

A new molecular phylogeny offers hope for a stable family level classification of the Noctuoidea (Lepidoptera)

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To examine the higher level phylogeny and evolutionary affinities of the megadiverse superfamily Noctuoidea, an extensive molecular systematic study was undertaken with special emphasis on Noctuidae, the most controversial group in Noctuoidea and arguably the entire Lepidoptera. DNA sequence data for one mitochondrial gene (cytochrome oxidase subunit I) and seven nuclear genes (Elongation Factor-1 α , *wingless*, Ribosomal protein S5, Isocitrate dehydrogenase, Cytosolic malate dehydrogenase, Glyceraldehyde-3-phosphate dehydrogenase and Carbamoylphosphate synthase domain protein) were analysed for 152 taxa of principally type genera/species for family group taxa. Data matrices (6407 bp total) were analysed by parsimony with equal weighting and model-based evolutionary methods (maximum likelihood), which revealed a new high-level phylogenetic hypothesis comprising six major, well-supported lineages that we here interpret as families: Oenosandridae, Notodontidae, Erebidae, Nolidae, Euteliidae and Noctuidae.

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Introduction

The classification of the diversity of life on Earth is one of the major ongoing undertakings 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. Although there has been some discussion of abandoning the 250-year-old Linnaean system for such classification, focusing more on genetic diversity, most researchers still prefer to use this hierarchical system. It provides a framework for access to a massive information resource on the biology, ecology and economic importance of all species, perhaps epitomized today by the Encyclopaedia of Life initiative (Wilson 2003). 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.

Lepidoptera are one of the four major Orders of insects, and Noctuoidea are the largest superfamily within the Order with between 42 000 (Heppner 1991) and 70 000 (Kitching & Rawlins 1998) described species. The next most numerous superfamily is Geometroidea with about 21 500 species, followed by Pyraloidea, Papilionoidea and Gelechioidea each with between 15 000 and 16 000 species (Heppner 1991). In contrast, the total number of terrestrial vertebrates is approximately 21 500 species (Maddison 2007).

The monophyly of Noctuoidea, based on the presence of a single apomorphic character, the metathoracic tympanal organ (Miller 1991) and its associated abdominal structures, seems well established (Kitching & Rawlins 1998; Mitchell *et al.* 2006). However, the limits and content of the constituent families, and the evolutionary relationships amongst and within these, are very poorly understood (Mitchell *et al.* 2006).

Noctuid species are placed in approximately 4200 genera (Kitching & Rawlins 1998) but there are numerous undescribed species, particularly from tropical regions. For example, the noctuid species total for Borneo now stands at about 2800, an increase of over 50% on a total estimated from a previous survey (1980) of the collections of The Natural History Museum in London (J. D. Holloway, unpublished data). This increase is the result of a quarter of a century of taxonomic effort on a major input of fresh survey material from Borneo, leading to a series of monographs on the Macrolepidoptera, those on the noctuids mostly cited in this paper. Taking as a minimum the calculations of the total Bornean Lepidoptera fauna by Robinson & Tuck (1993, 1996), this figure for noctuids represents about one quarter of that total. The proportion of Noctuoidea in the global total is likely to be similar.

The larvae of many noctuid genera include armyworms, cutworms, bollworms and stem borers, that collectively have a massive economic impact annually (Kitching 1984). The adults of other genera damage fruit crops by piercing the skins to suck juices (Bänziger 1982). Noctuids constitute one quarter of the approximately 6000 Lepidoptera species noted to be of economic importance by Zhang (1994). Though many of these can be assigned to what Mitchell *et al.* (2006) termed the 'pest clade', many more are distributed across the whole superfamily in over 500 genera (Zhang 1994). Therefore, resolution of stable, extrapolative higher level classificatory structure for the superfamily may prove to be an important prerequisite for studies of pest bionomics across the group.

Numerous classifications of the family groups of Noctuoidea have been proposed. 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). Miller (1991) recognized seven families: Oenosandridae, Doidae, Notodontidae, Lymantriidae, Arctiidae, Aganainae and Noctuidae. Scoble (1992) included six families, placing Aganainae as a subfamily within Noctuidae. Kitching & Rawlins (1998) later recognized three fundamental lineages of Noctuoidea: Oenosan-

dridae, Doidae + Notodontidae, and the quadrifid families (those where vein MA2 arises very close to, or is stalked with, MP1 in the forewing, i.e., Arctiidae, Lymantriidae, Noctuidae, Nolidae and Pantheidae). Most recently, three landmark publications (Fibiger & Lafontaine 2005; Lafontaine & Fibiger 2006; Mitchell *et al.* 2006) presented detailed phylogenies and revised the classification of Noctuoidea three times, each classification having its own limitations and strengths (Roe *et al.* 2010). Fibiger & Lafontaine (2005) proposed a new classification with ten families: Oenosandridae, Doidae, Notodontidae, Strepsimanidae, Nolidae, Lymantriidae, Arctiidae, Erebidae, Micronoctuidae and Noctuidae. 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.

Within the superfamily, the most controversial family group taxon is Noctuidae. Many of the traditional subfamilies are now recognized as unnatural (Kitching 1984; Beck 1991, 1992; Lafontaine & Poole 1991; Speidel *et al.* 1996; Kitching & Rawlins 1998; Fibiger & Lafontaine 2005; Mitchell *et al.* 2006). Indeed, the composition and monophyly of many subfamilies is still open to question, and in particular, the taxonomic composition of the quadrifine noctuids (those with a strong vein MA2 in the hindwing) has remained notoriously difficult to establish. The situation has been reviewed recently by several authors (Speidel & Naumann 1995; Fibiger 2003; Kühne & Speidel 2004; Holloway 2005, 2008), who have suggested that the monophyly of the group was highly doubtful. At a noctuid workshop in Denmark in 2002 (Holloway 2005), it was decided that, prior to any further attempts to redefine family groups across the superfamily, it was necessary to gain a clearer understanding of the higher taxonomic diversity involved by attempting to identify on morphological grounds more potentially monophyletic groupings of genera within the immense diversity of the trifold section of the superfamily, particularly amongst the much less well worked quadrifine richness in the tropics. Studies of this kind would provide a basis for a sampling strategy for future phylogenetic studies across the group as a whole, exemplars being selected from significant groupings of genera and morphologically well-supported concepts of higher taxa (and subgroups thereof) such as the traditional Arctiidae and Lymantriidae. This approach was adopted

by Holloway (2005) when exploring a broad cross-section of the Oriental tropical quadrifine fauna from Borneo, relating it as far as possible to type taxa of available family group names globally.

Several molecular studies have examined higher level relationships within the Noctuidae *sensu lato*. Weller *et al.* (1994), using partial sequences of nuclear 28S rRNA (300 bp) and mitochondrial ND1 (320 bp) from 26 noctuid species, including 10 noctuids, noted that, despite low levels of support, parsimony analyses consistently grouped quadrifine noctuids with Arctiidae, and often Lymantriidae, rather than with trifine noctuids (those with vein MA2 in the hindwing usually vestigial or absent so that the cubital vein appears to branch into three veins), suggesting paraphyly of Noctuidae. However, vein reduction in this region also occurs in some Arctiidae and Nolidae as we discuss later. Subsequent studies based on sequences of two nuclear genes, *Elongation Factor-1 α* (EF-1 α) and *Dopa Decarboxylase* (DDC) (Friedlander *et al.* 1994; Mitchell *et al.* 1997, 2000, 2006; Fang *et al.* 2000) provided further evidence for the paraphyly of Noctuidae. Mitchell *et al.* (2006) found a strongly supported clade of quadrifine noctuid moths that 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 noctuids, but 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 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 in question, it is crucial to sample the type genera of each family, subfamily and tribe to assess the taxonomic limits of a given category.

Previous molecular studies have used only a small number of molecular markers, usually one to three gene regions (Wahlberg & Wheat 2008). Here, we present a phylogenetic hypothesis for higher taxa of Noctuoidea using new molecular data from eight gene regions.

Materials and methods

We sampled 152 representatives of many major lineages of the Noctuoidea complex. These comprise four outgroup taxa and 148 Noctuoidea species representing four families (Oenosandridae, Notodontidae, Noctuidae and Micro-noctuidae), 50 subfamilies and 51 tribes, as recognized by

Lafontaine & Fibiger (2006), as well as 16 taxa of uncertain position (Table 1). Based on the results of Regier *et al.* (2009) and Mutanen *et al.* (2010), as well as our own preliminary analyses, we did not include the family Doidae. We were unable to sample some scarce taxa with restricted distributions and/or low species richness (e.g., subfamilies Cocytiinae, Eucocytiinae and Strepsimaninae and the type genera of a few tribes/subtribes). To test the monophyly of the Noctuoidea, we included four species from three other superfamilies, namely Drepanoidea, Bombycoidea and Geometroidea. We rooted the cladograms with *Thyatira batis* (Drepanidae).

