa slightly curved at distal 1/3; sacculus with a small triangular bulge at basal 1/3 (Fig. 25c). Saccus digitate. Aedeagus (Fig. 26) slender, of even width throughout, narrower than saccus, apex oblique, slightly bent medially; with a zone of minute-spinulate cornuti 1/5 as long as aedeagus.

Female genitalia (Fig. 32) (2 preparations examined) **–** S8 slightly oblique laterally, weakly sclerotized, with a pair of setose humps posteromedially; interspace between S8 humps with minute thorns; a pair of semicircular pleats lateroposteriorly (indicated with an asterisk in Fig. 32). Apophysis posterioris 4x longer than apophysis anterioris excluding basal Y-fork; longer branch of Y-fork 3x longer than shorter branch, 2.5x longer than apophysis anterioris. Ductus bursae 2x longer than corpus; antrum in posterior 1/6 of ductus bursae, cylindrical, with minute thorns on inner wall (Fig. 32a); ductus seminalis weakly sclerotized at connection with ductus bursae; bulla seminalis absent. Corpus bursae globular; signum absent.

Distribution. Costa Rica (high elevations of Cartago Province).

Etymology. The new species is named after Dr. Jerry A. Powell, director emeritus of the Essig Museum of Entomology, the University of California, Berkeley, in appreciation of his assistance with the first author’s work.

Eucalantica pumila **Sohn, sp. n.**

(Figures 13, 29 & 30)

Type material. Holotype ♂ – COSTA RICA: Heredia, Volcan Barva, 6 km ENE from Vara Blanca, 10˚11′ N; 84˚07′W, alt. 1950-2050 m, 20 February 2002, BN-INB0003219355, GSN [SJC 808] (INBIO).

Diagnosis. This new species is easily distinguished from all other species of *Eucalantica* by its smaller size and in having a triangular, dark brown dorsal patch on the forewings. The male genitalia of *E. pumila* is similar to *E. costaricae*, but spines on the socii and the aedeagus is slender in the former.

Description (Fig. 13). Forewing length 5.8 mm (n=1); costal streak on basal 1/10 of costal margin, black; dorsal patch subtriangular, dark brown, upper border extended to the lower side of the discal cell; terminal line with three dark brown dots between veins. Hindwing anterior margin 2.2x longer than maximum width, pale gray except dark gray apical area.

Male genitalia (Figs 29 & 30) – Uncus subpentagonal, convex posteriorly, with a papilliform projection apically; socii semielliptical, straight ventrally, 1.5x longer than saccus, long-hairy dorsally, with four slender terminal spines in a row, gradually smaller from basal to terminal spine (Fig. 29b). Tegumen subtrapezoidal; subscaphium (Fig. 29d) slightly bulged. Valva elongate, of even width throughout, narrowly rounded apically; costa slightly convex at basal 1/3; sacculus ending at basal 1/4 of ventral margin of valva; an arched setal area above basal area of sacculus (Fig. 29c). Saccus slender, 2x longer than uncus. Aedeagus (Fig. 30) slender, narrower in distal half, almost straight, obtuse terminally; a zone of minute-spinulate cornuti 1/2 as long as aedeagus.

Female – unknown.

Distribution. Costa Rica (only known from the type locality).

Etymology. The specific epithet is derived from the Latin *pumilus*, meaning "little", and refers to its small size relative to other *Eucalantica*.

Eucalantica vaquero Sohn, sp. n.

(Figures 14, 27–28 & 34)

Type material. Holotype ♂ – USA: New Mexico, Pecos National Forest, 35˚53′N; 105˚38′W, alt. 3048 m, 24 August 1916, C Heinrich, GSN [USNM-96389] (USNM). Paratypes (2♂3♀) – USA: 1♀, New Mexico, same as holotype, abdomen missing (USNM). 1♂, Arizona, White Mts., Summit of Mt. Thomas, 33˚54′22″N; 109˚33′46″W, alt. 11500 ft, 20 August 1925, OC Poling (USNM). MEXICO: 1♀, Tepalcates, 48 km W from Durango, Dgo, 24˚01′N; 104˚40′W, alt. 2560 m, 4–8 August 1972, J Powell, D Veirs, & CD MacNeill, GSN [EMEC-JCS 011] (EMEC). 1♂, Veracruz, Cañón Las Minas, 13 km NE from Perote, 19˚29′52″N; 52˚97′09″W, alt. 2150 m, 19 August 1987, J Brown & J Powell (EMEC); 1♀, Veracruz, 7 km NW from Banderilla, 19˚35′N; 95˚56′W, alt. 1680 m, 13 July 1974, J Powell & J Chemsak (EMEC).

Diagnosis. This new species is superficially indistinguishable from some variants of *E. polita* and in such cases, examination of the genitalia is necessary for a reliable identification. *E. vaquero* is also similar to *E. costaricae* in having a reduced dorsal patch on the forewings but differs from the latter by having the fewer black spots on the forewing, mainly around the CuP fold. The male genitalia of *E. vaquero* differ from ones of *E. polita* and *E. costaricae* in having a bulge on apex of the uncus and stouter saccus. In the female genitalia, *E. vaquero* is distinguished from the latter two in having keel-like signum in the corpus bursae.

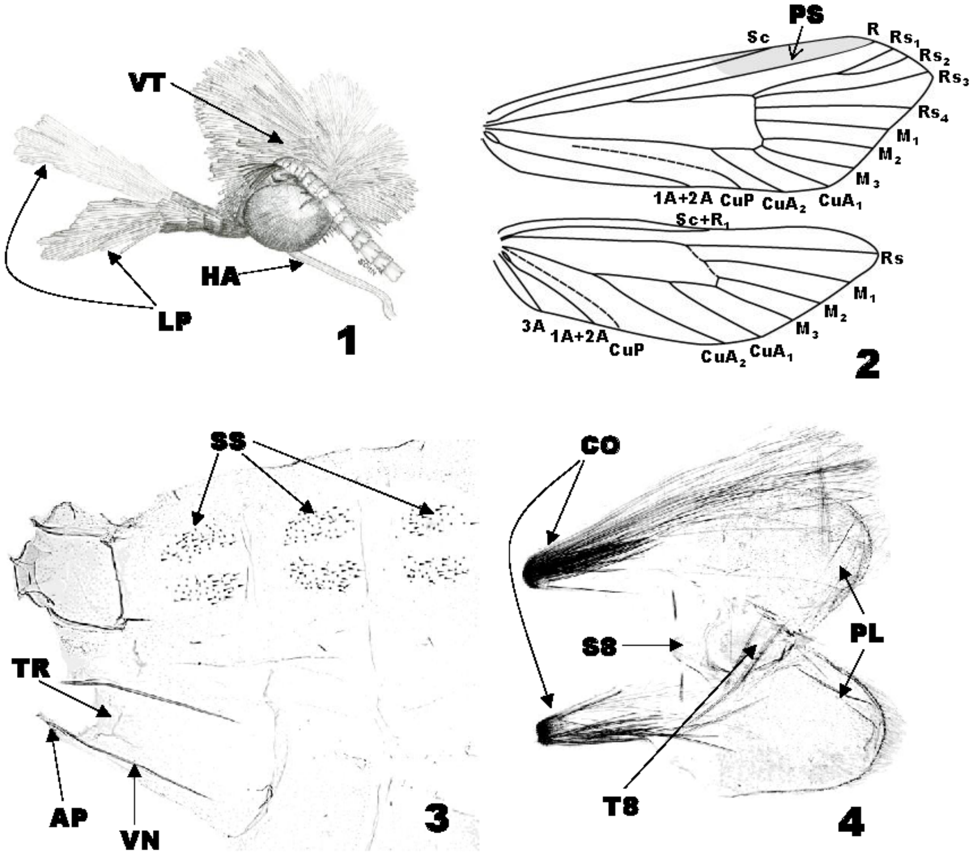
Description (Fig. 14). Forewing length 7.5–8.0mm (mean=7.65mm, n=4); costal streak on basal 1/3 narrow; dorsal patch reduced to a small, oblique, reddish brown band intermixed with black spots or absent; fringes white in basal 2/3, pale gray in distal 1/3. Hindwing anterior margin 2x longer than maximum width; fringes pale gray.

Male genitalia (Figs 27 & 28) (4 preparations examined) – Uncus (Fig. 27a) linguiform, bulged dorsoapically, lateral lobes upcurved, digitate; socii digitate, as long as saccus, long-hairy dorsally, with four terminal spines, all of them almost equal in size (Fig. 27b). Tegumen parallel laterally, 2x broader than uncus; tuba analis with minute thorns on inner wall; subscaphium (Fig. 27d) strongly bulged ventrad. Valva slightly broadened in distal half, narrowly round apically, saccular margin round in distal 1/3, almost straight in basal 2/3; costa slightly concave at middle; sacculus slightly bulged inward at basal 1/3; a semicircular setose area above saccular base; a longitudinal fold at base of valva, adjoining with a small dentiform process (Fig. 27c). Saccus digitate, robust. Aedeagus (Fig. 28) dillated at distal 1/3, almost straight; a zone of minute-spinulate cornuti 1/3 as long as aedeagus.

Female genitalia (Fig. 34) (2 preparations examined) – S8 quadrate, sclerotized, with a pair of semicircular, setose humps. Minute thorns on S8 humps and an area connecting S8 humps and ostium bursae. Apophysis posterioris 4x longer than apophysis anterioris excluding basal Y-fork; both branches of Y-fork almost equal in length, 2x longer than apophysis anterioris. Ductus bursae 4/5 as long as corpus; antrum in posterior 1/4 of ductus bursa, conical, with minute thorns internally (Fig. 34a); bulla seminalis as long as ductus bursae; a sclerite at connection between bulla seminalis and ductus bursae (Fig. 34d). Corpus bursae ellipsoid; signum keel-like on middle of corpus, base narrow-elliptical, with a few denticles (Fig. 34c).

Distribution. USA (New Mexico, Arizona) and Mexico.

Etymology. The species name *vaquero* is a noun in apposition, meaning the Mexican cowboy, and refers to the distribution range of the new species roughly matching with the regions under ‘vaquero’ traditions.



Figures 1-4. Generic characteristics of *Eucalantica*. **1** head of *E. polita* (lateral view) **2** wing venation of *E. polita* (gray shade – pterostigma) **3** abdominal segment II-IV of *E. costaricae* sp. n. **4** abdominal segment VIII of *E. costaricae* sp. n. Abbreviations: AP = apodeme; CO = coremata; LP = labial palpus; HA = haustellum; PL = pleural lobe; PS = pterostigma; S8 = eighth sternite; SS = spiniform setae; T8 = eighth tergite; TR = transverse ridge; VN = venula.

Figures 5-14. Adults of *Eucalantica*. **5** *Eucalantica costaricae* sp. n., resting on underside of *Vaccinium floribundum*, Cerro de la Muerte, Costa Rica **6** *E. ehecatlella* sp. n. (male, holotype) **7-9** *E. polita* **7** lectotype (male) **8** pale variant (female) **9** maculate variant (male) **10** *E. costaricae* sp. n. (female, paratype) **11** *E. icarusella* sp. n. (male, holotype) **12** *E. powelli* sp. n. (female, paratype) **13** *E. pumila* sp. n. (male, holotype) **14** *E. vaquero* sp. n. (female, paratype). Abbreviations: CS = costal streak; DP = dorsal patch; DS = discal spot; PS = posterior suffusion.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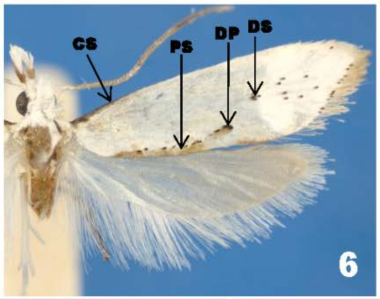

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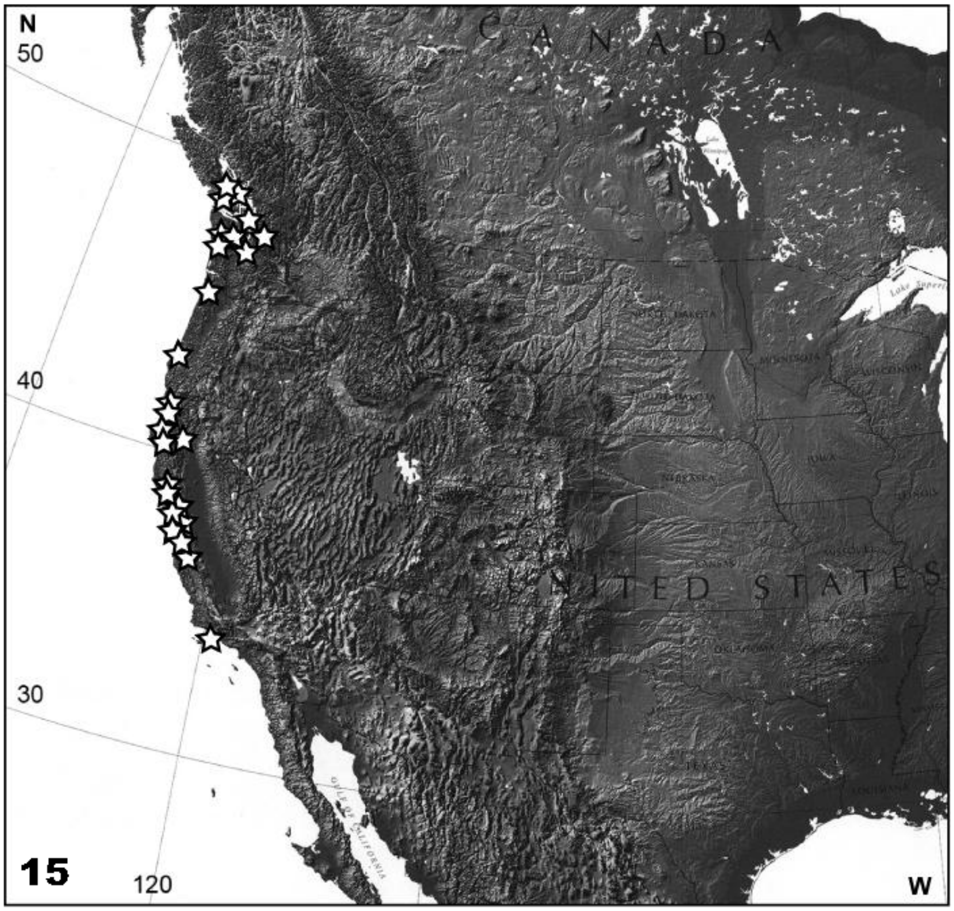


Figure 15. Distribution of *Eucalantica polita* (white star). Map from www.nationalatlas.gov.

