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MOLECULAR SYSTEMATICS OF NOCTUOIDEA (INSECTA, LEPIDOPTERA)

REZA ZAHIRI

TURUN YLIOPISTO
UNIVERSITY OF TURKU
Turku 2012

From the Laboratory of Genetics, Division of Genetics and Physiology, Department of Biology, University of Turku, FIN-20012, Finland

Supervised by:
Docent Niklas Wahlberg
University of Turku
Finland

Co-advised by:
Ph.D. J. Donald Lafontaine
Canadian National Collection of Insects, Arachnids and Nematodes
Canada

Ph.D. Ian J. Kitching
Natural History Museum
U.K.

Ph.D. Jeremy D. Holloway
Natural History Museum
U.K.

Reviewed by:
Professor Charles Mitter
University of Maryland
U.S.A.

Dr. Tommi Nyman
University of Eastern Finland
Finland

Examined by:
Dr. Erik J. van Nieukerken
Netherlands Centre for Biodiversity Naturalis, Leiden
The Netherlands

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To Maryam, my mother and father

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Reza Zahiri

This thesis is based on the following original research contributions, which are referred to in the text by their Roman numerals:

I Zahiri, R, Kitching, IJ, Lafontaine, JD, Mutanen, M, Kaila, L, Holloway, JD & Wahlberg, N (2011) A new molecular phylogeny offers hope for a stable family-level classification of the Noctuoidea (Lepidoptera). ***Zoologica Scripta***, 40, 158–173

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IV Zahiri, R, Lafontaine, JD, Holloway, JD, Kitching, IJ, Schmidt, BC, Kaila, L, & Wahlberg, N. Major lineages of Nolidae (Lepidoptera, Noctuoidea) elucidated by molecular phylogenetics. *Submitted manuscript*

V Zahiri, R, Lafontaine, JD, Kitching, IJ, Holloway, JD, Schmidt, BC, Mutanen, M & Wahlberg, N. Relationships of the early lineages of Noctuidae (Lepidoptera, Noctuoidea) based on eight gene regions. *Manuscript*

Abstract

In this thesis, I conduct a series of molecular systematic studies on the large phytophagous moth superfamily Noctuoidea (Insecta, Lepidoptera) to clarify deep divergences and evolutionary affinities of the group, based on material from every zoogeographic region of the globe. Noctuoidea are the most speciose radiations of butterflies and moths on earth, comprising about a quarter of all lepidopteran diversity. The general aim of these studies was to apply suitably conservative genetic markers (DNA sequences of mitochondrial—mtDNA—and nuclear gene—nDNA—regions) to reconstruct, as the initial step, a robust skeleton phylogenetic hypothesis for the superfamily, then build up robust phylogenetic frameworks for those circumscribed monophyletic entities (i.e., families), as well as clarifying the internal classification of monophyletic lineages (subfamilies and tribes), to develop an understanding of the major lineages at various taxonomic levels within the superfamily Noctuoidea, and their inter-relationships. The approaches applied included: i) stabilizing a robust family-level classification for the superfamily; ii) resolving the phylogeny of the most speciose radiation of Noctuoidea: the family Erebidae; iii) reconstruction of ancestral feeding behaviors and evolution of the vampire moths (Erebidae, Calpinae); iv) elucidating the evolutionary relationships within the family Nolidae and v) clarifying the basal lineages of Noctuidae *sensu stricto*. Thus, in this thesis I present a well-resolved molecular phylogenetic hypothesis for higher taxa of Noctuoidea consisting of six strongly supported families: Oenosandridae, Notodontidae, Euteliidae, Erebidae, Nolidae, and Noctuidae. The studies in my thesis highlight the importance of molecular data in systematic and phylogenetic studies, in particular DNA sequences of nuclear genes, and an extensive sampling strategy to include representatives of all known major lineages of entire world fauna of Noctuoidea from every biogeographic region. This is crucial, especially when the model organism is as species-rich, highly diverse, cosmopolitan and heterogeneous as the Noctuoidea, traits that represent obstacles to the use of morphology at this taxonomic level.

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"In scientific investigations, it is permitted to invent any hypothesis and, if it explains various large and independent classes of facts, it rises to the rank of a well-grounded theory"

Charles Darwin

1. INTRODUCTION

1.1 Why Noctuoidea?

I quote a magnificent passage from Charles Darwin who said ''*all the organic beings which have ever lived on this earth have descended from some one primordial form.*'' It can be obviously interpreted from this simple and meaningful passage that every characteristic of every species on Earth is the outcome of an evolutionary history (Futuyma, 2005). The evolutionary perspective and phylogenetic relationships have illuminated every subject in biology, from the molecular and morphology level to ecosystem and beyond. The geneticist Theodosius Dobzhansky (1973) famously argued that ''*Nothing in biology makes sense, except in the light of evolution.*'' Evolution governs diversity on Earth, and insects are the most diverse organisms in the whole history of life (Grimaldi & Engel, 2005). Consequently, insects should provide profound insights into evolution.

The Order Lepidoptera (moths and butterflies) is one of four super-radiations of insects (along with beetles, flies and wasps) that account for the majority of animal life on Earth. Noctuoidea are the largest superfamily within Lepidoptera—belonging to a large ditrysian clade that also includes e.g., geometroids and bombycoids (Regier *et al.*, 2009, Mutanen *et al.*, 2010)—with approximately 45,000 described (Nieukerken *et al.*, 2011) and many unknown as well as unnamed species, particularly from tropical regions.

To understand Noctuoidea evolution, their systems of evolutionary relationships—phylogenies based on extensive evidence from living lineages of noctuoids—must be recognized. Fortunately, the monophyly of Noctuoidea is firmly established. It is based on the presence of a single apomorphic character, the metathoracic tympanal organ (Miller, 1991). This organ is a highly specialized hearing apparatus that detects the echolocation signals of bats (Kitching & Rawlins, 1998); however, there is increasing evidence that the tympanum may also be involved in reception of mating signals (Kitching & Rawlins, 1998).

Noctuoidea, like most lepidopterans, are plant feeding as caterpillars and nectar feeding as adults, and they are a prominent element of terrestrial ecosystems, functioning as herbivores, pollinators and prey, as well as being one of the most damaging groups of pests to agriculture (Regier *et al.*, 2009). Of the approximately 6,000 Lepidoptera species noted to be of economic importance by Zhang (1994), about one-quarter belong to Noctuoidea. Although a large number of these can be assigned to what Mitchell *et al.* (2006) termed the 'pest clade', many more are distributed across the whole superfamily Noctuoidea in over 500 genera (Zhang, 1994). The caterpillars of many noctuoid genera have massive economic impact annually (Kitching, 1984). In addition, the adults of some genera damage fruit crops by piercing the skins to suck juices (Baenziger, 1982).

The study of relationships among major lineages of organisms—phylogenetic analysis—has been closely associated with the classification and naming of the diversity of life on Earth (i.e., taxonomy), which both are a branch of the science of systematics. The classification of organisms has been one of the major ongoing accomplishments of human society (Wilson, 2000), but is still far from completion, both in terms of the inventory of species and of the classification of those species in a hierarchical system that has a phylogenetic basis. However, there has been a striking improvement in the theory and computational methodology for inferring phylogenies (Regier *et al.*, 1995). In particular, the use of molecular data, in particular DNA sequences, is becoming increasingly important for testing and improving classifications, especially for highly diverse groups of organisms such as insects.

The main theme of my thesis, as well as my ongoing research, is to improve our understanding of the reasons and causes behind the flourishing diversification of Noctuoidea on Earth. To address tens of such questions—diversity of their adaptations, biomass, species-richness, ecological and economical impacts, etc.—it is necessary, as a first step, to place Noctuoidea and its major lineages in a phylogenetic context, by reconstructing a strong phylogenetic hypothesis. The resolution of a stable, extrapolative higher-level classificatory structure for the major lineages of Noctuoidea, and understanding their phylogenetic relationships, is also of importance for pest bionomic studies.

1.2 Status of Noctuoidea

Historically, the classification of noctuoid moths has been highly unstable, with different classification systems being used by different authors. It seems that the fundamental distinction between the different systems is based on the use of unsatisfactory (occasionally plesiomorphic) characters in phylogenetic reconstruction. Various authors have recognized between five and thirteen families, and strikingly, no two publications have agreed on the same divisions of the superfamily into families (Kitching & Rawlins, 1998, Lafontaine & Fibiger, 2006). For instance, in Figure 1, I have summarized most recent Noctuoidea classifications and have compared them with the most recent one, which is presented in this thesis (**I**). Kitching (1984) published a historical review of noctuid subfamily relationships and showed that the higher classifications of Noctuidae used up to that time had been based upon superficial resemblance and vaguely defined characters, rather than on rigorous application of cladistic principles. Subsequently, Speidel and co-workers attempted to progress beyond the age of traditional morphological noctuid taxonomy by initiating investigations based mainly on the male genitalia and the tympanal region, which they considered particularly useful in elucidating the basic relationships of the noctuid subfamilies (Speidel & Naumann, 1995, Speidel *et al.*, 1996, Kühne & Speidel, 2004, 2005).

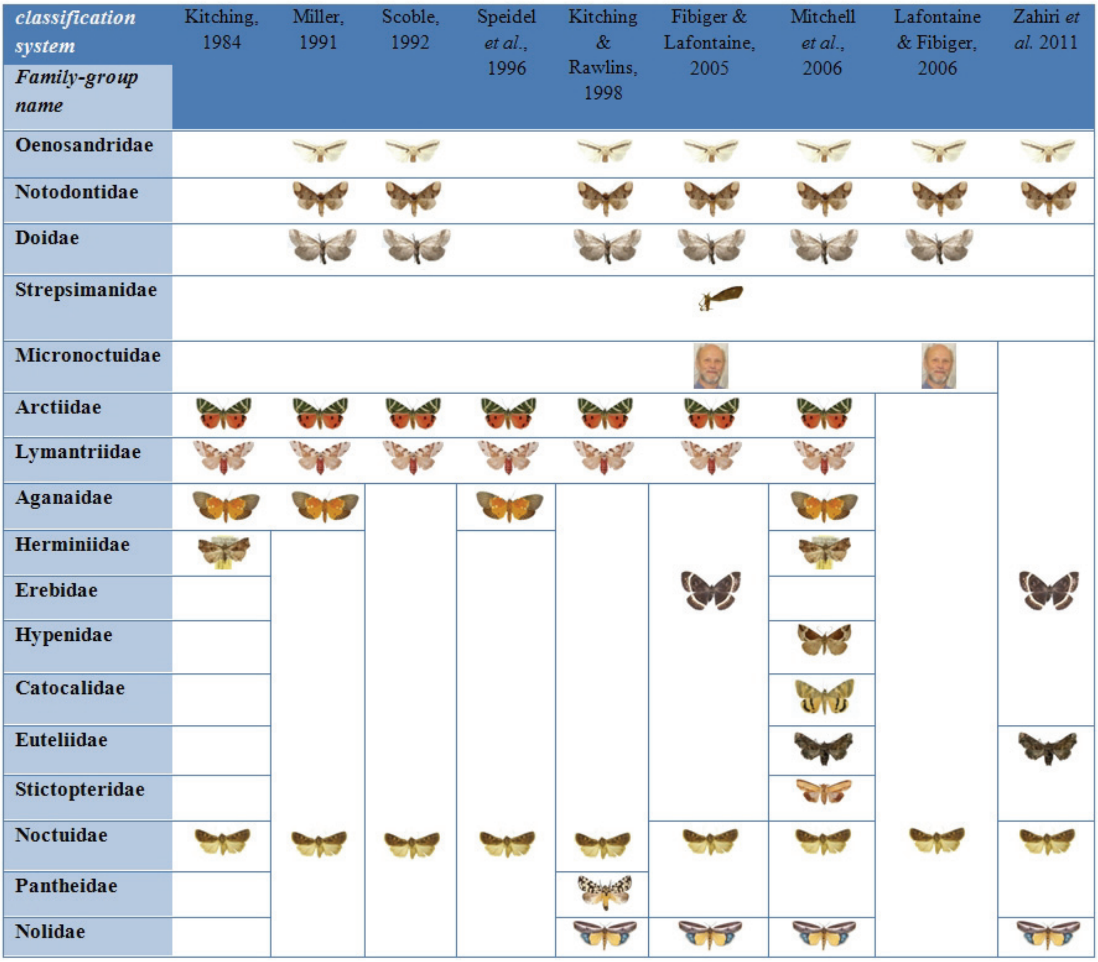


Figure 1 Different classification systems of the superfamily Noctuoidea that have been used since Kitching (1984) to date (**I**). In every classification moths (except the one for Micronoctuidae for which the author's portrait—the late Michael Fibiger—is used) indicate family-group name being used in the system.

Their work set the stage for the study of the systematics of noctuoids, and made it clear that increased character and taxon sampling were necessary to resolve the relationships of the diverse clades.

Recently, three landmark publications (Fibiger & Lafontaine, 2005, Lafontaine & Fibiger, 2006, Mitchell *et al*., 2006) presented detailed phylogenetic hypotheses and revised the classification of Noctuoidea three times (Figure 1), each classification having its own limitations and strengths (Roe *et al*., 2010). Fibiger & Lafontaine (2005) proposed a rather new classification with ten families: Oenosandridae, Doidae, Notodontidae, Strepsimanidae, Nolidae, Lymantriidae, Arctiidae, Erebidae, Micronoctuidae and Noctuidae (Figure 1). Later on, Lafontaine & Fibiger (2006) proposed a further revision to the classification of the families of Noctuoidea, in which Nolidae, Strepsimanidae, Arctiidae, Lymantriidae and Erebidae sensu Fibiger & Lafontaine (2005) were downgraded to subfamily status within an expanded family concept of Noctuidae based on the quadrifid venation of the forewing and the presence of a tympanal sclerite in the tympanal membrane. In their view, the superfamily should consist of five families: Oenosandridae, Doidae, Notodontidae, Micronoctuidae and Noctuidae (Figure 1).

To resolve the dominant complexity of relationships in higher systematics of Noctuoidea, it was crucial to understand their phylogenetic relationships by building a robust skeleton phylogenetic hypothesis, i.e., a phylogeny that was based on certain specialized features, and that had a common ancestor and unique evolutionary history. To achieve a more robust phylogenetic hypothesis, one strategy is to increase the number of characters to obtain a dataset with a strong phylogenetic signal. In molecular systematics, datasets with a weak phylogenetic 'signal' tend to be strongly influenced by the assumptions made by the analytical methods applied, whereas datasets with a strong phylogenetic signal are not influenced as much (Wahlberg & Wheat, 2008). One avenue for acquiring more characters is to use morphology. However, a species-rich, cosmopolitan and heterogeneous group such as the Noctuoidea (Speidel & Naumann, 1995) with a vast number of species presents obstacles to the use of morphology at this taxonomic level. The adults and larvae of species in Noctuoidea exhibit a bewildering diversity of size, coloration, adaptation, behaviour and ecology (Kitching & Rawlins, 1998). Morphological data are thus often difficult to homologize and code, require great experience to identify character states correctly and can be subject to extensive homoplasy (character convergence and reversal). As a result, morphological analyses have often failed to determine relationships among most groups with confidence.

1.3 Initiation of molecular phylogenetic approaches

As noted above, until recently, the higher systematics of Noctuoidea had been based primarily on morphological characters with a predominantly phenetic approach, until the introduction and application of cladistic philosophy by Kitching (1984, 1987) and Miller (1991). More recently, molecular data, in particular DNA sequences of mitochondrial and nuclear genes (mtDNA and nDNA, respectively), have opened new and fruitful avenues for the study of phylogenetic relationships. Molecular studies have often been based on a small number of molecular markers, usually between one and three genes (Sperling, 2003, Wahlberg & Wheat, 2008). The utility of using many mitochondrial genes alone is certainly questionable, as they have a shared evolutionary history, and even entire mitochondrial genomes (15,000–20,000 bp in insects) fail to provide robust inferences at deep levels (Cameron *et al.*, 2004). However, they are useful in the recognition of cryptic species and sometimes resolve relationships among closely related species and genera (Lafontaine & Schmidt, 2010). They have proven most valuable for relatively recent divergences, especially those of mid-Tertiary and later age, although they have also been applied, albeit infrequently, at deeper levels (Wiegmann *et al.*, 2000). In contrast, protein-coding nuclear genes generally have slower mutation rates compared with mtDNA. They are most frequently used to study older evolutionary divergences and are particularly good at resolving deeper nodes in phylogenetic hypotheses, where they have been important in establishing the family, subfamily and tribal classification of Lepidoptera (Regier *et al.*, 2009, Wahlberg *et al.*, 2009, Mutanen *et al.*, 2010). Over the past few years, a series of papers have been published with a shared objective: to contribute to the development of a more satisfactory classification of Noctuoidea at levels above that of the genus and particularly the 'quadrifid' part—those noctuoids with forewing vein M2 arises closer to the origin of M3 than M1, in the lower part of the discal cell—of the superfamily. It began with the exploration of molecular markers by Weller *et al.* (1994), who were then followed by Mitchell *et al.* (1997, 2000, 2006). The utility of DNA sequences was undeniable, and systematists were able to gain fascinating insights that were not obvious before, e.g., the polyphyly of the old concept of Noctuidae (Mitchell *et al.*, 1997). Mitchell *et al.* (2006) found a strongly supported clade of quadrifine noctuid moths that also included the families Lymantriidae and Arctiidae. They termed this the L.A.Q. clade (Lymantriidae, Arctiidae and Quadrifine Noctuidae).

Two recent molecular studies on ditrysian Lepidoptera sampled members of Noctuoidea and found that the enigmatic family Doidae did not group with the other noctuoids, but instead appeared to be related to Drepanoidea (Regier *et al.*, 2009, Mutanen *et al.*, 2010). Otherwise both studies found Noctuoidea to be monophyletic, with Oenosandridae being sister to the rest and Notodontidae the next lineage branching off.

However, all of these studies had very poor sampling of the higher taxa putatively belonging to the L.A.Q. clade, and critically they did not sample type genera of many higher taxa. Given that the monophyly of many named groups remains questionable, it is crucial to sample the type genera of each family, subfamily and tribe to assess the taxonomic limits of a given category. Furthermore, previous molecular studies have used only a small number of molecular markers, usually one to three gene regions (Wahlberg & Wheat, 2008).

1.4 Outline of the thesis

In this thesis, I employed the methods of molecular phylogenetics using eight markers for genomic DNA extractions of Lepidoptera to study the evolution of Noctuoidea and reconstruct a skeleton phylogenetic hypothesis for its major lineages. The first chapter gives a comprehensive overview of the higher-level phylogeny and evolutionary affinities of noctuoid moths, in an extensive sampling strategy of the entire Noctuoidea (**I**). It reveals a new high-level phylogenetic hypothesis comprising six major, well-supported lineages that are interpreted as families (**I**). The second chapter aims to understand the higher-level phylogeny and elucidate the evolutionary history of the moth family Erebidae, the most controversial group among the newly circumscribed families (**II**). Erebidae is a massive clade and includes a diverse groups exhibiting a broad range of feeding behaviors, including those that can be considered 'piercers' of fruits or other hosts (skin-piercers: hematophagous) and 'tear feeders' (lachryphagous) (**III**). Within butterflies and moths, adult hematophagy is limited to species within the vampire moth genus *Calyptra*

Ochsenheimer, which are placed within the subfamily Calpinae, Erebidae. Paper **III** focused on the subfamily Calpinae using both morphological and molecular data to reconstruct ancestral feeding behaviors within Calpinae as well as whether fruit-piercing behavior and associated modifications of the tongue have evolved independently in different groups of Erebidae (**III**). The fourth chapter seeks to elucidate the deep divergences and evolutionary relationships of the major lineages within the moth family Nolidae (**IV**). As a result of expanded sampling, a new lineage (i.e., Diphtherinae) within Noctuoidea—which includes taxa of previously uncertain affinity—was recovered. Diphtherinae is considered to be the plesiomorphic sister lineage to the rest of Nolidae (**IV**), thus a new phylogenetic hypothesis for Nolidae is presented (**IV**). The fifth chapter elucidates the evolutionary relationships of the basal lineages of the moth family Noctuidae (**V**). A summary flow chart is presented in Fig. 2, representing my thesis process with their main outputs.

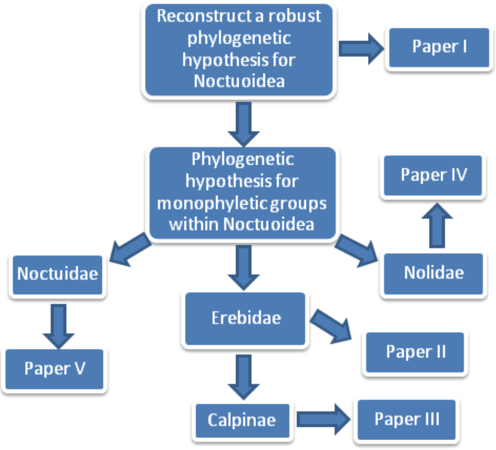


Figure 2 A flow chart summarizing five chapters included in this thesis.