We extracted DNA from one or two legs, dried or freshly preserved in 96% ethanol, using the DNeasy tissue extraction kit (QIAGEN, Hilden, Germany). For each specimen, we sequenced the *cytochrome oxidase subunit I* gene (COI) from the mitochondrial genome, and the EF-1 α , 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. All genes are protein coding and have been found to be highly informative for phylogenetic analyses at the level of families and superfamilies (Wahlberg & Wheat 2008; Wahlberg *et al.* 2009; Mutanen *et al.* 2010). PCR and sequencing protocols follow Wahlberg & Wheat (2008). Resulting chromatograms were checked and DNA sequences aligned by eye using the program BioEdit (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.

The gene regions were analysed separately and combined in various partitions using parsimony and maximum likelihood (ML) methods. The data were combined in three ways: all gene regions together, all nuclear genes together (i.e., the mitochondrial gene COI excluded) and all gene regions together with third codon positions excluded.

Parsimony analyses were undertaken by performing New Technology heuristic searches in the program TNT (Goloboff *et al.* 2003). All characters were treated as unordered and equally weighted. Clade robustness was estimated by Bremer support (Bremer 1988, 1994) using a script (Peña *et al.* 2006) in TNT. Model-based phylogenetic analyses were implemented using ML and a GTR+G+I model was chosen as the most appropriate model of sequence evolution for each gene partition using FindModel (<http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html>). However, we assigned all partitions with the GTR+G model, as the parameters I (proportion of Invariant positions) and G (Gamma distribution) are strongly correlated

Table 1 List of taxa with voucher codes and GenBank accession numbers. The families are classified as indicated for Figs 1 and 2

Family	Subfamily	Tribe: subtribe	Species	Specimen ID	COI- LCO	COI- Jerry	EF-1 α - begin	EF-1 α - end	Wingless	GAPDH	Rps5	MDH	CAD	IDH	Type status	Locality
			Outgroup													
Drepanidae	Thyatirinae		<i>Thyatira batris</i>	MM00027	GU828580	GU828380	GU828919	GU829212	GU829481	GU829743	GU830597	GU830293	GU828083	GU829969	TG/TS	Finland
Sphingidae	Sphinginae		<i>Sphinx ligustri</i>	NW141-12	EU141358	EU141358	EU136665	EU141239	EU141494	EU141391	EU141391	EU141615	EU141313	EU141550	TG/TS	Finland
Bombycidae	Bombycinae		<i>Bombyx mori</i>	NW149-1	EU141360	EU141360	EU136667	EU141241	EU141495	EU141393	EU141393	EU141617	EU141315	EU141552	TG/TS	USA
Geometridae	Archaearinae		<i>Archaearis parthenias</i>	NW107-1	DQ018928	DQ018928	DQ018899	DQ018899	DQ018869	EU141485	EU141381	EU141604	EU141303	EU141539	TG/TS	Sweden
Oenosandridae			Ingroup													
			<i>Oenosandra boisduvalli</i>	MM07590	GU828791	GU929762	GU829098	GU829377	GU829651	GU829871	GU830751	GU830492	GU828266	GU830173	TG/TS	Australia
Oenosandridae			<i>Discophlebia</i> sp.	RZ403	HQ006217	HQ006921	HQ006313	HQ006404	HQ006825	HQ006480	HQ006729	HQ006638	–	HQ006551		Australia
Notodontidae	Phalerinae		<i>Phalera bucephala</i>	MM00122	GU828607	GU828405	GU828941	GU829235	GU829502	–	GU830617	GU830318	GU828108	GU829995	TG/TS	Finland
Notodontidae	Heterocampinae		<i>Stauropus fagi</i>	MM00981	GU828651	GU828449	GU828983	GU829266	GU829539	GU829780	GU830650	GU830357	GU828148	GU830038	TS	Finland
Notodontidae	Notodontinae		<i>Notodonta dromedarius</i>	MM00998	GU828653	GU828451	GU828984	GU829268	GU829540	GU829781	GU830652	GU830359	GU828150	GU830040	TG/TS	Finland
Notodontidae	Pygaerinae		<i>Clostera pigra</i>	MM01005	GU828654	GU828452	GU828985	GU829269	GU829541	GU829782	GU830653	GU830360	GU828151	GU830041		Finland
Notodontidae	Thaumetopoeinae		<i>Epicoma melanosicta</i>	MM07592	GU828792	GU929763	GU829099	GU829378	GU829652	GU829872	GU830752	GU830493	GU828267	GU830174		Australia
Notodontidae	Thaumetopoeinae		<i>Thaumetopoea sollitaria</i>	MM09888	GU828843	GU929807	GU829144	–	GU829692	GU829904	GU830791	GU830534	GU828307	GU830223	TG	Greece
Notodontidae	Dudusinae		<i>Crinodes besckei</i>	05-smp-57213	GU828527	–	GU828873	GU829175	GU829434	–	GU830563	GU830251	GU828039	GU829918		Costa Rica
Notodontidae	Nystaleinae		<i>Nystalea striata</i>	05-smp-4443	GU828525	–	GU828871	GU829173	GU829432	GU829717	GU830561	GU830249	GU828037	GU829916	TG	Costa Rica
Notodontidae	Diopinae		<i>Scotura leucophleps</i>	06-smp-22781	GU828532	GU828334	GU828878	GU829179	GU829439	GU829721	GU830568	GU830256	GU828044	GU829923		Costa Rica
Erebidae	Rivulinae		<i>Rivula sericealis</i>	MM01404	GU828664	GU828462	GU828995	GU829278	–	GU829791	–	GU830370	GU828161	GU830051	TG/TS	Finland
Erebidae	Boletobiinae		<i>Parascotia fuliginaria</i>	MM00340	HQ006154	HQ006862	HQ006253	HQ006347	HQ006764	HQ006436	HQ006672	HQ006583	HQ006954	HQ006505	TG/TS	Finland
Erebidae	Hypenodinae		<i>Hypenodes humidalis</i>	MM01780	GU828671	GU828469	–	GU829285	GU829556	–	GU830666	–	GU828168	GU830058	TG/TS	Finland
Erebidae	Hypenodinae		<i>Schrankia costaestrigalis</i>	RZ27	HQ006192	HQ006896	HQ006288	HQ006382	HQ006800	HQ006461	HQ006705	HQ006613	HQ006987	–		Hong Kong
Erebidae	Araeopterinae		<i>Araeopteron</i> sp.	RZ137	HQ006170	HQ006874	HQ006267	HQ006361	HQ006779	–	HQ006686	–	HQ006966	HQ006515	TG	Indonesia
Erebidae	Eublemminae	Eublemmini	<i>Eublemma purpurina</i>	RZ7	HQ006237	HQ006940	HQ006332	HQ006424	HQ006845	HQ006491	HQ006748	HQ006655	–	HQ006569	TG	Hungary
Erebidae	Hermiinae		<i>Polypogon strigilatus</i>	MM01286	GU828663	GU828461	GU828994	GU829277	GU829549	GU829790	GU830660	GU830369	GU828160	GU830050	TG/TS	Finland
Erebidae	Hermiinae		<i>Paracolax tristalis</i>	RZ5	HQ006224	HQ006927	HQ006319	HQ006411	HQ006832	–	HQ006736	–	HQ007013	–		Hungary
Erebidae	Hermiinae		<i>Hermia tarsicrinalis</i>	RZ6	HQ006232	HQ006935	HQ006327	HQ006419	HQ006840	HQ006489	–	–	–	–	TG	Hungary
Erebidae	Hermiinae		<i>Simplicia pachycera</i>	RZ166	HQ006175	HQ006879	HQ006272	HQ006366	–	HQ006448	HQ006691	HQ006599	HQ006971	HQ006520		Ghana

Table 1 (Continued)