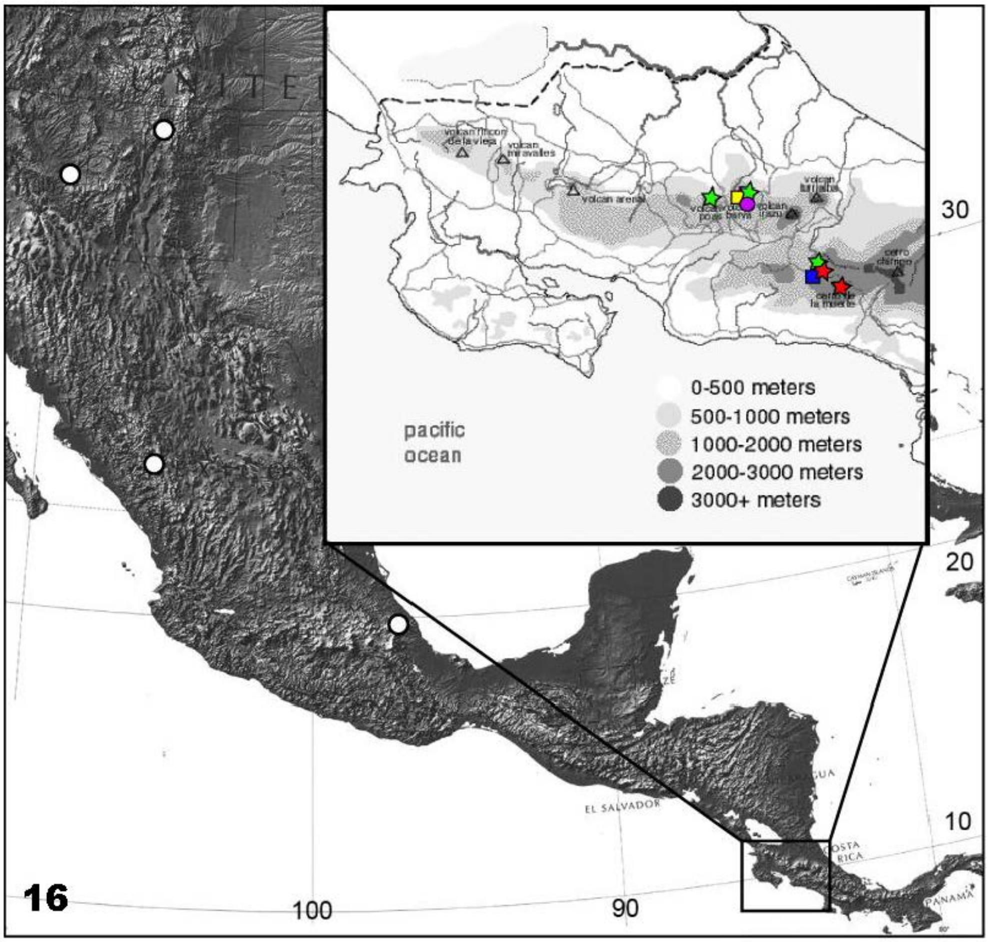
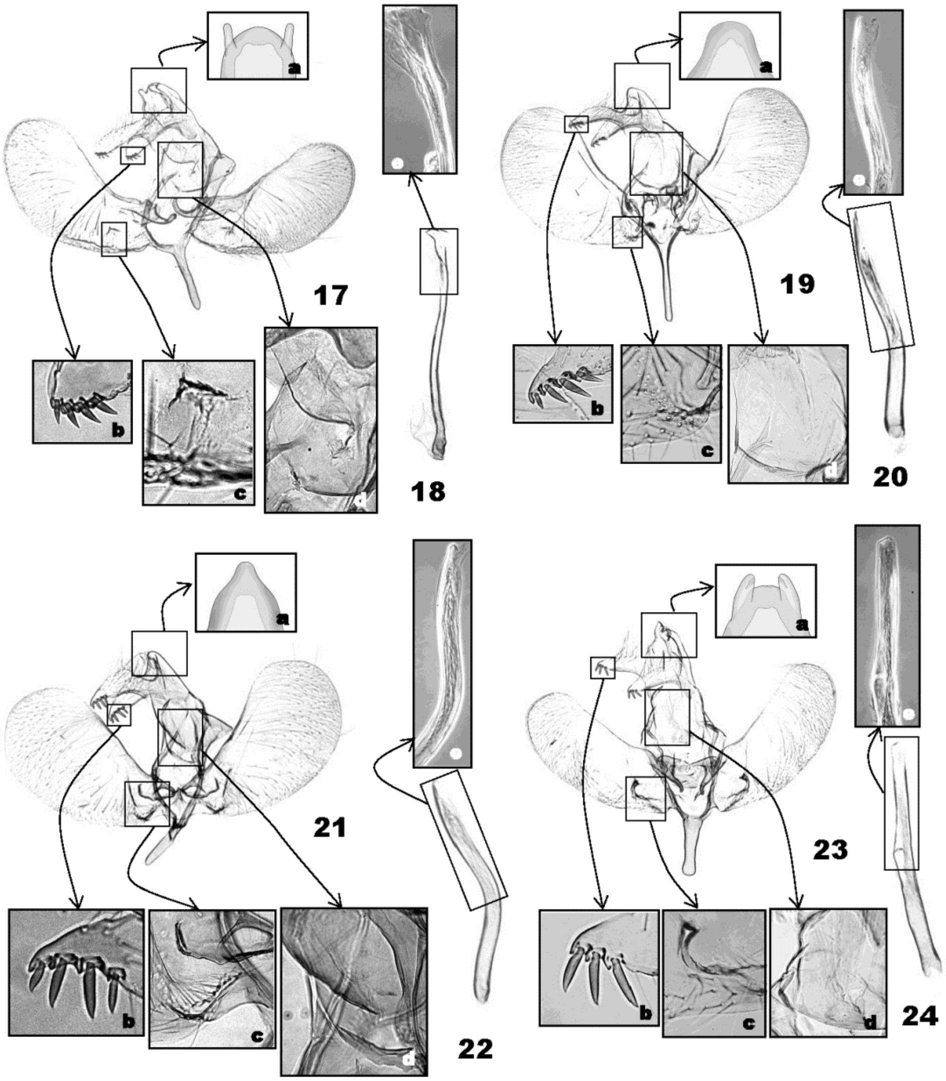
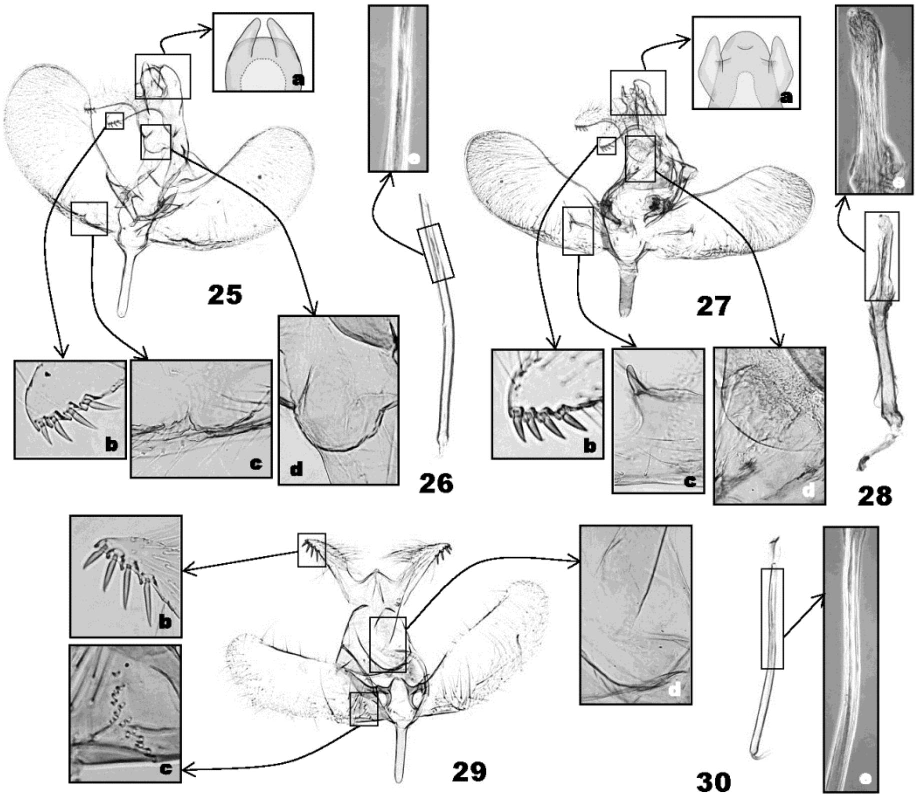


Figure 16. Distribution of *Eucalantica costaricae* sp. n. (red star), *E. ehecatlella* sp. n. (yellow box), *E. icarusella* sp. n. (green star), *E. powelli* sp. n. (blue box), *E. pumila* sp. n. (purple circle), and *E. vaquero* sp. n. (white circle). Maps from www.nationalatlas.gov and www.costa-rica-guide.com.

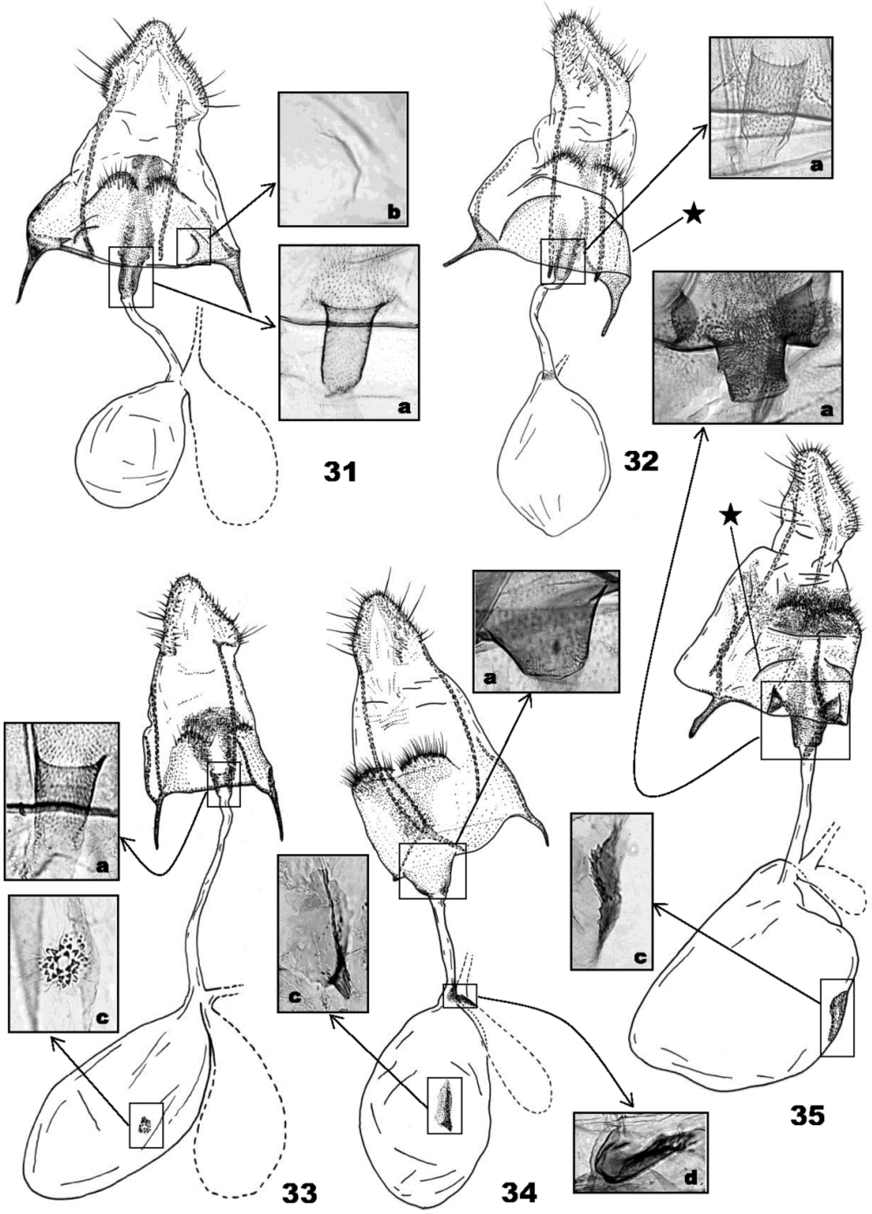


Figures 17-24. Male genitalia of *Eucalantica*. **17-18.** *E. polita* **19-20** *E. costaricae* sp. n. (holotype) **21-22** *E. ehecatlella* sp. n. (holotype) **23-24** *E. icarusella* sp. n. (holotype). **18, 20, 22, 24** aedeagus. Close-up boxes: a – apical region of uncus; b – terminal spines on socius; c – grooves or projections above sacculus; d – subscaphium; e – terminal part of aedeagus and cornuti (transmitted light phase contrast image).



Figures 25-30. Male genitalia of *Eucalantica*. **25-26** *E. powelli* sp. n. (holotype) **27-28** *E. vaquero* sp. n. (holotype) **29-30** *E. pumila* sp. n. (holotype). **26, 28, 30** aedeagus. See figures 17-24 for close-up boxes.

Figures 31-35. Female genitalia of *Eucalantica*. **31** *E. polita*. **32** *E. powelli* sp. n. (paratype) **33** *E. costaricae* sp. n. (paratype) **34** *E. vaquero* sp. n. (paratype) **35** *E. icarusella* sp. n. (paratype). Ductus seminalis and bulla seminalis contoured by dotted line. Asterisk = semicircular fold. Close-up boxes: a – antrum and thorny area around ostium; b – semicircular depression on eighth sternite; c – signum; d – sclerite at connection between ductus bursa and bulla seminalis.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A new species of *Atemelia* Herrich-Schäffer (Lepidoptera, Yponomeutoidea, Praydidae) feeding on an ornamental shrub *Mahonia* (Berberidaceae) from Chile

Sohn, J.-C. and M. Peralta, 2013 (in submission to Ann. Ent. Soc. Amer.)

Introduction

Atemelia Herrich-Schäffer is a genus of Praydidae (van Nieukerken et al., 2011), once a subfamily of Yponomeutidae sensu Kyrki (1990). Friese (1960) found that *Atemelia* differs from Yponomeutidae, based on four characteristics: the lack of the spiniform setae on the tergites; the lack of the longitudinal suture before the transverse suture of the adult head vertex; the presence of the socii without terminal spine in the male genitalia; and the greatly reduced apophyses anteriores in the female genitalia. He further suggested that *Atemelia* is associated with *Prays* Hübner in superficial and genital characters and that both genera are associated with Plutellidae. This hypothesis, however, was challenged by Moriuti (1977) who separated the so-called *Prays*-group from Plutellidae (Plutellinae of authors) and gave them a subfamily name, Praydinae. Recent molecular estimations of yponomeutoid phylogeny (Mutanen et al., 2010; Sohn et al., 2013) reconfirmed the distinctness of the *Prays*-group from Yponomeutidae and Plutellidae.

Atemelia had been monobasic until Kyrki (1990) found that the Nearctic *Orinympha* Meyrick is a synonym. This proposition has been supported by a recent molecular study (Sohn et al., 2013). Therefore, *Atemelia* now comprises two species: *torquatella* Lienig & Zeller from Europe and *aetherias* Meyrick from USA. These species are very different from each other in forewing patterns: fuscous with pale grayish patches in *torquatella* versus gray with reticulate streaks and a dark dorsal patch in *aetherias*. The biology of *Atemelia* is known only for *torquatella* which is a common leaf mining pest on *Betula* and *Ulmus* in certain parts of Europe. The larvae, however, rarely cause damage of economic significance.

The purpose of this paper is to describe a new species of *Atemelia* from Chile, including its immature stages. This is the first record of the genus from the Neotropical region. The new species is compared with *A. torquatella* in the adult, larval and pupal characteristics. It is possibly of economic importance due to feeding on *Mahonia* trees which are widely cultivated in gardens. We provide keys to the world species of *Atemelia* to facilitate their identification.

Materials and methods

Six larvae were collected with the host plant leaves and reared in captivity by the second author (MP). Three of the larvae were killed and fixed using boiling water and then stored in 80% ETOH. Two emerged adults were killed by freezing and prepared as dried specimens. All specimens examined were deposited in the Smithsonian National Museum of Natural History, Washington, DC (USNM). The genitalia slides were prepared following Clarke (1941), except that chlorazol black was used for staining and euparal resin for permanent slide mounting. Dissection of larval heads follows Corrette & Neunzig (1979). Since intact pupae were unavailable for our study, pupal exuvia were examined instead. All specimens were examined with a Leica MZ APO stereoscope. Slide-mounted specimens were examined with a Leica LETTZ-DMRX microscope. Images were captured using the VDBK digital imaging systems, adopted by the Systematic Entomology Laboratory (United States Department of Agriculture) and installed in the Department of Entomology, Smithsonian National Museum of Natural History.

Terms for genitalia, larvae, and pupae follow Klots (1970), Stehr (1987) and Mosher (1916), respectively. Larval thoracic and abdominal segments were abbreviated as ‘T’ and ‘AB’ respectively. References for morphological comparisons include Werner (1958) and Grandi (1933) for the larvae of *Atemelia torquatella*; Moriuti (1977) for the larvae and pupae of *Prays iota* and *P. lamda*; Patočka (1997) for the pupae of *Prays fraxinella* and *A. torquatella*.

Results

Genus *Atemelia* Herrich-Schäffer

Atemelia Herrich-Schäffer, 1853: 9, 33

Type species: *Oecophora torquatella* Lienig & Zeller, 1846, by subsequent designation by Fletcher (1929: 26)

= *Orinympha* Meyrick, 1927: 360. Synonymized by Kyrki (1990: 36).