2. MATERIAL AND METHODS

2.1 Sampling strategy

The sampling strategy that I adopted has treated the world fauna. I attempted to include representatives of all known major lineages of quadrifine Noctuoidea from every biogeographic region. This strategy is being used to establish priorities for ongoing studies, to test further the robustness of the major clades of Noctuoidea, both in relation to each other and internally.

Based on the results of recent publications (Fibiger & Hacker, 2005, Lafontaine & Fibiger, 2006, Mitchell *et al.*, 2006, Lafontaine & Schmidt, 2010), 152, 237, 35, 120 and 76 terminal taxa were sampled as representatives of the most recognized Noctuoidea lineages for papers **I–V**, respectively. Furthermore, there were numerous unplaced taxa of uncertain status that were included in each paper. Indeed, the allocation of the unplaced taxa into any higher taxa of Noctuoidea, however tentatively, could not be determined in previous classifications. I was unable to sample/amplify a few rare taxa with restricted distributions and/or low species richness (e.g., Strepsimaninae, Afridinae, Camptolominae). Where possible, a representative of the type genus of each lineage is included, but this was not possible for a few tribes/subtribes, in which case a closely related genus was selected.

Appendix 1 summarizes all 393 terminal taxa that are used in the five papers with their voucher codes and GenBank accession numbers.

To test the monophyly of the target taxon under study in the different papers, I included representatives from the most closely related taxa of other families of Lepidoptera (papers **I, II, IV, V**) or subfamilies of Erebidae (**III**). I rooted the cladograms, in different papers, with different taxa, which represents what I consider to be the putative sister family to the remainder of the terminal taxa.

2.2 Molecular markers

The total genomic DNA from one or two legs, dried or freshly preserved in 96% ethanol, was extracted using the DNeasy tissue extraction kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. For each specimen, I sequenced *cytochrome c oxidase subunit I* (COI) from the mitochondrial genome, and *elongation factor-1α* (EF-1α), *ribosomal protein S5* (RpS5), *carbamoylphosphate synthase domain protein* (CAD), *cytosolic malate dehydrogenase* (MDH), *glyceraldehyde-3-phosphate dehydrogenase* (GAPDH), *isocitrate dehydrogenase* (IDH) and *wingless* genes from the nuclear genome. For paper **III**, I sequenced an additional gene, the D2 region of the nuclear ribosomal RNA (rRNA) 28S region. All genes—except 28S, which is multiple-copy and encodes ribosomal RNA—are single-copy, protein-coding exons and have previously been found to be highly informative in phylogenetic analyses of Lepidoptera at higher taxonomic levels (Wahlberg *et al.*, 2009, Mutanen *et al.*, 2010, **I**, **II**).

DNA amplification (PCR) and sequencing protocols follow Wahlberg & Wheat (2008). Sequencing was performed mainly with an ABI 3730XL capillary sequencer (Macrogen, Seoul, Korea), and a smaller part with an ABI PRISMR 3130XL capillary sequencer (Turku, Finland). The resulting chromatograms were checked and DNA sequences aligned by eye using BioEdit v. 7.0.4.1 (Hall, 1999). Alignment was trivial and the few insertion/deletion events that were detected were of entire codons (in CAD, IDH and RpS5), and could be easily aligned. To minimize the risk of any kind of confusion during the sequencing protocol and errors in alignments, I constructed neighbor-joining and Maximum Likelihood trees separately for each gene region and checked them carefully for identical sequences and other doubtful patterns. In addition, to minimize the risk of misidentification, all the specimens were cross-checked with their DNA barcodes (COI) in BOLD (Barcode of Life Data System, http://www.boldsystems.org/views/login.php) (Ratnasingham & Hebert, 2007), where reference specimens were available for many of the species used in this study.

2.3 Phylogenetic analyses and character optimizations

The gene regions were analyzed using various phylogenetic approaches including model-based (Maximum Likelihood, ML; and Bayesian Inference, BI), and non model-based (i.e., parsimony) methods. Initially, the data matrices were analysed in various combinations using ML to explore their phylogenetic signal. Single genes were analyzed on their own, nuclear genes were combined, third codon positions were removed, data was partitioned into mtDNA and nDNA and finally the data was partitioned by gene regions (8 partitions). The effects of varying taxon and gene combinations were compared against the analyses of the full, combined and partitioned by gene data. Based on these data explorations, it was decided to include all genes and third codon positions as well as to partition the data by genes (8 partitions) in the ML analyses, and by nDNA and mtDNA (two partitions) in the BI analyses.

Parsimony analyses (MP) were undertaken using New Technology heuristic searches implemented in the program, TNT v 1.1 (Goloboff *et al.*, 2003). New technology searches (Goloboff, 1999) consisted of Tree Fusion, Ratchet, Tree Drifting and Sectorial Searches performed, with default parameters applied, until the minimal tree was found 1000 times. All characters were treated as unordered and equally weighted, and robustness of the hypothesis was assessed through the bootstrap (BP) with 1000 pseudoreplicates (Felsenstein, 1985). In addition, in papers **I** and **II** clade support was estimated by Bremer support (BS) (Bremer, 1988, 1994) using a script (Peña *et al.*, 2006) in TNT. Model-based phylogenetic analyses were performed using ML and a GTR + Γ model was selected as the most appropriate model of sequence evolution for each gene partition based on the Akaike Information Criterion using FindModel (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html). ML analyses were conducted using the default settings on the web-server RAxML III BlackBox (Stamatakis *et al.*, 2008). ML bootstrap analysis with 1000 pseudoreplicates (Felsenstein, 1985) was also conducted with RAxML III.

BI was not used for papers **I** and **II**. In the other papers, BI analyses were carried out using the software MrBayes v3.1 (Ronquist *et al.*, 2005) on the freely available Bioportal server (http://www.bioportal.uio.no). The dataset was divided into two partitions: mtDNA and nDNA, as partitioning by gene resulted in poor mixing of chains and problems with convergence of likelihoods. I modeled the evolution of sequences according to the GTR + Γ model independently for the two partitions using the "unlink" command in MrBayes. The Bayesian analyses were separately run two times for five, 23 and 20 million generations for papers **III−V**, respectively, with every 1000th generation sampled. Clade robustness was estimated by posterior probabilities (PP) in MrBayes. Convergence was determined when the standard deviation of split frequencies went below 0.05 and the PSRF (Potential Scale Reduction Factor) approached 1, and both runs had properly converged to a stationary distribution after the burn-in stage (which was 1,000 sampled generations).

To understand character evolution in higher noctuoids, a character optimization analysis based on parsimony was undertaken in paper **IV** using the software Mesquite v2.75 (Maddison & Maddison, 2011). Ancestral state reconstructions and character transformations were optimized onto the topology resulting from the Bayesian analysis (**IV**).

All laboratory procedures and phylogenetic data analyses are detailed in the original papers.

3. RESULTS AND DISCUSSION

3.1 Phylogenetic hypothesis for Noctuoidea

In the initial study, I aimed, as a first step, to reconstruct a robust phylogenetic hypothesis for higher taxa of Noctuoidea. The results strongly supported the monophyly of Noctuoidea. The major groups within the Noctuoidea clade all shared a particular morphological synapomorphy—a metathoracic tympanal organ. I found six strongly supported major lineages within Noctuoidea that deserved family status. These are Oenosandridae, Notodontidae, Euteliidae, Erebidae, Nolidae and Noctuidae (Fig. 3). The first two major lineages are well-recognized taxa that have often been considered families within Noctuoidea. Oenosandridae are a small family, only known from Australia, comprising eight species in four genera (Nielsen *et al.*, 1996), which mainly feed on Myrtaceae (Miller, 1991). Notodontidae contain approximately 3,800 species (Nieukerken *et al.*, 2011) and occur worldwide. The other four lineages have been split into as many as 10 families, with arctiines, lymantriines and nolines frequently being considered to be sufficiently distinct from the rest to warrant full family status. My phylogenetic hypothesis (**I**) placed previously recognized families—arctiines, lymantriines, aganaines, herminiines and micronoctuines—into the strongly supported Erebidae clade. Within Erebidae, relationships of only a few lineages (e.g., Arctiinae, Aganainae and Herminiinae) were well supported (**I**). The low support for some nodes within Erebidae and Noctuidae probably stems from high levels of homoplasy (particularly in the third codon position) and very sparse sampling.

At this stage, with well-supported monophyletic groups established within a phylogenetic framework, the question arose of how best to apply the Linnaean system of nomenclature to the structure of that framework, by making decisions on the content and arrangement of families, subfamilies, tribes and subtribes in a manner that was most likely to optimize the stability of that system and facilitate access to its information content (**II**). In particular, the establishment of a well-founded family-level noctuoid classification is certainly an issue of considerable practical importance, because it affects the classification of about a quarter of the world's lepidopteran species, according to current estimates (Nieukerken *et al.*, 2011). In paper **II**, I discussed in detail reasons for applying the six family-group system to the higher systematics of Noctuoidea with their advantages and drawbacks.

One of the most striking features of the application of molecular data in my thesis was uncovering the phylogenetic relationships of many unplaced taxa of uncertain affinity. Molecular phylogenetic techniques allowed the easy allocation of these taxa, which had remained 'incertae sedis' or with uncertain limits for many years. For example, the position of a number of taxa characterized by the pseudoquadrifine hindwing venation had been unstable for a long time (**IV**–**V**). Most of these groups (i.e., pseudoquadrifine Noctuidae) were previously assumed to be related to erebid subfamilies (Fibiger & Lafontaine, 2005, Lafontaine & Fibiger, 2006) (**II**) or even considered as distinct families (e.g., Pantheidae) (Kitching & Rawlins, 1998) (**V**). The results of papers **IV**–**V** placed them in a basal position within the family Noctuidae with strong support.

3.2 Pattern of relationships among major lineages of Noctuoidea

Notodontidae are found to be the sister group of all other Noctuoidea, with Oenosandridae branching off next (**I**). However, this pattern of relationships relative to the rest of Noctuoidea is not well supported in all papers. Both Oenosandridae and Notodontidae have a trifid forewing venation similar to that of Geometridae, a character state that appears to be plesiomorphic relative to the quadrifid forewing venation found in the other noctuoid families. All these terms are discussed and defined in detail in paper **II**.

The results of paper **I** recovered the six recognized families within Noctuoidea and the monophyly of the quadrifid Noctuoidea (i.e., Euteliidae, Erebidae, Nolidae, and Noctuidae). Although, the relationships amongst the remaining four families are not clear, they formed a monophyletic group (i.e., quadrifid Noctuoidea clade) with very strong support (Fig. 3) and shared a synapomorphy (i.e., quadrifid forewing venation). The relationships of the four clades of quadrifid lineage remained somewhat ambiguous in papers **I**–**II**, although the results of papers **IV**–**V** suggested a basal position for Euteliidae in all three phylogenetic methods (MP, ML and BI). In paper **I**, Euteliidae were sister to Noctuidae in ML analyses (Fig. 3), and sister to the other three families together in MP analyses. Similarly, in papers **IV**–**V**, Euteliidae were placed as sister to the rest of the quadrifid clade with moderately good support in MP, ML and BI analyses (Figs 4–5). In paper **I**, Nolidae were sister to Erebidae in ML analyses, but form a trichotomy with Erebidae and Noctuidae in MP analyses.

The short internal nodes, with little or no support for many basal divergences, in all quadrifid Noctuoidea lineages (**I, II, IV, V**), suggest that these groups diversified rapidly within a relatively short period of time (Whitfield & Kjer, 2008). Evolutionary rates in basal divergences appear punctuated and such explosive radiations are generally interpreted in two different ways: (i) there is an historical explanation (e.g., rapid radiation or the signature of a mass extinction event) or (ii) it is simply an artefact. Under the rapid radiation scenario, it is hypothesized that the lineages diverged so rapidly and within such a narrow time window that there was little opportunity for the ancestors of each monophyletic group to evolve distinctive apomorphies (Futuyma, 2005). However, such a pattern of short internal nodes and lineages with low support can be produced by other factors, such as inadequate data quality, poor and sparse sampling strategy, conflict within or among datasets (data inconsistency), incongruence between the real evolutionary process and the assumed models of sequence evolution, or even lack of phylogenetic signal due to accumulation of overlapping mutations (i.e., the probability of substitutional saturation at a given site).

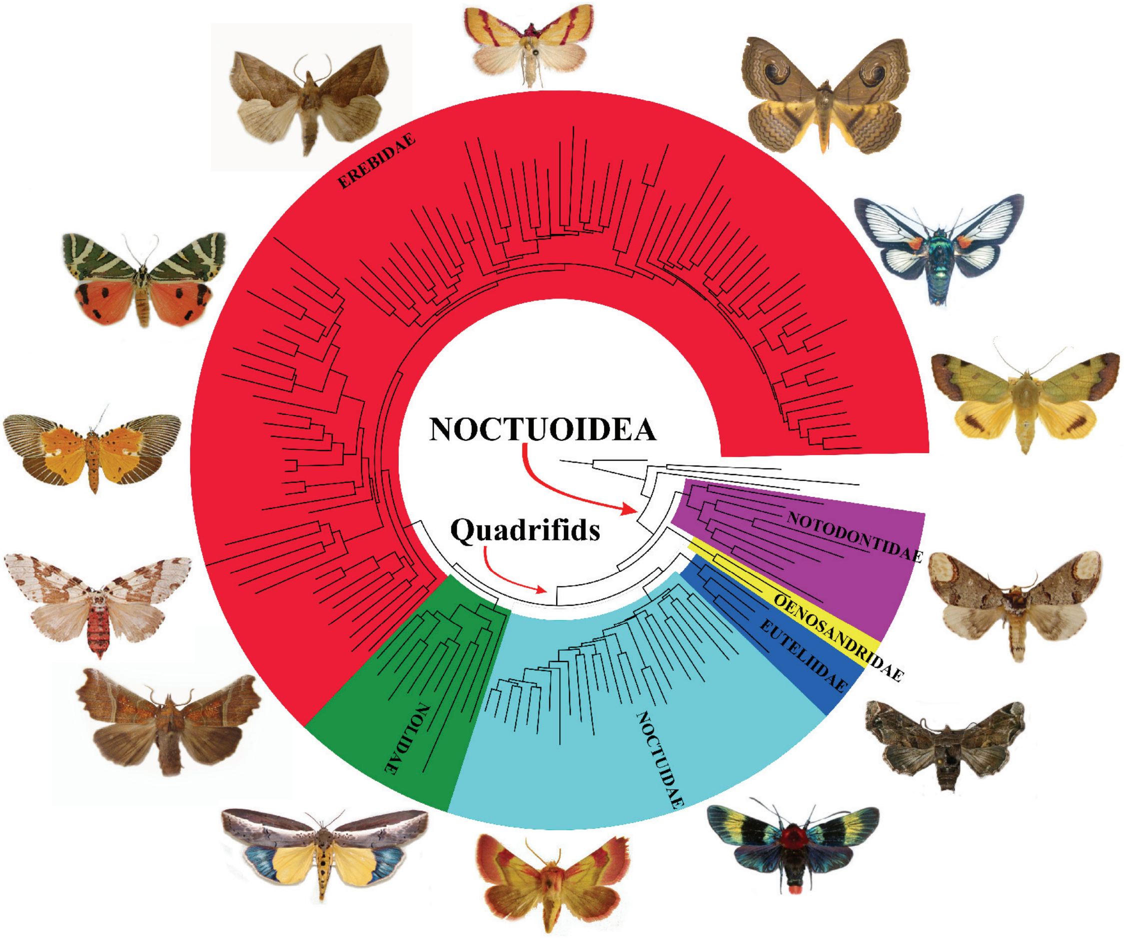


Figure 3 The phylogenetic hypothesis of the superfamily Noctuoidea based on a maximum likelihood analysis, along with outgroups. Clades representing families are coloured. The six families recognized here are indicated. Names of moths shown in figure clockwise are: Notodontidae: *Phalera* Hübner; Euteliidae: *Eutelia* Hübner, Noctuidae: *Eucocytia* Rothschild & Jordan (Pantheinae), *Periphanes* Hübner (Heliothinae); Nolidae: *Eligma* Hübner (Eligminae); Erebidae: *Scoliopteryx* Germar (Scoliopteryginae), *Lymantria* Hübner (Lymantriinae), *Peridrome* Walker (Aganainae), *Euplagia* Hübner (Arctiinae), *Calyptra* Ochsenheimer (Calpinae), *Phytometra* Haworth (Boletobiinae), *Spirama* Guenée (Erebinae), *Cocytia* Boisduval (Erebinae), and *Ophiusa* Ochsenheimer (Erebinae).

In addition, a recent study indicates that such phylogenetic patterns may well be signature of mass extinction events (Crisp & Cook, 2009), because mass extinction produces a sharp drop in the cumulative fossil diversity and is commonly thought to stimulate subsequent adaptive radiation, creating a sharp increase in the rate of diversification (Benton & Emerson, 2007).

3.3 Phylogenetic hypothesis for quadrifid Noctuoidea

Paper **I** revealed an urgent need for a comprehensive series of revisions for the higher classifications of quadrifid Noctuoidea families used up to that time. My results in paper **I** almost failed to recover some previously recognized subfamilies within Erebidae as monophyletic groups. For instance, they suggested that some recent concepts of subfamilies Calpinae, Catocalinae, Erebinae and Phytometrinae were polyphyletic (**I**). Consequently, the focus in paper **II** was designed to elucidate the higher-level phylogeny and evolutionary relationships of the massive Erebidae clade (**II**). I thus conducted a large-scale molecular phylogenetic analysis, which uncovered a well-resolved skeletal phylogenetic hypothesis. I thus presented a new phylogenetic hypothesis for Erebidae consisting of 18 moderate to strongly supported subfamilies (Fig. 4): Scoliopteryginae, Rivulinae, Anobinae, Hypeninae, Lymantriinae, Pangraptinae, Herminiinae, Aganainae, Arctiinae, Calpinae, Hypocalinae, Eulepidotinae, Toxocampinae, Tinoliinae, Scolecocampinae, Hypenodinae, Boletobiinae and Erebinae (Fig. 4). Where possible, I diagnosed apomorphic morphological character states for each monophyletic lineage (**II**).

Paper **II** provides strong support for subordinating five taxa where previously treated as families—Arctiidae, Lymantriidae, Micronoctuidae, Herminiidae and Aganaidae—within Erebidae. One of the most striking features, a strong association among three of them, was shown in papers **I**–**II**: Aganainae + Herminiinae + Arctiinae are recovered as monophyletic clade (Fig. 4), in which Arctiinae have a sister relationship with a strongly supported pairing of Aganainae and Herminiinae. The clade also has a morphological synapomorphy in the prespiracular position of the counter-tympanal hood, which was until then thought to be plesiomorphic. Adults of many aganaines and arctiines are visually striking and aposematic, and aganaines and herminiines share long labial palps and a bare lower frons. Herminiinae are generally cryptic, feeding on vegetable detritus, and Aganainae are aposematic, feeding on the same suite of toxic cardenolide-synthesizing plant families (Apocynaceae and Moraceae) as the danaine Nymphalidae and other moth genera such as *Glyphodes* (Crambidae) and *Agathia* (Geometridae) (Holloway, 2008).

Another interesting result from paper **II** was the placement of the new established family Micronoctuidae. Hypenodinae are enlarged to incorporate Micronoctuini as a tribe, corroborating the findings of paper **I**. The subfamily Erebinae, brings together the core catocalines (with the exceptions of Hypocalinae, Toxocampinae and Tinoliinae).