Family	Subfamily	Tribe: subtribe	Species	Specimen ID	COI- LCO	COI- Jerry	EF-1 α - begin	EF-1 α - end	Wingless	GAPDH	RpS5	MDH	CAD	IDH	Type status	Locality
Erebidae	Scolecocampinae		<i>Scolecocampa liburna</i>	RZ9	HQ006242	HQ006944	HQ006336	HQ006429	HQ006850	HQ006495	HQ006753	HQ006660	HQ007025	HQ006573	TG	USA
Erebidae	Hypeninae		<i>Hypena proboscidalis</i>	MM01545	GU828668	GU828466	GU828999	GU829282	GU829553	GU829794	GU830664	GU830374	GU828165	GU830055	TG/TS	Finland
Erebidae	Phytometrinae		<i>Phytometra viridaria</i>	RZ129	HQ006165	HQ006962	HQ006262	HQ006356	HQ006774	HQ006442	HQ006681	HQ006591	HQ006962	HQ006512	TG	Finland
Erebidae	Phytometrinae		<i>Colobochyla salicalis</i>	RZ4	HQ006215	HQ006919	HQ006311	HQ006402	HQ006823	HQ006478	HQ006727	HQ006636	HQ007005	–	TS	Hungary
Erebidae	Phytometrinae		<i>Oxyccilla ondo</i>	RZ24	HQ006184	HQ006888	HQ006280	HQ006375	HQ006792	HQ006456	–	HQ006607	HQ006980	HQ006529	–	USA
Erebidae	Pangraptnae		<i>Pangrapta bicornuta</i>	RZ40	HQ006216	HQ006920	HQ006312	HQ006403	HQ006824	HQ006479	HQ006728	HQ006637	HQ007006	HQ006550	TG	Hong Kong
Erebidae	Pangraptnae		<i>P. decoralis</i>	RZ66	HQ006236	HQ006939	HQ006331	HQ006423	HQ006844	–	HQ006747	–	HQ007022	HQ006568	TG/TS	USA
Erebidae	Aventinae		<i>Laspeyria flexula</i>	RZ3	HQ006197	HQ006901	HQ006293	HQ006386	HQ006805	HQ006463	HQ006710	HQ006618	HQ006990	HQ006536	TG/TS	Hungary
Erebidae	Aventinae		<i>Corgatha mitens</i>	RZ36	HQ006211	HQ006915	HQ006307	HQ006398	HQ006819	HQ006474	HQ006723	HQ006632	HQ007001	HQ006547	–	Hong Kong
Erebidae	Aventinae		<i>Prolophota trigonifera</i>	RZ37	HQ006212	HQ006916	HQ006308	HQ006399	HQ006820	HQ006475	HQ006724	HQ006633	HQ007002	–	TS	Hong Kong
Erebidae	Aventinae		<i>Meraemene albipunctata</i>	RZ41	HQ006218	HQ006922	HQ006314	HQ006405	HQ006826	HQ006481	HQ006730	HQ006639	HQ007007	HQ006552	–	Hong Kong
Erebidae	Aventinae	Trisateini	<i>Trisateles emortualis</i>	MM04877	GU828707	GU828502	GU829030	GU829319	GU829583	GU829821	GU830695	GU830411	GU828195	GU830093	TG/TS	Finland
Erebidae	Erebinae		<i>Erebus ephesperis</i>	RZ11	HQ006161	HQ006866	HQ006258	HQ006353	HQ006770	HQ006440	HQ006677	HQ006587	HQ006959	HQ006510	TG	Taiwan
Erebidae	Unassigned	Anobini	<i>Anoba anguliplaga</i>	RZ332	HQ006206	HQ006910	HQ006302	HQ006395	HQ006814	HQ006469	–	HQ006627	–	HQ006544	TG	Ghana
Erebidae	Unassigned	Anobini	<i>Marcipa</i> sp.	RZ177	HQ006177	HQ006881	–	HQ006368	HQ006785	HQ006450	–	HQ006601	HQ006973	HQ006522	–	Ghana
Erebidae	Unassigned	Episparis group	<i>Masca abactalis</i>	RZ18	HQ006178	HQ006882	HQ006274	HQ006369	HQ006786	HQ006451	HQ006693	–	HQ006974	HQ006523	TS	Indonesia
Erebidae	Unassigned		<i>Ugia insuspecta</i>	RZ45	HQ006221	HQ006925	–	HQ006408	HQ006829	HQ006484	HQ006733	HQ006642	HQ007010	HQ006555	–	Hong Kong
Erebidae	Unassigned	Saroba group	<i>Saroba pustulifera</i>	RZ104	HQ006160	HQ006865	HQ006257	HQ006352	HQ006769	–	HQ006676	–	–	HQ006509	TS	Hong Kong
Erebidae	Unassigned		<i>Sphingomorpha chlorea</i>	RZ291	HQ006195	HQ006899	HQ006291	HQ006385	HQ006803	–	HQ006708	HQ006616	–	–	TS	Tanzania
Erebidae	Unassigned	Eulepidotini	<i>Eulepidotis rectimargo</i>	RZ12	HQ006162	HQ006960	HQ006259	HQ006354	HQ006771	–	HQ006678	HQ006588	HQ006960	HQ006511	TG	Costa Rica
Erebidae	Unassigned	Thysaniini	<i>Thysania zenobia</i>	RZ53	HQ006225	HQ006928	HQ006320	HQ006412	HQ006833	HQ006486	HQ006737	HQ006645	HQ007014	HQ006558	TG	Costa Rica
Erebidae	Unassigned		<i>Oxidaria toxea</i>	RZ295	HQ006196	HQ006900	HQ006292	–	HQ006804	–	HQ006709	HQ006617	HQ006989	–	TS	Costa Rica
Erebidae	Calpinae	Scoliopterygini	<i>Scoliopteryx libatrix</i>	MM00407	GU828641	GU828439	GU828975	GU829260	GU829532	–	GU830643	GU830348	GU828140	GU830028	TG/TS	Finland
Erebidae	Calpinae	Anomini	<i>Anomis involuta</i>	RZ13	HQ006166	HQ006963	HQ006263	HQ006357	HQ006775	–	HQ006682	HQ006592	HQ006963	–	TG	Tanzania
Erebidae	Calpinae	Anomini	<i>A. metaxantha</i>	RZ55	HQ006227	HQ006930	HQ006322	HQ006414	HQ006835	–	HQ006739	HQ006647	HQ007016	HQ006560	TG	Taiwan
Erebidae	Calpinae	Phylloclini	<i>Phylloclades eyndhovi</i>	RZ56	HQ006228	HQ006931	HQ006323	HQ006415	HQ006836	–	HQ006740	HQ006648	–	HQ006561	TG	Taiwan
Erebidae	Calpinae	Phylloclini	<i>Miriodes phaeosoma</i>	RZ153	HQ006173	HQ006877	HQ006270	HQ006364	HQ006782	HQ006446	HQ006689	HQ006597	HQ006969	HQ006518	–	Ghana
Erebidae	Calpinae	Calpini	<i>Calypra thalictri</i>	MM00963	HQ006156	HQ006861	HQ006252	HQ006348	HQ006763	HQ006435	HQ006671	HQ006582	HQ006955	HQ006504	TG/TS	Finland

Table 1 (Continued)