Type species: *Orinympha aetherias* Meyrick, 1927, by monotypy

Key to the species of *Atemelia*, based on superficial characteristics

1. Forewing fuscous -- *torquatella* (Fig. 3)
   Forewing gray or pale gray -- 2
2. Forewing with dark brown, reticulate streak --------------------- *aetherias* (Fig. 4)
   Forewing with dark gray mottles --------------------- *mahonivora* n. sp. (Figs 1–2)

Atemelia mahonivora Sohn et Peralta, n. sp.

(Figs 1–2, 5–11)

Type Material. Holotype: ♂, Chile: Region de Valparaíso, Provincia de San Antonio, Comuna de Santo Domingo (33˚38´9″S 71˚37´41″W), 10 II 2009 (larva), reared on *Mahonia* sp., genitalia slide USNM 115094.

Paratypes (7♂, 2♀): 1♀, same as holotype, genitalia slide USNM 115095; 4 ♂, Chile: Curico, 20 km east from Potrero Grande, Buchen, 11 Jan. 1955 (LE Peña); 3♂, 1♀, Chile, Bio-Bio Prov., Lago El Barco, Guallali, Sta Barbara, 1200m, 25-28 Feb. 1981 (LE Peña), genitalia slide USNM 115075 (♀), 115077 (♂), 115083 (♂). All types are deposited in the United States National Museum of Natural History, Washington DC, USA.

Diagnosis. The new species is similar to *Atemelia aetherias* (Meyrick) in having the forewing pale gray with a fuscous dorsal patch but differs in having dark gray mottles (dark brown reticulation in *aetherias*). The male genitalia of *A. mahonivora* are distinguished from *A. aetherias* and *A. torquatella* in the lack of a pair of processes extended from the ventral side of the uncus. In the female genitalia, *A. mahonivora* differs from *A. torquatella* in having a smaller signum and a nearly straight anterior margin of ninth sternite (medially emarginated in *torquatella*).

Description. Head: Vertex pale brownish gray; frons dark brown with white margins. Antenna 3/4 as long as forewing, dark brown, tinged with gray on basal half of dorsal side; scape and pecten pale brownish gray. Labial palpus slightly upcurved, dark brownish gray, intermixed with pale gray, obtuse apically; 2nd segment 1.5x longer than 3rd.

Thorax: Patagium, tegula, metanotum pale brownish gray; basal half of tegula dark brown; a broad dark brown band on mesocutellum. Foreleg dark brown with a pale brownish gray band on the middle of femur, at 1/3 and 3/2 of tibia and on the base of 1st tarsomere. Midleg dark brown; femur tinged with brownish white ventrally; tibia with three pale brownish gray bands, each basally, medially and terminally; tarsomeres pale brownish gray ventrally. Hindleg brownish gray dorsally, brownish white ventrally, with luster. Forewing length 5.4–7.0mm (average = 6.5; n = 10), pale yellowish gray in male, white in female, costa almost straight; apex on anterior 1/3 of outer margin; brownish gray mottles along subbasal line, costal area except terminal 1/5 and around the distal end of discal cell; costal strigulae darker in female; oblique reddish brown band surrounded black, adjoining outward with triangular gray marking and dark brown strigulae; a triangular marking with mixture of dark gray, reddish brown and black around tornus; apical area tinged with dark gray and reddish brown; fringe dark brown. Hindwing dark brown, brownish gray to base; fringe grayish brown.

Male eighth abdominal segment and genitalia (Figs 9A–E): Eighth tergite rectangular, 1.5x longer than width; anterior margin roundly emarginated to 1/3 of its length medially, lateral projection round apically; medial projection on posterior margin slender, slightly enlarged to base, bifid apically. Eighth sternite quadrate, 3x wider than eighth tergal sclerite; anterior margin inverted-M-shaped, medial emargination round, 1/2 as deep as its length, lateral projections round apically; posterior margin roundly emarginated medially, lateral costa slightly concave near base, extended to a bent rod posterolaterally. Uncus subtriangular, with sparsely long-hairs dorsally, shoulder with lobe folded inward; socii falcate, almost straight ventrally, with two spines on ventral top, terminal spine larger than subterminal spine. Tegumen trapezoidal, lower margin broadly round. Juxta

U-shaped, with a small, rectangular extension anteriorly. Valva elongate, round apically, 3.5x longer than socii, sparsely setose on terminal 1/3; costa slightly convex and sclerotized in basal 2/3, gradually broadened to base; sacculus broad, strongly sclerotized, curved medially, basal half expanded like fin inward, distal end with two lobes and a dentiform projection. Vinculum broadly round; saccus digitate, as long as socius. Phallus 2x longer than saccus, broader in basal half, slightly bent medially; coecum absent; a zone of spinulate cornuti 1/3 as long as phallus.

Female eighth abdominal segment and genitalia (Fig. 9F): Papillae anales subtrapezoidal, sclerotized; ninth tergite scletotized, as long as papillae anales, basal 2/3 semi-circular, strengthened along margin, distal 1/3 quadrate. Eighth abdominal segment strongly sclerotized; tergite as a pair of semicircular sclerites, membranous medially; pleural area emarginated; sternite with a pair of very shallow humps posteromedially. Ostium bursae connected with ductus bursae a cylindrical sclerite, 1/6 as long as ductus bursae. Ductus bursae as long as corpus bursae, enlarged in basal half. Corpus bursae long, elliptical, cervix slightly bulging; signum near to connection with ductus bursae, as a small, circular, scobinate plate.

Larva (Figs 5 & 10): Length 8.1–9.0 mm (n = 3). Head grayish orange, mottled with brown. Body reddish brown dorsally, pale purplish gray ventrally; irregularly waved, longitudinal streaks on subdorsal and lateral areas pale purplish gray; subdorsal band dark brown after SD pinaculum of T2, reaching at posterior end of AB9; microtrichiae densely covered on ventral and subventral areas; all pinacula dark brown; spiracle on T1 1.5x larger than spiracle of AB8, 2x larger than spiracles on AB1–AB7. Anal shield dark brown.

Head (Figs 10C & 10F): Hypognathous, epicranial suture 1/2 as long as frontoclypeus, epicranial notch 1/2 as long as epicranial suture, forming two large, rounded hemispheres; AF-group bisetose, with no puncture on adfrontal sclerite; AF1 1.5x longer than AF2; F1 on basal 2/5 of frons; P1 in horizontal line with AF2; P2 ventrolateral to P1, equidistant to A2 and A3; Pb above and lateral to P1; V-group trisetose; C2 lateral to C1, both lower than A1; A2 slightly lateral to A1; A3 above stemma 1 and in nearly horizontal line with A2; L1 dorsolateral to A3; stemma 1 close to stemma 2, both dorso lateral to stemma 3; stemma 3–6 situated in sharp arc, stemma 4 close to stemma 5, stemma 4–6 smaller than stemma 3; S2 ventrolateral to stemma 1; S1 close to stemma 2; SS1 close to antennal base; SS2 below stemma 6, equidistant to SS1 and SS3; MG1 above and slightly lateral to MGa. Hypopharygeal complex (Fig. 10D) with dark brown patches on maxillae near to labium. Mandibles (Figs 10G & 10H) with two setae, one 4x longer than the other.

Thorax (Figs 10A & 10B): T1 with Thoracic shield not clearly defined; D2 2.5x longer than D1; XD1 dorsolateral to XD2, 1.5x longer than XD2; SD1 on large pinaculum, 1.5x longer than SD2; SD2 dorsoposterior to SD1; L-group trisetose, anterior to spiracle; L1 about 2x longer than L2 and L3, ventroposterior to L2; L3 in horizontal line with L2; SV1 3x longer than SV2, both on separate, small pinacula; MV2 anterior to coxa; V1 on small pinaculum, ventroposterior to coxa. T2–3 with D2 very close to D1, both on separate small pinacula; D2 almost

3x longer than D1; SD1 close to SD2, both on the same pinaculum; SD1 almost 4x longer than SD2; L1 dorsoposterior to L2, both on the same pinaculum; L3 dorsoposterior to L1, L1 1.5x longer than L3, 2x longer than L2; SV1 on pinaculum; MV2 anterior to coxa; V1 on small pinaculum, ventroposterior to coxa. Thoracic legs with band-like sclerites along coxal margin (Fig. 10E); tarsal claw simple.

Abdomen (Figs 10A & 10B): AB1 with D2 4x longer than D1, both on separate pinacula; SD1 as long as D2, dorsoanterior to spiracle; SD2 absent; L1 2x longer than L2, below spiracle, both in horizontal line; L3 on pinaculum, 3.5x longer than and ventroposterior to L1; SV1 5x longer than and ventroposterior to SV2, both on same pinaculum; V1 equidistant to SV1 and SV2, as long as SV2. AB2–AB7 same as AB1 except the presence of SV3 on its own pinaculum, 1/5 as long as SV1; SV2 2/3 as long as SV1; V1 on AB3-6 anterior to prolegs, below SV2. Proleg crochets biordinal, transverse bands. AB8 with setae as AB1 except L1 3.5x longer than L2; SV-group unisetose, below L1; V1 ventroanterior to SV1. AB9 with D2 5x longer than D1, both close to each other; SD1 in near vertical line with D1, L-group, SV1, and V1, as long as D2; L1 3x longer than L2, closer to L2 than to L3; L3 as long as L1; SV1 as long as L2 and also V1. AB10 anal shield with D2 3x longer than D1; SD1 as long as D2 and also SD2, all three in diagonal line; L1 above SV4; anal leg with PP1, SV1–SV4, crochet biordinal, semi-circle, open posteriorly.

Pupa (Fig. 11): Length 3.9–4.3mm, maximum width 1.2-1.8mm (n = 3). Pupation in a loosely-meshed, fusiform cocoon (Fig. 7). Head dark brown, with pale, blotched pattern on vertex and frons; thorax yellowish brown; wing sheaths dark brown, darker in hind wings, extending to anterior margin of AB4; abdomen yellowish brown with three narrow, longitudinal bands, one on medial line of dorsum of AB1–AB5 and AB7–AB8, two laterally on dorsum of AB6–7; small, dark brown spots interior to sub-lateral setae dorsally on AB2–6. Antennal sclerites nearly extending to the tips of the forewings. Spiracles dorsally protuberant. Tenth abdominal segment with 16 terminally-curled setae, 6 on dorsal side, 4 in a row at the middle and 6 along posteromarginal area of ventral side; cremaster with four hook-tipped setae, two apically and one on each side.

Distribution. Chile (Bio-Bio, Curico, and San Antonio).

Host plants. *Mahonia* sp. (Berberidaceae)

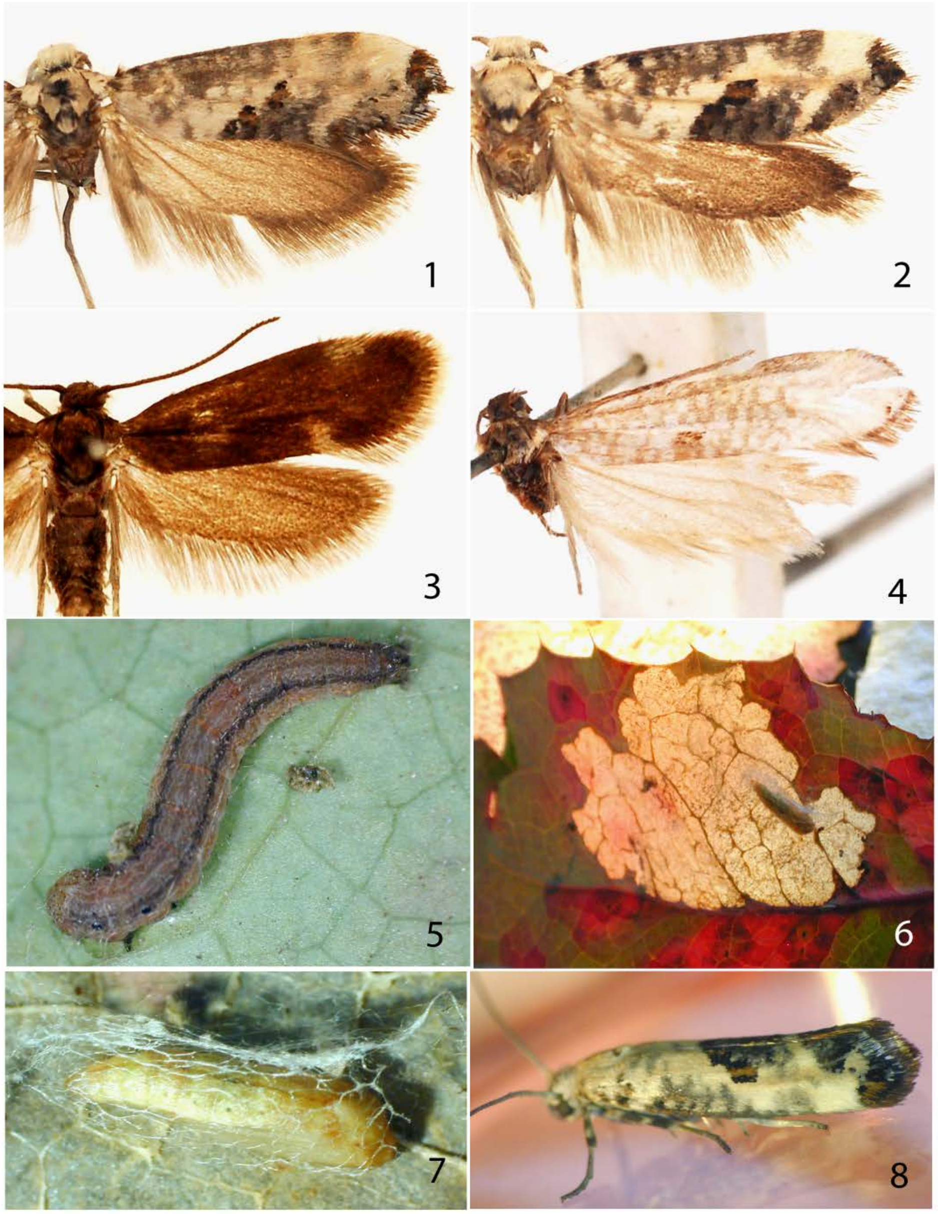
Discussion

Atemelia and *Orinympha* are associated with Praydidae due to the presence of an enlarged male sternite VIII, an autapomorphy for the family (Moriuti, 1977; Kyrki, 1984). Those two genera had been treated as the separate, monotypic groups, until Kyrki (1990) found them to be synonymous. Kyrki's proposal, however, appeared simply in a generic checklist with no detail and thus was not widely accepted. Our examination of all known praydid genera revealed that both *Atemelia* and *Orinympha* are indeed more closely related with each other than with *Prays*. Agassiz (1996) pointed out that *Atemelia torquatella* differs from *Prays* by the presence of pecten on the antennal scape. In *Orinympha*, the characteristic is consistent with *Atemelia*. Both genera are also common in possessing a medial process on the posterior margin of the male eighth tergite, whereas members of *Prays* lack it. A close relationship of *Atemelia* and *Orinympha* is further supported by a recently published molecular phylogeny of Yponomeutoidea (Sohn et al., 2013). All these findings justify the synonymy of *Atemelia* and *Orinympha*, although they differ remarkably in forewing patterns. Another Nearctic praydid, *Eucatagma*, is superficially similar to *Orinympha*. Their true relationship however remains uncertain, since the male genital features of *Eucatagma* are still unknown.