Calpinae *sensu* Lafontaine & Fibiger (2006) consisted of four tribes, Anomini, Scoliopterygini, Calpini and Phyllodini on the basis of the sharing of peculiar morphological adaptations. A robust, highly developed fruit-piercing (and in some cases skin-piercing and blood sucking) proboscis is found widely in Calpini and in some of the more robust scoliopterygines such as *Anomis* Hübner, with many similar features in the structure. However, my phylogenetic analysis

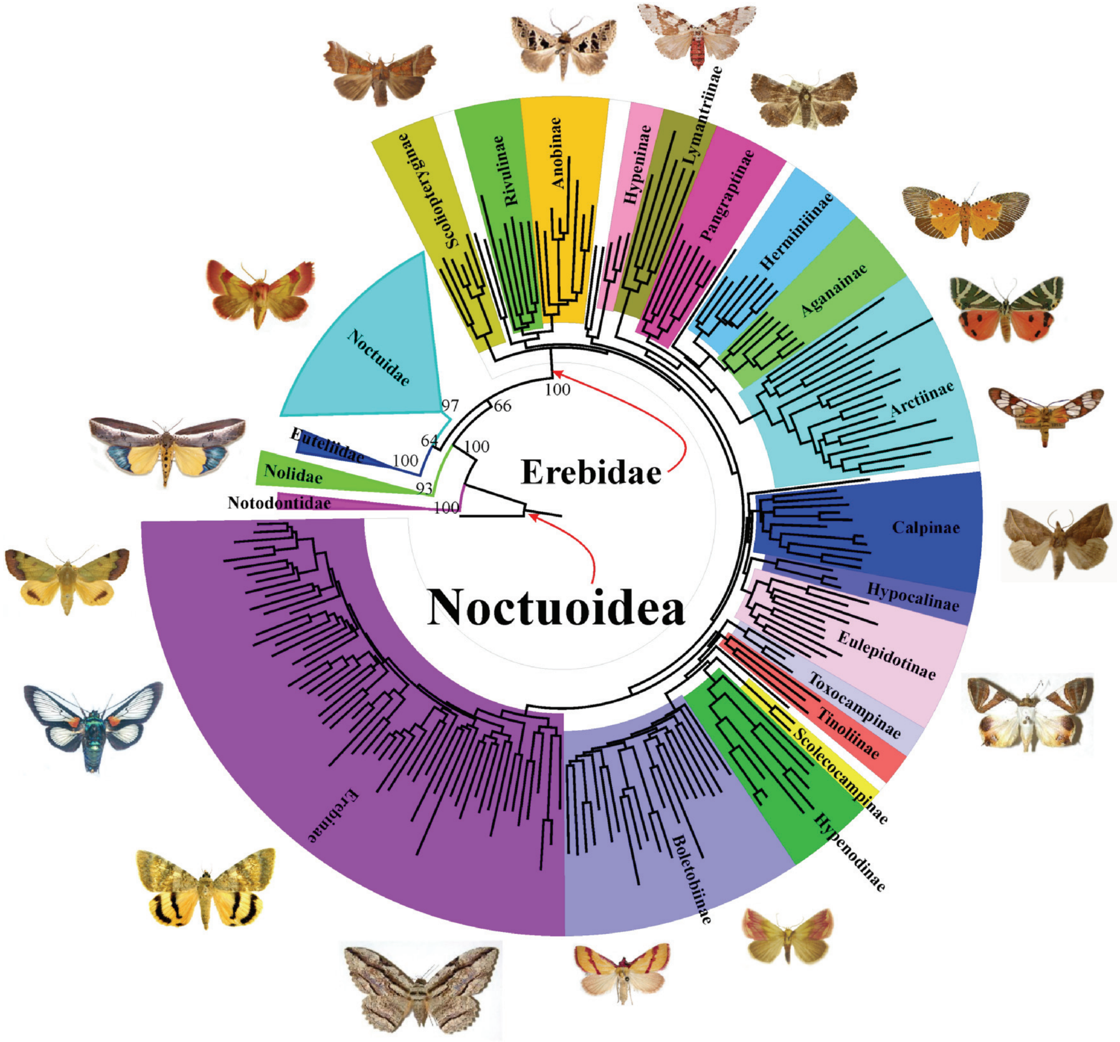


Figure 4 Phylogenetic hypothesis of the moths family Erebidae, based on ML analysis. Clades representing the major clades are coloured. Support values (bootstrap) are shown next to the branches. Names of moths shown in figure clockwise are: Nolidae: *Eligma* (Eligminae); Noctuidae: *Periphanes* (Heliothinae); Erebidae: *Scoliopteryx* (Scoliopteryginae), *Anoba* Walker (Anobinae), *Lymantria* (Lymantriinae), *Pangrapta* Hübner (Pangraptinae), *Peridrome* (Aganainae), *Euplagia* Hübner (Arctiinae), *Syntomis* Ochsenheimer (Arctiinae), *Calyptra* (Calpinae), *Eulepidotis* Hübner (Eulepidotinae), *Eublemma* Hübner (Boletobiinae), *Phytometra* (Boletobiinae), *Thysania* Dalman (Erebinae), *Catocala* Schrank (Erebinae), *Cocytia* (Erebinae), and *Ophiusa* (Erebinae).

confirmed the polyphyly of the old concept of Calpinae, and supports a monophyletic Calpinae that places members of Anomini and Scoliopterygini in other noctuid subfamilies (**II–III**). These results suggesting that the fruit-piercing behavior and the associated modifications of the tongue seen in moths of both groups have evolved independently (**III**). The phylogenetic hypothesis suggested three subclades for the subfamily Calpinae that were treated as tribes: Phyllodini, Ophiderini and Calpini (**II**). The polyphyly of the former concept of Calpinae provides an object lesson in how the sharing of peculiar morphological adaptations may mislead classifications, and how shared features of a more subtle nature may be overlooked in an unchallenged traditional classification. Within the entire Lepidoptera, adult hematophagy—the ability to pierce mammalian tissue and extract a blood meal—is limited to species within the vampire moth genus *Calyptra* Ochsenheimer, which belongs to the subfamily Calpinae. In paper **III**, we tested whether hematophagy in *Calyptra* arose from plant (e.g., fruit-piercing) or animal-related behaviors (e.g., tear feeding or lachryphagy). To do that, we subjected the resulting phylogenetic trees to a Bayesian method of ancestral state reconstruction to reconstruct ancestral feeding behaviors within Calpinae and test competing hypotheses regarding their evolution. The results supported the hypothesis that blood feeding in vampire moth evolved from the fruit-piercing habit as opposed to tear feeding or other animal-related feeding behaviors (e.g., dung feeding, urine feeding) (**III**).

In paper **IV**, I aimed to elucidate the higher-level phylogeny of Nolidae and to clarify relationships in basal lineages of Noctuidae (**V**). My phylogenetic hypothesis (**I**) had already recovered Nolidae and Noctuidae as well-supported monophyletic clades (Fig. 3). The results were fascinating and fairly robust. Many genera previously placed in Nolidae and the former subfamily Ophiderinae (Erebidae) were placed with strong support within Noctuidae, in the subfamily Bagisarinae, supporting an expanded concept of the subfamily (**V**). In addition, by increasing taxon sampling of several unassigned Neotropical taxa, I uncovered a previously unknown lineage of Noctuoidea with Neotropical origins (*Diphthera* Hübner + *Lepidodes* Guenée) with strong support. This lineage appears to be the sister group to Nolidae, and it shares an unambiguous feature and the most characteristic Nolidae apomorphy yet proposed—the structure of the boat-shaped cocoon with a vertical, anterior exit slit—, suggesting that the clade could be included in the family Nolidae as the subfamily Diphtherinae (**IV**). Diphtherinae is considered to be the plesiomorphic sister lineage to the rest of Nolidae, characterized by the loss of the proximal pair of tibial spurs on the hindlegs of males, and the presence of a frontal tubercle or process, which is presumably associated with a derived strategy of emergence from the cocoon (**IV**). My analyses (**IV**) revealed a well-resolved phylogenetic hypothesis for Nolidae, allowing me to present a new classification for Nolidae consisting of eight strongly supported subfamilies: Diphtherinae, Risobinae, Collomeninae, Beaninae, Eligminae, Westermanniinae, Nolinae, and Chloephorinae. Among these, two groups are suggested as new subfamilies (i.e., Collomeninae and Beaninae). I also defined each monophyletic group by autapomorphic morphological character states.

3.4 Character optimizations

The higher systematics of the quadrifid Noctuoidea is often discussed in terms of whether the hindwings have a trifine or quadrifine venation. To understand character evolution in higher noctuoids and major nolids, I undertook a character optimization analysis based on parsimony using the software Mesquite v2.75 (Maddison & Maddison, 2011). My results of ancestral-state reconstructions and character optimization (Fig. 5) showed that most traits—those characters that are considered to be of phylogenetic significance—are clearly synapomorphic for major lineages of quadrifids, except the hindwing venation which was an ambiguous character state (**IV**). It is generally thought that the pseudoquadrifine condition is the ancestral state for Noctuoidea. This condition concerns the position of three veins (M2, M3 and CuA1), in which M2 arises about one-third of the way up the discal cell, and M2 is strong and parallel to M3. My character examinations indicated that the pseudoquadrifine condition is shared by the basal lineages of Noctuidae s.s. (i.e., Bagisarinae, Plusiinae, Dilobinae and Pantheinae) (**V**), and a few erebid subfamilies (Hypeninae, Herminiinae, Scoliopteryginae and Rivulinae) (**II**), as well as Diphtherinae (Nolidae) (**IV**). I evaluated the distribution patterns and evolutionary trends of this complex trait under the two most commonly used character optimization algorithms of parsimony analysis: ACCTRAN—accelerated transformation—and DELTRAN—delayed transformation—(Agnarsson & Miller, 2008). I finally favoured DELTRAN optimization (**IV**), which minimizes reversals and maximizes convergences and parallel evolution. This favours the acquisition of the derived quadrifine state—base of M2 close to M3—independently in Erebidae, Nolidae (with Diphtherinae excluded), and Euteliidae (Fig. 5). In other words, the plesiomorphic condition of M2 in the hindwing of the four quadrifid lineages is the form found in Diphtherinae and basal lineages of Noctuidae, and arguably some basal lineages of Erebidae. This trend of character evolution can be traced by checking the position of the vein M2 in different groups of quadrifids. For instance, the condition of M2 in Diphtherinae is exactly the same condition that occurs in Pantheinae, Plusiinae, Dilobinae and Bagisarinae (**V**), where M2 is very slightly reduced. In higher noctuids (i.e., Hadeninae) the vein is still visible in exactly the same position, but is even more reduced, and then entirely lost in Noctuinae (Fibiger & Lafontaine, 2005). In the Erebidae lineage, M2 is seen in this condition in some primitive lineages (e.g., Rivulinae, Hypeninae, and Herminiinae). As a consequence, the quadrifine (M2 adjacent to M3) form of venation must have been independently gained several times within Erebidae, acquired once in Nolidae (after the Diphtherinae lineage branched off), and once in Euteliidae (Fig. 5). Thus, all these so-called primitive lineages have retained the ancestral (symplesiomorphic) hindwing venation trait with a pseudoquadrifine condition (Fig. 5).

3.5 Evolution of host-plant associations in Noctuoidea

There have been few attempts to study the evolution of host-plant use in Noctuoidea. The results from the character optimizations (**IV**) drove me to learn more about the evolution of feeding habits in higher noctuoids. One feature that has been suggested as the prime factor governing the evolution of butterfly-host plant associations, is host growth form, which appears, on the whole, to be more conserved phylogenetically than host-plant taxon affiliation (Janz & Nylin, 1998). Given its prevalence among the deeper lineages, woody-plant feeding can be

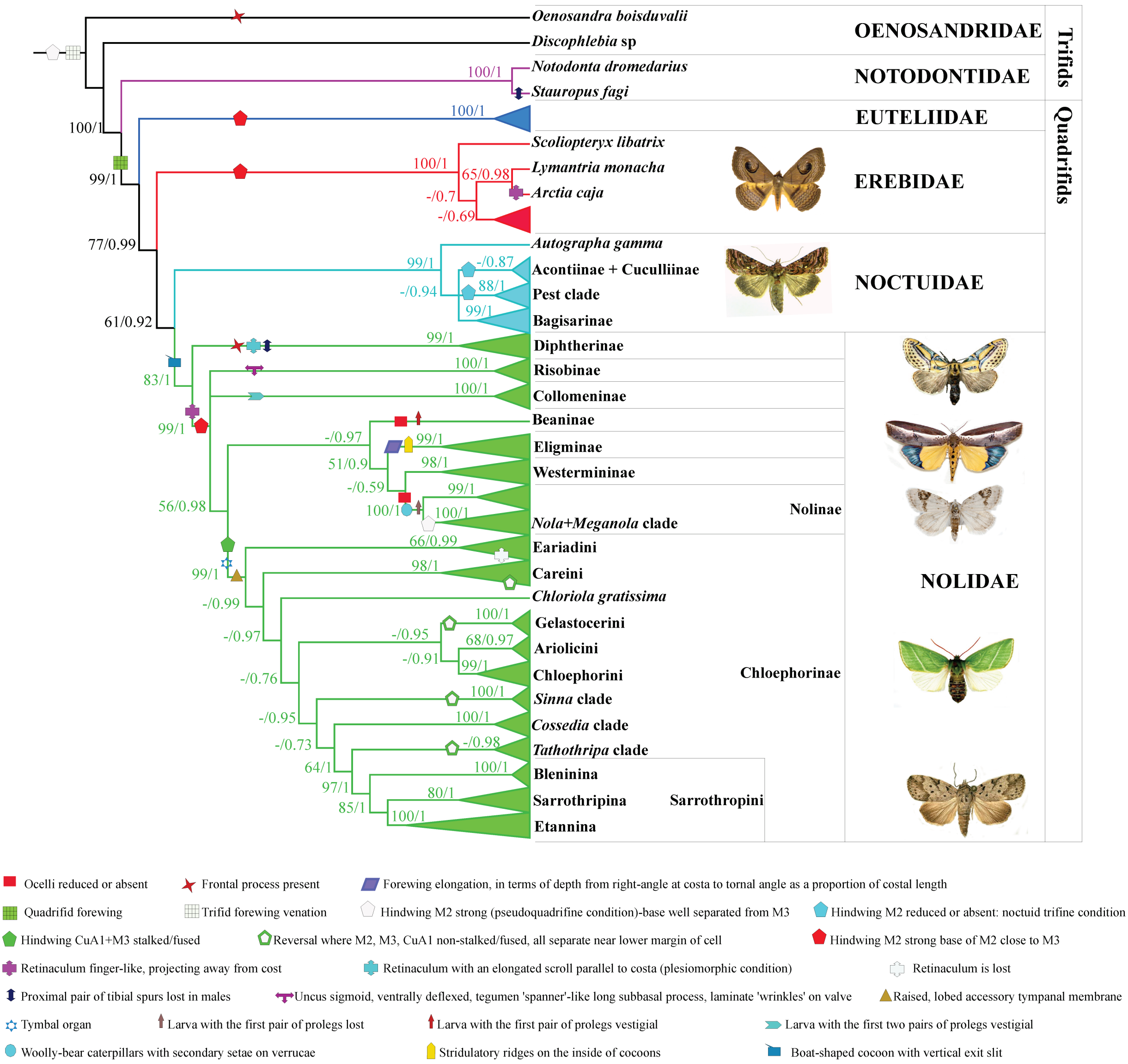


Fig. 5 Summary of ancestral states reconstruction on Bayesian tree under DELTRAN optimization. Clades representing higher taxa (i.e., families) are coloured. Support values under the two support measures (bootstrap/posterior probabilities) shown next to the branches. Coloured characters on terminal branches and internal nodes indicate the presence of morphological traits as shown below the tree. Names of moths shown in figure from top to bottom are: *Spirama* (Erebidae, Erebinae), *Autographa* Hübner (Noctuidae, Plusiinae), *Diphthera* (Nolidae: Diphtherinae), *Eligma* Hübner (Nolidae: Eligminae), *Nola* Leach (Nolidae, Nolinae), *Pseudoips* Hübner (Nolidae, Chloephorinae, Chloephorini), *Giaura* Walker (Nolidae, Chloephorinae, Sarrothripini).

reasonably inferred as ancestral for entire Noctuoidea (Holloway, 1989, Mitchell *et al.*, 2006), as it is, apparently, for most other macrolepidopteran superfamilies (Powell *et al.*, 1998).

Within Noctuoidea, arboreal feeding is predominant among the oldest and basal lineages in trifid families—Oenosandridae and Notodontidae—and, within quadrifids, in diverse lineages of Erebidae (e.g., many Erebinae, Aganainae, Lymantriinae, etc.) as well as Euteliidae (Table 1). My results corroborate those of previous results (Forbes, 1923, Holloway, 1987, Weller, 1989, Miller, 1991, Richards, (1933) 1932) in accepting that trifids are the plesiomorphic sister lineage to the rest of Noctuoidea (i.e. quadrifid Noctuoidea) (**I, II, IV, V**). For example, the family Oenosandridae—only known from Australia—mainly feeds on the woody plant family Myrtaceae (Miller, 1991). In Notodontidae—with a worldwide distribution but more diverse in tropics and especially the Neotropics (Weller, 1989, Miller, 1991)—almost all species feed on trees, and only a few are found on herbaceous plants (Miller, 1991). Within Euteliidae, Euteliinae most commonly feed on Anacardiaceae (Powell *et al.*, 1998), a plant family that contains trees and shrubs with highly poisonous flowers. Among their other prominent hosts are Burseraceae (includes both shrubs and trees), Dipterocarpaceae (mainly tropical lowland rainforest trees), Moraceae and Hamamelidaceae (which consists of small trees and shrubs) (Holloway, 1985, Powell *et al.*, 1998). Stictopterinae, the sister group of Euteliinae, is associated primarily with Dipterocarpaceae and Clusiaceae (Table 1). Within quadrifids, where tree feeding is probably also ancestral, it seems clear that there have been many independent colonizations and subsequent radiations on herbaceous plants, most spectacularly in Arctiinae (Erebidae) and derived trifine lineages (e.g., the pest clade). Although, the great majority of quadrifids feed on living higher plants, consumption of lower plants and detritus has arisen in several groups, most notably Erebidae (**II**). For example, lichen-feeding is predominant among lithosiines (Arctiinae) and a number of Aventiini (Boletobiinae) species (Wagner *et al.*, 2008), while detritivory, mycophagy and algivory is dominant in Herminiinae and Boletobiinae (**II**) and recurs sporadically in other noctuid subfamilies (e.g., some Bryophilinae, see Table 1) (**V**).

The results in paper **V** also suggested that Noctuidae included a number of lineages that are exclusively arboreal feeders, such as Dilobinae (Rosaceae), Raphiinae (Salicaceae), Pantheinae (Pinaceae) and Acronictinae (polyphagous but mostly on trees) (Table 1). The first three of these groups are associated with basal Noctuidae lineages in my phylogenetic hypothesis (Fig. 6)—those characterized by the plesiomorphic pseudoquadrifine condition of the hindwing venation. There are also a few groups among the derived noctuid lineages that generally feed on trees and shrubs, such as some Xylenini, Psaphidini (Mitchell *et al.*, 2006), and Orthosiini. Some other subfamilies are more specialized; for example, Agaristinae, often show a strong preference for Vitaceae (Holloway, 1989). My review of major trends in feeding habits in the subfamily Dyopsinae (Table 1) indicates that most of them feed on the plant family Urticaceae, a flowering plant family of mostly trees and shrubs. In contrast, herbaceous-feeding larvae are predominant in the higher trifines (i.e., the ‘pest clade’, Amphipyrinae, Metoponiinae, etc.).

Table 1 Larval host-plant families for Noctuidae study taxa. Zoogeographic regions are abbreviated as follows: P = Palaearctic; O = Oriental; Au = Australasia; Nea = Nearctic; Neo = Neotropical; Af = Afrotropical.

Family	Subfamily	Tribe	Species	Main host-plant family	Main Host-plants	Host growth form	Typical distribution
			Outgroup				
Notodontidae	Notodontinae		*Notodonta dromedarius*	Betulaceae	*Betula*	Trees	P
Notodontidae	Thaumetopoeinae		*Thaumetopoea solitaria*	Pinaceae/Anacardiaceae	*Pistacia*	Trees	P/O/Af
Euteliidae	Euteliinae		*Eutelia adulatrix*	Anacardiaceae/Hamamelidaceae	*Rhus/Liquidambar/ Altingia*	Trees	P
Euteliidae	Euteliinae		*Targalla subocellata*	Myrtaceae	*Eugenia* spp	Trees	O/Au
Euteliidae	Stictopterinae		*Lophoptera squammigera*	Dipterocarpaceae/Euphorbiaceae/ Malvaceae	*Shorea/Grewia*	Herbs/Trees	O
Euteliidae	Stictopterinae		*Stictoptera columba*	Clusiaceae (=Guttiferae)	*Calophyllum/Garcinia/Mesua*	Trees	O
Erebidae	Erebinae	Catocalini	*Catocala sponsa*	Fagaceae	*Quercus*	Trees	P
Erebidae	Lymantriinae	Lymantriini	*Lymantria monacha*	Polyphagous	Polyphagous	Trees	P
Erebidae	Arctiinae	Arctiini	*Arctia caja*	Polyphagous	Polyphagous	Herbs/Trees	P/Nea
Erebidae	Calpinae	Calpini	*Calyptra thalictri*	Ranunculaceae/Menispermaceae	*Thalictrum/* vines	Herbs	P
Nolidae	Collomeninae		*Neostictoptera nigropuncta*	–	–	–	Neo
Nolidae	Collomeninae		*Collomena siopera*	Combretaceae	*Terminalia*	Trees	Neo
Nolidae	Eligminae		*Eligma narcissus*	Simaroubaceae	*Ailanthus*	Trees	O
Nolidae	Chloephorinae	Chloephorini	*Pseudoips prasinana*	Fagaceae/Salicaceae	*Fagus/Quercus/Populus*	Trees	P
			Ingroup				
Noctuidae	Dyopsinae	Dyopsini	*Dyops chromatophila*	Urticaceae	*Cecropia*	Trees	Neo
Noctuidae	Dyopsinae	Arcteini	*Pseudoarcte melanis*	–	–	–	Af
Noctuidae	Dyopsinae	Arcteini	*Arcte modesta*	Urticaceae/Ulmaceae	*Boehmeria/Debregeasia/Trema*	Shrubs/small trees	O
Noctuidae	Dyopsinae	Arcteini	*Pararcte schneideriana*	Urticaceae	*Cecropia*	Trees	Neo
Noctuidae	Dyopsinae	Ceroctenini	*Belciana kala*	Malvaceae	*Grewia/Heritiera*	Trees	O
Noctuidae	Dyopsinae	Ceroctenini	*Belciana biformis*	Malvaceae	*Grewia/Heritiera*	Trees	O
Noctuidae	Dyopsinae	Ceroctenini	*Cyclodes omma*	Arecaceae	palm trees	Trees	O
Noctuidae	Dyopsinae	Ceroctenini	*Ceroctena amynta*	Meliaceae	*Trichilia*	Shrubs/trees	Neo
Noctuidae	Dyopsinae	Ceroctenini	*Sosxetra grata*	Meliaceae	*Trichilia*	Shrubs/trees	Neo
Noctuidae	Plusiinae	Plusiini	*Autographa gamma*	Polyphagous	Polyphagous	Herbs/Shrubs	P/Nea
Noctuidae	Plusiinae	Abrostolini	*Abrostola tripartita*	Urticaceae	*Urtica dioica*	Herbs	P
Noctuidae	Eustrotiinae		*Deltote uncula*	Cyperaceae	*Carex*	Herbs	P
Noctuidae	Cuculliinae		*Cucullia umbratica*	Asteraceae	Oligophagous	Herbs	P
Noctuidae	Dilobinae		*Diloba caeruleocephala*	Rosaceae	*Malus/Prunus/Pyrus/Sorbus*	Trees	P
Noctuidae	Raphiinae		*Raphia abrupta*	Salicaceae/Betulaceae	*Populus/Betula*	Trees	Nea
Noctuidae	Pantheinae	Eucocytiini	*Eucocytia meeki*	–	–	–	Au
Noctuidae	Pantheinae	Pantheini	*Thiacidas* sp.	Rhamnaceae/Fabaceae	*Ziziphus/Acacia*	Shrubs/Trees	O
Noctuidae	Pantheinae	Pantheini	*Antitrisuloides catocalina*	–	–	–	O
Noctuidae	Pantheinae	Pantheini	*Panthea coenobita*	Pinaceae	*Pinus*	Trees	P
Noctuidae	Acontiinae		*Emmelia trabealis*	Convolvulaceae	*Convolvulus*	Herbs	P
Noctuidae	Acontiinae		*Acontia lucida*	Convolvulaceae	*Convolvulus*	Herbs	P
Noctuidae	Bagisarinae		*Amyna octo*	Polyphagous	Polyphagous	Herbs	Neo/Nea/O/Au/Af

Continuation of **Table 1**.