Family	Subfamily	Tribe:	Species	Specimen ID	COI- LCO	COI- Jerry	EF-1 α - begin	EF-1 α - end	Wingless	GAPDH	RpS5	MDH	CAD	IDH	Type status	Locality
Erebidae	Calpinae	Calpini	<i>Eudocima fullonia</i>	RZ16	HQ006174	HQ006878	HQ006271	HQ006365	HQ006783	HQ006447	HQ006690	HQ006598	HQ006970	HQ006519		Malaysia
Erebidae	Calpinae	Calpini	<i>Plusiodonta nitissima</i>	RZ333	HQ006207	HQ006911	HQ006303	-	HQ006815	HQ006470	HQ006719	HQ006628	-	-		Costa Rica
Erebidae	Calpinae	Calpini	<i>Gonodonta uxor</i>	RZ335	HQ006208	HQ006912	HQ006304	-	HQ006816	HQ006471	HQ006720	HQ006629	-	HQ006545		Costa Rica
Erebidae	Calpinae	Calpini	<i>Oraesia emarginata</i>	RZ102	HQ006159	HQ006864	HQ006256	HQ006351	HQ006768	HQ006439	HQ006675	HQ006586	HQ006958	HQ006508	TS	Hong Kong
Erebidae	Calpinae	Unassigned	<i>Hyponopha homos</i>	RZ17	HQ006176	HQ006880	HQ006273	HQ006367	HQ006784	HQ006449	HQ006692	HQ006600	HQ006972	HQ006521		USA
Erebidae	Catocalinae	Serrodos group	<i>Serrodos campana</i>	RZ318	HQ006202	HQ006906	HQ006298	HQ006391	HQ006810	HQ006467	HQ006715	HQ006623	HQ006995	HQ006540		Taiwan
Erebidae	Catocalinae	Unassigned	<i>Erygia apicalis</i>	RZ29	HQ006194	HQ006898	HQ006290	HQ006384	HQ006802	-	HQ006707	HQ006615	HQ006988	HQ006535	TS	Hong Kong
Erebidae	Catocalinae	Unassigned	<i>Sympis rufibasis</i>	RZ48	HQ006223	-	HQ006318	HQ006410	HQ006831	HQ006485	HQ006735	HQ006644	HQ007012	HQ006557	TS	Hong Kong
Erebidae	Catocalinae	Unassigned	<i>Anisoneura salebrosa</i>	RZ38	HQ006213	HQ006917	HQ006309	HQ006400	HQ006821	HQ006476	HQ006725	HQ006634	HQ007003	HQ006548	TS	Hong Kong
Erebidae	Catocalinae	Catocalini	<i>Catocala sponsa</i>	MM04358	GU828700	GU828495	GU829023	GU829312	GU829576	GU829816	GU830688	GU830404	GU828189	GU830086	TG	Finland
Erebidae	Catocalinae	Catocalini	<i>Ulotrichopus macula</i>	RZ241	HQ006185	HQ006889	HQ006281	-	HQ006793	HQ006457	HQ006699	HQ006608	-	HQ006530		Taiwan
Erebidae	Catocalinae	Toxocampini	<i>Lygephila pastinum</i>	MM05092	GU828711	GU828506	-	GU829323	GU829587	-	GU830699	GU830415	GU828199	GU830097	TG	Finland
Erebidae	Catocalinae	Toxocampini	<i>L. maxima</i>	RZ57	HQ006229	HQ006932	HQ006324	HQ006416	HQ006837	HQ006487	HQ006741	HQ006649	-	HQ006562	TG	Japan
Erebidae	Catocalinae	Toxocampini	<i>Pantylia diemeni</i>	RZ309	HQ006199	HQ006903	HQ006295	HQ006388	HQ006807	HQ006464	HQ006712	HQ006620	HQ006992	HQ006538		Australia
Erebidae	Catocalinae	Acantholipini	<i>Acantholipes circumdata</i>	RZ248	HQ006189	HQ006893	HQ006285	HQ006379	HQ006797	-	HQ006702	-	HQ006984	HQ006531	TG	UAE
Erebidae	Catocalinae	Acantholipini	<i>A. regularis</i>	RZ135	HQ006168	HQ006872	HQ006265	HQ006359	HQ006777	-	HQ006684	-	-	-	TG/TS	Russia
Erebidae	Catocalinae	Melipotini	<i>Melipotis jucunda</i>	RZ58	HQ006230	HQ006933	HQ006325	HQ006417	HQ006838	-	HQ006742	HQ006650	HQ007017	HQ006563	TG/TS	USA
Erebidae	Catocalinae	Panopodini	<i>Azeta ceramina</i>	RZ22	HQ006182	HQ006886	HQ006278	HQ006373	HQ006790	-	HQ006697	HQ006605	HQ006978	HQ006527		Costa Rica
Erebidae	Catocalinae	Panopodini	<i>Panopoda rufimargo</i>	RZ59	HQ006231	HQ006934	HQ006326	HQ006418	HQ006839	HQ006488	HQ006743	HQ006651	HQ007018	HQ006564	TG	USA
Erebidae	Catocalinae	Ophiusini	<i>Achaea sena</i>	RZ19	HQ006179	HQ006883	HQ006270	HQ006370	HQ006787	HQ006452	HQ006694	HQ006602	HQ006975	HQ006524		Malaysia
Erebidae	Catocalinae	Ophiusini	<i>Heteropalpia acrosticta</i>	RZ243	HQ006186	HQ006890	HQ006282	HQ006376	HQ006794	-	HQ006700	-	HQ006981	-		UAE
Erebidae	Catocalinae	Ophiusini	<i>Ophiusa coronata</i>	RZ21	HQ006181	HQ006885	HQ006277	HQ006372	HQ006789	HQ006454	HQ006696	HQ006604	HQ006977	HQ006526	TG	Malaysia
Erebidae	Catocalinae	Ophiusini	<i>O. tirhaca</i>	RZ246	HQ006187	HQ006891	HQ006283	HQ006377	HQ006795	HQ006458	HQ006701	HQ006609	HQ006982	-	TG/TS	UAE
Erebidae	Catocalinae	Ophiusini	<i>Clytie devia</i>	RZ247	HQ006188	HQ006892	HQ006284	HQ006378	HQ006796	HQ006459	-	HQ006610	HQ006983	-		UAE
Erebidae	Catocalinae	Pandesmini	<i>Pandesma robusta</i>	RZ321	HQ006204	HQ006908	HQ006300	HQ006393	HQ006812	-	HQ006717	HQ006625	HQ006997	HQ006542	TG/TS	Spain
Erebidae	Catocalinae	Ophiusini	<i>Artena dotata</i>	RZ46	HQ006222	HQ006926	HQ006317	HQ006409	HQ006830	-	HQ006734	HQ006643	HQ007011	HQ006556		Hong Kong
Erebidae	Catocalinae	Euclidiini	<i>Mocis latipes</i>	RZ20	HQ006180	HQ006884	HQ006276	HQ006371	HQ006788	HQ006453	HQ006695	HQ006603	HQ006976	HQ006525		Costa Rica
Erebidae	Catocalinae	Euclidiini	<i>Callistegia mi</i>	MM05469	HQ006150	HQ006857	HQ006248	HQ006343	HQ006759	-	HQ006667	HQ006578	HQ006950	HQ006500	TS	Finland
Erebidae	Catocalinae	Euclidiini	<i>Euclidia glyphica</i>	RZ82	HQ006239	HQ006942	HQ006333	HQ006426	HQ006847	-	HQ006750	HQ006657	HQ007023	HQ006570	TG	Finland
Erebidae	Catocalinae	Audeini	<i>Audea bipunctata</i>	RZ60	HQ006233	HQ006936	HQ006328	HQ006420	HQ006841	-	HQ006744	HQ006652	HQ007019	HQ006565	TG/TS	Congo
Erebidae	Catocalinae	Sypniini	<i>Synpoides fumosa</i>	RZ313	HQ006201	HQ006905	HQ006269	HQ006390	HQ006809	HQ006466	HQ006714	HQ006622	HQ006994	HQ006539		Japan
Erebidae	Catocalinae	Hypopyriini	<i>Hypopyria capensis</i>	RZ149	HQ006172	HQ006876	HQ006267	HQ006363	HQ006781	-	HQ006688	HQ006596	HQ006968	HQ006517	TG	Ghana
Erebidae	Catocalinae	Hulodini	<i>Ericia subcinerea</i>	RZ39	HQ006214	HQ006918	HQ006310	HQ006401	HQ006822	HQ006477	HQ006726	HQ006635	HQ007004	HQ006549		Hong Kong
Erebidae	Catocalinae	Hulodini	<i>Hulodes caranea</i>	RZ126	HQ006163	-	HQ006260	-	HQ006772	-	HQ006679	HQ006589	-	-	TG	Malaysia
Erebidae	Catocalinae	Pericymini	<i>Pericyma cruegeri</i>	RZ99	HQ006244	HQ006946	HQ006338	HQ006431	HQ006852	HQ006497	HQ006755	HQ006662	HQ007027	HQ006575	TG	Hong Kong
Erebidae	Catocalinae	Catephiini	<i>Catephia alchymista</i>	RZ127	HQ006164	HQ006961	HQ006261	HQ006355	HQ006773	HQ006441	HQ006680	HQ006590	HQ006961	-	TG/TS	Germany
Erebidae	Catocalinae	Ercheini	<i>Ercheia cyllaria</i>	RZ33	HQ006205	HQ006909	HQ006301	HQ006394	HQ006813	-	HQ006718	HQ006626	HQ006998	HQ006543	TG	Hong Kong
Erebidae	Aganainae		<i>Asota caricae</i>	MM00145	GU828615	GU828413	GU828949	GU829240	GU829509	-	GU830624	GU830325	GU828115	GU830003	TG/TS	Thailand

Table 1 (Continued)