Atemelia mahonivora, the new species described here, is very similar to *Atemelia aetherias* (Meyrick), the type species of *Orinympha*, in external and genital features (see the diagnoses of the new species for the similarities). The larval characteristics of *A. mahonivora* reinforce the praydid association of *Atemelia*. Dugdale et al. (1998a) noted that praydid larvae possess the cranial seta MD1 as small as MD2; P1 situated in or above a line between Af2 and P2 setae. Both characteristics are observed on *A. mahonivora*, although the latter characteristic is not the case for *Atemelia torquatella*, if Grandi (1933) correctly illustrated the head setae. Comparing to *Prays* (represented by two species, *Prays iota* Moriuti and *P. lamda* Moriuti in this study), the larvae of *A. mahonivora* and *A. torquatella* share the lack of the SD2 seta on the abdominal segments; the SD1 seta on the anal shield as long as the SD2 (1/2 as long as in both *Prays* species); and the presence of the SV3 seta on AB2. Additional uniquely shared features of the two *Atemelia* species from *Prays* (represented by three species, *P. fraxinella*, *P. iota*, and *P. lamda* here) are found in their pupae, including the presence of the protruding cremaster with 4 setae (6 in *Prays*); and 4 terminally-curled setae on the ventral side of AB10 (6 in *Prays*). All these characteristics provide additional support to the synonymy of *Atemelia* and *Orinympha* (represented by *Atemelia mahonivora*).

Together with the similarities, several differences in larval and pupal morphologies can also be found between *A. mahonivora* and *A. torquatella*, including the larval setae longer in *A. torquatella* than in *A. mahonivora*; the lack of MD3 on the larval head of *A. mahonivora*; the larval seta D1 1/2 as long as D2 in *A. torquatella*, 1/4 as long as in *A. mahonivora*; on larval T2 and T3, the seta L3 as long as D2 in *A. torquatella*, 1/5 in *A. mahonivora*. It is known that the larvae of *Atemelia torquatella* feed in large, communal blotch mine beneath which a light web is spun and, then maturing, construct circular cocoons within the mine (Agassiz, 1996). Differing from this, the larvae of *A. mahonivora* consume the lower epidermal and parenchymous tissues of the host plant foliages, leaving window feeding traces, and pupate within fusiform cocoons attached on the undersides of the host leaves (Fig. 4).

The host plant families of *Prays* include Juglandaceae, Caprifoliaceae, Rutaceae, and Oleaceae, the latter two of which are most frequently used by the moths (Dugdale et al., 1998a). *Atemelia torquatella* is associated with Betulaceae and Ulmaceae (Agassiz, 1996). *Eucatagma amyrisella* was described from the larvae feeding on *Amyris floridana* belonging to Burseraceae. Berberidaceae is recorded for the first time as a host plant family for Praydidae, based on our observation for *Atemelia mahonivora*. The larvae fed on the leaves of *Mahonia* of which some species are popular garden shrubs. However, there has been no extensive damage by *A. mahonivora* on Mahonia trees reported from Chile so far.



Figures 1-8. *Atemelia* species. 1-4) Adults. 1) *A. mahonivora* n. sp., male holotype, 2) *A. mahonivora* n. sp., female paratype, 3) *A. torquatella*, male, 4) *A. aetherias*, male, 5-8) *A. mahonivora* n. sp. 5) larva, 6) feeding damage on a leaf of *Mahonia* sp. with a cocoon attached, 7) pupa within cocoon, 8) adult male on resting.

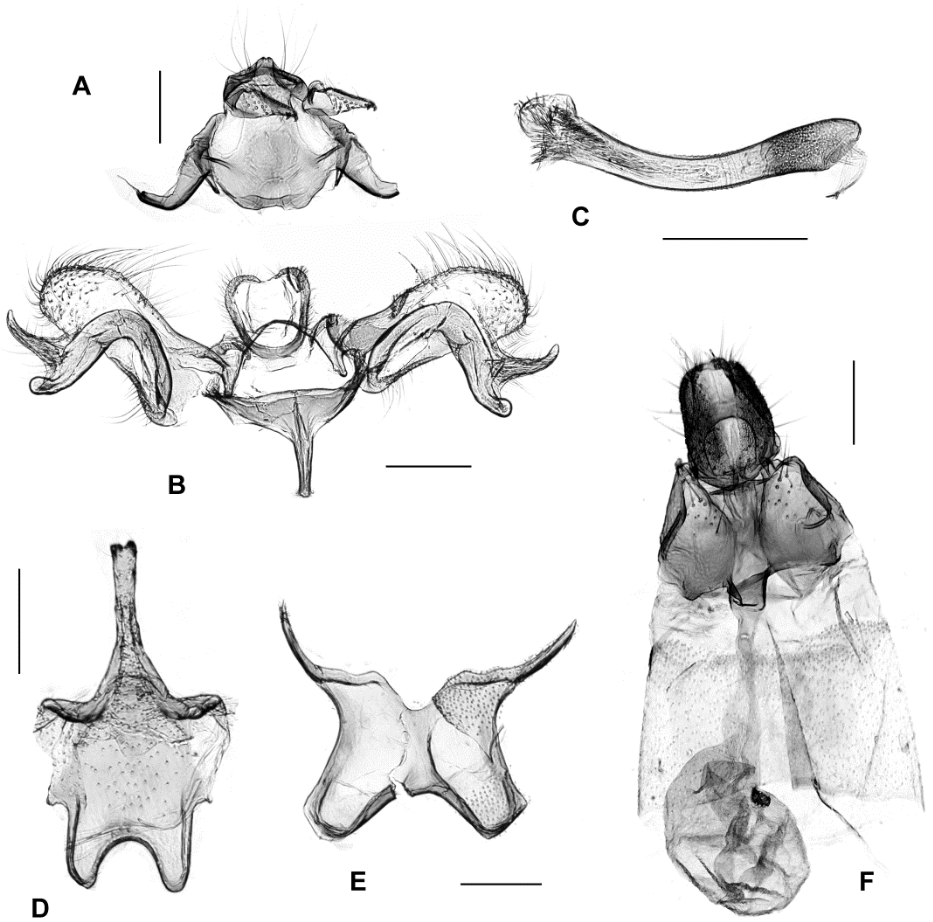


Figure 9. Male (A–E, holotype) and female (F, paratype) genitalia and eighth abdominal segment of *Atemelia mahonivora* n. sp. A) uncus and tegumen, B) juxta, vinculum, saccus, and valvae, C) phallus, D) eighth tergite, E) eighth sternite, F) female genitalia. Scale bars = 0.25mm.

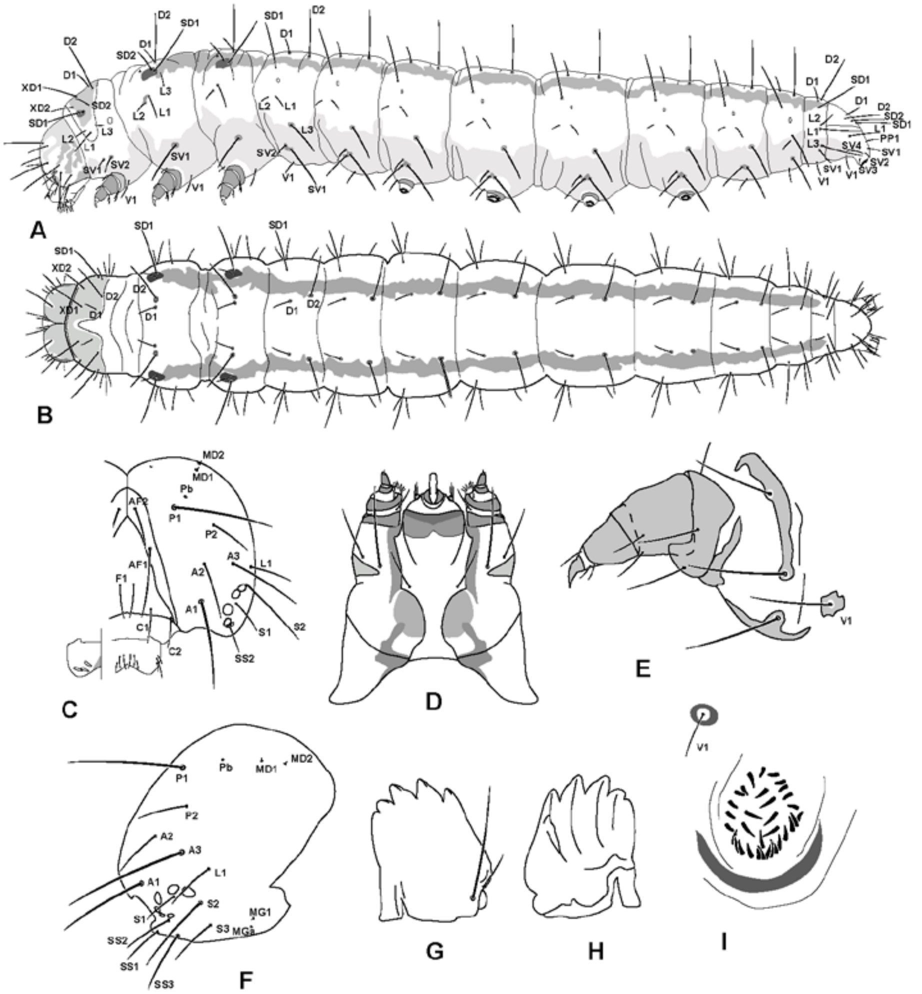


Figure 10. Larva of *Atemelia mahonivora* n. sp. A) entire larva, lateral view, B) entire larva, dorsal view, C) head, frontal view, inset = left half of epipharynx, D) hypopharyngeal complex and maxillae, E) right leg on T2, ventral view, F) head, ventrolateral view, G) left mandible, dorsal view, H) right mandible, ventral view, I) right proleg on AB3, ventral view.

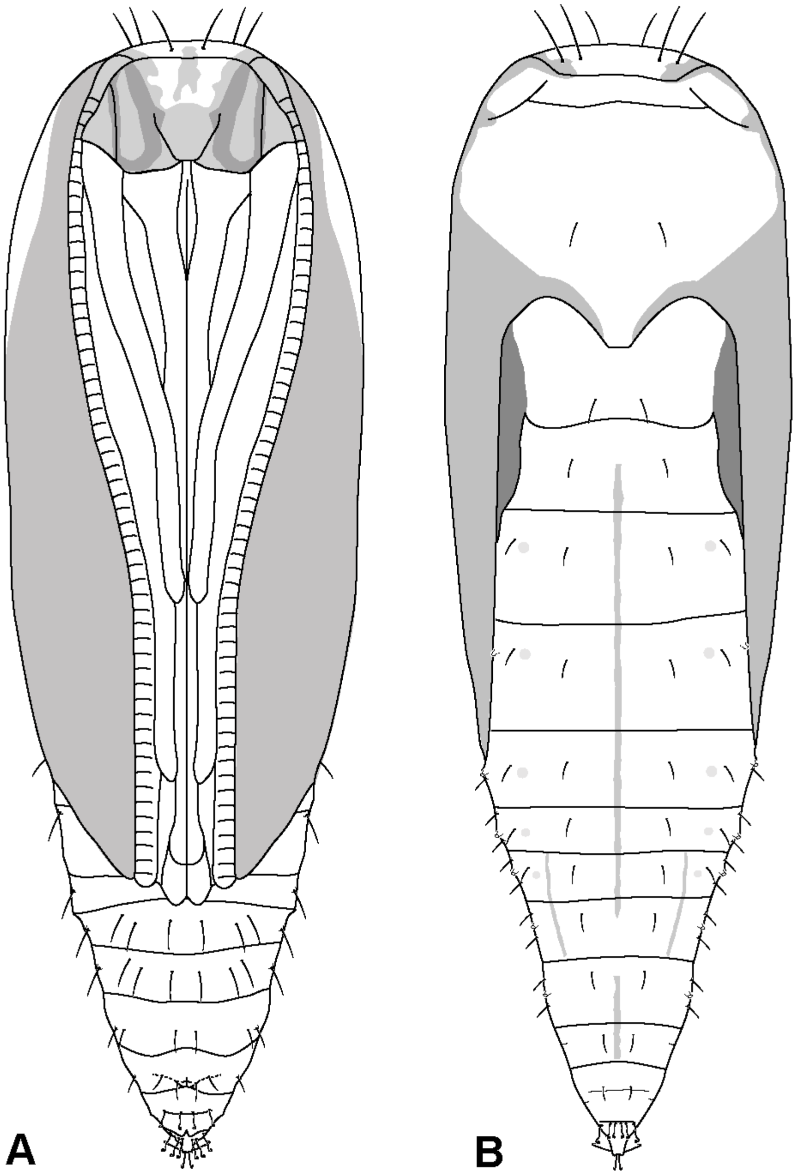


Figure 11. Pupa of *Atemelia mahonivora* n. sp. A) ventral view, B) dorsal view.

Appendix

Species concept adopted in Chapter 4

There are several ways to define species (reviewed in Coyne & Orr, 2004), of which the biological and the phylogenetic species concepts are currently two most popular ones. They differ principally in how to view species: biological species are groups of actually or potentially interbreeding natural populations that are reproductively isolated from populations of other species, whereas phylogenetic species are clusters of individuals that are diagnosably distinct from other such clusters in which there is a parental pattern of ancestry and descent (Futuyma, 2009). There are, however, practical limitations in applying these concepts directly to taxonomic studies for which testing reproductive isolation or evolutionary divergence is seldom feasible. Therefore, morphological and other phenotypic differences have been used as proxies for biological or phylogenetic species. My taxonomic studies follow the morphological proxy for the phylogenetic species concept by using apomorphies and autapomorphies in species delimitation (Wheeler and Meier, 2000). Such characteristics are corresponding to the clearly diagnosable morphological features within populations descendent from a common ancestor. These are shared by all individuals among conspecific populations and thus distinguished from intraspecific variation.

For insects, differences in genitalia are the most widely used evidence for diagnosing species (Klot, 1970). These characteristics have been suggested as good markers for reproductive isolation due to their role in mechanical fitting (the Lock-and-Key hypothesis: reviewed in Masly, 2011) or sexual selection (Arnqvist, 1997). Genital structures, once properly interpreted, can be a rich source of apomorphies (Friese, 1960). From these reasons, species distinction based on genital characteristics has long served as a standard for the taxonomy of Yponomeutoidea (e.g. Friese, 1960; Moriuti, 1977). Likewise, my taxonomic works have emphasized genital characters in species delineation.

Spurious morphological differences in genitalia can result from artifacts in specimen preparation, especially caused by the embedding or fixing process in permanent resin. This problem can be alleviated or avoided by examining the three-dimensional structures of dissected genitalia before their fixation in permanent mount. This helps to identify structures easily distorted during the preparation of slide mounts.

It has been assumed that genitalia are relatively stable within interbreeding populations due to their role in reproduction. This assumption is sometimes violated for some species which show intraspecific variations in genital characters. In such cases, Gilligan & Wenzel (2008) suggested a statistical approach to distinguish interspecific variations from intraspecific variations. Examination of multiple samples from different populations is necessary to use this approach. Whenever a large number of specimens was available, I dissected multiple individuals to discern the autaphomorphic features in genitalia from intraspecific variations. Several yponomeutoids are, however, so rare that their taxonomic identity has been inevitably defined using few individuals. In such cases, I delimitated species by the following proxies: i) the presence/absence of a particular feature in the genitalia rather than the metric differences; ii) the intraspecifically constant characteristics identified from the specimen-rich congeners; and iii) the differences in more than two independent genital features. It must be noticed that genitalia cannot be used as the sole factor in delineating species. Life history traits (Kaila, 2011) and genetic markers, notably DNA barcodes (Hebert et al., 2003), are useful sources for species delineation in addition to genital morphology. Such data, if available, have been considered in my taxonomic works for finding cryptic species undetected by morphology.

References

Arnqvist, G. (1997) The evolution of animal genitalia: distinguishing between hypotheses by single species studies. *Biological Journal of the Linnean Society* 60: 365–379.

Aberer, A. J. (2011) RogueNaRok. https://github.com/aberer/RogueNaRok/wiki. (Accessed: November, 2011).

Aberer, A. J., Stamatakis, A. (2011) A simple and accurate method for rogue taxon identification. *IEEE BIBM* 2011: 118–122.

Aberer, A. J., Krompaß, D., Stamatakis, A. (2011) RogueNaRok: An efficient and exact algorithm for rogue taxon identification. *Heidelberg Institute for Theoretical Studies*: Exelixis-RRDR-2011-10, November 2011 (http://sco.h-its.org/exelixis/publications.html).

Agassiz, D. J. L. (1996) Yponomeutidae. In: Emmet, A. M. (ed.) *The Moths and Butterflies of Great Britain and Ireland*. Vol. 3. Yponomeutidae-Elachistidae. Harley Books. pp. 39-114.