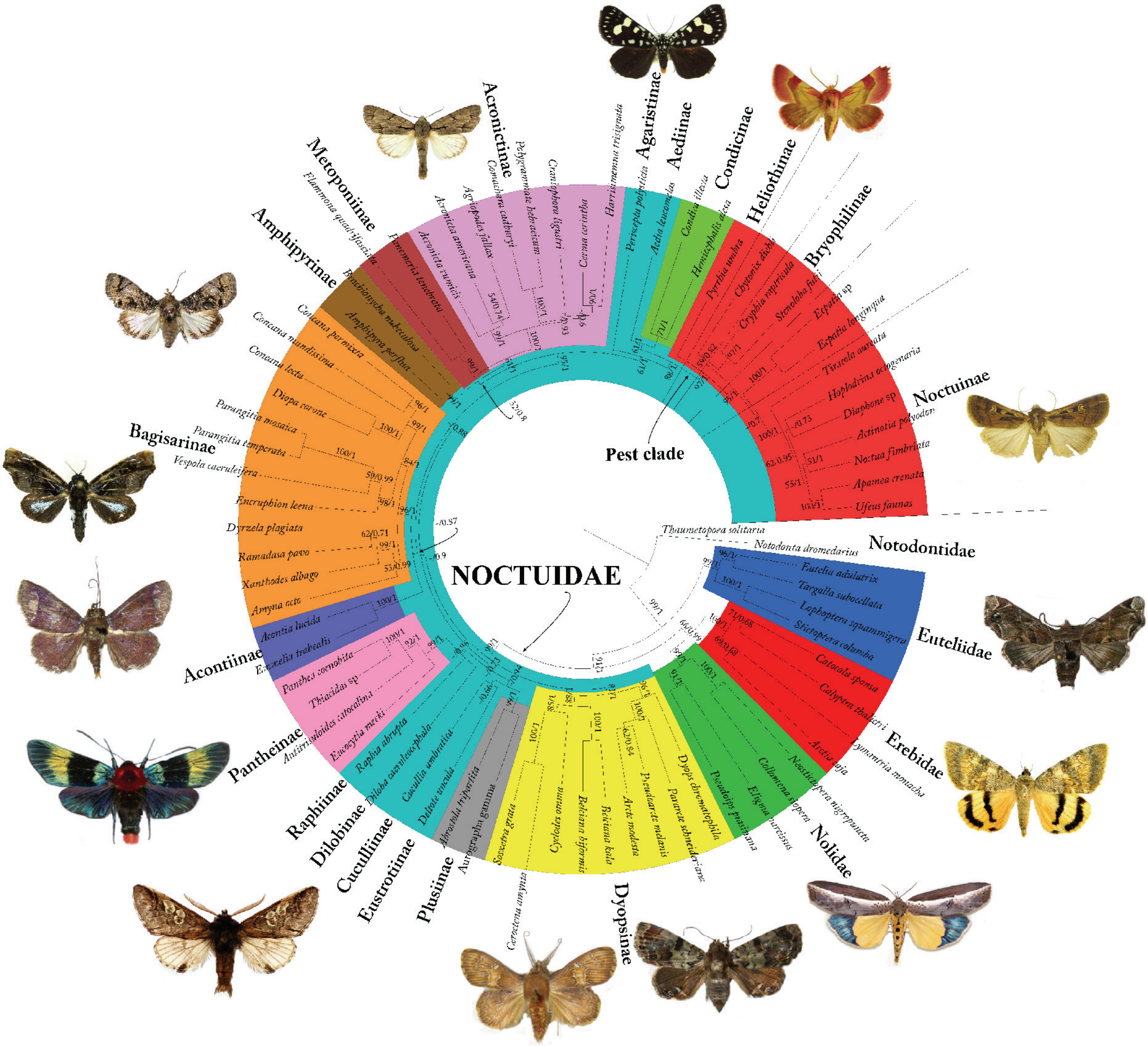
Noctuidae	Bagisarinae		*Xanthodes albago*	Malvaceae	Oligophagous	Herbs	O/Af//Au
Noctuidae	Bagisarinae		*Ramadasa pavo*	–	–	–	O
Noctuidae	Bagisarinae		*Dyrzela plagiata*	Malvaceae	*Grewia*	Trees	O
Noctuidae	Bagisarinae		*Encruphion leena*	Malvaceae	*Luehea*	Trees	Neo
Noctuidae	Bagisarinae		*Vespola caeruleifera*	Malvaceae	*Ceiba pentandra*	Trees	Neo
Noctuidae	Bagisarinae		*Parangitia temperata*	Moraceae	*Maclura*	Trees	Neo
Noctuidae	Bagisarinae		*Parangitia mosaica*	Malvaceae/Moraceae	–	Trees	Neo
Noctuidae	Bagisarinae		*Diopa corone*	Ochnaceae/Malvaceae	*Cespedesia/Pachira*	Shrubs/Trees	Neo
Noctuidae	Bagisarinae		*Concana mundissima*	Malpighiaceae	*Heteropterys/Byrsonima*	Shrubs/Trees	Neo
Noctuidae	Bagisarinae		*Concana lecta*	Malpighiaceae	*Banisteriopsis*	Trees	Neo
Noctuidae	Bagisarinae		*Concana permixta*	Malpighiaceae	–	–	Neo
Noctuidae	Amphipyrinae	Amphipyrini	*Amphipyra perflua*	Polyphagous	Polyphagous	Shrubs	P
Noctuidae	Amphipyrinae	Psaphidini	*Brachionycha nubeculosa*	Polyphagous	Polyphagous	Shrubs/Trees	P
Noctuidae	Metoponiinae		*Flammona quadrifasciata*	Orchidaceae	orchids	Epiphytes	O
Noctuidae	Metoponiinae		*Panemeria tenebrata*	Caryophyllaceae	*Cerastium*	Herbs	P
Noctuidae	Acronictinae		*Craniophora ligustri*	Betulaceae/Oleaceae	*Alnus/Fraxinus*	Trees	P
Noctuidae	Acronictinae		*Acronicta americana*	Polyphagous	Polyphagous	Trees	Nea
Noctuidae	Acronictinae		*Acronicta rumicis*	Polyphagous	Polyphagous	Trees	P
Noctuidae	Acronictinae		*Cerma cerintha*	Rosaceae	*Prunus/ Malus*	Trees	Nea
Noctuidae	Acronictinae		*Comachara cadburyi*	Cornaceae	*Nyssa sylvatica*	Trees	Nea
Noctuidae	Acronictinae		*Harrisimemna trisignata*	Polyphagous	Polyphagous	Trees	Nea
Noctuidae	Acronictinae		*Polygrammate hebraeicum*	Cornaceae	*Nyssa sylvatica*	Trees	Nea
Noctuidae	Acronictinae		*Agriopodes fallax*	Adoxaceae	*Viburnum*	Shrubs	Nea
Noctuidae	Agaristinae		*Periscepta polysticta*	Dilleniaceae	*Hibbertia*	Shrubs	Au
Noctuidae	Aediinae		*Aedia leucomelas*	Convolvulaceae	*Ipomoea/Convolvulus*	Herbs	Au/O
Noctuidae	Condicinae		*Condica illecta*	Asteraceae	*Carthamus/Coreopsis*	Herbs	O
Noctuidae	Condicinae		*Hemicephalis alesa*	Boraginaceae	*Cordia panamensis*	Shrubs	Nea
Noctuidae	Heliothinae		*Pyrrhia umbra*	Polyphagous	Polyphagous	Shrubs	P
Noctuidae	unassigned		*Chytonix diehli*	–	–	–	O
Noctuidae	Bryophilinae		*Cryphia raptricula*	Lichenes	Lichenes	Lichenes	P
Noctuidae	Bryophilinae		*Stenoloba futii*	Lichenes	Lichenes	Lichenes	O
Noctuidae	unassigned		*Ecpatia* sp.	Phyllanthaceae	–	shrubby	O
Noctuidae	unassigned		*Ecpatia longinquua*	Phyllanthaceae	*Antidesma*	shrubby	O
Noctuidae	Noctuinae		*Tiracola aureata*	Polyphagous	Polyphagous	Herbs	O
Noctuidae	Noctuinae		*Actinotia polyodon*	Hypericaceae	*Hypericum*	Herbs	P
Noctuidae	Noctuinae		*Hoplodrina octogenaria*	Polyphagous	Polyphagous	Herbs	P
Noctuidae	Noctuinae		*Diaphone* sp.	Polyphagous	Polyphagous	Herbs	Af
Noctuidae	Noctuinae	Apameini	*Apamea crenata*	Poaceae	Oligophagous	Grass	P
Noctuidae	Noctuinae		*Ufeus faunas*	Salicaceae	*Salix/Populus*	Trees	Nea
Noctuidae	Noctuinae	Noctuini	*Noctua fimbriata*	Polyphagous	Polyphagous	Herbs	P

These results are also widely corroborated by the study of Mitchell *et al.* (2006), who studied the role of ecological and geographical factors in the diversification of Noctuoidea. They presented a provisional synopsis of species diversity, latitudinal distribution, and host-plant use for major noctuoid groups sampled in their study, superimposed onto the phylogeny. It is revealed that the growth form (i.e., woody-plant feeding vs. herb-feeding) of the host-plant appears on the whole more conserved phylogenetically than host-plant taxon affiliation, where woody-plant feeding can be reasonably inferred as ancestral for Noctuoidea, as it is, apparently, for most other macrolepidopteran superfamilies.

In general, herbaceous-feeding larvae are predominant in the higher trifines (i.e., the ‘pest clade’, Amphipyrinae, Metoponiinae, etc.), whereas in the basal noctuid and basal trifines lineages arboreal feeding is predominant. This evolutionary pattern of feeding habits, postulating a general evolutionary trend from a tree feeding to a herb feeding habit, has also been shown for butterflies (Janz & Nylin, 1998). Thus it can be suggested that the host-growth form in Noctuoidea is more evolutionarily conservative than host affiliation (Mitchell *et al.*, 2006). However, my preliminary study of host-plant associations showed that in a few Noctuidae subfamilies a strong preference toward feeding on a specific plant family can be seen, such as Bagisarinae which feed mainly on Malvaceae.

One of the fundamental reasons for studying the evolutionary history of noctuoid moths is to determine the main driving forces behind the diversification of this species-rich group. It has become apparent that the evolution of host-plant use has likely been a key ecological mechanism behind the rapid diversification and evolutionary divergence in the butterfly families (Janz & Nylin, 1998, Janz *et al.*, 2006). Noctuoidea are about three times more diverse than the butterflies, and the role of host plant specialization in the diversification of the moths has yet to be studied in detail. With the phylogenetic relationships of the major lineages of Noctuoidea becoming clearer (**I, II, IV, V**), questions about host plant associations and diversification can now be addressed for this megadiverse clade.

Fig. 6 Phylogenetic hypothesis of the basal Noctuidae subfamilies, based on a Bayesian inference analysis. Clades representing major lineages are coloured. Support values under the two support measures (Bootstrap/posterior probabilities) shown next to the branches. Names of moths shown in figure clockwise are: *Eutelia* (Euteliidae); *Catocala* (Erebidae); *Eligma* (Nolidae); *Dyops* (Noctuidae Dyopsinae, Dyopsini), *Sosxetra* Walker (Dyopsinae, *Ceroctena* clade), *Diloba* Boisduval (Dilobinae), *Eucocytia* (Pantheinae), *Amyna* Guenée (Bagisarinae), *Vespola* Walker (Bagisarinae), *Concana* Walker (Bagisarinae), *Acronicta* Ochsenheimer (Acronictinae), *Periphanes* (Heliothinae), *Euxoa* Hübner (Noctuinae).


NOCTUIDAE
Pest clade
Agaristinae
Aediinae
Condicinae
Heliothinae
Bryophilinae
Noctuinae
Notodontidae
Euteliidae
Erebidae
Nolidae
Dyopsinae
Plusiinae
Eustrotiinae
Cuculliinae
Dilobinae
Raphiinae
Pantheinae
Acontiinae
Bagisarinae
Amphipyrinae
Metoponiinae
Acronictinae
Harrisimemna trisignata
Cerma cerintha
Craniophora ligustri
Polygrammate hebraeicum
Comachara cadburyi
Agriopodes fallax
Acronicta americana
Acronicta rumicis
Panemeria tenebrata
Flammona quadrifasciata
Brachionycha nubeculosa
Amphipyra perflua
Conceana permixta
Conceana mundissima
Conceana lecta
Diopa carone
Parangitia mosaica
Parangitia temperata
Vespola caeruleifera
Encruphion leena
Dyrzela plagiata
Ramadasa pavo
Xanthodes albago
Amyna octo
Acontia lucida
Emmelia trabealis
Panthea coenobita
Trichosea / Thiacidas sp
Antitrisuloides catocalina
Euocytia mecki
Raphia abrupta
Diloba caeruleocephala
Cucullia umbratica
Deltote uncula
Abrostola tripartita
Autographa gamma
Ceratiena amyntas
Sosxetra grata
Cyclodes omma
Baileyna bijiformis
Beintania kala
Arcte modesta
Pseudarcte malanis
Paracte schneideriana
Dyops dromatophila
Pseudoips prasinana
Elygea narcissus
Collomena filifera
Neostictoptera nigropuncta
Lymantria monacha
Arctia caja
Calyptra thalictri
Catocala sponsa
Stictoptera columba
Lophoptera squammigera
Targalla subocellata
Eutelia adulatrix
Notodonta dromedarius
Thaumetopoea solitaria
Periscepta polysticta
Aedia leucomelas
Condica illecta
Hemicephalis alesa
Pyrrhia umbra
Chytonix diabi
Cryphia raptricula
Stenoloba fibrilla
Ecpatia sp
Ecpatia longinquua
Tiracola aureata
Hoplodrina octogenaria
Diaphone sp
Actinotia polyodon
Noctua fimbriata
Apamea crenata
Ufeus faunus

4. CONCLUSIONS AND FUTURE DIRECTIONS

4.1 Conclusions

To conclude my Ph.D. thesis, I have summarized a number of distinctive issues and strategies that I have employed in this thesis that are different from those in previous works.

First of all and probably the most important scheme was the taxon sampling strategy. Elucidating the evolutionary history of the massive superfamily Noctuoidea clade (potentially including 45,000 species) required extensive taxon sampling. A deliberate and carefully considered sampling strategy could only be accomplished by selecting exemplars from significant groupings of genera and morphologically well-supported concepts of higher taxa. In my five projects, I chose up to 393 taxa (Appendix 1) of 45,000 noctuoids that have been formally described, covering almost all recognized major clades of Noctuoidea, as representatives for major lineages of Noctuoidea. This extensive taxon sampling was made possible through the extensive network that I built up during my studies. One of the main causes for the previous low support of phylogenetic relationships for some massive clades probably stems from very sparse sampling.

The second feature was the obstacles that are met in applying morphological traits, in particular, in a species-rich, cosmopolitan and heterogeneous taxon such as Noctuoidea. The high number of species presents complications to the use of morphology and any other kinds of phenotypic traits at this taxonomic level. Morphological data are thus often difficult to homologize and code, require great experience to identify character states correctly and can be subject to extensive homoplasy (character convergence and reversal). Consequently, despite their major role in inferring phylogenies, morphological analyses have often failed to determine relationships among most groups with confidence. On the other hand, phenotypic traits (e.g., morphological, ecological, host-plant associations, behavioural characters, etc.) and synapomorphies can be properly recognized from molecular phylogeny-based systems. In the context of such a robust evolutionary hypothesis, morphological, ecological and behavioural characters can be better understood. For example, I demonstrated that the prespiracular counter-tympanal hood of Aganainae, Herminiinae and Arctiinae is not the result of convergent (independent) evolutionary events, as previously thought (**I**–**II**). I proved that this is the result of a common ancestry of these groups within the family Erebidae (**II**). Polyphyly of the old concept of Calpinae was another clear case (**II**–**III**). My results recovered a monophyletic subfamily Calpinae that was restricted to three monophyletic tribes (i.e., Phyllodini, Ophiderini and Calpini) (**III**), and placed all other groups that had previously been placed as tribes within Calpinae (e.g., Anobini, Anomini and Scoliopterygini), as independent and distant well-defined lineages (i.e., Scoliopteryginae and Anobinae) within Erebidae (**II**). Calpinae sensu lato was traditionally restricted to the fruit-piercing (and in some cases skin piercing and blood sucking) moths (Kitching & Rawlins, 1998). However, my molecular phylogeny revealed that this feeding behavior, as well as its associated modifications of the proboscis and adaptations (**III**), have evolved independently in Calpinae, Scoliopteryginae (including Anomini), Anobinae and some Erebinae (**II**). This provides again an object lesson on how the sharing of peculiar morphological adaptations may mislead in classification, and how shared features of a more subtle nature may be overlooked in an unchallenged traditional classification (**I**). Other examples of discovering morphological apomorphies based on my molecular phylogeny results were in Diphtherinae—characterized by the loss of the proximal pair of tibial spurs on the hindlegs of males and the presence of a frontal tubercle—(**IV**), Nolidae—construction of a boat-shaped cocoon with a vertical exit slit, and finger-like retinaculum on the forewings of the males—(**IV**), trifid and quadrifid lineages—condition of vein M2 in forewing—(**I, II, IV, V**), host-plant associations—e.g., detritivory, lichen-feeding, mycophagy and algivory—in Boletobiinae (Erebidae) (**II**) and finally speculation for a potential broad evolutionary feeding habit trend in Noctuoidea from tree feeding in trifid lineages toward herb feeding in more derived lineages (i.e., pest clade in Noctuidae), similar to the pattern that has been suggested for butterflies (Janz & Nylin, 1998).

A third issue was related to determining the evolutionary relationships of noctuoid taxa of uncertain systematic position using molecular data. In particular, those taxa characterized by the pseudoquadrifine hindwing venation, which have been previously assigned to various noctuoid groups (**IV**–**V**). Molecular phylogenetics methods illustrate how easy is it can be to pinpoint their certain phylogenetic position.

To conclude, I had been able to address a massive and long-recalcitrant phylogenetic problem, that of the relationships among and within major lineages of the largest superfamily of Lepidoptera, Noctuoidea. The phylogenetic analyses that I employed were well designed, and many relatively deep nodes are strongly resolved and substantial progress has been made on the backbone phylogeny of Noctuoidea. This group of insects is of major economic and ecological importance. It constitutes an exemplar case in which molecular methods, which seem to be highly informative at this level, have been of enormous help, in part because the sheer size of the group has greatly impeded progress via the morphological approach.