Family	Subfamily	Tribe: subtribe	Species	Specimen ID	COL- LCO	COL- Jerry	EF-1 α - begin	EF-1 α - end	Wingless	GAPDH	RpS5	MDH	CAD	IDH	Type status	Locality
Erebidae	Aganinae		<i>A. heliconia</i>	RZ44	HQ006220	HQ006924	HQ006316	HQ006407	HQ006828	HQ006483	HQ006732	HQ006641	HQ007009	HQ006554	TG	Hong Kong
Erebidae	Arctiinae	Lithosiini	<i>Brunia antica</i>	RZ28	HQ006193	HQ006897	HQ006289	HQ006383	HQ006801	HQ006462	HQ006706	HQ006614	–	HQ006534	TS	Hong Kong
Erebidae	Arctiinae	Arctiini:	<i>Antichloris viridis</i>	MM05380	HQ006151	HQ006858	HQ006249	HQ006344	HQ006760	HQ006433	HQ006668	HQ006579	HQ006951	HQ006501	–	Ecuador
Erebidae	Arctiinae	Ctenuchina														
Erebidae	Arctiinae	Arctiini:	<i>Ctenucha virginica</i>	AM-94-0396	GU828535	GU828337	GU828881	GU829181	GU829442	GU829722	GU830570	–	–	GU829926	TG	USA
Erebidae	Arctiinae	Ctenuchina														
Erebidae	Arctiinae	Syntomini	<i>Apisa canescens</i>	MM05843	HQ006146	HQ006853	–	HQ006339	HQ006765	–	HQ006663	–	–	–	TS	Oman
Erebidae	Arctiinae	Syntomini	<i>Syntomis ptegea</i>	RZ8	HQ006238	HQ006941	–	HQ006425	HQ006846	HQ006492	HQ006749	HQ006656	–	–	TG/TS	Hungary
Erebidae	Arctiinae	Syntomini	<i>Dysauxes famula</i>	MM00154	GU828619	GU828417	GU828954	GU829244	GU829514	–	–	GU830328	GU828120	HQ830008	–	Greece
Erebidae	Arctiinae	Arctiini:	<i>Coscimia cibraria</i>	MM05671	HQ006149	HQ006856	HQ006247	HQ006342	HQ006758	–	HQ006666	–	HQ006949	HQ006499	–	Finland
Erebidae	Arctiinae	Callimorphina														
Erebidae	Arctiinae	Arctiini:	<i>Callimorpha dominula</i>	RZ136	HQ006169	HQ006873	HQ006266	HQ006360	HQ006778	HQ006444	HQ006685	HQ006594	HQ006965	HQ006514	TG/TS	Russia
Erebidae	Arctiinae	Callimorphina														
Erebidae	Arctiinae	Arctiini:	<i>Cretonotos transiens</i>	RZ30	HQ006198	HQ006902	HQ006294	HQ006387	HQ006806	–	HQ006711	HQ006619	HQ006991	HQ006537	–	Hong Kong
Erebidae	Arctiinae	Arctiini:	<i>Arctia caja</i>	MM03713	GU828693	GU828489	–	GU829305	GU829573	GU829813	–	GU830398	GU828185	GU830080	TG/TS	Finland
Erebidae	Arctiinae	Arctiini:	<i>Dysschema leucophaea</i>	RZ88	HQ006240	–	HQ006334	HQ006427	HQ006848	HQ006493	HQ006751	HQ006658	–	HQ006571	–	Costa Rica
Erebidae	Arctiinae	Unassigned	<i>Pseudophaloe troetschi</i>	06-smp-35191	GU828534	GU828336	GU828880	GU829180	GU829441	–	GU830569	GU830258	GU828046	GU829925	–	Costa Rica
Erebidae	Lymantriinae	Lymantriini	<i>Lymantria monacha</i>	MM01048	GU828655	GU828453	GU828986	GU829270	GU829542	–	GU830654	GU830361	GU828152	GU830042	TG	Finland
Erebidae	Lymantriinae	Leucomini	<i>Leucoma salicis</i>	MM06740	GU828748	GU929722	GU829062	GU829347	GU829611	–	GU830719	GU830449	GU828232	GU830132	TG/TS	Finland
Erebidae	Lymantriinae	Nygmiiini	<i>Nygmia plana</i>	RZ34	HQ006209	HQ006913	HQ006305	HQ006396	HQ006817	HQ006472	HQ006721	HQ006630	HQ006999	HQ006546	TG	Hong Kong
Erebidae	Lymantriinae	Orgyiini	<i>Orgyia antiqua</i>	RZ130	HQ006167	HQ006964	HQ006264	HQ006358	HQ006776	HQ006443	HQ006683	HQ006593	HQ006964	HQ006513	TG/TS	Finland
Erebidae	Lymantriinae	Arctomithini	<i>Arctormis</i> sp.	RZ89	HQ006241	HQ006943	HQ006335	HQ006428	HQ006849	HQ006494	HQ006752	HQ006659	HQ007024	HQ006572	TG	Japan
Erebidae	Micronoctuinae	Micronoctuini	<i>Micronoctua</i> sp.	RZ138	HQ006171	HQ006875	HQ006268	HQ006362	HQ006780	HQ006445	HQ006687	HQ006595	HQ006967	HQ006516	TG	Indonesia
Nolidae	Chloephorinae	Chloephorini	<i>Pseudops prasina</i>	MM00107	GU828600	GU828399	GU828934	GU829229	GU829496	GU829754	GU830611	GU830312	GU828101	GU829989	TG	Finland
Nolidae	Chloephorinae	Sarrothripini	<i>Nycteola degenerana</i>	MM00135	GU828612	GU828410	GU828946	GU829238	GU829506	GU829760	GU830621	GU830323	GU828113	GU830000	TG	Finland
Nolidae	Chloephorinae	Sarrothripini	<i>Giaura robusta</i>	RZ31	HQ006200	HQ006904	HQ006296	HQ006389	HQ006808	HQ006465	HQ006713	HQ006621	HQ006993	–	–	Hong Kong
Nolidae	Chloephorinae	Ariolicini	<i>Paracrama dulcissima</i>	RZ43	HQ006219	HQ006923	HQ006315	HQ006406	HQ006827	HQ006482	HQ006731	HQ006640	HQ007008	HQ006553	TS	Hong Kong
Nolidae	Chloephorinae	Ariolicini	<i>Ariolica argentea</i>	RZ63	HQ006234	HQ006937	HQ006329	HQ006421	HQ006842	–	HQ006745	HQ006653	HQ007020	HQ006566	TG	Japan
Nolidae	Bleninae		<i>Blenina octo</i>	RZ64	HQ006235	HQ006938	HQ006330	HQ006422	HQ006843	HQ006490	HQ006746	HQ006654	HQ007021	HQ006567	TG	Sumatra
Nolidae	Westermanniinae		<i>Negeta signata</i>	RZ26	HQ006191	HQ006895	HQ006381	HQ006799	HQ006460	HQ006704	HQ006704	HQ006612	HQ006986	HQ006533	–	Hong Kong
Nolidae	Eligmiinae		<i>Eligma narcissus</i>	RZ97	HQ006243	HQ006945	HQ006337	HQ006430	HQ006851	HQ006496	HQ006754	HQ006661	HQ007026	HQ006574	TG/TS	Hong Kong
Nolidae	Unassigned		<i>Selepa molybdea</i>	RZ32	HQ006203	HQ006907	HQ006299	HQ006392	HQ006811	HQ006468	HQ006716	HQ006624	HQ006996	HQ006541	–	Hong Kong
Nolidae	Nolini	Nolini	<i>Nola aerugula</i>	MM01776	GU828670	GU828468	GU829001	GU829284	GU829555	–	GU830665	GU830376	GU828167	GU830057	TG	Finland
Nolidae	Eariadinae		<i>Earias clorana</i>	MM06650	GU828747	GU929721	GU829061	GU829346	GU829610	GU829845	GU830718	GU830448	GU828231	GU830131	TG/TS	Finland
Euteliidae	Euteliinae		<i>Eutelia adulatrix</i>	MM00160	GU828621	GU828419	GU828956	GU829246	GU829516	GU829764	GU830629	GU830330	GU828122	GU830010	TG/TS	Greece
Euteliidae	Euteliinae		<i>Marathyssa basalis</i>	RZ23	HQ006183	HQ006887	HQ006279	HQ006374	HQ006791	HQ006455	HQ006698	HQ006606	HQ006979	HQ006528	TS	USA
Euteliidae	Euteliinae		<i>Targalla subocellata</i>	RZ35	HQ006210	HQ006914	HQ006306	HQ006397	HQ006818	HQ006473	HQ006722	HQ006631	HQ007000	–	–	Hong Kong

Table 1 (Continued)