Alonso, C., Vuorisalo, T., Wilsey, B., Honkanen, T. (2000) *Yponomeuta evonymellus* outbreaks in southern Finland: spatial synchrony but different local magnitudes. *Annales Zoologici Fennici* 37: 178–188.

Andersen, N. M., Andersen, S. (1996) Kampemyrer og andre danekra fra Limfjordens askeserie–Studiet af en uddød insektfauna fra Danmarks Palaeogen. *Naturens Verden* 11/12: 417–432.

Ansorge, J. (2002) Revision of the “Trichoptera” described by Geinitz and Handlirsch from the Lower Toarcian of Dobbertin (Germany) based on new material. *Proceedings of the 10th International Symposium on Trichoptera, Nova Supplementa Entomologica* 15: 55–74.

APG III (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161: 105–121.

Azar, D., Gèze, R., El-Samrani, A., Maalouly, J., Nel, A. (2010) Jurassic amber in Lebanon. *Acta Geologica Sinica* 84: 977–983.

Bachofen-Echt, A. (1949) *Der Bernstein und Seine Einschlüsse*. Springer-Verlag, Vienna.

Balmford, A. M., Jayasuriya, A. M. H., Green, M. J. B. (1996) Using higher-taxon richness as a surrogate for species richness: II. Local applications. *Proceedings of the Royal Society (B)* 263: 1571–1575.

Bazinet, A. L., Cummings, M. P. (2009) The Lattice Project: a Grid research and production environment combining multiple Grid computing models. Distributed & Grid Computing. In: Weber, M. H. W. (ed.) *Science Made Transparent for Everyone*. Principles, Applications and Supporting Communities. Tectum Publishing House, Marburg. pp. 2–13.

Bazinet, A. L., Cummings, M. P. (2011) Computing the Tree of Life - Leveraging the power of desktop and service grids. In: *2011 IEEE International Symposium on Parallel and Distributed Processing Workshops and PhD Forum*. pp. 1896–1902.

Berendt, G. C. (1830) *Die Insekten im Bernstein ein Beitrag zur Thiergeschichte der Vorwelt*. Nicolai, Danzig, 38 pp.

Bigot, L., Nel, A., Nel, J. (1986) Description de la première espèce fossile connue de Ptérophore (Lepidoptera, Pterophoridae). *Alexanor* 14: 283–288.

Blair, K. G. (1927) Insect remains from oil sand in Trinidad. *Transactions of the Entomological Society of London* 75: 137–141.

Börner, C. (1939) Die Grundlagen meines Lepidopterensystems. *Verhandlungen der VII Internationaler Kongress für Entomologie, Berlin* 2: 1372–1424.

Bonde, N., Andersen, S., Hald, N., Jakobsen, S. L. (2008) *Danekra – Danmarks bedste fossiler*. Gyldendal, Copenhagen.

Braby, M. F., Vila, R., Pierce, N. E. (2006) Molecular phylogeny and systematics of the Pieridae (Lepidoptera: Papilionoidea): higher classification and biogeography. *Zoological Journal of the Linnean Society* 147: 239–275.

Brock, J. P. (1971) A contribution towards an understanding of morphology and phylogeny of the ditrysian Lepidoptera. *Journal of Natural History* 5: 29–102.

Brocklehurst, N., Upchurch, P., Mannion, P. D., O’Connor, J. (2012) The completeness of the fossil record of Mesozoic birds: Implications for early avian evolution. *PLoS One* 7: e39056. doi:10.1371/journal.pone.0039056

Brown, W. M. (1985) The mitochondrial genome of animals. In: MacIntyre, R. J. (ed.), Molecular evolutionary genetics. Plenum Publishing Co., New York. pp. 95–130.

Bruand, C. T. (1851) Catalogue systématique et synonymique des Lépidoptères du Department du Doubs. Tineides. *Mémoirs de la Société d'emulation du Doubs* 3(3): 23–68.

Burgeff, H. (1951) Die meeralpengrenze der Zygaenen (Lep.), eine mit Hilfe der Populationsanalyse der Arten der Gattung *Zygaena* (Lepidoptera) durchelführte Untersuchungen über die lokalisation und die Beudeutung geographischer Rassen in ihrem Zussammenhang mit der Eiszeit. *Biologisches Zentralblatt* 70: 1–23.

Busck, A. (1904) Tineid moths from British Columbia. *Proceedings of the U.S. National Museum* 27: 745–778.

Carpenter, F. M. (1930) A review of our present knowledge of the geological history of the insects. *Psyche* 37: 15–34.

Carpenter, F. M. (1992) *Treatise on Invertebrate Paleontology,* Part R (Arthropoda–4), 3 and 4 (Superclass Hexapoda). Geological Society of America and the University of Kansas, Boulder, Colorado and Lawrence, Kansas.

Carpenter, F. M., Burnham, L. (1985) The geological record of insects. *Annual Review of Earth and Planetary Sciences* 13: 297–314.

Chambers, V. T. (1882) Burrowing larvae. *Nature* 25: 529.

Cho, S., Zwick, A., Regier, J., Mitter, C., Cummings, M., Yao, J., Du, Z., Hong, Z., Kawahara, A., Weller, S., Davis, D., Baixeras, J., Brown, J., Parr, C. (2011) Deliberately unequal gene sampling: boon or bane for phylogenetics of Lepidoptera (Hexapoda)? *Systematic Biology* 60: 782–796.

Clarke, J. F. C. (1941) The preparation of slides of the genitalia of Lepidoptera. *Bulletin of the Brooklyn Entomological Society* 36: 149–161.

Cockerell, T. D. A. (1914) Fossil Saturniidae. *Memoir of the National Academy of Science* 12: 171.

Cockerell, T. D. A. (1916) Some American fossil insects. *Proceedings of the United States National Museum* 51: 89–106.

Cockerell, T. D. A. (1919) Two interesting insects in Burmese amber. *The Entomologist* 52: 193–195.

Cockerell, T. D. A. (1922) A fossil moth from Florissant, Colorado. *American Museum Novitates* 34: 1–2.

Cockerell, T. D. A. (1926) A new fossil moth from Florissant. *Psyche* 33: 16–17.

Common, I. F. B. (1970) Lepidoptera. In: Mackerras, I. M. (ed.) *The Insects of Australia*. CISRO, Canberra. pp. 765–866.

Corrette, K. B., Neunzig, H. H. (1979) Descriptions of and notes on larval habits of four immature phycitines in the Southeastern United States (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America* 72: 690–699.

Coyne, J. A., Orr, H. A. (2004) *Speciation*. Sinauer Associates, Inc., Sunderland. 545 pp.

Cummings, M. P., Huskamp, J. C. (2005) Grid computing. *EDUCAUSE review* 40: 116–117.

Davis, D. R., Robinson, G. S. (1998) The Tineoidea and Gracillarioidea. In: Kristensen, N. P. (ed.) Lepidoptera, Moths and Butterflies. Vol. 1: Evolution, Systematics, and Biogeography. *Handbook of Zoology* 4: 91–117.

de Jong, R. (2007) Estimating time and space in the evolution of the Lepidoptera. *Tijdschrift voor Entomologie* 150: 319–346.

de Serres, M. (1829) *Géognosie des Terrains Tertiaires ou Tableau des Principaux Animaux Invertébrés des Terrains Marins Tertiaires, du Midi de la France*. Romathio-Durville, Montpellier & Paris.

Donoghue, P. C. J., Benton, M. J. (2007) Rocks and clocks: calibrating the Tree of Life using fossils and molecules. *Trends in Ecology and Evolution* 22: 424–431.

Douglas, S. D., Stockey, R. A. (1996) Insect fossils in middle Eocene deposits from British Columbia and Washington State: faunal diversity and geological range extensions. *Canadian Journal of Zoology* 74: 1140–1157.

Dugdale, J. S., Kristensen, N. P., Robinson, G. S., Scoble, M. J. (1998a) The Yponomeutidae. In: Kristensen, N. P. (ed.) Lepidoptera, Moths and Butterflies. Vol. 1: Evolution, Systematics, and Biogeography. *Handbook of Zoology* 4: 119–130.

Dugdale, J. S., Kristensen, N. P., Robinson, G. S., Scoble, M. J. (1998b) The smaller Microlepidoptera-grade superfamilies. In: Kristensen, N. P.

(ed.) Lepidoptera, Moths and Butterflies. Vol. 1: Evolution, Systematics, and Biogeography. *Handbook of Zoology* 4: 217–232.

Duncan, I. J. (1997) *The Taphonomy of Insects*. Ph. D. thesis, Department of Geology, University of Bristol. Bristol, United Kingdom, xvi+328 pp.

Durden, C. J., Rose, H. (1978) Butterflies from the middle Eocene: the earliest occurrence of fossil Papilionoidea (Lepidoptera). *Pearce-Sellards Series, Texas Memorial Museum* 29: 1–25.

Edwards, E. D. (1996) Yponomeutidae, Argyresthiidae, Plutellidae, and Glyphipterigidae. In: Nielsen, E. S., Edwards, E. D., Rangsi, T. V. (eds) Checklist of the Lepidoptera of Australia. *Monographs on Australian Lepidoptera* 4: 50–55.

Elias, S. A. (1992) *Quaternary Insects and their Environments*. Smithsonian Institution Press, Washington and London.

Engel, M. S., Kinzelbach, R. K. (2008) A primitive moth from the earliest Eocene Fur Formation (“Mo-clay”) of Denmark (Lepidoptera: Micropterygidae). *Linzer biologische Beiträge* 40: 1443–1448.

Evans, W. P. (1931) Traces of a lepidopterous insect from Middle Waikato Coal-Measures. *Transactions and Proceedings of the New Zealand Institute* 62: 99–101.

Evenhuis, N. L. (2004) *Catalogue of the Fossil Flies of the World (Insecta: Diptera)*. URL http://hbs.bishopmuseum.org/fossilcat [accessed on 25 May 2012].

Fernández-Rubio, F., Nel, A. (2000) *Neurosymploca*? *oligocenica*, a new fossil species of Lepidoptera Zygaenoidea of the Oligocene of Céreste (Lubéron, France). *Boletín Sociedad Entomológica Aragones*a 27: 7–16.

Fernández-Rubio, F., Peñalver, E. (1994) Un nuevo ejemplar fósil de *Zygaena*? *turolensis* Fernández-Rubio, Peñalver & Martínez-Delclòs, 1991 (Lepidoptera: Zygaenidae). *Estudios del Museo de Ciencias Naturales de Alava* 9: 39–48.

Fernández-Rubio, F., Peñalver, E., Martínez-Delclòs, X. (1991) *Zygaena*? *turolensis* una nueva especie de Lepidoptera Zygaenidae del Mioceno de Rubielos de Mora (Teruel). Descripción y filogenia. *Estudios del Museo de Ciencias Naturales de Álava* 6: 77–93.

Fletcher, T. B. (1929) A list of generic names used for the Microlepidoptera. *Memoirs of the Department of Agriculture of India (Entomology)* 11: 1–244.

Fossil Insect Research Group for Nojiri-ko Excavation (1990) Fossil insects obtained from the Nojiri-ko Formation during the 10th Nojiri-ko and the 5th Hill Site excavation. *Monograph of the Association for Geologic Collaboration in Japan* 37: 93–110.

Fracker, S. B. (1915) The Classification of lepidopterous larvae. *Illinois Biological Monographs* 2(1): 1–161.

Friese, G. (1960) Revision der paläarktischen Yponomeutidae unter besonderer Berücksichtigung der Genitalien (Lepidoptera). *Beiträge zur Entomologie* 10: 1–131.

Friis, E. M., Crane, P. R., Pederson, N. M. (2011) *Early Flowers and Angiosperm Evolution*. Cambridge University Press, Cambridge U.K.

Fritsch, A. (1882) Fossile Arthropoden aus der Steinkohlen- und Kreideformation Böhmens. *Beiträge zur Paläontologie Österreich-Ungarns* 2: 1–7, pls. 1–2.

Fu, D.-Z., Yang, Y., Zhu, G.-H. (2004) A new scheme of classification of living Gymnosperms at family level. *Kew Bulletin* 59: 111–116.

Futuyma, D. J. (2009) *Evolution*, 2nd edition. Sinauer Associates, Inc., Sunderland. 633 pp.

Gaedike, R. (1997) *Lepidopterorum Catalogus (New Series)*. Fas. 55 Acrolepiidae. Scientific Publishers, Gainsville. 20 pp.

Gall, L. F., Tiffney, B. H. (1983) A fossil noctuid moth egg from the Late Cretaceous of eastern North America. *Science* 219: 507–509.

Gaston, K. J. (1991) The magnitude of global insect species richness. *Conservation Biology* 5: 283–296.

Gerasimov, A. M. (1952) Caterpillars, Part 1. *Fauna SSSR*, Vol. 56, Insects, Lepidoptera (n.s.) 1(2): 1–338 [in Russian].

Gershenson, Z. S., Ulenberg, S. A. (1998) The Yponomeutinae (Lepidoptera) of the World exclusive of the Americas. *Koninklijke Nederlandse Akademie van Weternschappen Verhandelingen Afdeling Naturrkunde* 99: 1–202.

Gilligan, T. M., Wenzel, J. W. (2008) Extreme intraspecific variation in *Hystrichophora* (Lepidoptera: Tortricidae) genitalia – questioning the lock-and-key hypothesis. *Annales Zoologici Fennici* 45: 465–477.

Givulescu, R. (1984) Pathological elements on fossil leaves from Chiuzbaia (galls, mines and other insect traces). *Dãri de Seamã ale Şedinţelor, Institute of Geology and Geophysics* 18: 123–133.

Gradstein, F. M., Ogg, J. G., Smith, A. G. (2004) *A Geologic Time Scale 2004*. Cambridge University Press, Cambridge.

Grandi, G. (1933) Morfologia ed etologia comparata di Insectti a regime specializzato. IV. La morfologia comparata di vari stati larvali di 30 Microlepidotteri minatori appartenenti a 15 generi ed a 11 famiglie. *Bollettino del Laboratorio di Entomologia del R. Istituto Superiore Agrario di Bologna* 5: 143-307.

Gravenhorst, H. (1835) Bericht der entomologischen Sektion. *Schlesische Gesellschaft für Vaterländische Kultur Jahresberichte* 1834: 88–95.

Griffiths, C. S. (1999) The effect of structure and function of a protein on evolution in protein-coding genes: Problems in retrieving phylogenetic signal. In: Adams, N. J., Slotow, R. H. (eds) *Proceedings of the 22nd International Ornithological Congress, Durban*. BirdLife South Africa, Johannesburg. pp. 754–761.

Grimaldi, D. (1999) The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Annals of the Missouri Botanical Garden* 86: 373–406.

Grimaldi, D., Engel, M. S. (2005) Evolution of the Insects. Cambridge University Press, Cambridge. 755 pp.

Grimaldi, D. A., Nascimbene, P. C. (2010) Raritan (New Jersey) amber. In: Penny, D. (ed.) *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester. pp. 167–191.

Hall, J. P. W., Robbins, R. K., Harvey, D. J. (2004) Extinction and biogeography in the Caribbean: new evidence from a fossil riodinid butterfly in Dominican amber. *Proceedings of the Royal Society of London (B)* 271: 797–801.

Hammond, P. M. (1992) Species inventory. In: Groombridge, B. (ed.) *Global Biodiversity Status of the Earth's Living Resources*. Chapman & Hall, London. pp. 17–39.

Handlirsch, A. (1925) Systematische Übersicht. In: Schröder, C. (ed.) *Handbuch der Entomologie*, Vol. 3. Gustav Fischer, Jena. pp. 377–1143.

Harris, A. C., Raine, J. I. (2002) A sclerite from a late Cretaceous moth (Insecta: Lepidoptera) from Raikaia Gorge, Canterbury, New Zealand. *Journal of the Royal Society of New Zealand* 32: 457–462.

Hebert, P. D. N., Cywinska, A., Ball, S. l., deWaard, J. R. (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society B, Biological Sciences* 270 (1512): 313–321.

Heer, O. (1849) *Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien.* Volume 2. Wilhelm Engelmann, Leipzig.