4.2 Future directions

This Ph.D. thesis addressed several phylogenetic problems concerning the evolution of Noctuoidea, but there are still many unanswered questions. For example, it is crucial to determine where, when and how the major groups of noctuoids diverged and evolved. The common factors that influence the speciation process and identifying possible reasons for this remarkable and extraordinary diversity of species among other herbivorous insects are not yet understood. Likewise, the patterns of diversification, the main driving forces behind the diversification of this species-rich group, and plausible explanations for the differences in diversity among the various groups within Noctuoidea have yet to be determined—for instance, why does a family such as Euteliidae contain about 500 species, but another like Erebidae contains 25,000 species? It would be of great interest to know whether major climatic changes and mass extinction events over geological time scales have had a major impact on the diversification of Noctuoidea. And it would be most interested to infer a scenario of the evolutionary history and biogeography of noctuoids, based on all available data (i.e., morphology, DNA sequences, ecological data, geographical distributions, and geological and paleontological information).

Further studies are also needed to identify the reasons and causes for the short basal branches, i.e., whether there is a historical explanation behind them (e.g., rapid radiation), or whether it is simply an artefact of insufficient data.

The use of novel tools in DNA sequencing technologies, such as Next-Generation Sequencing (NGS) methods and relatively new field of phylogenomics, might be able to address the state of uncertainty in Noctuoidea diversification and their rapid radiations. Phylogenomics is useful for evolutionary studies, in particular resolving ambiguous phylogenies and for verifying relationships created on the basis of a few gene regions (Hackett *et al.*, 2008). Since the cost of whole genome sequencing is decreasing, anticipation of total genome sequences from the major lineages of interest, is no longer a distant dream (Murphy *et al.*, 2004).

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APPENDIX

Family	Subfamily	Species	Paper	Specimen ID	COI-LCO	COI-Jerry	EF1 −α-begin	EF1 −α-end	Wingless	GAPDH	RpS5	MDH	CAD	IDH	Type status	Locality
		Outgroup														
Drepanidae	Thyatirinae	*Thyatira batis*	**I**	MM00027	GU828580	GU828380	GU828919	GU829212	GU829481	GU829743	GU830597	GU830293	GU828083	GU829969	TG/TS	FINLAND
Sphingidae	Sphinginae	*Sphinx ligustri*	**I**	NW141-12	EU141358	EU141358	EU136665	EU136665	EU141239	EU141494	EU141391	EU141615	EU141313	EU141550	TG/TS	FINLAND
Bombycidae	Bombycinae	*Bombyx mori*	**I**	NW149-1	EU141360	EU141360	EU136667	EU136667	EU141241	EU141495	EU141393	EU141617	EU141315	EU141552	TG/TS	USA
Geometridae	Archiearinae	*Archiearis parthenias*	**I**	NW107-1	DQ018928	DQ018928	DQ018899	DQ018899	DQ018869	EU141485	EU141381	EU141604	EU141303	EU141539	TG/TS	SWEDEN
		Ingroup														
Oenosandridae		*Oenosandra boisduvali*	**I,II,IV**	MM07590	GU828791	GU929762	GU829098	GU829377	GU829651	GU829871	GU830751	GU830492	GU828266	GU830173	TG/TS	AUSTRALIA
Oenosandridae		*Discophlebia sp.*	**I,IV**	RZ403	HQ006217	HQ006921	HQ006313	HQ006404	HQ006825	HQ006480	HQ006729	HQ006638	–	HQ006551		AUSTRALIA
Notodontidae	Phalerinae	*Phalera bucephala*	**I,II**	MM00122	GU828607	GU828405	GU828941	GU829235	GU829502	–	GU830617	GU830318	GU828108	GU829995	TG/TS	FINLAND
Notodontidae	Heterocampinae	*Stauropus fagi*	**I,II,IV**	MM00981	GU828651	GU828449	GU828983	GU829266	GU829539	GU829780	GU830650	GU830357	GU828148	GU830038	TS	FINLAND
Notodontidae	Notodontinae	*Notodonta dromedarius*	**I,II,IV,V**	MM00998	GU828653	GU828451	GU828984	GU829268	GU829540	GU829781	GU830652	GU830359	GU828150	GU830040	TG/TS	FINLAND
Notodontidae	Pygaerinae	*Clostera pigra*	**I**	MM01005	GU828654	GU828452	GU828985	GU829269	GU829541	GU829782	GU830653	GU830360	GU828151	GU830041		FINLAND
Notodontidae	Thaumetopoeinae	*Epicoma melanosticta*	**I**	MM07592	GU828792	GU929763	GU829099	GU829378	GU829652	GU829872	GU830752	GU830493	GU828267	GU830174		AUSTRALIA
Notodontidae	Thaumetopoeinae	*Thaumetopoea solitaria*	**I,V**	MM09888	GU828843	GU929807	GU829144	–	GU829692	GU829904	GU830791	GU830534	GU828307	GU830223	TG	GREECE
Notodontidae	Dudusinae	*Crinodes besckei*	**I**	05-SRNP-57213	GU828527	–	GU828873	GU829175	GU829434	–	GU830563	GU830251	GU828039	GU829918		COSTA RICA
Notodontidae	Nystaleinae	*Nystalea striata*	**I**	05-SRNP-4443	GU828525	–	GU828871	GU829173	GU829432	GU829717	GU830561	GU830249	GU828037	GU829916	TG	COSTA RICA
Notodontidae	Dioptinae	*Scotura leucophleps*	**I**	06-SRNP-22781	GU828532	GU828334	GU828878	GU829179	GU829439	GU829721	GU830568	GU830256	GU828044	GU829923		COSTA RICA
Euteliidae	Euteliinae	*Eutelia adulatrix*	**I,II,V**	MM00160	GU828621	GU828419	GU828956	GU829246	GU829516	GU829764	GU830629	GU830330	GU828122	GU830010	TG/TS	GREECE
Euteliidae	Euteliinae	*Eutelia geyeri*	**IV**	RZ508	X	X	X	X	X	X	X	X	–	X	TG	HONG KONG
Euteliidae	Euteliinae	*Marathyssa basalis*	**I**	RZ23	HQ006183	HQ006887	HQ006279	HQ006374	HQ006791	HQ006455	HQ006698	HQ006606	HQ006979	HQ006528	TS	USA
Euteliidae	Euteliinae	*Targalla subocellata*	**I,II,IV,V**	RZ35	HQ006210	HQ006914	HQ006306	HQ006397	HQ006818	HQ006473	HQ006722	HQ006631	HQ007000	–		HONG KONG
Euteliidae	Stictopterinae	*Aegilia describens*	**II**	RZ287	JN401234	JN401118	JN401352	–	JN400927	JN401566	JN401873	JN401772	JN401036	–	TS	INDONESIA
Euteliidae	Stictopterinae	*Lophoptera hemithyris*	**I,II**	MM07614	GU828802	GU929772	GU829107	GU829385	GU829661	GU829879	GU830759	GU830501	GU828274	GU830183		AUSTRALIA
Euteliidae	Stictopterinae	*Lophoptera squammigera*	**IV,V**	RZ120	X	X	X	X	X	X	X	X	–	X	TG	HONG KONG
Euteliidae	Stictopterinae	*Stictoptera columba*	**IV,V**	RZ541	X	X	X	X	X	–	X	X	–	X	TG	MALAYSIA
Erebidae	Scoliopteryginae	*Scoliopteryx libatrix*	**I,II,IV**	MM00407	GU828641	GU828439	GU828975	GU829260	GU829532	–	GU830643	GU830348	GU828140	GU830028	TG/TS	FINLAND
Erebidae	Scoliopteryginae	*Ossonoba torpida*	**II**	RZ411	JN401252	JN401134	JN401369	JN401480	JN400939	JN401582	JN401893	–	JN401050	–	TS	MALAYSIA
Erebidae	Scoliopteryginae	*Rusicada fulvida*	**II**	RZ101	JN401253	JN401135	JN401370	JN401481	JN400983	JN401583	JN401894	JN401790	JN401051	JN401683		HONG KONG
Erebidae	Scoliopteryginae	*Rusicada metaxantha*	**I,II**	RZ55	HQ006227	HQ006930	HQ006322	HQ006414	HQ006835	–	HQ006739	HQ006647	HQ007016	HQ006560	TG	TAIWAN
Erebidae	Scoliopteryginae	*Gonitis involuta*	**I,II**	RZ13	HQ006166	HQ006963	HQ006263	HQ006357	HQ006775	–	HQ006682	HQ006592	HQ006963	–	TG	TANZANIA
Erebidae	Scoliopteryginae	*Anomis flava*	**II**	RZ100	JN401254	JN401136	JN401371	JN401482	JN400981	JN401584	–	–	JN401052	JN401684		HONG KONG
Erebidae	unassigned	*Rhesala imparata*	**II**	RZ265	JN401255	JN401137	JN401372	JN401483	JN400940	JN401585	–	JN401791	JN401053	JN401685	TS	HONG KONG
Erebidae	unassigned	*Nychioptera noctuidalis*	**II**	RZ283	JN401256	JN401138	JN401373	–	JN400941	–	–	JN401792	–	–	TS	USA
Erebidae	Rivulinae	*Rivula sericealis*	**I,II**	MM01404	GU828664	GU828462	GU828995	GU829278	–	GU829791	–	GU830370	GU828161	GU830051	TG/TS	FINLAND

Erebidae	Rivulinae	*Rivula ochrea*	**II**	RZ159	JN401257	JN401139	JN401374	JN401484	JN400979	JN401586	–	JN401793	JN401054	–	TG	GHANA
Erebidae	Rivulinae	*Oxycilla ondo*	**I,II**	RZ24	HQ006184	HQ006888	HQ006280	HQ006375	HQ006792	HQ006456	–	HQ006607	HQ006980	HQ006529		USA
Erebidae	Rivulinae	*Bocula bifaria*	**II**	RZ413	JN401258	JN401140	JN401375	JN401485	JN400942	JN401587	–	–	JN401055	JN401686		MALAYSIA
Erebidae	Rivulinae	*Oglasa ansorgei*	**II**	RZ167	JN401259	JN401141	JN401376	JN401486	JN400986	JN401588	–	–	JN401056	JN401687		GHANA
Erebidae	Rivulinae	*Alesua etialis*	**II**	RZ94	JN401260	JN401142	JN401377	JN401487	JN400943	JN401589	–	JN401794	–	JN401688	TS	COSTA RICA
Erebidae	Anobinae	*Anoba anguliplaga*	**I,II**	RZ332	HQ006206	HQ006910	HQ006302	HQ006395	HQ006814	HQ006469	–	HQ006627	–	HQ006544	TG	GHANA
Erebidae	Anobinae	*Marcipa* sp.	**I,II**	RZ177	HQ006177	HQ006881	–	HQ006368	HQ006785	HQ006450	–	HQ006601	HQ006973	HQ006522		GHANA
Erebidae	Anobinae	*Marcipa* sp.	**II**	RZ200	JN401261	JN401143	JN401378	JN401488	JN400944	JN401590	–	JN401795	–	JN401689		GHANA
Erebidae	Anobinae	*Plecoptera major*	**II**	RZ183	JN401262	JN401144	–	JN401489	JN400945	JN401591	–	JN401796	–	JN401690		GHANA
Erebidae	Anobinae	*Crithote prominens*	**II**	RZ109	JN401263	JN401145	JN401379	JN401490	JN400946	JN401592	–	JN401797	JN401057	JN401691		HONG KONG
Erebidae	Anobinae	*Rema costimacula*	**II**	RZ103	JN401264	JN401146	JN401380	JN401491	JN400947	JN401593	–	JN401798	JN401058	JN401692	TS	HONG KONG
Erebidae	Anobinae	*Baniana strigata*	**II**	RZ92	JN401265	JN401147	JN401381	JN401492	JN400948	JN401594	–	JN401799	JN401059	JN401693		COSTA RICA
Erebidae	Anobinae	*Deinopa signiplena*	**II**	RZ311	JN401266	JN401148	JN401382	JN401493	JN400949	JN401595	–	JN401800	JN401060	JN401694		COSTA RICA
Erebidae	Hypeninae	*Hypena proboscidalis*	**I,II**	MM01545	GU828668	GU828466	GU828999	GU829282	GU829553	GU829794	GU830664	GU830374	GU828165	GU830055	TG/TS	FINLAND
Erebidae	Hypeninae	*Hypena baltimoralis*	**II**	RZ367	JN401267	JN401149	JN401383	JN401494	JN400993	JN401596	JN401895	JN401801	JN401061	JN401695	TG	USA
Erebidae	Hypeninae	*Hypena laceratalis*	**II**	RZ368	JN401268	JN401150	JN401384	JN401495	JN400950	–	JN401896	–	JN401062	JN401696	TG	HONG KONG
Erebidae	unassigned	*Cultripalpa* sp.	**II**	RZ394	JN401269	JN401151	JN401385	JN401496	JN400951	JN401597	JN401897	JN401802	–	JN401697		MALAYSIA
Erebidae	unassigned	*Colobochyla salicalis*	**I,II**	RZ4	HQ006215	HQ006919	HQ006311	HQ006402	HQ006823	HQ006478	HQ006727	HQ006636	HQ007005	–	TS	HUNGARY
Erebidae	Lymantriinae	*Lymantria monacha*	**I,II,IV,V**	MM01048	GU828655	GU828453	GU828986	GU829270	GU829542	–	GU830654	GU830361	GU828152	GU830042	TG	FINLAND
Erebidae	Lymantriinae	*Leucoma salicis*	**I,II**	MM06740	GU828748	GU929722	GU829062	GU829347	GU829611	–	GU830719	GU830449	GU828232	GU830132	TG/TS	FINLAND
Erebidae	Lymantriinae	*Nygmia plana*	**I,II**	RZ34	HQ006209	HQ006913	HQ006305	HQ006396	HQ006817	HQ006472	HQ006721	HQ006630	HQ006999	HQ006546	TG	HONG KONG
Erebidae	Lymantriinae	*Orgyia antiqua*	**I,II**	RZ130	HQ006167	HQ006964	HQ006264	HQ006358	HQ006776	HQ006443	HQ006683	HQ006593	HQ006964	HQ006513	TG/TS	FINLAND
Erebidae	Lymantriinae	*Arctornis* sp.	**I,II**	RZ89	HQ006241	HQ006943	HQ006335	HQ006428	HQ006849	HQ006494	HQ006752	HQ006659	HQ007024	HQ006572	TG	JAPAN
Erebidae	Pangraptinae	*Pangrapta bicornuta*	**I,II**	RZ40	HQ006216	HQ006920	HQ006312	HQ006403	HQ006824	HQ006479	HQ006728	HQ006637	HQ007006	HQ006550	TG	HONG KONG
Erebidae	Pangraptinae	*Pangrapta decoralis*	**I,II**	RZ66	HQ006236	HQ006939	HQ006331	HQ006423	HQ006844	–	HQ006747	–	HQ007022	HQ006568	TG/TS	USA
Erebidae	Pangraptinae	*Chrysograpta igneola*	**II**	RZ408	JN401270	JN401152	JN401386	JN401497	JN400952	JN401598	JN401898	JN401803	–	–	TS	MALAYSIA
Erebidae	Pangraptinae	*Hyposemansis singha*	**II**	RZ279	JN401271	JN401153	JN401387	JN401498	JN400953	JN401599	JN401899	JN401804	JN401063	JN401698	TS	MALAYSIA
Erebidae	Pangraptinae	*Gracilodes caffra*	**II**	RZ292	JN401272	JN401154	JN401388	JN401499	JN400954	JN401600	JN401900	JN401805	JN401064	JN401699	TS	TANZANIA
Erebidae	Pangraptinae	*Episparis costistriga*	**II**	RZ319	JN401273	JN401155	JN401389	JN401500	JN400955	JN401601	JN401901	–	–	JN401700		MALAYSIA
Erebidae	Pangraptinae	*Masca abactalis*	**I,II**	RZ18	HQ006178	HQ006882	HQ006274	HQ006369	HQ006786	HQ006451	HQ006693	–	HQ006974	HQ006523	TS	INDONESIA
Erebidae	unassigned	*Schistorhynx argentistriga*	**II**	RZ119	JN401274	JN401156	JN401390	JN401501	JN400956	JN401602	JN401902	JN401806	JN401065	JN401701	TS	HONG KONG
Erebidae	Herminiinae	*Polypogon strigilatus*	**I,II**	MM01286	GU828663	GU828461	GU828994	GU829277	GU829549	GU829790	GU830660	GU830369	GU828160	GU830050	TG/TS	FINLAND
Erebidae	Herminiinae	*Paracolax tristalis*	**I,II**	RZ5	HQ006224	HQ006927	HQ006319	HQ006411	HQ006832	–	HQ006736	–	HQ007013	–		HUNGARY
Erebidae	Herminiinae	*Herminia tarsicrinalis*	**I,II**	RZ6	HQ006232	HQ006935	HQ006327	HQ006419	HQ006840	HQ006489	–	–	–	–	TG	HUNGARY
Erebidae	Herminiinae	*Simplicia* sp.	**I,II**	RZ166	HQ006175	HQ006879	HQ006272	HQ006366	–	HQ006448	HQ006691	HQ006599	HQ006971	HQ006520		GHANA
Erebidae	Herminiinae	*Idia aemula*	**II**	RZ271	JN401275	JN401157	JN401391	JN401502	JN400957	–	–	JN401807	JN401066	JN401702	TS	USA
Erebidae	Herminiinae	*Lysimelia neleusalis*	**II**	RZ260	JN401276	JN401158	–	JN401503	JN400958	JN401603	–	JN401808	JN401067	JN401703	TS	HONG KONG
Erebidae	Herminiinae	*Nodaria verticalis*	**II**	RZ180	JN401277	JN401159	JN401392	JN401504	JN400959	JN401604	–	–	–	JN401704		GHANA