Family	Subfamily	Tribe: subtribe	Species	Specimen ID	COI- LCO	COI- Jery	EF-1 α - begin	EF-1 α - end	Wingless	GAPDH	RpS5	MDH	CAD	IDH	Type status	Locality
Euteliidae	Stictopterinae		<i>Lophoptera hemithyris</i>	MM07614	GU828802	GU929772	GU829107	GU829385	GU829661	GU829879	GU830759	GU830501	GU828274	GU830183		Australia
Noctuidae	?Pantheinae	Arctini	<i>Arcte modesta</i>	RZ54	HQ006226	HQ006929	HQ006321	HQ006413	HQ006834	–	HQ006738	HQ006646	HQ007015	HQ006559	TG	Malaysia
Noctuidae	?Erebinae	Dyopsini	<i>Dyops chromatophila</i>	RZ10	HQ006158	–	HQ006255	HQ006350	HQ006767	HQ006438	HQ006674	HQ006585	HQ006957	HQ006507	TG	Costa Rica
Noctuidae	?Aedinae		<i>Epatia longinqua</i>	RZ25	HQ006190	HQ006894	HQ006286	HQ006380	HQ006798	–	HQ006703	HQ006611	HQ006985	HQ006532		Hong Kong
Noctuidae	Metoponiinae		<i>Panemeria tenebrata</i>	MM00005	HQ006152	HQ006863	HQ006254	HQ006349	HQ006766	HQ006437	HQ006673	HQ006584	HQ006956	HQ006506		Finland
Noctuidae	Acontinae	Acontini	<i>Acontia lucida</i>	MM00152	GU828617	GU828415	GU828952	GU829243	GU829512	GU829763	GU830627	GU830327	GU828118	GU830006	TG	Greece
Noctuidae	Acontinae	Acontini	<i>Emmella trabecalis</i>	MM09893	HQ006147	HQ006854	HQ006245	HQ006340	HQ006756	–	HQ006664	HQ006576	HQ006947	–		Sardinia
Noctuidae	Agaristinae		<i>Periscepta polysicta</i>	MM07669	GU828820	GU929788	GU829125	GU829400	GU829674	GU829892	GU830773	GU830519	GU828289	GU830201	TG/TS	Australia
Noctuidae	Plusiinae	Abrostolini	<i>Abrostola tripartita</i>	MM05132	HQ006152	HQ006859	HQ006250	HQ006345	HQ006761	–	HQ006669	HQ006580	HQ006952	HQ006502	TG	Finland
Noctuidae	Plusiinae	Plusiini	<i>Autographa gamma</i>	MM00328	GU828636	GU828434	GU828970	GU829256	GU829528	–	GU830640	GU830344	GU828135	GU830023	TG/TS	Finland
Noctuidae	Amphipyriinae	Psaphidini	<i>Brachionycha rubeculosa</i>	MM01542	GU828667	GU828465	GU828998	GU829281	GU829552	GU829793	GU830663	GU830373	GU828164	GU830054	TS	Finland
Noctuidae	Amphipyriinae	Amphipyriini	<i>Amphipyra perflua</i>	MM01162	GU828660	GU828458	GU828991	GU829275	GU829546	GU829787	GU830657	GU830366	GU828157	GU830047	TG	Finland
Noctuidae	Xyleninae	Apameini	<i>Apamea crenata</i>	MM01170	GU828661	GU828459	GU828992	GU829276	GU829547	GU829788	GU830658	GU830367	GU828158	GU830048	TG	Finland
Noctuidae	Xyleninae	Caradimini	<i>Hoplodrina octogenaria</i>	MM01651	HQ006153	HQ006860	HQ006251	HQ006346	HQ006762	HQ006434	HQ006670	HQ006581	HQ006953	HQ006503		Finland
Noctuidae	Xyleninae	Xylenini: Ufeina	<i>Ufeus faunas</i>	RR-98-0914	GU828860	GU929822	GU829163	GU829425	GU829709	GU829911	GU830807	GU830552	GU828320	GU830238	TG	USA
Noctuidae	Xyleninae	Actinotini	<i>Actinotia polyodon</i>	MM05153	GU828714	GU828509	–	GU829326	GU829590	GU829827	GU830702	GU830418	GU828202	GU830100	TG	Finland
Noctuidae	Bryophilinae		<i>Cryphia raptricula</i>	MM04919	GU828708	GU828503	GU829031	GU829320	GU829584	GU829822	GU830696	GU830412	GU828196	GU830094		Finland
Noctuidae	Acronictinae		<i>Acronicta rumicis</i>	MM01529	GU828666	GU828464	GU828997	GU829280	GU829551	GU829792	GU830662	GU830372	GU828163	GU830053	TG	Finland
Noctuidae	Acronictinae		<i>Cranioophora ligustri</i>	MM06745	HQ006148	HQ006855	HQ006246	HQ006341	HQ006757	HQ006432	HQ006665	HQ006577	HQ006948	HQ006498	TS	Finland
Noctuidae	Raphiinae		<i>Raphia abrupta</i>	CWM-94-0372	GU828548	GU828350	GU828893	GU829193	GU829455	GU829728	GU830579	GU830270	GU828059	GU829939	TG	USA
Noctuidae	Cucullinae		<i>Cucullia umbratica</i>	MM04543	GU828701	GU828496	GU829024	GU829313	GU829577	GU829817	GU830689	GU830405	GU828190	GU830087	TG/TS	Finland
Noctuidae	Pantheinae		<i>Panthea coenobita</i>	MM04583	GU828702	GU828497	GU829025	GU829314	GU829578	–	GU830690	GU830406	GU828191	GU830088	TG/TS	Finland
Noctuidae	Eustrotinae		<i>Deltole uncula</i>	MM04601	GU828703	GU828498	GU829026	GU829315	GU829579	GU829818	GU830691	GU830407	GU828192	GU830089		Finland
Noctuidae	Noctuidae		<i>Noctua fimbriata</i>	MM04752	GU828705	GU828500	GU829028	GU829317	GU829581	GU829820	GU830693	GU830409	GU828194	GU830091	TG	Finland
Noctuidae	Condicinae		<i>Condica vecors</i>	CWM-95-0471	GU828550	GU828352	GU828895	GU829194	GU829457	–	GU830581	–	GU828061	GU829941	TG	USA
Noctuidae	Heliothinae		<i>Pyrrhia umbra</i>	MM05114	GU828712	GU828507	GU829034	GU829324	GU829588	GU829825	GU830700	GU830416	GU828200	GU830098		Finland
Noctuidae	Hadeninae	Glottulini	<i>Diaphone capillamentum</i>	MF-05-0053	GU828571	GU828372	GU828913	GU829206	GU829475	GU829738	GU830591	GU830285	GU828076	GU829960		Tanzania
Noctuidae	Bagisarinae		<i>Xanthodes albago</i>	MM09894	GU828844	GU929808	GU829145	GU829412	GU829693	–	GU830792	GU830535	GU828308	GU830224		Sardinia

–, gene region was not amplified for specimen; TG, type genus; TS, type species; COI, cytochrome oxidase subunit I gene; EF-1 α , Elongation Factor-1 α ; RpS5, Ribosomal protein S5; CAD, Carbamoylphosphate synthase domain protein; MDH, Malate dehydrogenase; GAPDH, Glyceraldehyde-3-phosphate dehydrogenase; IDH, Isocitrate dehydrogenase.

and deeply intertwined such that it is impossible to tease them apart (Ren *et al.* 2005; Kelchner & Thomas 2007), making it likely that complications arise in estimating values for these parameters. The gamma function is enough for correcting for the rate variations amongst sites, including sites which do not change at all in the dataset. ML analyses were conducted using the web-server RAxML (Stamatakis *et al.* 2008). ML bootstrap analysis with 1000 pseudoreplicates (Felsenstein 1985) was conducted with RAxML.

Results

Our analyses are based on sequence data from seven nuclear gene regions (1240 bp of EF-1 α , 400 bp of *wingless*, 617 bp of RpS5, 850 bp of CAD, 410 bp of MDH, 691 bp of GAPDH and 710 bp of IDH) and one mitochondrial gene region (1477 bp of COI), for a total of 6407 aligned nucleotide sites (Table 2). We were not able to amplify some genes for some taxa (Tables 1 and 2).

The optimal cladograms found by the two methods (parsimony and ML) for the combined, complete datasets are very similar, but show novel relationships not previously suggested (Figs 1 and 2). The monophyly of Noctuoidea is strongly supported (BP ≥ 96 ; BS ≥ 18), within which we find six strongly supported clades that we feel deserve family status. These are Oenosandridae, Notodontidae, Erebidae, Nolidae, Euteliidae stat. rev. and Noctuidae (Figs 1 and 2). The Notodontidae are found to be the sister group of all other Noctuoidea, with the Australian family Oenosandridae branching off next. However, this pattern of relationships relative to the rest of Noctuoidea is not well supported. Both Oenosandridae and Notodontidae have a trifold 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 noctuid families. Relationships amongst the remaining four families are not clear, although they form a monophyletic group with very strong support (Fig. 1). Euteliidae are sister to Noctuidae in ML analyses (Fig. 1), and sister to the other three families together in parsimony analyses. Similarly, Nolidae are sister to Erebidae in ML analyses, but form a trichotomy with Erebidae and Noctuidae in parsimony analyses.

The six strongly supported clades are also found when only nuclear gene regions are analysed (i.e., the mitochondrial gene is excluded) and when third codon positions are excluded (Supporting information, Appendices S1 and S2). However, the relationships amongst the clades we are designating as families (Oenosandridae, Notodontidae, Euteliidae, Erebidae, Nolidae and Noctuidae) are not stable. The two analyses now place Oenosandridae as sister to the rest of Noctuoidea, with Notodontidae branching off next, and this arrangement is quite well supported (BP ≥ 87 for the node Notodontidae + the rest) when the third codon positions are excluded (Supporting information, Appendix S2). The four remaining families always form a well-supported clade, but their relationships once again vary. Nuclear gene regions place Nolidae as sister to the rest and Erebidae as sister to Euteliidae + Noctuidae, whereas when third codon positions are removed, Euteliidae are sister to the rest and Erebidae are sister to Nolidae + Noctuidae. Of the single gene analyses only CAD recovers all six family clades as monophyletic (Supporting information, Appendix S3), although most members of the clades recovered in the combined analyses do tend to remain together in a clade with the other genes, and the non-monophyly of the families is not strongly supported. As the results of these analyses do not show strongly supported conflict with the combined, complete analysis, we henceforth describe in detail only the latter results.

Nolidae come out as a well-supported monophyletic clade (BP ≥ 97 ; BS ≥ 10) contra Beck (2009). Nolinae (represented by type genus) are placed as sister to the rest of the family. Eligminae are confirmed as belonging to this family, though they lack most of the diagnostic characteristics listed by Holloway (1998, 2003) and are associated with *Selepa*, a genus unassigned to any subfamily by Holloway. The subfamily Chloephorinae forms a major clade that also includes two further groups given subfamily status by Holloway: Bleninae, placed as sister to Sarrothripini; and Eariadinae, placed with representatives of Chloephorini and Ariolicini. The subfamily Westermaniinae remains separate; the subfamilies Afridinae, Collomeninae and Risobinae were not sampled.

Euteliidae are strongly supported as a monophyletic group (BP ≥ 100 ; BS ≥ 9). The clade consists of two subfamilies, Stictopterinae and Euteliinae.