Heer, O. (1856) Ueber die fossilen Insekten von Aix in der Provence. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich* 1: 1–40.

Heer, O. (1861) *Recherches sur le Climat et la Végétation du Pays Tertiaire*. Winterthur, Geneva & Paris, 220 pp.

Heppner, J. B. (1977) The status of the Glyphipterigidae and a reassessment of relationships in Yponomeutoid families and Ditrysian superfamiles. *Journal of the Lepidopterists' Society* 31: 124–134.

Heppner, J. B. (1984) *Atlas of Neotropical Lepidoptera Checklist*. Part I Micropterigoidea–Immoidea. Dr. W. Junk Publishers, Gainesville. 112 pp.

Heppner, J. B. (1995) Lacturidae, new family (Lepidoptera: Zygaenoidea). *Tropical Lepidoptera* 6(2): 146–148.

Heppner, J. B. (1998) Classification of Lepidoptera, Part 1. Introduction. *Holarctic Lepidoptera* 5 (Suppl. 1): 1–148.

Heppner, J. B. (2005) Primitive sedge moths from New Zealand and Tasmania: Transfer of *Proditrix* and relatives to Orthotelinae (Lepidoptera: Glyphipterigidae). *Lepidoptera News* 2003 (1-2): 31–42.

Heppner, J. B. (2011) Lepidoptera of Florida Checklist. *Lepidoptera Novae* 4(2-4): 61–193.

Heppner, J. B., Duckworth, W. D. (1983) Yponomeutoidea. In: Hodges, R. W. (ed.) *Check List of the Lepidoptera of America North of Mexico*. E. W. Classey Ltd., Washington, DC: & The Wedge Entomological Research Foundation, London. pp. 26–28.

Herrich-Schäffer, G. A. W. (1853) *Systematische Bearbeitung der Schmetterlinge von Europa, Zugleich als Text, Revision und Supplement zu Jacob Hubners Sammlung europaischer Schmetterlinge*, Vol. 5. G.J. Manz, Regensburg. 394 pp.

Heyden, C. (1862) Gliederthiere aus der Braunkohle des Niederrhein's, der Wetterau und der Röhn. *Palaeontographica* 10: 62–82.

Hickey, L. J., Hodges, R. W. (1975) Lepidopteran leaf mine from the early Eocene Wind River Formation of northeastern Wyoming. *Science* 189: 718–720.

Ho, S. Y. W., Phillips, M. J. (2009) Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. *Systematic Biology* 58: 367–380.

Hoebeke, E. R. (1987) *Yponomeuta cagnagella* (Lepidoptera: Yponomeutidae): A Palearctic ermine moth in the United States, with notes on its recognition, seasonal history, and habitats. *Annals of the Entomological Society of America* 80: 462–467.

Holder, M. T., Zwickl, D. J., Dessimoz, C. (2008) Evaluating the robustness of phylogenetic methods to among-site variability in substitution processes. *Philosophical Transactions of the Royal Society B* 363: 4013–4021.

Hsu, Y.-F., Powell, J. A. (2005) Phylogenetic relationships within Heliodinidae and systematics of moths formerly assigned to *Heliodines* Stainton

(Lepidoptera: Yponomeutoidea). *University of California Publications, Entomology* 124: 1–158.

Huang, D., Nel, A., Minet, J. (2010) A new family of moths from the Middle Jurassic (Insecta: Lepidoptera). *Acta Geologica Sinica* 84: 874–885.

Hurd, P. D. J., Smith, R. F., Durham, J. W. (1962) The fossiliferous amber of Chiapas, Mexico. *Ciencia* 21: 108–118.

Imada, Y., Kawakita, A., Kato, M. (2011) Allopatric distribution and diversification without niche shift in a bryophyte-feeding basal moth lineage (Lepidoptera: Micropterigidae). *Proceedings of the Royal Society B* 278: 3026–3033.

Jablonski, D., Roy, K., Valentine, J. W., Price, R. M., Anderson, P. S. (2003) The impact of the pull of the recent on the history of marine diversity. *Science* 300: 1133–1135.

Janz, N. (2011) Ehrlich and Raven revisited: mechanisms underlying codiversification of plants and enemies. *Annual Review of Ecology, Evolution, and Systematics* 42: 71–89.

Janz, N., Nylin, S. (1998) Butterflies and plants: a phylogenetic study. *Evolution* 52: 486–502.

Jarzembowski, E. A. (1976) Report of Easter Field Meeting: the Lower Tertiaries of the Isle of Wight, 27–31.III.1975. *Tertiary Research* 1: 11–16.

Jarzembowski, E. A. (1980) Fossil insects from the Bembridge Marls, Palaeogene of the Isle of Wight, southern England. *Bulletin of the British Museum of Natural History (Geology)* 33: 237–293.

Jarzembowski, E. A. (1989) A century plus of fossil insects. *Proceedings of the Geologists' Association* 100: 433–449.

Jarzembowski, E. A. (1995) Checklist of Tertiary insects from Dorset. *Proceedings of the Dorset Natural History and Archaeological Society* 116: 145–146.

Joseph, N. C. (1986) Eocene flora and fauna unearthed at Republic. *Washington Geologic Newsletter* 14: 3–5.

Kaila, L. (2011) Elachistine Moths of Australia (Lepidoptera: Gelechioidea: Elachistidae). *Monographs on Australian Lepidoptera*, Vol. 11. CSIRO Publishing, Collingwood. 443 pp.

Kapoor, V. C. (1981) *Origin and Evolution of Insects*. Kalyani Publishers, New Delhi & Ludhiana.

Karsholt, O., Razowski, J. (1996) *The Lepidoptera of Europa, A Distributional Checklist*. Apollo Books, Stenstrup. 380 pp. & CD-ROM.

Kawahara, A. Y., Ohshima, I., Kawakita, A., Regier, J. C., Mitter, C., Cummings, M. P., Davis, D. R., Wagner, D. L., De Prins, J., Lopez-Vaamonde, C. (2011) Increased gene sampling strengthens support for higher-level groups within leaf-mining moths and relatives (Lepidoptera: Gracillariidae). *BMC Evolutionary Biology* 11: 182.

Kernbach, K. (1967) Über die bischer im Pliozän von Willershausen gefundenen Schmetterlings- und Raupenreste. *Bericht der Naturhistorischen Gesellschaft zu Hannover* 111: 103–108.

Klebs, R. (1890) Ueber die Fauna des Bernsteins. *Versammlung Deutscher Naturforscher und Ärzte in Heidelberg* 18: 268–271.

Kloet, G. S., Hincks, W. D. (1945) *A check list of British insects*. Kloet and Hincks, Stockport. 483 pp.

Klots, A. B. (1970) Lepidoptera. In: Tuxen, S. L. (ed.) *Taxonomist's Glossary of Genitalia in Insects*. Munksgaard, Copenhagen. pp. 115–130.

Knowlton, F. H. (1917) A fossil flora from the Frontier Formation of southwestern Wyoming. *United States Geological Survey Professional Paper* 108: 73–95, pls. 1–39.

Koponen, M., Nuorteva, M. (1973) Über subfossile Waldinsekten aus dem Moor Piionsuo in Südfinnland. *Acta Entomologica Fennica* 29: 1–84.

Kozhanchikov, I. V. (1957) Novy predstavitel' sem Cossidae iz Miotsenovikh otlozheny Kavkaza (Lepidoptera, Insecta). *Doklady Akademiya Nauk SSSR* 113: 675–677.

Kozlov, M. V. (1987) Noviye Molevidniye Cheshuyekriliye iz Baltiiskogo Yantara. *Paleontologicheskiy Zhurnal* 1987(4): 59–67.

Kozlov, M. V. (1988) Paleontology of the Lepidoptera and problems of phylogeny of the order Papilionoidea. In: Ponomarenko, A.G. (ed.) *The Cretaceous Biocoenotic Crisis and the Evolution of Insects*. Nauka Press, Moscow. pp. 16–69 [in Russian].

Kozlov, M. V. (1989) New Lepidoptera (Papilionoidea) from the Upper Jurassic and Lower Cretaceous. *Paleontologicheskiy Zhurnal* 4: 37–42 [in Russian].

Kozlov, M. V., Ivanov, V. D., Rasnitsyn, A. P. (2002) Order Lepidoptera Linné, 1758. The butterflies and moths (= Papilionida Laicharting, 1781). In: Rasnitsyn, A. P., Quicke, D. L. J. (eds) *History of Insects*. Kluwer Academic Publishers, Dordrecht, Boston & London. pp. 220–227.

Krassilov, V. A. (2007) Mines and galls on fossil leaves from the Late Cretaceous of southern Negev, Israel. *African Invertebrates* 48: 13–22.

Krassilov, V., Shuklina, S. (2008) Arthropod trace diversity on fossil leaves from the mid-Cretaceous of Negev, Israel. *Alavesia* 2: 239–245.

Kristensen, N. P. (1997) Early evolution of the Lepidoptera+Trichoptera lineage: phylogeny and the ecological scenario. *Mémoires du Muséum National d'Histoire Naturelle* 173: 253–271.

Kristensen, N. P., Skalski, A. W. (1998) Phylogeny and palaeontology. In: Kristensen, N.P. (ed) *Handbook of Zoology*, Vol. IV Arthropoda: Insecta, Part 35, Lepidoptera, Moths and Butterflies, Vol. 1: Evolution, Systematics, and Biogeography. Walter de Gruyter, Berlin & New York. pp. 7–25.

Kristensen, N. P., Scoble, M., Karsholt, O. (2007) Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. *Zootaxa* 1668: 699–747.

Kritsky, G., Cherry, R. (2000) *Insect Mythology*. Writers Club Press, Lincoln, Nebraska.

Kühne, W. G., Kubig, L., Schlüter, T. (1973) Eine Micropterygide (Lepidoptera, Homoneura) aus mittelcretazischem Harz Westfrankreichs. *Mitteilungen der Deutschen Entomologischen Gesellschaft* 32: 61–64.

Kunz, P. (2010) 30 ans déjà. *ASAM Bulletin* 2010: 39–45.

Kupryjanowicz, J. (2001) The Amber Treasure Trove, Part I. Arthropods in Baltic amber and their photographic record. *Museum of the Earth Documentary Studies* 18: 19–59.

Kuroko, H. (1964) Revisional studies on the family Lyonetiidae of Japan (Lepidoptera). *Esakia* 4: 1–61, 17 pls.

Kurz, M. A., Kurz, M. E. (2010) *Micropteryx gertraudae* Kurz M. A. & M. E. Kurz, 2010. Taxonomy Online. Available from http://www.nkis.info/nkis/extaustaxonshow.cgi?uid=guest&tax=161783&lang=e/ (accessed 13 August 2011).

Kuznetzov, V. I., Stekolnikov, A. A. (1977) Phylogenetic relationships between the superfamilies Psychoidea, Tineoidea and Yponomeutoidea in the light of the functional morphology of the male genitalia. Part 2. Phylogenetic relationships of the families and subfamilies. *Entomologicheskoe Obozrenie* 56: 19–30.

Kuznetzov, V. I., Kozlov, M. V., Seksjaeva, S. V. (1988) To the systematics and phylogeny of mining moths Gracillariidae, Bucculatricidae and Lyonetiidae (Lepidoptera) with consideration of functional and comparative morphology of male genitalia. *Proceedings of the Zoological Institute, Leningrad* 176: 52–71.

Kusnezov, N. (1928) *Oligamatites martynovi*, gen. et sp. n., a fossil amatid lepidopteron from the Oligocene beds of Central Asia. *Doklady Akademiya Nauk SSSR* 20: 431–436.

Kusnezov, N. (1941) *A Revision of Amber Lepidoptera*. Paleontological Institute, Academy of Sciences, Moscow & Leningrad.

Kyrki, J. (1984) The Yponomeutoidea: a reassessment of the superfamily and its suprageneric groups (Lepidoptera). *Entomologica scandinavica* 15: 71–84.

Kyrki, J. (1988) The systematic position of *Wockia* Heinemann, 1870, and related genera (Lepidoptera: Ditrysia: Yponomeutidae auct.). *Nota Lepidopterologica* 11(1): 45–69.

Kyrki, J. (1990) Tentative reclassification of holarctic Yponomeutoidea (Lepidoptera). *Nota Lepidopterologica* 13(1): 28–42.

Kyrki, J., Itämies, J. (1986). Immature stages and the systematic position of *Orthotelia sparganella* (Thunberg) (Lepidoptera: Yponomeutoidea). *Systematic Entomology* 11: 93–105.

Labandeira, C. C. (1994) A compendium of fossil insect families. *Milwaukee Public Museum Contributions in Biology and Geology* 88: 1–71.

Labandeira, C. C. (1998) Plant-insect associations from the fossil record. *Geotimes* 43: 18–24.

Labandeira, C. C. (1999) Insects and other hexapods. In: Singer, R. (ed.) *Encyclopedia of Paleontology*. Fitzroy-Dearborn Publishers, Chicago. pp. 603–624.

Labandeira, C. C. (2002a) Paleobiology of middle Eocene plant-insect associations from the Pacific Northwest: A preliminary report. *Rocky Mountain Geology* 37: 31–59.

Labandeira, C. C. (2002b) The history of associations between plants and animals. In: Herrera, C. M., Pellmyr, O. (eds) *Plant–Animal Interactions: An Evolutionary Approach*. Blackwell Science, London. pp. 28–74, 248–261.

Labandeira, C. C. (2005) The fossil record of insect extinction: new approaches and future directions. *American Entomologist* 51: 14–29.

Labandeira, C. C., Dilcher, D. L., Davis, D. R., Wagner, D. L. (1994) Ninety-seven million years of angiosperm-insect association: Paleobiological insights into the meaning of coevolution. *Proceedings of the National Academy of Sciences, USA* 91: 12278–12282.

Labandeira, C. C., Johnson, K. R., Lang, P. J. (2002a) Preliminary assessment of insect herbivory across the Cretaceous–Tertiary boundary: Major extinction and minimum rebound. *Geological Society of America Special Paper* 361: 297–327.

Labandeira, C. C., Johnson, K. R., Wilf, P. (2002b) Impact of the terminal Cretaceous event on plant-insect associations. *Proceedings of the National Academy of Sciences, USA* 99: 2061–2066.

Labandeira, C. C., Sepkoski, Jr., T.J. (1993) Insect diversity in the fossil record, *Science* 261: 310–315.

Labandeira, C. C., Wilf, P., Johnson, K. R., Marsh, F. (2007) *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils*. Version 3.0—Spring 2007. Smithsonian Institution, Washington, DC. http://paleobiology.si.edu/insects/index.html

Lacki, M. J., Johnson, J. S., Dodd, L. E., Baker, M. D. (2007) Prey consumption of insectivorous bats in coniferous forests of North-Central Idaho. *Northwest Science* 81: 199–205.

Lancucka-Srodoniowa, M. (1964) Tertiary coprolites imitating fruits of the Araliaceae. *Acta Societatis Botanicorum Poloniae* 33: 469–473.

Larsson, S. G. (1975) Paleobiology and mode of burial of the insects of the Lower Eocene Mo-clay of Denmark. *Bulletin of the Geological Society of Denmark* 24: 193–209.

Leakey, L. S. B. (1952) Lower Miocene invertebrates from Kenya. *Nature* 169: 624–625.

Leather, S. R. (1986) Insects on bird cherry I. The bird cherry ermine moth, *Yponomeuta evonymellus* (L.) (Lepidoptera: Yponomeutidae). *Entomologist's Gazette* 37: 209–213.

Leestmans, R. (1983) Les lépidoptères fossiles trouvés en France (Insecta Lepidoptera). *Linneana Belgica* 9: 64–89.

Lemmon, A. R., Brown, M. M., Stanger-Hall, K., Lemmon, E. M. (2009) The effect of ambiguous data on phylogenetic estimates obtained by maximum likelihood and Bayesian inference. *Systematic Biology* 58: 501–508.

Lewis, S. E. (1976) Lepidopterous feeding damage of live oak leaf (*Quercus convexa* Lesquereux) from the Ruby River Basin (Oligocene) of southwestern Montana. *Journal of Paleontology* 50: 345–346.