Erebidae	Aganainae	*Asota caricae*	**I,II**	MM00145	GU828615	GU828413	GU828949	GU829240	GU829509	–	GU830624	GU830325	GU828115	GU830003	TG/TS	TAHILAND
Erebidae	Aganainae	*Asota heliconia*	**I,II**	RZ44	HQ006220	HQ006924	HQ006316	HQ006407	HQ006828	HQ006483	HQ006732	HQ006641	HQ007009	HQ006554	TG	HONG KONG
Erebidae	Aganainae	*Neochera inops*	**II**	RZ346	JN401278	JN401160	JN401393	–	JN400960	JN401605	–	JN401809	JN401068	JN401705		JAPAN
Erebidae	Aganainae	*Euplocia membliaria*	**II**	RZ345	JN401279	JN401161	JN401394	JN401505	JN400961	JN401606	–	JN401810	–	JN401706	TS	MALAYSIA
Erebidae	Aganainae	*Peridrome orbicularis*	**II**	RZ280	JN401280	JN401162	JN401395	JN401506	JN400962	JN401607	JN401903	JN401811	–	JN401707	TS	MALAYSIA
Erebidae	Aganainae	*Mecodina praecipua*	**II**	RZ268	JN401281	JN401163	JN401396	JN401507	JN400963	JN401608	–	JN401812	JN401069	JN401708		HONG KONG
Erebidae	Aganainae	*Psimada quadripennis*	**II**	RZ47	JN401282	JN401164	JN401397	JN401508	JN400964	–	JN401904	JN401813	JN401070	JN401709	TG/TS	HONG KONG
Erebidae	Arctiinae	*Brunia antica*	**I,II**	RZ28	HQ006193	HQ006897	HQ006289	HQ006383	HQ006801	HQ006462	HQ006706	HQ006614	–	HQ006534	TS	HONG KONG
Erebidae	Arctiinae	*Garudinia simulana*	**II**	RZ399	JN401283	JN401165	JN401398	JN401509	JN400965	JN401609	JN401905	JN401814	JN401071	JN401710		MALAYSIA
Erebidae	Arctiinae	*Eugoa bipunctata*	**II**	RZ400	JN401284	JN401166	JN401399	JN401510	JN400966	–	JN401906	JN401815	JN401072	JN401711		MALAYSIA
Erebidae	Arctiinae	*Cyana* sp	**II**	RZ398	JN401285	JN401167	JN401400	JN401511	JN400967	JN401610	JN401876	JN401816	JN401073	JN401712		MALAYSIA
Erebidae	Arctiinae	*Barsine* sp	**II**	RZ397	JN401286	JN401168	JN401401	JN401512	JN400968	–	JN401878	JN401817	JN401074	JN401713		MALAYSIA
Erebidae	Arctiinae	*Apisa canescens*	**I,II**	MM05843	HQ006146	HQ006853	–	HQ006339	HQ006765	–	HQ006663	–	–	–	TS	OMAN
Erebidae	Arctiinae	*Syntomis phegea*	**I,II**	RZ8	HQ006238	HQ006941	–	HQ006425	HQ006846	HQ006492	HQ006749	HQ006656	–	–	TG/TS	HUNGARY
Erebidae	Arctiinae	*Dysauxes famula*	**I,II**	MM00154	GU828619	GU828417	GU828954	GU829244	GU829514	–	–	GU830328	GU828120	GU830008		GREECE
Erebidae	Arctiinae	*Antichloris viridis*	**I,II**	MM05380	HQ006151	HQ006858	HQ006249	HQ006344	HQ006760	HQ006433	HQ006668	HQ006579	HQ006951	HQ006501		ECUADOR
Erebidae	Arctiinae	*Ctenucha virginica*	**I,II**	AM-94-0396	GU828535	GU828337	GU828881	GU829181	GU829442	GU829722	GU830570	–	–	GU829926	TG	USA
Erebidae	Arctiinae	*Coscinia cribraria*	**I,II**	MM05671	HQ006149	HQ006856	HQ006247	HQ006342	HQ006758	–	HQ006666	–	HQ006949	HQ006499		FINLAND
Erebidae	Arctiinae	*Pseudophaloe troetschi*	**I,II**	06-SRNP-35191	GU828534	GU828336	GU828880	GU829180	GU829441	–	GU830569	GU830258	GU828046	GU829925		COSTA RICA
Erebidae	Arctiinae	*Dysschema leucophaea*	**I,II**	RZ88	HQ006240	–	HQ006334	HQ006427	HQ006848	HQ006493	HQ006751	HQ006658	–	HQ006571		COSTA RICA
Erebidae	Arctiinae	*Nyctemera baulus*	**II**	RZ387	JN401287	JN401169	JN401402	JN401513	JN400969	JN401611	JN401909	JN401818	–	JN401714		MALAYSIA
Erebidae	Arctiinae	*Callimorpha dominula*	**I,II**	RZ136	HQ006169	HQ006873	HQ006266	HQ006360	HQ006778	HQ006444	HQ006685	HQ006594	HQ006965	HQ006514	TG/TS	RUSSIA
Erebidae	Arctiinae	*Creatonotos transiens*	**I,II**	RZ30	HQ006198	HQ006902	HQ006294	HQ006387	HQ006806	–	HQ006711	HQ006619	HQ006991	HQ006537		HONG KONG
Erebidae	Arctiinae	*Arctia caja*	**I,II,IV,V**	MM03713	GU828693	GU828489	–	GU829305	GU829573	GU829813	–	GU830398	GU828185	GU830080	TG/TS	FINLAND
Erebidae	Arctiinae	*Amerila astreus*	**II**	RZ404	JN401288	JN401170	JN401403	JN401514	–	JN401612	JN401910	–	–	JN401715	TS	MALAYSIA
Erebidae	Unassigned	*Epitausa dilina*	**II**	RZ93	JN401289	JN401171	JN401404	JN401515	JN400970	JN401613	JN401911	JN401819	–	JN401716		COSTA RICA
Erebidae	Calpinae	*Phyllodes eyndhovii*	**I,II,III**	RZ56	HQ006228	HQ006931	HQ006323	HQ006415	HQ006836	–	HQ006740	HQ006648	–	HQ006561	TG	TAIWAN
Erebidae	Calpinae	*Phyllodes imperialis*	**II,III**	RZ546	JN674869	JN674851	JN674886	JN674902	JN674968	JN674919	JN674950	JN674934	–	JN674991	TG	AUSTRALIA
Erebidae	Calpinae	*Miniodes phaeosoma*	**I,II,III**	RZ153	HQ006173	HQ006877	HQ006270	HQ006364	HQ006782	HQ006446	HQ006689	HQ006597	HQ006969	HQ006518		GHANA
Erebidae	Calpinae	*Hemiceratoides sittaca*	**II,III**	RZ155	JN401290	JN401172	JN401405	JN401516	JN400971	JN401614	JN401912	JN401820	–	JN401717		GHANA
Erebidae	Calpinae	*Eudocima salaminia*	**II,III**	RZ338	JN401291	JN401173	JN401406	JN401517	JN400990	JN401615	JN401913	JN401821	–	JN401740	TG/TS	HONG KONG
Erebidae	Calpinae	*Eudocima fullonia*	**I,II,III**	RZ16	HQ006174	HQ006878	HQ006271	HQ006365	HQ006783	HQ006447	HQ006690	HQ006598	HQ006970	HQ006519	TG	MALAYSIA
Erebidae	Calpinae	*Eudocima divitiosa*	**III**	RZ210	JN674870	JN674852	JN674887	JN674903	JN674969	JN674920	JN674951	–	–	JN674992	TG	GHANA
Erebidae	Calpinae	*Eudocima tyrannus*	**III**	RZ430	JN674871	JN674853	JN674888	JN674904	JN674970	JN674921	JN674952	JN674935	–	JN674993	TG	RUSSIA
Erebidae	Calpinae	*Gonodonta uxor*	**I,II,III**	RZ335	HQ006208	HQ006912	HQ006304	–	HQ006816	HQ006471	HQ006720	HQ006629	–	HQ006545		COSTA RICA
Erebidae	Calpinae	*Gonodonta lincus*	**III**	RZ417	JN674872	JN674854	JN674889	JN674905	JN674971	JN674922	JN674953	JN674936	–	JN674994		BRAZIL
Erebidae	Calpinae	*Gonodonta milla*	**III**	RZ421	JN674873	JN674855	JN674890	JN674906	JN674972	JN674923	JN674954	JN674937	–	JN674995		BRAZIL
Erebidae	Calpinae	*Gonodonta syrna*	**III**	RZ420	JN674874	JN674856	JN674891	JN674907	JN674973	JN674924	JN674955	JN674938	–	JN674996		BRAZIL

Erebidae	Calpinae	*Gonodonta fulvangula*	**III**	RZ423	JN674875	JN674857	JN674892	JN674908	JN674974	–	JN674957	JN674940	–	JN674997		BRAZIL
Erebidae	Calpinae	*Gonodonta nutrix*	**III**	RZ432	JN674876	JN674858	JN674893	JN674909	JN674975	–	JN674956	JN674939	JN674985	JN674998		USA
Erebidae	Calpinae	*Gonodonta sicheas*	**III**	RZ419	JN674877	JN674859	JN674894	JN674910	JN674976	JN674925	JN674959	JN674941	–	JN674999		ECUADOR
Erebidae	Calpinae	*Calyptra thalictri*	**I,II,III,IV,V**	MM00963	HQ006156	HQ006861	HQ006252	HQ006348	HQ006763	HQ006435	HQ006671	HQ006582	HQ006955	HQ006504	TG/TS	FINLAND
Erebidae	Calpinae	*Calyptra hokkaida*	**II,III**	RZ336	JN401292	JN401174	JN401407	JN401518	JN400972	JN401616	JN401914	JN401823	JN401075	JN401718	TG	JAPAN
Erebidae	Calpinae	*Calyptra lata*	**III**	RZ431	JN674884	JN674866	JN674900	JN674917	JN674982	JN674931	JN674965	JN674947	JN674988	–	TG	RUSSIA
Erebidae	Calpinae	*Calyptra canadensis*	**III**	CTW2	–	JN674867	–	–	JN674983	JN674933	JN674967	JN674949	JN674989	JN675005	TG	USA
Erebidae	Calpinae	*Calyptra minuticornis*	**III**	RZ514	JN674885	JN674868	JN674901	JN674918	JN674984	JN674932	JN674966	JN674948	JN674990	JN675006	TG	MALAYSIA
Erebidae	Calpinae	*Plusiodonta nitissima*	**I,II,III**	RZ333	HQ006207	HQ006911	HQ006303	–	HQ006815	HQ006470	HQ006719	HQ006628	–	–		COSTA RICA
Erebidae	Calpinae	*Plusiodonta coelonota*	**III**	RZ106	JN674878	JN674860	JN674895	JN674911	JN674977	JN674926	JN674960	JN674942	–	JN675000		HONG KONG
Erebidae	Calpinae	*Plusiodonta casta*	**III**	RZ429	JN674879	JN674861	JN674896	JN674912	JN674978	JN674927	JN674961	JN674943	–	JN675001		RUSSIA
Erebidae	Calpinae	*Oraesia emarginata*	**I,II,III**	RZ102	HQ006159	HQ006864	HQ006256	HQ006351	HQ006768	HQ006439	HQ006675	HQ006586	HQ006958	HQ006508	TS	HONG KONG
Erebidae	Calpinae	*Oraesia excavata*	**II,III**	RZ337	JN401293	JN401175	JN401408	JN401519	JN400987	JN401617	JN401915	JN401824	JN401076	JN401719		HONG KONG
Erebidae	Calpinae	*Oraesia excavate*	**III**	RZ434	JN674880	JN674862	–	JN674913	–	–	JN674958	–	JN674986	–		USA
Erebidae	Calpinae	*Oraesia nobilis*	**III**	RZ422	JN674881	JN674863	JN674897	JN674914	JN674979	JN674928	JN674962	JN674944	–	JN675002		BRAZIL
Erebidae	Calpinae	*Oraesia glaucocheila*	**III**	RZ418	JN674882	JN674864	JN674898	JN674915	JN674980	JN674929	JN674963	JN674945	JN674987	JN675003		BRAZIL
Erebidae	Calpinae	*Oraesia rectristria*	**III**	RZ433	JN674883	JN674865	JN674899	JN674916	JN674981	JN674930	JN674964	JN674946	–	JN675004		NEPAL
Erebidae	Hypocalinae	*Hypsoropha hormos*	**I,II,III**	RZ17	HQ006176	HQ006880	HQ006273	HQ006367	HQ006784	HQ006449	HQ006692	HQ006600	HQ006972	HQ006521		USA
Erebidae	Hypocalinae	*Hypocala deflorata*	**II**	RZ105	JN401294	JN401176	JN401409	JN401520	JN400985	JN401618	JN401916	JN401825	JN401077	JN401720	TG/TS	HONG KONG
Erebidae	Hypocalinae	*Hypocala andremona*	**II,III**	RZ340	JN401295	JN401177	JN401410	JN401521	JN400980	JN401619	JN401917	JN401826	JN401078	JN401721	TG	COSTA RICA
Erebidae	Eulepidotinae	*Tautobriga glaucopis*	**II**	RZ354	JN401296	JN401178	–	–	JN400977	–	–	JN401827	–	–		COSTA RICA
Erebidae	Eulepidotinae	*Panopoda rufimargo*	**I,II,III**	RZ59	HQ006231	HQ006934	HQ006326	HQ006418	HQ006839	HQ006488	HQ006743	HQ006651	HQ007018	HQ006564	TG	USA
Erebidae	Eulepidotinae	*Antiblemma fuscireticulata*	**II,III**	RZ334	JN401297	JN401179	JN401411	–	JN400975	JN401620	JN401918	JN401828	–	–		COSTA RICA
Erebidae	Eulepidotinae	*Sanys irrosca*	**II**	RZ343	JN401298	JN401180	JN401412	–	JN400973	JN401621	JN401919	JN401829	JN401079	JN401722		COSTA RICA
Erebidae	Eulepidotinae	*Eulepidotis rectimargo*	**I,II,III**	RZ12	HQ006162	HQ006960	HQ006259	HQ006354	HQ006771	–	HQ006678	HQ006588	HQ006960	HQ006511	TG	COSTA RICA
Erebidae	Eulepidotinae	*Anticarsia gemmatalis*	**II**	RZ267	JN401299	JN401181	JN401413	JN401522	JN400974	JN401622	JN401920	JN401830	–	JN401723	TS	USA
Erebidae	Eulepidotinae	*Anticarsia irrorata*	**II**	RZ370	JN401300	JN401182	JN401414	JN401523	JN400995	JN401623	JN401921	JN401831	JN401080	JN401724		HONG KONG
Erebidae	Eulepidotinae	*Hemeroplanis finitima*	**II**	RZ298	JN401301	JN401183	JN401415	JN401524	JN401004	JN401624	JN401922	JN401832	–	JN401725		USA
Erebidae	Eulepidotinae	*Oxidercia toxea*	**I,II**	RZ295	HQ006196	HQ006900	HQ006292	–	HQ006804	–	HQ006709	HQ006617	HQ006989	–	TS	COSTA RICA
Erebidae	Eulepidotinae	*Azeta ceramina*	**I,II,III**	RZ22	HQ006182	HQ006886	HQ006278	HQ006373	HQ006790	–	HQ006697	HQ006605	HQ006978	HQ006527		COSTA RICA
Erebidae	Toxocampinae	*Autophila chamaephanes*	**II**	RZ276	JN401302	JN401184	JN401416	JN401525	JN401005	JN401625	JN401923	JN401833	JN401081	JN401726		COSTA RICA
Erebidae	Toxocampinae	*Lygephila pastinum*	**I,II**	MM05092	GU828711	GU828506	–	GU829323	GU829587	–	GU830699	GU830415	GU828199	GU830097	TG	FINLAND
Erebidae	Toxocampinae	*Lygephila maxima*	**I,II**	RZ57	HQ006229	HQ006932	HQ006324	HQ006416	HQ006837	HQ006487	HQ006741	HQ006649	–	HQ006562	TG	JAPAN
Erebidae	Tinoliinae	*Tinolius eburneigutta*	**II**	RZ331	JN401303	JN401185	JN401417	–	–	–	JN401924	JN401834	JN401082	–	TG/TS	THAILAND
Erebidae	Tinoliinae	*Poeta denotalis*	**II**	RZ445	JN401304	JN401186	JN401418	JN401526	JN401006	JN401626	JN401925	–	–	JN401727	TS	MALAYSIA
Erebidae	Tinoliinae	*Tamsia hieroglyphica*	**II**	RZ389	JN401305	JN401187	JN401419	JN401527	JN401007	JN401627	JN401907	JN401835	JN401083	JN401728		MALAYSIA
Erebidae	Unassigned	*Platyjionia mediorufa*	**II**	RZ111	JN401306	JN401188	JN401420	JN401528	JN400991	JN401628	JN401926	–	JN401084	JN401729		HONG KONG
Erebidae	Scolecocampinae	*Scolecocampa liburna*	**I,II**	RZ9	HQ006242	HQ006944	HQ006336	HQ006429	HQ006850	HQ006495	HQ006753	HQ006660	HQ007025	HQ006573	TG	USA

Erebidae	Scolecocampinae	*Gabara stygialis*	**II**	RZ297	JN401307	JN401189	JN401421	JN401529	–	JN401629	JN401927	JN401836	JN401085	JN401730		USA
Erebidae	Hypenodinae	*Hypenodes humidalis*	**I,II**	MM01780	GU828671	GU828469	–	GU829285	GU829556	–	GU830666	–	GU828168	GU830058	TG/TS	FINLAND
Erebidae	Hypenodinae	*Schrankia costaestrigalis*	**I,II**	RZ27	HQ006192	HQ006896	HQ006288	HQ006382	HQ006800	HQ006461	HQ006705	HQ006613	HQ006987	–		HONG KONG
Erebidae	Hypenodinae	*Luceria striata*	**II**	RZ42	JN401308	JN401190	JN401422	JN401530	JN401008	–	JN401928	–	–	–		HONG KONG
Erebidae	Hypenodinae	*Luceria oculalis*	**II**	RZ369	JN401309	JN401191	JN401423	JN401531	JN401009	–	JN401929	–	JN401086	JN401731		HONG KONG
Erebidae	Hypenodinae	*Anachrostis* sp.	**II**	RZ288	JN401310	JN401192	JN401424	–	–	–	JN401930	JN401837	JN401087	–		INDONESIA
Erebidae	Hypenodinae	*Micronoctua* sp.	**I,II**	RZ138	HQ006171	HQ006875	HQ006268	HQ006362	HQ006780	HQ006445	HQ006687	HQ006595	HQ006967	HQ006516	TG	INDONESIA
Erebidae	Hypenodinae	*Biuncus* sp. 1	**II**	RZ475	–	JN401193	JN401425	JN401532	JN400992	JN401630	JN401931	JN401838	JN401088	JN401732		GHANA
Erebidae	Hypenodinae	*Biuncus* sp. 2	**II**	RZ476	JN401311	JN401194	JN401426	–	JN400994	JN401631	JN401908	JN401839	JN401089	JN401733		GHANA
Erebidae	Boletobiinae	*Saroba pustulifera*	**I,II**	RZ104	HQ006160	HQ006865	HQ006257	HQ006352	HQ006769	–	HQ006676	–	–	HQ006509	TS	HONG KONG
Erebidae	Boletobiinae	*Condate* sp.	**II**	RZ393	JN401312	JN401195	JN401427	JN401533	JN401010	JN401632	JN401932	JN401840	JN401090	JN401734		MALAYSIA
Erebidae	Boletobiinae	*Corgatha nitens*	**I,II**	RZ36	HQ006211	HQ006915	HQ006307	HQ006398	HQ006819	HQ006474	HQ006723	HQ006632	HQ007001	HQ006547		HONG KONG
Erebidae	Boletobiinae	*Phytometra viridaria*	**I,II**	RZ129	HQ006165	HQ006962	HQ006262	HQ006356	HQ006774	HQ006442	HQ006681	HQ006591	HQ006962	HQ006512	TG	FINLAND
Erebidae	Boletobiinae	*Laspeyria flexula*	**I,II**	RZ3	HQ006197	HQ006901	HQ006293	HQ006386	HQ006805	HQ006463	HQ006710	HQ006618	HQ006990	HQ006536	TG/TS	HUNGARY
Erebidae	Boletobiinae	*Zurobata rorata*	**II**	RZ385	JN401313	JN401196	JN401428	JN401534	JN400996	–	JN401933	JN401841	JN401091	JN401735	TS	MALAYSIA
Erebidae	Boletobiinae	*Homodes crocea*	**II**	RZ412	JN401314	JN401197	JN401429	JN401535	JN401011	–	JN401934	JN401842	JN401092	JN401736	TS	MALAYSIA
Erebidae	Boletobiinae	*Enispodes purpurea*	**II**	RZ390	JN401315	JN401198	JN401430	–	JN401012	JN401633	JN401935	JN401843	JN401093	JN401737	TS	MALAYSIA
Erebidae	Boletobiinae	*Tamba mnionomera*	**II**	RZ415	JN401316	JN401199	JN401431	JN401536	–	JN401634	JN401936	JN401844	–	JN401738		MALAYSIA
Erebidae	Boletobiinae	*Parolulis absimilis*	**II**	RZ392	JN401317	JN401200	JN401432	JN401537	–	JN401635	JN401937	JN401845	–	JN401739		MALAYSIA
Erebidae	Boletobiinae	*Araeopteron* sp.	**I,II**	RZ137	HQ006170	HQ006874	HQ006267	HQ006361	HQ006779	–	HQ006686	–	HQ006966	HQ006515	TG	INDONESIA
Erebidae	Boletobiinae	*Araeopteron* sp.	**II**	RZ410	JN401318	JN401201	JN401433	JN401538	JN401013	JN401636	JN401938	JN401846	JN401094	–	TG	MALAYSIA
Erebidae	Boletobiinae	*Eublemma purpurina*	**I,II**	RZ7	HQ006237	HQ006940	HQ006332	HQ006424	HQ006845	HQ006491	HQ006748	HQ006655	–	HQ006569	TG	HUNGARY
Erebidae	Boletobiinae	*Eublemma anachoresis*	**II**	RZ98	JN401319	JN401202	JN401434	JN401539	JN400989	JN401637	JN401939	JN401847	–	JN401741	TG	HONG KONG
Erebidae	Boletobiinae	*Eublemma albifascia*	**II**	RZ220	JN401320	JN401203	JN401435	JN401540	JN401014	JN401638	JN401940	–	–	JN401742	TG	GHANA
Erebidae	Boletobiinae	*Parascotia fuliginaria*	**I,II**	MM00340	HQ006154	HQ006862	HQ006253	HQ006347	HQ006764	HQ006436	HQ006672	HQ006583	HQ006954	HQ006505	TG/TS	FINLAND
Erebidae	Boletobiinae	*Metalectra edilis*	**II**	RZ372	JN401321	JN401204	JN401436	JN401541	JN401015	JN401639	JN401941	JN401848	–	JN401744		FINLAND
Erebidae	Boletobiinae	*Trisateles emortualis*	**I,II**	MM04877	GU828707	GU828502	GU829030	GU829319	GU829583	GU829821	GU830695	GU830411	GU828195	GU830093	TG/TS	FINLAND
Erebidae	Boletobiinae	*Prolophota trigonifera*	**I,II**	RZ37	HQ006212	HQ006916	HQ006308	HQ006399	HQ006820	HQ006475	HQ006724	HQ006633	HQ007002	–	TS	HONG KONG
Erebidae	Boletobiinae	*Hypenagonia ?brachypalpia*	**II**	RZ409	JN401322	–	JN401437	JN401542	JN401016	JN401640	JN401942	JN401849	–	–		MALAYSIA
Erebidae	Boletobiinae	*Metaemene atrigutta*	**I,II**	RZ41	HQ006218	HQ006922	HQ006314	HQ006405	HQ006826	HQ006481	HQ006730	HQ006639	HQ007007	HQ006552		HONG KONG
Erebidae	Boletobiinae	*Mataeomera semialba*	**II**	RZ107	JN401323	JN401205	JN401438	–	–	JN401641	–	JN401850	JN401095	JN401745		HONG KONG
Erebidae	Erebinae	*Euaontia semirufa*	**II**	RZ285	JN401324	JN401206	JN401439	JN401543	JN401017	JN401642	JN401943	–	JN401096	JN401746	TS	USA
Erebidae	Erebinae	*Acantholipes circumdata*	**I,II**	RZ248	HQ006189	HQ006893	HQ006285	HQ006379	HQ006797	–	HQ006702	–	HQ006984	HQ006531	TG	UAE
Erebidae	Erebinae	*Acantholipes regularis*	**I,II**	RZ135	HQ006168	HQ006872	HQ006265	HQ006359	HQ006777	–	HQ006684	–	–	–	TG/TS	RUSSIA
Erebidae	Erebinae	*Hypospila bolinoides*	**II**	RZ116	JN401325	JN401207	JN401440	JN401544	JN400997	JN401643	JN401944	JN401851	–	JN401743	TS	HONG KONG
Erebidae	Erebinae	*Ugia insuspecta*	**I,II**	RZ45	HQ006221	HQ006925	–	HQ006408	HQ006829	HQ006484	HQ006733	HQ006642	HQ007010	HQ006555		HONG KONG
Erebidae	Erebinae	*Ugiodes cinerea*	**II**	RZ326	JN401326	JN401208	–	–	–	JN401644	JN401945	–	JN401097	–	TS	GHANA