Table 2 Basic statistics for the eight gene regions used in this study

Gene region	Number of base pairs	Number of taxa sequenced	Number of parsimony informative sites
COI	1477	152	607
EF-1 α	1240	152	386
Wingless	400	146	215
RpS5	617	142	255
GAPDH	691	98	290
CAD	859	127	429
IDH	716	117	337
MDH	407	139	194
Total	6407	1073	2713

COI, cytochrome oxidase subunit I gene; EF-1 α , *Elongation Factor-1 α* ; RpS5, Ribosomal protein S5; GAPDH, *Glyceraldehyde-3-phosphate dehydrogenase*; CAD, *Carbamoylphosphate synthase domain protein*; IDH, *Isocitrate dehydrogenase*; MDH, *Cytosolic malate dehydrogenase*.

The Noctuidae clade, as delimited in Fig. 1, has strong support (BP ≥ 99 ; BS ≥ 10), the most striking feature of which is the inclusion of a clade comprising two quadrifine tribes, Arcteini (represented by type genus) and Dyopsini (represented by type genus), which were previously assumed to be related to Erebiniae *sensu* Lafontaine & Fibiger (2006). Otherwise, this clade is made up of trifine noctuids. The ‘pest clade’ of Mitchell *et al.* (2006) (Heliothinae to Xyleninae) has strong BP (100) but weak BS (1) support.

Our results provide strong support (BP ≥ 99 ; BS ≥ 9) for the monophyly of Erebidae. Strikingly, many of the basal divergences in the family show very short branches with no or low support. Some traditionally recognized families, subfamilies and tribes show clear evolutionary relationships with strong BS and BP support. For example, there is clear support for a clade with Pangraptinae (represented by its type genus) as sister to another well-supported clade comprising Aganainae (represented by its type genus) + Herminiinae (represented by its type genus and three other core herminiines) and Arctiinae (represented by 12 genera including the type genus) (Fig. 2). The systematic position of what traditionally has been recognized as the family Lymantriidae is clearly within Erebidae (Fig. 2), consistent with the findings of previous molecular studies. *Oxyzilla*, a genus recently excluded from Rivulinae by Fibiger & Lafontaine (2005), is grouped with *Rivula* (type genus of Rivulinae) with strong support values (BP ≥ 96 ; BS ≥ 20). Both ML and parsimony analyses place the recently discovered family Micronoctuidae within subfamily Hypenodinae (BP ≥ 89 ; BS ≥ 14). A strongly supported clade (BP ≥ 98 ; BS ≥ 18), which we term the boletobiine clade, places together a large number of taxa with very diverse feeding habits, including detritivory, fungivory, lichenivory, frugivory, pod-boring, predation on other insects and carrion feeding as well as defoliation; association of many of these taxa was suggested by Holloway (2005, 2009).

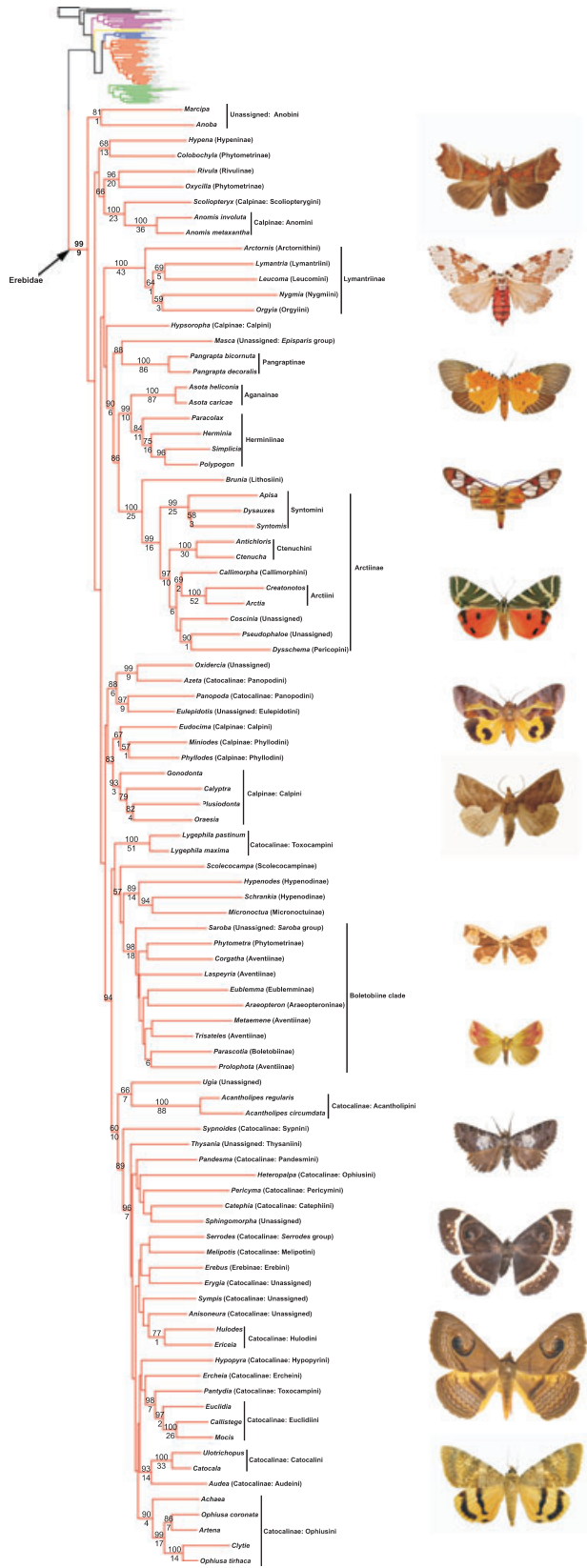
Our analyses fail to recover some previously recognized subfamilies within Erebidae as monophyletic groups (Fig. 2). Both parsimony and ML analyses suggest that some recent concepts of subfamilies Calpinae, Catocalinae,

Erebiniae and Phytometrinae are polyphyletic. For example, Calpinae *sensu* Lafontaine & Fibiger (2006) consisted of four tribes, Anomini, Scoliopterygini, Calpini and Phyllo-dini. Our results placed two of these tribes, Anomini and Scoliopterygini, into a strongly supported monophyletic group (BP ≥ 100 ; BS ≥ 23) as in Holloway (2005). This is well separated from the clade that comprises the five genera of Calpini and two Phyllo-dini (BP ≥ 83). Within this clade, four Calpini (*Calyptra thalictri*, the type genus; *Gonodonta*, *Plusiodonta*, *Oraesia*) constitute a monophyletic group with some support (BP ≥ 93 ; BS ≥ 3), whereas the fifth calpine, *Eudocima*, was clustered with the two genera of Phyllo-dini (*Phyllodes* and *Miniodes*), albeit with low branch support (BP ≥ 67 ; BS ≥ 1).

Discussion

Until recently, the higher classification of the Noctuoidea has been based on morphological characters with a predominantly phenetic approach until the review by Kitching (1984). Higher taxa have been defined on alternative states of particular adult characters such as ones of wing venation mentioned earlier, but also: the orientation of the thoracic tympanum (ventral vs. posterior); the position of the counter-tympanal hood relative to the spiracle of A1 (anterior vs. posterior); spining of the mid-tibia (present vs. absent); genitalic structures including everted vesicae and expanded corpus bursae (Fibiger & Lafontaine 2005). However, these characters were often found to be in conflict, or both states were found to occur in taxa that otherwise would be considered congeneric, leading to debate about the relative weight each should be accorded. Genitalic characters, including structures of the everted vesica and within the corpus bursae, have also augmented the body of morphological information available, providing autapomorphies for all or major parts of many higher taxa within the superfamily, though not significantly so at the family level, except possibly for Euteliidae and Nolidae. For Erebidae, Fibiger (2003) and Holloway (2005) came to somewhat different conclusions about classification of the traditional quadrifine noctuids, even though these were based in part on the same collection of over 2000 genitalia slides from the Oriental fauna and from the type species

Fig. 1 The phylogenetic hypothesis of the superfamily Noctuoidea based on a maximum likelihood analysis, along with outgroups. Clades representing families are coloured. Numbers given above branches are bootstrap values (>50%) and numbers below the branch are Bremer support values for the node. Nodes without Bremer support values do not appear in the most parsimonious trees. The six families recognized here are indicated. The Erebidae clade (in red) is shown in more detail in Fig. 2. Family group ranking within each follows from this (i.e., subfamily and below), though assignment of individual taxa reflect previous classifications, particularly Fibiger & Lafontaine (2005), Lafontaine & Fibiger (2006) and Holloway (2005, 2009). The three taxa transferred in the analysis from the old ‘quadrifine’ noctuid concept to the more restricted one for Noctuidae in the analysis are indicated by asterisks. Names of moths shown in figure from top to bottom are: *Dioptis* (Dioptinae), *Oenosandra* (Oenosandridae), *Targalla* (Euteliinae), *Euchalcia* (Plusiinae), *Moma* (Acronictinae), *Periphanes* (Heliothinae), *Euxoa* (Noctuinae), *Eligma* (Eligminae) and *Hypopyra* (Hypopyrini).



of genera on which global family group names were based (Holloway 2005). There has also been disagreement about the relative value of larval vs. adult characteristics (e.g. Beck 2009), although several larval characteristics have been found to be of significance for higher classification (Kitching & Rawlins 1998). Besides early stages and adult characters, there is now another important new set of characters provided by molecular sequences. The increasing availability of molecular information has brought new insights into the relationships of noctuid taxa (Weller *et al.* 1994; Mitchell *et al.* 1997, 2006), such as the paraphyly of the old concept of Noctuidae.