Lewis, S. E. (1985) Miocene insects from the Clarkia deposits of northern Idaho. In: Smiley, C.J. (ed.) *Late Cenozoic History of the Pacific Northwest*. American Association for the Advancement of Science, Pacific Division, Oregon. pp. 245–264.

Lewis, S. E. (1992) Insects of the Klondike Mountain Formation, Republic, Washington. *Washington Geology* 20: 15–19.

Liebhold, A. M., Voney, W. J. A., Schorn, H. E. (1982) An unidentified leaf mine in fossil *Mahonia reticulata* (Berberidaceae). *The Canadian Entomologist* 114: 455–456.

Liu, L., Pearl, D. K. (2007) Species trees from gene trees: reconstructing Bayesian posterior distributions of a species phylogeny using estimated gene tree distributions. *Systematic Biology* 56(3): 504–514.

Marshall, C. R. (1997) Confidence intervals on stratigraphic ranges with nonrandom distributions of fossil horizons. *Paleobiology* 23: 165–173.

Martínez-Delclós, X., Arillo, A., Ortuño, V., Peñalver, E. (1999) El ámbar del Cretácico Inferior de Peñacerrada (Álava, España). *Temas Geológico-Mineros ITGE* 26: 13–17.

Martins-Neto, R. G. (1989) Novos insetos Terciários do Estado de São Paulo. *Revista Brasileira de Geociências* 19: 375–386.

Martins-Neto, R. F. (1998a) A paleontomofauna da Formação Tremembé (Bacia de Taubaté), Oligoceno do Estado de São Paulo: descrição de novos lepidópteros (Insecta). *Acta Geologica Leopoldensia* 41: 75–82.

Martins-Neto, R. F. (1998b) A paleontomofauna da Formação Tremembé (Bacia de Taubaté), Oligoceno do Estado de São Paulo: novos Hemiptera, Auchenorrhyncha, Hymenoptera, Coleoptera e Lepidoptera (Insecta). *Revista Universidade Guarulhos, Geosciências* 3: 58–70.

Martins-Neto, R. F., Kucera-Santos, J. C., de Moraes Vieira, F. R., de Campos-Fragosa, L. M. (1993) Nova espécie de borboleta (Lepidoptera: Nymphalidae: Satyrinae [sic] da Formação Tremembé, Oligoceno do Estado de São Paulo. *Acta Geologica Leopoldensia* 16: 5–16.

Martins-Neto, R. F. & Vulcano, M. A. (1989) Amphiesmenoptera (Trichoptera + Lepidoptera) na Formação Santana (Cretáceo Inferior) Bacia do Araripe, Nordeste do Brasil. I. Lepidoptera (Insecta*). Anais da Academia Brasileira de Ciências* 61: 459–466.

Masly, J. P. (2011) 170 years of “lock-and-key”: genital morphology and reproductive isolation. *International Journal of Evolutionary Biology* 2012 (247352): 1–10.

Mason, P. G., Appleby, M., Juneja, S., Allen, J., Landry, J.-F. (2010) Biology and development of *Acrolepiopsis assectella* (Lepidoptera: Acrolepiidae) in eastern Ontario. *The Canadian Entomologist* 142: 393–404.

McNamara, M., Briggs, D. E. G., Orr, P. J., Wedmann, S., Noh, H., Cao, H. (2011) Fossilized biophotonic nanostructures reveal the original colors of 47-million-year-old moths. *PLoS Biology* 9: e1001200.

Menge, A. (1856) *Lebenszeichen Vorweltlicher, im Bernstein Eingeschlossener Thiere*. A.W. Kafemann, Danzig.

Menken, S. B. J., Herrebout, W. M., Wiebes, J. T. (1992) Small ermine moths (*Yponomeuta*): Their host relations and evolution. *Annual Review of Entomology* 37: 41–66.

Menken, S. B. J., Boomsma, J. J., Nieukerken, E. J. van (2009) Large-scale evolutionary patterns of host plant associations in the Lepidoptera. *Evolution* 64: 1098–1119.

Mérit, X., Mérit, M. (2008) *Problongos baudiliensis* genus novus & species nova: un nouveau Lépidoptère fossile découvert dans la diatomite du Miocène Supérieur de Saint-Bauzile (Ardèche, F-07) (Lepidoptera, Geometridae, Ennominae). *Revue dans Lépidoptéristes de France* 17(39): 29–33.

Mey, W. (2006) Revision of the genus *Phyllobrostis* Staudinger, 1859 (Lepidoptera, Lyonetiidae). *Deutsche Entomologische Zeitschrift* 53(1): 114–147.

Mey, W. (2007) Microlepidoptera: Smaller families. In: Mey, W. (ed.) The Lepidoptera of the Brandberg Massif in Namibia. *Esperiana Memoir* 4: 9–30.

Mey, W. (2011a) Basic pattern of Lepidoptera diversity in southwestern Africa. *Esperiana Memoir* 6: 7–316.

Mey, W. (2011b) On the systematic position of *Baltimartyria* Skalski, 1995, and description of a new species from Baltic amber (Lepidoptera, Micropterygidae). *ZooKeys* 130: 331–342.

Meyer, H. W. (2003) *The Fossils of Florissant*. Smithsonian Books, Washington & London.

Meyrick, E. (1914) *Lepidopterorum Catalogus*. Vol. 19. Hyponomeutidae, Plutellidae and Amphitheridae. W. Junk, Berlin. 63 pp.

Meyrick, E. (1927) *Exotic Microlepidoptera,* Vol. 3. Taylor and Francis, London. 640 pp.

Meyrick, E. (1928) *A revised handbook of British Lepidoptera*. Watkins and Doncaster, London. 914 pp.

Miller, S. E., Hodges, R. W. (1990) Primary types of microlepidoptera in the Museum of Comparative Zoology (with a discursion [sic] on V. T. Chambers' work). *Bulletin of the Museum of Comparative Zoology* 152: 45-87.

Minet, J. (1983) Étude morphologique et phylogénétique des organs tympaniques des Pyraloidea. I – généralités et homologies (Lep. Glossata). *Annales de la Société Entomologique de France (New Series)* 19: 175–207.

Minet, J. (1986) Ebauche d'une classification moderne de l'ordre des Lépidoptères. *Alexanor* 14: 291–313.

Moriuti, S. (1977) *Fauna Japonica, Yponomeutidae s. lat. (Insecta, Lepidoptera).* Keigaku Publishing Co., Tokyo. 327 pp.

Mosher, E. (1916) A classification of the Lepidoptera based on characters of the pupa. *Bulletin of the Illinois State Laboratory of Natural History* 12: 17–159.

Mutanen, M., Wahlberg, N., Kaila, L. (2010) Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. *Proceedings of the Royal Society B* 277: 2839–2848.

Nekrutenko, Y. P. (1965) A new Tertiary nymphalid (Lepidoptera, Rhopalocera). *Palentologicheskiy Zhurnal* 4: 97–99.

Nel, A., Descimon, H. (1994) Une nouveau espèce de Lépidoptère fossile du Stampien de Céreste (Lepidoptera–Satyrinae). *Géologie Méditerranèene* 11: 287–293.

Nel, A., Nel, J. (1986) A propos de deux Lépidoptère fossile du Stampien d’ Aix-en-Provence (Lepidoptera–Hesperidae et Nymphalidae Satyrinae). *Bulletin du Muséum National d’Histoire Naturelle, Paris* (4) 8: 343–350.

Nel, A., Nel, J., Balme, C. (1993) Un noveau lépidoptère Satyrinae fossile de l’Oligocene du sud-est de la France (Insecta, Lepidoptera, Nymphalidae). *Linneana Belgica* 14: 20–36.

Nielsen, E. S. (1996) Heliodinidae and Lyonetiidae. In: Nielsen, E. S., Edwards, E. D., Rangsi, T. V. (eds) Checklist of the Lepidoptera of Australia. *Monographs on Australian Lepidoptera* 4: 56–57.

Nieukerken. E. J. van, 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. A., Brown, J. W., Bucheli, S. R., Davis, D. R., De Prins, J., De Prins, W., Epstein, M. E., Gentili-Poole, P., Gielis, C., Hattenschwiler, 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 Linnaeus, 1758. In: Zhang, Z.-Q. (ed.) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. *Zootaxa* 3148: 212–221.

Nishida, K., Rotheray, G., Thompson, F. C. (2002) First non-predaceous syrphine flower fly (Diptera: Syrphidae): a new leaf-mining *Allograpta* from Costa Rica. *Studia dipterologica* 9 (2): 421−436.

Nuorteva, M., Kinnunen, K. A. (2008) Insect frass in Baltic amber. *Bulletin of the Geological Society of Finland* 80: 105–124.

Ollerton, J. (1999) La evolución de las relaciones polinizador-planta en los artrópodos. *Boletín de la Sociedad Entomológica Aragonesa* 26: 741–758.

Opler, P. A. (1973) Fossil lepidopterous leaf mines demonstrate the age of some insect-plant relationships. *Science* 179: 1321–1323.

Opler, P. A. (1982) Fossil leaf-mines of *Bucculatrix* (Lyonetiidae) on *Zelkova* (Ulmaceae) from Florissant, Colorado. *Journal of the Lepidopterists' Society* 36: 145–147.

Oustalet, M. E. (1870) Recherches sur les insectes fossiles des Terrains Tertiares de la France. *Annales des Sciences Géologiques* 2: 1–175.

Patočka, J., 1997. Über die puppen der mitteleuropäischen Schmetterlinge (Insecta: Lepidoptera): Überfamilien Yponomeutoidea, Gelechioidea, Schreckensteinoidea, Epermenoidea und Copromorphoidea. *Linzer biologische Beiträge* 29(2): 715-751.

Peñalver, E., Delclós, X. (2004) Insectos del Mioceno inferior de Ribesalbes (Castellón, España). Interacciones planta-insecto. *Treballs del Museu de Geologia de Barcelona* 12: 69–95.

Peñalver, E., Engel, M. S. (2006) Two wasp families rare in the fossil record (Hymenoptera): Perilampidae and Megaspilidae from the Miocene of Spain. *American Museum Novitates* 3540: 1–12.

Peñalver, E., Grimaldi, D. A. (2006) New data on Miocene butterflies in Dominican amber (Lepidoptera: Riodinidae and Nymphalidae) with the description of a new nymphalid. *American Museum Novitates* 3519: 1–17.

Penney, D. (2010) *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester.

Pierce, F. N., Metcalfe, J. W. (1935) *The Genitalia of the Tineid Families of Lepidoptera of the British Islands*. Oundle, Northants. 116+22 pp., 68 pls.

Piton, L. (1936) Addition a la faune entomologique des cinerites du La Chambon (Puy-de -Dome). *Revue Scientifique du Bourbonnais et du Centre de la France* 1936: 16–24.

Piton, L. (1940) *Paléontologie du Gisement Éocene de Menat (Puy-de-Dome) (Flore et Faune)*. Imprimeries Paul Vallier, Clermont-Ferrand.

Poinar, Jr., G. O. (1992) *Life in Amber*. Stanford University Press, Stanford.

Poinar, Jr., G. O., Brown, A. E. (2002) *Hymenaea mexicana* sp. nov. (Leguminosae: Caesalpinioideae) from Mexican amber indicates Old World connections. *Botanical Journal of the Linnean Society* 139: 125–132.

Poinar, Jr., G. O., Brown, J. W. (1993) A new fossil tortricid (Lepidoptera: Tortricidae) from Dominican amber. *Entomologica Scandinavica* 23: 25–29.

Posada, D. (2008) jModelTest: Phylogenetic Model Averaging. *Molecular Biology and Evolution* 25: 1253–1256.

Powell, J. A., Opler, P. A. 2009. Superfamily Yponomeutoidea. In: *Moths of Western North America*. University of California Press, Berkeley. pp. 104–113.

Powell, J. A., Mitter, C., Farrell, B. D. (1998) Evolution of larval food preferences in Lepidoptera. In: Kristensen, N.P. (ed.) *Handbook of*

Zoology, Vol. 4, Lepidoptera, moths and butterflies, Vol. 1: Evolution, systematics, and biogeography. Walter de Gruyter, Berlin & New York. pp. 403–422.

Proctor, M., Yeo, P., Lack, A. (1996) *The Natural History of Pollination*. Harper Collins Publishers, London.

Prokop, J. (2003) Remarks on palaeoenvironmental changes based on reviewed Tertiary insect associations from the Krušné hory piedmont basins and the České středhoří Mts in northwestern Bohemia (Czech Republic). *Acta Zoological Cracoviensia* 46 (Supplement): 329–344.

Pyron, R. A. (2010) A likelihood method for assessing molecular divergence time estimates and the placement of fossil calibrations. *Systematic Biology* 59: 185–194.

Rambaut A (2009) FigTree v1.3.1. http://tree.bio.ed.ac.uk/software/figtree (Accessed: January 2010).

Rasnitsyn, A. P. (1983) Pervaya nakhodka babochki yurskogo vozrasta [First find of a moth from the Jurassic]. *Doklady Akademiya Nauk SSSR* 269: 467–471.

Rasnitsyn, A. P., Ross, A. J. (2000) A preliminary list of arthropod families present in the Burmese amber collection at the Natural History Museum, London. *Bulletin of the Natural History Museum, London (Geology)* 56: 21–24.

Rasnitsyn, A. P., Zherikhin, V. V. (2002) Appendix: Alphabetic list of selected insect fossil sites. Impression fossils. In: Rasnitsyn, A.P., Quicke, D. L.

J. (eds) *History of Insects*. Kluwer Academic Publishers, Dordrecht. pp. 437–444.

Raup, D. M. (1979) Biases in the fossil record of species and genera. *Carnegie Museum of Natural History Bulletin* 13: 85–91.

Rebel, H. (1898) Fossil Lepidopteren aus der Miocänformation von Gabbro. *Sitzungsberichte der kaiserlichen Akademie der Wissenschaften* 107: 731–745.

Rebel, H. (1934) Bernstein–Lepidopteren (aus der Sammlung Bachofen-Echt). *Paleobiologica* 6: 1–6, pl. 1.

Rebel, H. (1936) Mikrolepidopteren aus dem baltischen Bernstein. *Die Naturwissenschaften* 24: 519–520.

Regier, J. C. (2008) Protocols, concepts, and reagents for preparing DNA sequencing templates. V. 12/4/08 (http://www.umbi.umd.edu/users/jcrlab/PCR_primers.pdf).

Regier, J. C., Brown, J., Mitter, C., Baixeras, J., Cho, S., Cummings, M. P., Zwick, A. (2012a) A molecular phylogeny for the leaf-roller moths (Lepidoptera: Tortricidae) and its implications for classification and life history evolution. *PLoS One* 7 (4): e35574.

Regier, J. C., Cook, C. P., Mitter, C., Hussey, A. (2008a) A phylogenetic study of the 'bombycoid complex' (Lepidoptera) using five protein-coding nuclear genes, with comments on the problem of macrolepidoteran phylogeny. *Systematic Entomology* 33: 175–189.

Regier, J. C., Mitter, C., Solis, M. A., Hayden, J. E., Landry, B., Nuss, M., Simonsen, T., Yen, S.-H., Zwick, A., Cummings, M. P. (2012b) A molecular phylogeny for the pyraloid moths (Lepidoptera: Pyraloidea) and its implications for higher-level classification. *Systematic Entomology* 37 (4): 635-656.

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, high-level, molecular phylogenetic study of the insect order Lepidoptera (moths and butterflies). *PLoS One* (in press).

Regier, J. C., Shultz, J. W., Ganley, A. R. D., Hussey, A., Shi, D., Ball, B., Zwick, A., Stajich, J. E., Cummings, M. P., Martin, J. W., Cunningham, C. W. (2008b) Resolving Arthropod Phylogeny: Exploring phylogenetic signal within 41 kb of protein-coding nuclear gene sequence. *Systematic Biology* 57 (6): 920–938.

Regier, J. C., Shultz, J. W., Zwick, A., Hussey, A., Ball, B., Wetzer, R., Martin, J. W., Cunningham, C. W. (2010) Arthropod relationships revealed by phylogenomic analysis of nuclear proten-coding sequences. *Nature* 463: 1079–1083.

Regier, J. C., Zwick, A. (2011) Sources of signal in 62 protein-coding nuclear genes for higher-level phylogenetics of arthropods. *PLoS One* 6(8): e23408.