Erebidae	Erebinae	*Sypnoides fumosa*	**I,II**	RZ313	HQ006201	HQ006905	HQ006297	HQ006390	HQ006809	HQ006466	HQ006714	HQ006622	HQ006994	HQ006539		JAPAN
Erebidae	Erebinae	*Daddala lucilla*	**II**	RZ320	JN401327	JN401209	JN401441	JN401545	JN400998	JN401645	JN401946	JN401852	JN401098	JN401747		JAPAN
Erebidae	Erebinae	*Catephia alchymista*	**I,II**	RZ127	HQ006164	HQ006961	HQ006261	HQ006355	HQ006773	HQ006441	HQ006680	HQ006590	HQ006961	–	TG/TS	GERMANY
Erebidae	Erebinae	*Heteranassa* sp.	**II**	RZ350	JN401328	JN401210	JN401442	JN401546	JN401002	JN401646	JN401947	JN401860	–	JN401748		USA
Erebidae	Erebinae	*Zale bethunei*	**II**	RZ270	JN401329	JN401211	JN401443	JN401547	JN401018	JN401647	JN401948	JN401853	–	JN401749		USA
Erebidae	Erebinae	*Thysania zenobia*	**I,II**	RZ53	HQ006225	HQ006928	HQ006320	HQ006412	HQ006833	HQ006486	HQ006737	HQ006645	HQ007014	HQ006558	TG	COSTA RICA
Erebidae	Erebinae	*Toxonprucha* sp.	**II**	RZ307	JN401330	JN401212	JN401444	JN401548	–	JN401648	JN401949	JN401854	–	JN401750		USA
Erebidae	Erebinae	*Pseudbarydia crespula*	**II**	RZ91	JN401331	JN401213	JN401445	JN401549	JN401019	JN401649	JN401950	JN401855	JN401099	JN401751		COSTA RICA
Erebidae	Erebinae	*Pandesma robusta*	**I,II**	RZ321	HQ006204	HQ006908	HQ006300	HQ006393	HQ006812	–	HQ006717	HQ006625	HQ006997	HQ006542	TG/TS	SPAIN
Erebidae	Erebinae	*Heteropalpia acrosticta*	**I,II**	RZ243	HQ006186	HQ006890	HQ006282	HQ006376	HQ006794	–	HQ006700	–	HQ006981	–		UAE
Erebidae	Erebinae	*Sphingomorpha chlorea*	**I,II**	RZ291	HQ006195	HQ006899	HQ006291	HQ006385	HQ006803	–	HQ006708	HQ006616	–	–	TS	TANZANIA
Erebidae	Erebinae	*Pericyma cruegeri*	**I,II**	RZ99	HQ006244	HQ006946	HQ006338	HQ006431	HQ006852	HQ006497	HQ006755	HQ006662	HQ007027	HQ006575	TG	HONG KONG
Erebidae	Erebinae	*Sympis rufibasis*	**I,II**	RZ48	HQ006223	–	HQ006318	HQ006410	HQ006831	HQ006485	HQ006735	HQ006644	HQ007012	HQ006557	TS	HONG KONG
Erebidae	Erebinae	*Erebus ephesperis*	**I,II**	RZ11	HQ006161	HQ006866	HQ006258	HQ006353	HQ006770	HQ006440	HQ006677	HQ006587	HQ006959	HQ006510	TG	TAIWAN
Erebidae	Erebinae	*Erygia apicalis*	**I,II**	RZ29	HQ006194	HQ006898	HQ006290	HQ006384	HQ006802	–	HQ006707	HQ006615	HQ006988	HQ006535	TS	HONG KONG
Erebidae	Erebinae	*Bulia deducta*	**II**	RZ314	JN401332	JN401214	JN401446	JN401550	JN401020	JN401650	JN401951	JN401856	JN401100	JN401752		USA
Erebidae	Erebinae	*Forsebia perlaeta*	**II**	RZ284	JN401333	JN401215	JN401447	JN401551	JN401021	JN401651	JN401952	JN401857	JN401101	JN401753	TS	USA
Erebidae	Erebinae	*Melipotis punctifinis*	**II**	RZ342	JN401334	JN401216	JN401448	JN401552	JN401022	JN401652	JN401953	JN401858	JN401102	JN401754	TG	COSTA RICA
Erebidae	Erebinae	*Melipotis jucunda*	**I,II**	RZ58	HQ006230	HQ006933	HQ006325	HQ006417	HQ006838	–	HQ006742	HQ006650	HQ007017	HQ006563	TG/TS	USA
Erebidae	Erebinae	*Phoberia atomaris*	**II**	RZ286	JN401335	JN401217	JN401449	–	JN401023	–	JN401954	JN401859	JN401103	JN401755	TS	USA
Erebidae	Erebinae	*Audea bipunctata*	**I,II**	RZ60	HQ006233	HQ006936	HQ006328	HQ006420	HQ006841	–	HQ006744	HQ006652	HQ007019	HQ006565	TG/TS	CONGO
Erebidae	Erebinae	*Audea humeralis*	**II**	RZ290	JN401336	JN401218	JN401450	JN401553	JN401024	JN401653	JN401955	–	JN401104	JN401756	TG	TANZANIA
Erebidae	Erebinae	*Hypotacha brandbergensis*	**II**	RZ275	JN401337	JN401219	JN401451	JN401554	JN400999	JN401654	JN401956	–	JN401105	JN401757		NAMIBIA
Erebidae	Erebinae	*Catocala sponsa*	**I,II,IV,V**	MM04358	GU828700	GU828495	GU829023	GU829312	GU829576	GU829816	GU830688	GU830404	GU828189	GU830086	TG	FINLAND
Erebidae	Erebinae	*Ulotrichopus macula*	**I,II**	RZ241	HQ006185	HQ006889	HQ006281	–	HQ006793	HQ006457	HQ006699	HQ006608	–	HQ006530		TAIWAN
Erebidae	Erebinae	*Hypopyra capensis*	**II**	RZ149	HQ006172	HQ006876	HQ006269	HQ006363	HQ006781	–	HQ006688	HQ006596	HQ006968	HQ006517	TG	GHANA
Erebidae	Erebinae	*Spirama retorta*	**II**	RZ359	JN401338	JN401220	JN401452	–	JN401025	JN401655	JN401957	–	JN401106	JN401758		TAIWAN
Erebidae	Erebinae	*Calyptis idonea*	**II**	RZ473	JN401339	JN401221	JN401453	–	JN401000	JN401656	JN401958	JN401861	JN401107	JN401759		ECUADOR
Erebidae	Erebinae	*Ommatophora luminosa*	**II**	RZ407	JN401340	JN401222	JN401454	JN401555	JN401026	JN401657	JN401959	JN401862	JN401108	JN401760	TG/TS	MALAYSIA
Erebidae	Erebinae	*Pantydia diemeni*	**I,II**	RZ309	HQ006199	HQ006903	HQ006295	HQ006388	HQ006807	HQ006464	HQ006712	HQ006620	HQ006992	HQ006538		AUSTRALIA
Erebidae	Erebinae	*Mocis latipes*	**I,II**	RZ20	HQ006180	HQ006884	HQ006276	HQ006371	HQ006788	HQ006453	HQ006695	HQ006603	HQ006976	HQ006525		COSTA RICA
Erebidae	Erebinae	*Callistege mi*	**I,II**	MM05469	HQ006150	HQ006857	HQ006248	HQ006343	HQ006759	–	HQ006667	HQ006578	HQ006950	HQ006500	TS	FINLAND
Erebidae	Erebinae	*Euclidia glyphica*	**I,II**	RZ82	HQ006239	HQ006942	HQ006333	HQ006426	HQ006847	–	HQ006750	HQ006657	HQ007023	HQ006570	TG	FINLAND
Erebidae	Erebinae	*Ercheia cyllaria*	**I,II**	RZ33	HQ006205	HQ006909	HQ006301	HQ006394	HQ006813	–	HQ006718	HQ006626	HQ006998	HQ006543	TG	HONG KONG
Erebidae	Erebinae	*Hulodes caranea*	**I,II**	RZ126	HQ006163	–	HQ006260	–	HQ006772	–	HQ006679	HQ006589	–	–	TG	MALAYSIA
Erebidae	Erebinae	*Ericeia subcinerea*	**II**	RZ39	HQ006214	HQ006918	HQ006310	HQ006401	HQ006822	HQ006477	HQ006726	HQ006635	HQ007004	HQ006549		HONG KONG
Erebidae	Erebinae	*Platyja umminea*	**II**	RZ261	JN401341	JN401223	JN401455	JN401556	JN401027	JN401658	JN401960	JN401863	–	JN401761	TS	HONG KONG
Erebidae	Erebinae	*Anisoneura salebrosa*	**I,II**	RZ38	HQ006213	HQ006917	HQ006309	HQ006400	HQ006821	HQ006476	HQ006725	–	HQ007003	HQ006548	TS	HONG KONG

Erebidae	Erebinae	*Praxis porphyretica*	**II**	RZ308	JN401342	JN401224	JN401456	–	JN401028	JN401659	JN401961	JN401864	JN401109	JN401762		AUSTRALIA
Erebidae	Erebinae	*Ischyja manlia*	**II**	RZ269	JN401343	JN401225	JN401457	JN401557	JN401029	JN401660	JN401962	JN401822	JN401110	JN401763	TS	MALAYSIA
Erebidae	Erebinae	*Oxyodes scrobiculata*	**II**	RZ113	JN401344	JN401226	JN401458	JN401558	JN401030	JN401661	JN401963	JN401866	JN401111	JN401764	TS	HONG KONG
Erebidae	Erebinae	*Serrodes campana*	**I,II**	RZ318	HQ006202	HQ006906	HQ006298	HQ006391	HQ006810	HQ006467	HQ006715	HQ006623	HQ006995	HQ006540		TAIWAN
Erebidae	Erebinae	*Avatha uloptera*	**II**	RZ317	JN401345	JN401227	JN401459	JN401559	JN401003	JN401662	JN401964	JN401867	–	JN401765		MALAYSIA
Erebidae	Erebinae	*Cocytia durvillii*	**II**	RZ401	JN401346	JN401228	JN401460	JN401560	JN401031	JN401663	JN401965	JN401869	JN401112	JN401766	TG/TS	NEW GUINEA
Erebidae	Erebinae	*Bastilla praetermissa*	**II**	RZ306	JN401347	JN401229	JN401461	JN401561	JN401032	JN401664	JN401966	JN401868	JN401113	JN401767		MALAYSIA
Erebidae	Erebinae	*Achaea serva*	**I,II**	RZ19	HQ006179	HQ006883	HQ006275	HQ006370	HQ006787	HQ006452	HQ006694	HQ006602	HQ006975	HQ006524		MALAYSIA
Erebidae	Erebinae	*Chalciope mygdon*	**II**	RZ391	JN401348	JN401230	JN401462	JN401562	JN401001	JN401665	JN401967	JN401865	JN401881	JN401768	TS	MALAYSIA
Erebidae	Erebinae	*Allotria elonympha*	**II**	RZ294	JN401349	JN401231	JN401463	JN401563	JN401033	JN401666	JN401968	JN401870	JN401115	JN401769	TS	USA
Erebidae	Erebinae	*Clytie devia*	**I,II**	RZ247	HQ006188	HQ006892	HQ006284	HQ006378	HQ006796	HQ006459	–	HQ006610	HQ006983	–		UAE
Erebidae	Erebinae	*Ophiusa tirhaca*	**I,II,IV**	RZ246	HQ006187	HQ006891	HQ006283	HQ006377	HQ006795	HQ006458	HQ006701	HQ006609	HQ006982	–	TG/TS	UAE
Erebidae	Erebinae	*Thyas metaphaea*	**II**	RZ190	JN401350	JN401232	JN401464	JN401564	JN401034	JN401667	JN401969	JN401871	JN401116	JN401770		GHANA
Erebidae	Erebinae	*Ophiusa coronata*	**I,II**	RZ21	HQ006181	HQ006885	HQ006277	HQ006372	HQ006789	HQ006454	HQ006696	HQ006604	HQ006977	HQ006526	TG	MALAYSIA
Erebidae	Erebinae	*Artena dotata*	**I,II**	RZ46	HQ006222	HQ006926	HQ006317	HQ006409	HQ006830	–	HQ006734	HQ006643	HQ007011	HQ006556		HONG KONG
Nolidae	Diphtherinae	*Lepidodes gallopavo*	**IV**	RZ353	X	X	X	X	X	–	–	X	X	–		COSTA RICA
Nolidae	Diphtherinae	*Lepidodes limbulata* 1	**IV**	RZ628	–	–	X	X	X	X	–	X	X	X	TS	COSTA RICA
Nolidae	Diphtherinae	*Lepidodes limbulata* 2	**IV**	RZ630	X	–	X	X	X	X	–	X	X	X	TS	COSTA RICA
Nolidae	Diphtherinae	*Lepidodes limbulata* 3	**IV**	RZ594	X	X	–	–	X	–	–	–	–	–	TS	COSTA RICA
Nolidae	Diphtherinae	*Diphthera festiva* 2	**IV**	RZ465	X	X	X	X	X	X	–	X	X	X	TG/TS	COSTA RICA
Nolidae	Diphtherinae	*Diphthera festiva* 3	**IV**	RZ631	X	–	–	–	X	–	X	–	–	–	TG/TS	COSTA RICA
Nolidae	Diphtherinae	*Diphthera festiva* 1	**IV**	RZ633	X	–	X	–	X	–	–	–	–	–	TG/TS	COSTA RICA
Nolidae	Risobinae	*Risoba obstructa* 2	**II,IV**	RZ381	JN401233	JN401117	JN401351	–	JN400926	JN401565	JN401872	JN401771	JN401035	JN401668	TG	MALAYSIA
Nolidae	Risobinae	*Risoba obstructa* 1	**I,II,IV**	RZ65	X	X	X	X	X	X	X	X	–	X	TG	THAILAND
Nolidae	Risobinae	*Baileya levitans*	**IV**	RZ461	X	X	X	X	X	X	X	X	X	X		USA
Nolidae	Collomeninae	*Collomena siopera* 1	**IV**	RZ632	X	–	–	–	X	–	X	X	–	–	TG	COSTA RICA
Nolidae	Collomeninae	*Collomena siopera* 2	**IV,V**	RZ634	X	–	X	X	X	X	X	X	–	–	TG	COSTA RICA
Nolidae	Collomeninae	*Neostictopera nigropuncta*	**IV,V**	RZ469	X	X	X	X	X	X	X	X	X	X	TS	COSTA RICA
Nolidae	Beaninae	*Beana terminigera*	**IV**	RZ638	X	–	X	X	X	X	X	X	X	X	TG	THAILAND
Nolidae	Eligminae	*Baroa siamica*	**IV**	RZ396	X	X	X	X	X	X	X	X	X	X		MALAYSIA
Nolidae	Eligminae	*Selepa molybdea*	**I,IV**	RZ32	HQ006203	HQ006907	HQ006299	HQ006392	HQ006811	HQ006468	HQ006716	HQ006624	HQ006996	HQ006541		HONG KONG
Nolidae	Eligminae	*Selepa discigera/celtis*	**IV**	RZ500	X	X	X	X	X	–	X	X	X	X		HONG KONG
Nolidae	Eligminae	*Ptisciana seminivea*	**IV**	RZ516	X	X	X	X	X	X	X	X	–	X	TS	MALAYSIA
Nolidae	Eligminae	*Triorbis aureovitta*	**IV**	RZ360	X	X	X	X	X	X	X	X	X	X		MALAYSIA
Nolidae	Eligminae	*Eligma narcissus*	**I,II,IV,V**	RZ97	HQ006243	HQ006945	HQ006337	HQ006430	HQ006851	HQ006496	HQ006754	HQ006661	HQ007026	HQ006574	TG/TS	HONG KONG
Nolidae	Eligminae	*Elaeognatha argyritis*	**IV**	RZ462	X	X	X	–	X	X	X	X	–	–	TS	COSTA RICA
Nolidae	Eligminae	*Iscadia product*	**IV**	RZ361	X	X	–	–	X	–	X	X	–	–		COSTA RICA
Nolidae	Westermanniinae	*Pterogonia cardinalis*	**IV**	RZ522	X	X	X	X	X	X	X	X	X	–		MALAYSIA

Nolidae	Westermanniinae	*Miaromima cornucopia*	**IV**	RZ530	X	X	X	X	X	X	X	X	–	X		MALAYSIA
Nolidae	Westermanniinae	*Westermannia superba*	**IV**	RZ645	X	–	X	X	X	X	X	X	X	–	TG/TS	THAILAND
Nolidae	Westermanniinae	*Iragaodes nobilis*	**IV**	RZ483	X	X	X	X	X	X	X	–	–	–	TS	JAPAN
Nolidae	Westermanniinae	*Negeta contrariata* 2	**I,II,IV**	RZ26	HQ006191	HQ006895	HQ006287	HQ006381	HQ006799	HQ006460	HQ006704	HQ006612	HQ006986	HQ006533		HONG KONG
Nolidae	Westermanniinae	*Negeta abbreviata*	**IV**	RZ414	X	–	X	X	X	X	X	X	X	X		MALAYSIA
Nolidae	Westermanniinae	*Negeta contrariata* 1	**IV**	RZ487	X	X	X	–	X	X	X	X	–	X		TAIWAN
Nolidae	Westermanniinae	*Negeta contrariata* 3	**IV**	RZ504	X	X	X	X	X	X	X	X	X	X	TS	MALAYSIA
Nolidae	Nolinae	*Melanographia flexilineata*	**IV**	RZ498	X	X	X	X	X	X	X	X	X	X	TS	HONG KONG
Nolidae	Nolinae	*Membranola lampang*	**IV**	RZ626	X	X	X	X	X	X	X	X	–	X		THAILAND
Nolidae	Nolinae	*Alcanola tympanistes*	**IV**	RZ624	X	X	X	X	X	X	X	X	X	X		THAILAND
Nolidae	Nolinae	*Alcanola obscurata*	**IV**	RZ625	X	–	X	X	X	X	X	X	X	–		THAILAND
Nolidae	Nolinae	*Meganola minuscula*	**IV**	RZ485	X	X	X	X	X	X	X	–	–	X		USA
Nolidae	Nolinae	*Nola basinigra*	**IV**	RZ627	X	X	X	X	X	X	X	X	X	X	TG	THAILAND
Nolidae	Nolinae	unknown noline	**IV**	RZ526	X	X	X	X	X	X	X	–	X	X		MALAYSIA
Nolidae	Nolinae	*Nola aerugula*	**I,II,IV**	MM01776	GU828670	GU828468	GU829001	GU829284	GU829555	–	GU830665	GU830376	GU828167	GU830057	TG	FINLAND
Nolidae	Nolinae	*Nola minna*	**IV**	RZ488	X	X	X	X	X	X	X	X	–	X	TG	USA
Nolidae	Nolinae	*Nola cretacea*	**IV**	RZ493	X	X	X	–	X	X	X	–	X	–	TG	HONG KONG
Nolidae	Nolinae	*Nola analis*	**IV**	RZ494	X	X	–	X	X	X	–	–	X	–	TG	HONG KONG
Nolidae	Nolinae	*Nola lucidalis*	**IV**	RZ533	X	X	X	X	X	–	X	X	–	–	TG	MALAYSIA
Nolidae	Nolinae	*Nola fasciata*	**IV**	RZ534	X	–	X	X	X	X	X	X	–	X	TG	MALAYSIA
Nolidae	Nolinae	*Manoba brunellus*	**IV**	RZ495	X	X	X	X	X	X	–	X	X	X		HONG KONG
Nolidae	Chloephorinae	*Maceda mansueta*	**IV**	RZ641	X	–	–	–	X	–	X	X	–	–	TS	THAILAND
Nolidae	Chloephorinae	*Paracrama angulata*	**I,IV**	RZ43	HQ006219	HQ006923	HQ006315	HQ006406	HQ006827	HQ006482	HQ006731	HQ006640	HQ007008	HQ006553		HONG KONG
Nolidae	Chloephorinae	*Paracrama dulcissima*	**IV**	RZ648	X	–	X	X	X	X	X	X	–	–	TS	THAILAND
Nolidae	Chloephorinae	*Earias clorana*	**I,II,IV**	MM06650	GU828747	GU929721	GU829061	GU829346	GU829610	GU829845	GU830718	GU830448	GU828231	GU830131	TG/TS	FINLAND
Nolidae	Chloephorinae	*Earias roseifera*	**IV**	RZ480	X	X	X	X	X	X	X	X	X	X		TAIWAN
Nolidae	Chloephorinae	*Earias insulana*	**IV**	RZ492	X	X	X	–	X	X	–	X	X	X	TG	HONG KONG
Nolidae	Chloephorinae	*Maurilia iconica*	**IV**	RZ484	X	X	–	X	X	X	X	X	X	X		INDONESIA
Nolidae	Chloephorinae	*Tortriciforma razowskii*	**IV**	RZ586	X	X	X	X	X	X	X	X	–	–		MALAYSIA
Nolidae	Chloephorinae	*Didigua viridifascia*	**IV**	RZ525	X	X	X	X	X	X	X	X	–	X		MALAYSIA
Nolidae	Chloephorinae	*Xenochroa annae*	**IV**	RZ386	X	X	X	X	X	X	X	X	X	X		MALAYSIA
Nolidae	Chloephorinae	*Xenochroa xanthia*	**IV**	RZ503	X	X	X	X	X	X	X	X	X	X		MALAYSIA
Nolidae	Chloephorinae	*Diehlea tumida*	**IV**	RZ479	X	X	X	X	X	–	X	X	X	–	TS	MALAYSIA
Nolidae	Chloephorinae	*Chloriola gratissima*	**IV**	RZ531	X	X	X	X	X	X	X	X	X	X	TS	MALAYSIA
Nolidae	Chloephorinae	*Gelastocera viridimacula*	**IV**	RZ521	X	X	X	X	X	X	X	X	–	X	TG	MALAYSIA
Nolidae	Chloephorinae	*Beara tortriciformis*	**IV**	RZ515	X	X	X	X	X	X	X	X	–	X		MALAYSIA
Nolidae	Chloephorinae	*Ariolica argentea*	**I,IV**	RZ63	HQ006234	HQ006937	HQ006329	HQ006421	HQ006842	–	HQ006745	HQ006653	HQ007020	HQ006566	TG	JAPAN
Nolidae	Chloephorinae	*Gariga mirabilis*	**IV**	RZ114	X	X	X	–	X	X	X	X	–	–		HONG KONG

Nolidae	Chloephorinae	*Tympanistes fusimargo*	**IV**	RZ566	X	X	X	X	X	X	X	X	X	–		MALAYSIA
Nolidae	Chloephorinae	*Pseudoips prasinana* 2	**IV**	RZ128	X	–	X	X	X	X	X	–	–	–	TG/TS	GERMANY
Nolidae	Chloephorinae	*Pseudoips prasinana* 1	**I,IV,V**	MM00107	GU828600	GU828399	GU828934	GU829229	GU829496	GU829754	GU830611	GU830312	GU828101	GU829989	TG	FINLAND
Nolidae	Chloephorinae	*Clethrophora distincta*	**IV**	RZ478	X	X	X	X	X	X	X	X	X	X	TS	JAPAN
Nolidae	Chloephorinae	*Hylophilodes orientalis*	**IV**	RZ643	X	–	X	X	X	–	X	X	X	–	TS	THAILAND
Nolidae	Chloephorinae	*Chloroplaga sp.*	**IV**	RZ520	X	X	X	X	X	X	X	X	X	X		MALAYSIA
Nolidae	Chloephorinae	*Chloroplaga nygmia*	**IV**	RZ646	X	–	X	X	X	X	X	X	–	X	TS	THAILAND
Nolidae	Chloephorinae	*Sinna extrema*	**IV**	RZ490	X	X	X	X	X	X	X	X	X	X		JAPAN
Nolidae	Chloephorinae	*Sinna floralis*	**IV**	RZ529	X	X	X	X	X	X	X	X	–	X		MALAYSIA
Nolidae	Chloephorinae	*Siglophora ferreilutea*	**IV**	RZ489	X	X	X	X	X	X	X	X	X	–		JAPAN
Nolidae	Chloephorinae	*Chandica quadripennis*	**IV**	RZ579	X	X	X	X	X	X	X	X	–	X	TS	MALAYSIA
Nolidae	Chloephorinae	*Cossedia hyriodes*	**IV**	RZ524	X	X	X	X	X	X	X	X	–	–		MALAYSIA
Nolidae	Chloephorinae	*Labanda ceylusalis*	**IV**	RZ555	X	X	X	X	X	X	X	X	–	X		MALAYSIA
Nolidae	Chloephorinae	*Aquis orbicularis*	**IV**	RZ639	X	–	X	X	X	X	X	X	–	–		THAILAND
Nolidae	Chloephorinae	*Tathothripa continua*	**IV**	RZ640	–	–	X	X	X	X	X	X	–	–	TS	THAILAND
Nolidae	Chloephorinae	*Blenina donans*	**I,IV**	RZ64	HQ006235	HQ006938	HQ006330	HQ006422	HQ006843	HQ006490	HQ006746	HQ006654	HQ007021	HQ006567	TG	SUMATRA
Nolidae	Chloephorinae	*Blenina quinaria*	**IV**	RZ499	X	X	X	X	X	X	X	X	X	X	TG	HONG KONG
Nolidae	Chloephorinae	*Dilophothripa chrysorrhaea*	**IV**	RZ528	X	X	X	X	X	X	X	X	–	–	TS	MALAYSIA
Nolidae	Chloephorinae	*Egchiretes nomimus*	**IV**	RZ481	X	X	X	X	X	–	X	–	–	–	TS	COSTA RICA
Nolidae	Chloephorinae	*Nycteola degenerana*	**I,IV**	MM00135	GU828612	GU828410	GU828946	GU829238	GU829506	GU829760	GU830621	GU830323	GU828113	GU830000	TG	FINLAND
Nolidae	Chloephorinae	*Nycteola sinuosa*	**IV**	RZ501	X	X	X	X	X	X	X	X	–	–	TG	HONG KONG
Nolidae	Chloephorinae	*Nycteola indica*	**IV**	RZ539	X	X	X	X	X	X	X	X	–	X	TG	MALAYSIA
Nolidae	Chloephorinae	*Garella nilotica*	**IV**	RZ477	X	X	X	X	X	X	X	X	X	X		USA
Nolidae	Chloephorinae	*Garella ruficirra*	**IV**	RZ502	X	X	X	X	X	–	X	X	–	X		HONG KONG
Nolidae	Chloephorinae	*Giaura robusta*	**I,IV**	RZ31	HQ006200	HQ006904	HQ006296	HQ006389	HQ006808	HQ006465	HQ006713	HQ006621	HQ006993	–		HONG KONG
Nolidae	Chloephorinae	*Giaura nigrilineata*	**IV**	RZ519	X	–	X	X	X	X	X	X	–	X		MALAYSIA
Nolidae	Chloephorinae	*Giaura multipunctata*	**IV**	RZ496	X	X	X	X	X	X	X	X	X	X		HONG KONG
Nolidae	Chloephorinae	*Giaura niveidisca*	**IV**	RZ527	X	X	X	X	X	X	X	X	–	X		MALAYSIA
Nolidae	Chloephorinae	*Pardasena verna*	**IV**	RZ532	X	X	X	X	X	–	X	X	X	–		MALAYSIA
Nolidae	Chloephorinae	*Etanna clopaea*	**IV**	RZ486	X	X	X	X	X	X	X	X	–	X		AUSTRALIA
Nolidae	Chloephorinae	*Etanna breviuscula* 2	**IV**	RZ491	X	X	X	X	X	X	X	X	X	X		HONG KONG
Nolidae	Chloephorinae	*Etanna breviuscula* 1	**IV**	RZ497	X	X	X	X	X	X	X	X	–	X		HONG KONG
Nolidae	Chloephorinae	*Etanna breviuscula* 3	**IV**	RZ518	X	X	X	X	X	X	X	X	–	X		MALAYSIA
Noctuidae	Dyopsinae	*Dyops chromatophila*	**I,II,V**	RZ10	HQ006158	–	HQ006255	HQ006350	HQ006767	HQ006438	HQ006674	HQ006585	HQ006957	HQ006507	TG	COSTA RICA
Noctuidae	Dyopsinae	*Pseudoarcte melanis*	**II,V**	RZ147	JN401235	JN401119	JN401353	JN401465	JN400928	JN401567	JN401874	JN401773	JN401037	JN401669		GHANA
Noctuidae	Dyopsinae	*Arcte modesta*	**I,II,V**	RZ54	HQ006226	HQ006929	HQ006321	HQ006413	HQ006834	–	HQ006738	HQ006646	HQ007015	HQ006559	TG	MALAYSIA
Noctuidae	Dyopsinae	*Pararcte schneideriana*	**V**	RZ548	X	X	X	X	X	X	X	X	–	–	TS	COSTA RICA
Noctuidae	Dyopsinae	*Belciana kala*	**II,V**	RZ416	JN401238	–	JN401356	JN401468	JN400930	JN401570	JN401879	JN401776	JN401040	JN401672		MALAYSIA

Noctuidae	Dyopsinae	*Belciana biformis*	**II,V**	RZ384	JN401237	JN401121	JN401355	JN401467	JN400929	JN401569	JN401877	JN401775	JN401039	JN401671	TS	MALAYSIA
Noctuidae	Dyopsinae	*Cyclodes omma*	**V**	RZ636	X	X	X	X	X	X	X	X	–	X	TS	THAILAND
Noctuidae	Dyopsinae	*Ceroctena amynta*	**V**	RZ552	X	X	X	X	X	X	X	X	X	–	TS	ECUADOR
Noctuidae	Dyopsinae	*Sosxetra grata*	**II,V**	RZ281	JN401236	JN401120	JN401354	JN401466	JN400988	JN401568	JN401875	JN401774	JN401038	JN401670	TS	COSTA RICA
Noctuidae	Plusiinae	*Autographa gamma*	**I,II,IV,V**	MM00328	GU828636	GU828434	GU828970	GU829256	GU829528	–	GU830640	GU830344	GU828135	GU830023	TG/TS	FINLAND
Noctuidae	Plusiinae	*Abrostola tripartita*	**I,V**	MM05132	HQ006152	HQ006859	HQ006250	HQ006345	HQ006761	–	HQ006669	HQ006580	HQ006952	HQ006502	TG	FINLAND
Noctuidae	Eustroniinae	*Deltote uncula*	**I,V**	MM04601	GU828703	GU828498	GU829026	GU829315	GU829579	GU829818	GU830691	GU830407	GU828192	GU830089		FINLAND
Noctuidae	Cuculliinae	*Cucullia umbratica*	**I,IV,V**	MM04543	GU828701	GU828496	GU829024	GU829313	GU829577	GU829817	GU830689	GU830405	GU828190	GU830087	TG/TS	FINLAND
Noctuidae	Dilobinae	*Diloba caeruleocephala*	**II,V**	MM09267	JN401246	JN401128	JN401364	JN401475	JN400982	–	JN401887	JN401784	–	JN401678	TG/TS	FINLAND
Noctuidae	Raphiinae	*Raphia abrupt*	**I,II,V**	CWM-94-0372	GU828548	GU828350	GU828893	GU829193	GU829455	GU829728	GU830579	GU830270	GU828059	GU829939	TG	USA
Noctuidae	Pantheinae	*Eucocytia meeki*	**II,V**	RZ87	JN401247	JN401129	–	–	–	–	JN401888	JN401785	JN401047	–	TG/TS	INDONESIA
Noctuidae	Pantheinae	*Thiacidas* sp.	**II,V**	RZ459	JN401249	JN401131	JN401366	JN401477	JN400937	JN401579	JN401888	JN401787	–	JN401680	TG	INDIA
Noctuidae	Pantheinae	*Antitrisuloides catocalina*	**II,V**	RZ388	JN401248	JN401130	JN401365	JN401476	JN400936	JN401578	JN401889	JN401786	JN401048	JN401679	TG	MALAYSIA
Noctuidae	Pantheinae	*Panthea coenobita*	**I,II,V**	MM04583	GU828702	GU828497	GU829025	GU829314	GU829578	–	GU830690	GU830406	GU828191	GU830088	TG/TS	FINLAND
Noctuidae	Acontiinae	*Emmelia trabealis*	**I,V**	MM09893	HQ006147	HQ006854	HQ006245	HQ006340	HQ006756	–	HQ006664	HQ006576	HQ006947	–		SARDINIA
Noctuidae	Acontiinae	*Acontia lucida*	**I,IV,V**	MM00152	GU828617	GU828415	GU828952	GU829243	GU829512	GU829763	GU830627	GU830327	GU828118	GU830006	TG	GREECE
Noctuidae	Bagisarinae	*Amyna octo*	**II,V**	RZ50	JN401242	JN401125	JN401360	JN401471	JN400984	JN401574	JN401883	JN401780	JN401043	JN401675		MALAYSIA
Noctuidae	Bagisarinae	*Xanthodes albago*	**I,II,V**	MM09894	GU828844	GU929808	GU829145	GU829412	GU829693	–	GU830792	GU830535	GU828308	GU830224		SARDINIA
Noctuidae	Bagisarinae	*Ramadasa pavo*	**II,V**	RZ382	JN401241	JN401124	JN401359	JN401470	JN400978	JN401573	JN401882	JN401779	–	JN401674	TS	MALAYSIA
Noctuidae	Bagisarinae	*Dyrzela plagiata*	**II,V**	RZ395	JN401240	JN401123	JN401358	JN401469	JN400932	JN401572	JN401881	JN401778	JN401042	JN401673	TS	MALAYSIA
Noctuidae	Bagisarinae	*Encruphion leena*	**II,V**	RZ351	JN401243	JN401126	JN401361	JN401472	JN400933	JN401575	JN401884	JN401781	JN401044	JN401676		COSTA RICA
Noctuidae	Bagisarinae	*Vespola caeruleifera*	**V**	RZ595	X	X	X	X	X	–	X	X	X	–	TS	COSTA RICA
Noctuidae	Bagisarinae	*Parangitia temperata*	**II,IV,V**	RZ463	JN401244	JN401127	JN401362	JN401473	JN400934	JN401576	JN401885	JN401782	JN401045	–		COSTA RICA
Noctuidae	Bagisarinae	*Parangitia mosaica*	**II,IV,V**	RZ464	JN401245	–	JN401363	JN401474	JN400935	JN401577	JN401886	JN401783	JN401046	JN401677		COSTA RICA
Noctuidae	Bagisarinae	*Diopa corone*	**II,IV,V**	RZ472	JN401239	JN401122	JN401357	–	JN400931	JN401571	JN401880	JN401777	JN401041	–		FRENCH GUIANA
Noctuidae	Bagisarinae	*Concana mundissima*	**IV,V**	RZ621	X	X	X	X	X	X	X	–	–	X	TS	USA
Noctuidae	Bagisarinae	*Concana lecta*	**IV,V**	RZ474	X	–	–	X	X	–	X	X	–	–		COSTA RICA
Noctuidae	Bagisarinae	*Concana permixta*	**IV,V**	RZ482	X	X	X	X	X	X	X	X	–	X		GUATEMALA
Noctuidae	Amphipyrinae	*Amphipyra perflua*	**I,II,IV,V**	MM01162	GU828660	GU828458	GU828991	GU829275	GU829546	GU829787	GU830657	GU830366	GU828157	GU830047	TG	FINLAND
Noctuidae	Amphipyrinae	*Brachionycha nubeculosa*	**I,V**	MM01542	GU828667	GU828465	GU828998	GU829281	GU829552	GU829793	GU830663	GU830373	GU828164	GU830054	TS	FINLAND
Noctuidae	Metoponiinae	*Flammona quadrifasciata*	**V**	RZ596	X	X	X	X	X	X	X	X	X	X	TS	MALAYSIA
Noctuidae	Metoponiinae	*Panemeria tenebrata*	**I,V**	MM00005	HQ006157	HQ006863	HQ006254	HQ006349	HQ006766	HQ006437	HQ006673	HQ006584	HQ006956	HQ006506		FINLAND
Noctuidae	Acronictinae	*Craniophora ligustri*	**I,V**	MM06745	HQ006148	HQ006855	HQ006246	HQ006341	HQ006757	HQ006432	HQ006665	HQ006577	HQ006948	HQ006498	TS	FINLAND
Noctuidae	Acronictinae	*Acronicta americana*	**V**	RZ597	X	X	X	X	X	X	X	X	–	X	TG	USA
Noctuidae	Acronictinae	*Acronicta rumicis*	**I,V**	MM01529	GU828666	GU828464	GU828997	GU829280	GU829551	GU829792	GU830662	GU830372	GU828163	GU830053	TG	FINLAND
Noctuidae	Acronictinae	*Cerma cerintha*	**V**	RZ617	X	X	X	X	X	X	X	–	–	X		USA
Noctuidae	Acronictinae	*Comachara cadburyi*	**V**	RZ618	X	X	X	X	X	X	X	X	–	X	TS	USA

Noctuidae	Acronictinae	*Harrisimemna trisignata*	**V**	RZ619	X	X	X	X	X	X	X	X	–	X		USA
Noctuidae	Acronictinae	*Polygrammate hebraeicum*	**V**	RZ620	X	X	X	X	X	X	X	X	X	X	TS	USA
Noctuidae	Acronictinae	*Agriopodes fallax*	**V**	RZ616	X	X	X	X	X	X	X	X	–	X	TS	USA
Noctuidae	Agaristinae	*Periscepta polysticta*	**I,II,V**	MM07669	GU828820	GU929788	GU829125	GU829400	GU829674	GU829892	GU830773	GU830519	GU828289	GU830201	TG/TS	AUSTRALIA
Noctuidae	Aediinae	*Aedia leucomelas*	**II,V**	RZ277	JN401250	JN401132	JN401367	JN401478	JN400976	JN401580	JN401891	JN401788	–	JN401681	TS	JAPAN
Noctuidae	Condicinae	*Condica illecta*	**V**	RZ511	X	X	X	X	X	X	X	–	–	X	TG	MALAYSIA
Noctuidae	Condicinae	*Condica vecors*	**I,II**	CWM-95-0471	GU828550	GU828352	GU828895	GU829194	GU829457	–	GU830581	–	GU828061	GU829941	TG	USA
Noctuidae	Condicinae	*Hemicephalis alesa*	**II,V**	RZ341	JN401251	JN401133	JN401368	JN401479	JN400938	JN401581	JN401892	JN401789	JN401049	JN401682		COSTA RICA
Noctuidae	Heliothinae	*Pyrrhia umbra*	**I,V**	MM05114	GU828712	GU828507	GU829034	GU829324	GU829588	GU829825	GU830700	GU830416	GU828200	GU830098		FINLAND
Noctuidae	unassigned	*Chytonix diehli*	**V**	RZ517	X	X	X	X	X	X	X	X	–	X		MALAYSIA
Noctuidae	Bryophilinae	*Cryphia raptricula*	**I,V**	MM04919	GU828708	GU828503	GU829031	GU829320	GU829584	GU829822	GU830696	GU830412	GU828196	GU830094		FINLAND
Noctuidae	Bryophilinae	*Stenoloba futii*	**V**	RZ523	X	X	X	X	X	X	X	X	X	–		MALAYSIA
Noctuidae	unassigned	*Ecpatia* sp.	**V**	RZ545	X	X	X	X	X	X	X	X	–	X		MALAYSIA
Noctuidae	unassigned	*Ecpatia longinquua*	**I,II,V**	RZ25	HQ006190	HQ006894	HQ006286	HQ006380	HQ006798	–	HQ006703	HQ006611	HQ006985	HQ006532		HONG KONG
Noctuidae	Noctuinae	*Tiracola aureata*	**V**	RZ14	X	X	X	X	–	X	X	X	X	–		INDONESIA
Noctuidae	Noctuinae	*Actinotia polyodon*	**I,V**	MM05153	GU828714	GU828509	–	GU829326	GU829590	GU829827	GU830702	GU830418	GU828202	GU830100	TG	FINLAND
Noctuidae	Noctuinae	*Hoplodrina octogenaria*	**I,V**	MM01651	HQ006153	HQ006860	HQ006251	HQ006346	HQ006762	HQ006434	HQ006670	HQ006581	HQ006953	HQ006503		FINLAND
Noctuidae	Noctuinae	*Diaphone* sp.	**I,II,V**	MF-05-0053	GU828571	GU828372	GU828913	GU829206	GU829475	GU829738	GU830591	GU830285	GU828076	GU829960		TANZANIA
Noctuidae	Noctuinae	*Apamea crenata*	**I,IV,V**	MM01170	GU828661	GU828459	GU828992	GU829276	GU829547	GU829788	GU830658	GU830367	GU828158	GU830048	TG	FINLAND
Noctuidae	Noctuinae	*Ufeus faunas*	**I,V**	RR-98-0914	GU828860	GU929822	GU829163	GU829425	GU829709	GU829911	GU830807	GU830552	GU828320	GU830238	TG	USA
Noctuidae	Noctuinae	*Noctua fimbriata*	**I,II,IV,V**	MM04752	GU828705	GU828500	GU829028	GU829317	GU829581	GU829820	GU830693	GU830409	GU828194	GU830091	TG	FINLAND