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

Reiss, H. (1936) Ein Zygaenenfund aus der Tertiärzeit. *Entomologische Rundschau* 53: 554–556.

Ren, F., Tanaka, H., Yang, Z. (2005) An empirical examination of the utility of codon-substitution models in phylogeny reconstruction. *Systematic Biology* 54 (5): 808–818.

Richter, G., Storch, G. (1980) Beiträge zur Ernährungsbiologie eozäner Fledermäuse aus der "Grube Messel". *Natur und Museum* 110: 353–367.

Riek, E. F. (1970) *The Insects of Australia*. Melbourne University Press, Melbourne.

Robinson, G. S., Ackery, P. R., Kitching, I. J., Beccaloni, G. W., Hernández, L. M. (2010) HOSTS - A Database of the World's Lepidopteran Hostplants. Natural History Museum, London. http://www.nhm.ac.uk/hosts. (Accessed: 18 Aug.2010).

Ross, A. J., Mellish, C., York, P., Crighton, B. (2010) Burmese amber. In: Penny, D. (ed.) *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester. pp. 208–235.

Rozefelds, A. C. (1988) Lepidoptera mines in *Pachypteris* leaves (Corystospermaceae: Pteridospermophyta) from the Upper Jurassic/Lower Cretaceous Battle Camp Formation, north Queensland. *Proceedings of the Royal Society of Queensland* 99: 77–81.

Rust, J. (1998) Fossil insects from the Fur and Olst Formations (“Mo Clay”) of Denmark (upper Paleocene/lowermost Eocene). *Proceedings of the First International Palaeoentomological Conference, Moscow*. AMBA Projects International, Bratislava. pp. 135–139.

Rust, J. (1999) *Biologie der Insekten aus dem ältersten Tertiär Nordeuropas*. Habilitation Thesis, Biologische Fakultät der Georg-August, Universität Göttingen.

Sanderson, M. J., Shaffer, H. B. (2002) Troubleshooting molecular phylogenetic analyses. *Annual Review of Ecology and Systematics* 33: 49–72.

Sauquet, H., Ho, S. Y. W., Gandolfo, M. A., Jordan, G. J., Wilf, P., Cantrill, D. J., Bayly, M. J., Bromham, L., Brown, G. K., Carpenter, R. J., Lee, D. M., Murphy, D. J., Sniderman, J. M. K., Udovicic, F. (2012) Testing the impact of calibration on molecular divergence times using a fossil-rich group: the case of *Nothofagus* (Fagales). *Systematic Biology* 61: 289–313.

Schmidt, A. R., Jancke, S., Lindquist, E. E., Ragazzi, E., Roghi, G., Nascimbene, P. C., Schmidt, K., Wappler, T., Grimaldi, D. A. (2012) Arthropods in amber from the Triassic Period. *Proceedings of the National Academy of Sciences U.S.A.* 109: 14796–14801.

Scoble, M. J. (1992) *The Lepidoptera: Form, Function and Diversity*. Oxford University Press, Oxford.

Scudder, S. H. (1867) Results of an examination of a small collection of fossil insects obtained by Prof. Wm. Denton in the Tertiary beds of Green River, Colorado. *Proceedings of the Boston Society of Natural History* 11: 117–118.

Scudder, S. H. (1875) Fossil butterflies. *Memoirs of the American Association for the Advancement of Science* 1: 1–99.

Scudder, S. H. (1878) An account of some insects of unusual interest from the Tertiary rocks of Colorado and Wyoming. *Bulletin of the United States Geological Survey of the Territories* 4: 519–543.

Seilacher, A., Rief, W.-E., Westphal, F. (1985) Sedimentological, ecological and temporal patterns of fossil Lagerstätten. *Philosophical Transactions of the Royal Society of London B* 311: 5–23.

Seksyayeva, S. V. (1994) Comparative morphological analysis of the structure of male genitalia in the family Lyonetiidae (Lepidoptera). *Entomologicheskoe Obozrenie* 73 (3): 716–721.

Shcherbakov, D. E. (2008) Madygen, Triassic Lagerstätte number one, before and after Sharov. *Alavesia* 2: 113–114.

Shimodaira, H. (2002) An approximately unbiased test of phylogenetic tree selection. *Systematic Biology* 51: 492–508.

Shimodaira, H. (2011) CONSEL Home Page. http://www.is.titech.ac.jp/~shimo/prog/consel (Accessed: October, 2011).

Shimodaira, H., Hasegawa, M. (2001) CONSEL: for assessing the confidence of phylogenetic tree selection. *Bioinformatics* 17: 1246–1247.

Skalski, A. W. (1973a) Studies on the Lepidoptera from fossil resins. Part VI. *Tortricidrosis inclusa* gen. et spec. nov. from the Baltic amber (Lep., Tortricidae). *Deutsche Entomologische Zeitschrift, N. F.* 20: 339–344.

Skalski, A. W. (1973b) Studies on the Lepidoptera from fossil resins. Part II. *Epiborkhausenites obscurotrimaculatus* gen. et sp. nov. (Oecophoridae) and a tineid-moth discovered in the Baltic amber. *Acta Palaeontologica Polonica* 28: 153–160.

Skalski, A. W. (1974) Zwei neue Gattungen und Arten der Familie Tineidae aus dem Baltischen Bernstein. *Beiträge zur Entomologie* 24: 97–104.

Skalski, A. W. (1976a) Les lépidoptères fossiles de l'ambre, Etat actuel de nos connaissances (3^{me} partie et fin). *Linneana Belgica* 6: 221–233.

Skalski, A. W. (1976b) Les lépidoptères fossiles de l'ambre, Etat actuel de nos connaissances (2^{me} partie). *Linneana Belgica* 6: 195–208.

Skalski, A. W. (1977) Studies on the Lepidoptera from fossil resins. Part 1. General remarks and descriptivos of new genera and especies of the families Tineidae and Oecophoridae from the Baltic amber. *Prace Muzeum Ziemi* 26: 3–24.

Skalski, A. W. (1979a) Records of oldest Lepidoptera. *Nota Lepidopterologica* 2: 61–66.

Skalski, A. W. (1979b) Study on the lepidoptera from fossil resins. Part II. *Palaeodepressaria hannemanni* gen. et sp. nov. (Oecophoridae) from the Baltic amber. *Prace Muzeum Ziemi* 32: 101–107.

Skalski, A. W. (1985) Motyle (Lepidoptera) w bursztynie baltyckim. *Wiadomosci Entomologiczne* 6: 207–210.

Skalski, A. W. (1988) *Stauropolia nekrutenkoi* gen. et. sp. n. (Lepidoptera, Arctiidae)–a new fossil Tiger-moth from Miocene of the Caucasus. *Vestnik Zoologii* 1988: 21–25.

Skalski, A. W. (1990a) An annotated review of all fossil records of Lower Lepidoptera. *Bulletin of the Sugadaira Montane Research Center* 11: 125–128.

Skalski, A. W. (1990b) Lepidoptera in fossil resins with emphasis on new investigations. *Prace Muzeum Ziemi* 41: 163–164.

Skalski, A. W. (1992) Studies on the Lepidoptera from fossil resins. Part III. Two new genera and species of Tortricidae from the Baltic Amber. *Annals of the Upper Silesian Museum (Entomology)* 3: 137–146.

Skalski, A. W., Veggiani, A. (1990) Fossil resin in Sicily and the northern Apennines: geology and organic content. *Prace Muzeum Ziemi* 41: 37–49.

Simmons, M. P. (2012) Radical instability and spurious branch support by likelihood when applied to matrices with non-random distributions of missing data. *Molecular Phylogenetics and Evolution* 62: 472–484.

Smith, D. M. (1998) Comparative taphonomy and paleoecology of insects in lacustrine deposits. In: Zherikhin, V. V. (ed.) *Proceedings of the First International Palaeoentomological Conference*. AMBA Projects International, Bratislava & Paleontological Institute, Moscow. pp. 155–161,

Sobczyk, T., Kobbert, M.J. (2009) Die Psychidae des baltischen Bernsteins. *Nota lepidopterologica* 32: 13–22.

Sohn, J.-C., Labandeira, C., Davis, D., Mitter, C. (2012) An annotated catalog of fossil and subfossil Lepidoptera (Insecta: Holometabola) of the world. *Zootaxa* 3286: 1–132.

Sohn, J.-C., Nishida, K. (2011) A taxonomic review of Eucalantica Busck (Lepidoptera, Yponomeutidae) with descriptions of six new species. *ZooKeys* 118: 75–96.

Sohn, J.-C., Regier, J. C., Mitter, C., Davis, D., Landry, J.-F., Zwick, A., Cummings, M. (2013) A molecular phylogeny of Yponomeutoidea (Insecta, Lepidoptera, Ditrysia) and its implications for classification, biogeography and the evolution of host plant use. *PLoS One* 8(1): e55066.

Solomon, J. D. (1977) Frass characteristics for identifying insect borers (Lepidoptera: Cossidae and Sesiidae; Coleoptera: Cerambycidae) in living hardwoods. *Canadian Entomologist* 109: 295–303.

Stainton, H. T. (1854) *Insecta Britannica*. Lepidoptera: Tineina. Vol. 3. Reeve and Benham, London. 331 pp.

Stamatakis, A., Hoover, P., Rougemont, J. (2008) A fast bootstrapping algorithm for the RAxML Web-Servers. *Systematic Biology* 57(5): 758–771.

Staudinger, O., Rebel, H. (1901). *Catalog der Lepidopteren des Paläarktischen Faunengebietes*. Vol. 3. R. Friedländer & Sohn, Berlin, 368 pp.

Stehr, F. W. (1987) Order Lepidoptera. In: Stehr, F. W. (ed.) *Immature Insect*, Vol. 1. Kendall/Hunt Publishing Co., Dubuque. pp. 288-596.

Stephens, J. F. (1829). *A Systematic Catalogue of British Insects*. Baldwin and Cradock, London, 388 pp.

Stephenson, J. (1991) *Evidence of Plant/Insect Interactions in the Late Cretaceous and Early Tertiary*. Ph. D. Thesis, Department of Geology, University of London.

Straus, A. (1976) Eine Gangmine im Eozän von Messel. *Aufschluß* 27: 445–446.

Straus, A. (1977) Gallen, Minen und andere Fraßspuren im Pliozän von Willershausen am Harz. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg* 113: 43–80.

Sutherland, W. (2009) *Botanical Inclusions in Baltic Amber* [WWW document]. URL http://www.theedwardbulwerlyttoninstitute.org/uploads/1/7/5/8/1758444/botanical_inclusions_in_baltic_amber.pdf [accessed on 7 June 2012].

Swofford, D. L. (2002) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associate, Sunderland (http://paup.csit.fsu.edu).

Talekar, N. S., Shelton, A. M. (1993) Biology, ecology, and management of the Diamondback moth. *Annual Review of Entomology* 38: 275–301.

Théobald, N. (1937) *Les Insectes Fossiles des Terrains Oligocenes de France*. Imprimerie Georges Thomas, Nancy, France.

Tindale, N. B. (1985) A butterfly-moth (Lepidoptera, Castniidae) from the Oligocene shales of Florissant, Colorado. *Journal of Research on the Lepidoptera* 24: 31–40.

Turner, H., Lieshout, N., Ginkel, W. E. van, Menken, S. B. J. (2010) Molecular phylogeny of the small ermine moth genus *Yponomeuta* (Lepidoptera, Yponomeutidae) in the Palaearctic. *PLoS One* 5(3): e9933.

Ulenberg, S. A. (2009) Phylogeny of the *Yponomeuta* species (Lepidoptera, Yponomeutidae) and the history of their host plant associations. *Tijdschrift voor Entomologie* 152: 187–207.

Wahlberg, N., Weingartner, E., Nylin, S. (2003) Towards a better understanding of the higher systematics of Nymphalidae (Lepidoptera: Papilionoidea). *Molecular Phylogenetics and Evolution* 28: 473–484.

Walsingham, T. (1881) On some North-American Tineidae. *Proceedings of the Zoological Society of London* 1881: 301–325.

Warnock, R. C. M., Yang, Z., Donoghue, P. C. J. (2012) Exploring uncertainty in the calibration of the molecular clock. *Biology Letters* 8: 156–159.

Werner, K. (1958) Die Larvalsystematik einiger Kleinschmetterlingsfamilien (Hyponomeutidae, Orthoteliinae, Acrolepiidae, Tineidae, Incurvariidae und Adelidae). *Abhandlungden zur Larvalsystematik der Insekten,* Nr. 2. Akademie-Verlag, Berlin. 145 pp.

Whalley, P. E. S. (1978) New taxa of fossil and recent Micropterigidae with a discussion of their evolution and a comment on the evolution of Lepidoptera (Insecta). *Annals of the Transvaal Museum* 31: 71–86.

Whalley, P. E. S. (1985) The systematics and biogeography of the Lower Jurassic insects of Dorset, England. *Bulletin of the British Museum of Natural History (Geology)* 39: 107–189.

Wheeler, Q. D. (2004) Taxonomic triage and the poverty of phylogeny. *Philosophical Transactions of the Royal Society of London* B 359: 571–583.

Wheeler, Q. D., Meier, R. (2000) *Species Concepts and Phylogenetic Theory, a Debate*. Columbia University Press, New York. pp. 230.

Whiting, M. F. (2002) Phylogeny of the holometabolous orders. *Zoologica Scripta* 31: 3–15.

Wilf, P., Labandeira, C. C., Johnson, K. R., Cúneo, N. R. (2005) Richness of plant-insect associations in Eocene Patagonia: A legacy for South American biodiversity. *Proceedings of the National Academy of Sciences, USA* 102: 8944–8948.

Wilkinson, M. (1994) Common cladistic information and its consensus representation: Reduced Adams and reduced consensus trees and profiles. *Systematic Biology* 43(3): 343–368.

Wilkinson, M. (1995) More on Reduced Consensus Method. *Systematic Biology* 44(3), 435–439.

Wilkinson, M. (1996) Majority-rule reduced consensus trees and their use in bootstrapping. *Molecular Biology and Evolution* 13(3): 437–444.

Winkler, I. S., Mitter, C. (2008) The phylogenetic dimension of insect/plant interactions: a review of recent evidence. In: Tillmon, K. (ed.) *Specialization, Speciation, and Radiation: The Evolutionary Biology of Herbivorous Insects*. University of California Press, Berkeley. pp. 240–263.

Wootton, R. J. (1979) Function, homology and terminology in insect wings. *Systematic Entomology* 4: 81-93.

Zeller, P. C. (1839) Versuch einer naturgemassen Eintheilung der Schaben. *Isis von Oken* 3: 168–220.

Zeuner, F. E. (1927) Eine Sphingidenraupe aus dem Obermiozän von Böttingen. *Palaeontologische Zeitschrift* 8: 321–326.

Zeuner, F. E. (1942) Two new fossil butterflies of the family Pieridae. *Annals and Magazine of Natural History* 10: 140–144.

Zhang, J. (1989) *Fossil Insects from Shanwang, Shandong, China*. Shandong Science Technology Publishing House, Jinan, China.

Zhang, J., Sun, B., Zhang, X. (1994). *Miocene Insects and Spiders from Shanwang*. Science Press, Beijing.

Zherikhin, V. V., Sukacheva, I. D. (1973) On Cretaceous "ambers" (retinites) with insects of North Siberia. *Doklady na XXIV Ezhegodnom Tshtenii Pamiati N. A. Cholodkovskogo* 1971: 3–48.

Zuchowski, W. (2007) *Tropical Plants of Costa Rica*. A Zona Tropical Publication, San José, Costa Rica. 529 pp.

Zwick, A. (2010) Degeneracy Coding Web Site. PhyloTools. 10 FEB 2010. http://www.phylotools.com/ptdegen1webservice.htm (Accessed: 1 September 2011).

Zwick, A., Regier, J. C., Mitter, C., Cummings, M. P. (2011) Increased gene sampling yields robust support for higher-level clades within Bombycoidea (Lepidoptera). *Systematic Entomology* 36: 31–43.

Zwickl, D. J. (2011) GARLI 2.0. http://code.google.com/p/garli (Accessed: May, 2011).