Our results, with more molecular data than have been used previously for this group of moths, point to six well-supported major lineages that we have defined as families. Two of the major lineages are well-recognized taxa that have often been considered families within Noctuoidea, i.e., Oenosandridae and Notodontidae. 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). Miller (1991) excluded *Oenosandra* from Notodontidae based on the non-homology of scale tuft structures on the female tergite 7 (the hairs are used to cover the egg masses), placing it in a separate family. Notodontidae contain approximately 4200 species 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.

Wing venation has been thought to be informative of the phylogenetic relationships of noctuoids, with the quadrifine hindwing defining a group comprising our Nolidae, Erebidae and Euteliidae and the trifine hindwing defining Noctuidae. However, our results suggest that trifine moths have evolved from quadrifines multiple times, e.g., amongst some Erebidae, such as Arctiinae: Syntomini (Griveaud 1964; Holloway 1988), and Nolidae (Holloway 1998, 2003) show hindwing vein reduction in addition to

Fig. 2 Continuation of phylogram in Fig. 1. The phylogenetic hypothesis of the family Erebidae based on a maximum likelihood analysis. Numbers given above branches are bootstrap values (>50%) and numbers below the branch are Bremer support values for the node. Nodes without Bremer support values do not appear in the most parsimonious trees. Names of moths shown in figure from top to bottom are: *Scoliopteryx* (Scoliopterygini), *Lymantria* (Lymantriinae), *Peridrome* (Aganainae), *Syntomis* (Syntomini), *Euplagia* (Arctiinae), *Eudocima* (Calpinae), *Calyptra* (Calpinae), *Orusa* (Aventiinae), *Eublemma* (Eubleminae), *Sypna* (Sypnini), *Erebus* (Erebinae), *Spirama* (Hypopyrini) and *Catocala* (Catocalinae).

the Noctuidae sensu stricto. Furthermore, the tribes Arctiini and Dyopsini, previously classified as quadrifines, are part of a well-supported clade otherwise consisting of trifines (some of the more basal 'trifine' subfamilies, e.g., Plusiinae, Pantheinae, Bagisarinae also have a quadrifine hindwing). The placement of *Arcte* is corroborated by morphological characters (see Holloway 2005, 2009), whereas *Dyops* has not yet been investigated morphologically in this context.

We follow Fibiger & Lafontaine (2005) in employing the family name Erebidae, which was previously used as a subfamily name by Forbes (1954). The family group names Arctiidae, Herminiidae and Erebidae were described in the same publication (Leach 1815) and thus have equal priority, and all three have priority over Cato-calidae. However, both Arctiinae and Herminiinae are well-known taxa generally considered to be subfamily level (Holloway 2008) or family level (e.g. Kitching 1984) taxa, and thus we consider that it would generate less confusion to adopt the name Erebidae for the larger group of noctuoids that includes both Arctiinae and Herminiinae.

Within Erebidae, relationships of only a few lineages are well supported. The monophyly of Aganainae + Herminiinae + Arctiinae clade is strongly supported by our analyses. The association of Herminiinae (Renia) with arctiines was found in an earlier morphological study by Jacobson & Weller (2002). The clade also has a morphological synapomorphy in the prespiracular position of the counter-tympanal hood. Adults of many aganaines and arctiines are visually striking and aposematic, and aganaines and herminiines share long labial palps and a bare lower frons. Kitching (1984) was the first to exclude Aganainae and Herminiinae from Noctuidae based on the prespiracular hood, which was then thought to be plesiomorphic. In addition, the clade may be characterized by two further synapomorphies: modified foretibia in the males of most genera and a swollen metepimeron ventral to pocket IV (Kitching 1984). Holloway (2008) also discussed this grouping, commenting on biological differences between the groups, Herminiinae being generally cryptic, feeding on vegetable detritus, and Aganainae being aposematic, feeding on the same suite of toxic cardenolide-synthesizing plant families (Apocynaceae, Asclepiadaceae and Moraceae) as the danaine Nymphalidae and other moth genera such as *Glyphodes* (Crambidae) and *Agathia* (Geometridae). We have also found that Pangrap-tinae + *Masca*, a member of the *Episparis* group of genera of Holloway (2005), are sister to the Aganainae + Herminiinae + Arctiinae clade with good support. Pangrap-tinae were previously thought to be associated with Eublem-minae (Fibiger & Lafontaine 2005), but see Holloway (2005, 2008, 2009) and below.

The boletobiine clade (Fig. 2) has several potential morphological synapomorphies. Many of the included taxa have the central part of the valve heavily sclerotized with several processes arranged transversely, with the cucullus reduced to a membranous flap. In addition, the female genitalia often have a ring of claw-like spines in the corpus bursae, the base of which is frequently narrow and coiled to some degree. The larvae have the first two pairs of pro-legs reduced and are often warty or pubescent. They feed on a diversity of resources as mentioned above. Much of this clade is made up of a revised and enlarged concept of Aventiinae, together with Eublemminae (Holloway 2009), as well as many Araeopteroninae and Phytometrinae. We identify the clade as boletobiine from the oldest family group name amongst the included taxa (Boletobiinae). Phylogenetic relationships within the clade are in much need of study, and promise to reveal considerable insight into morphological and life history evolution in quadrifines.

The separation in the molecular results of the calpine clade from the scoliopterygine clade and the inclusion of Phyllodini in the former provides 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. A robust, highly developed fruit-piercing (and in some cases skin piercing and blood sucking) proboscis is found widely in Calpini and in some more robust scoliopterygines such as *Anomis*, with many similar features in the structure. But the molecular results point to this being a homoplasy.

Phyllodini, with a spined adult mid-tibia, were traditionally catocalines, and Calpini, with an unspined mid-tibia, were traditional ophiderines, indeed including the type genus thereof. The grouping of Phyllodini with *Eudocima* in the molecular analysis brings into greater prominence several features shared by these groups (Holloway 2005): leaf mimicry in the forewing and flash colouration in the hindwing of the adults; Menispermaceae as a favoured larval host family; a similar method of pupation in a leaf shelter.

The Euteliidae lineage is undoubtedly a well-defined group of noctuoids and is raised here to family level, thus supporting the findings of Mitchell *et al.* (2006). Kitching (1987) demonstrated that Euteliinae and Stictopterinae are related and form a monophyletic group, based on a large number of synapomorphies including: reduced female frenulum, modified basiconic sensilla on the proboscis, presence of a small oval plate in the ductus ejaculatorius, anal papillae modified so that their inner surfaces are directed posteriorly and the counter-tympanal hood has a unique double structure (Richards 1932; Holloway 1985;

Kitching 1987; Kitching & Rawlins 1998). The host plant range of the two subfamilies embraces mostly lactiferous plants, with Euteliinae favouring Anacardiaceae and Stictopterinae having distinct lineages on Calophyllaceae/Clusiaceae, Dipterocarpaceae and Euphorbiaceae (Holloway 1985).

The relationships of the six clades remain somewhat ambiguous, although it is clear that Euteliidae, Nolidae, Erebidae and Noctuidae together form a monophyletic group. The position of Oenosandridae varies in our analyses, with the nuclear only and third codon position excluded analyses placing it as sister to the rest of Noctuoidea. This position has also been found in the two recent studies on Ditrysiinae (Regier *et al.* 2009; Mutanen *et al.* 2010). Our full, combined dataset places Notodontidae in this position, with Oenosandridae diverging next, but this is not well supported. It appears that all poorly supported, unstable relationships are characterized by short basal branches, especially within Erebidae (Fig. 2). Such patterns of short branches and low support values have been thought to indicate rapid radiations (Tajima 1983; Wiens *et al.* 2008; Kodandaramaiah *et al.* 2010).

Elucidating the evolutionary history of the massive Erebidae clade (potentially including 40 000 species) will require more intensive sampling. Further studies are also needed to identify the reasons 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. Noctuoidea represent a unique opportunity to investigate the reasons underlying massive diversification in phytophagous insects, and a first step in such investigations is the identification of monophyletic groups and their interrelationships.

The sampling strategy that we have adopted, described in the introduction, is being used to establish priorities for ongoing studies, to test further the robustness of the four major clades, both in relation to each other and internally. Work in progress on an increased sample of taxa, particularly in Erebidae, shows that the clades remain distinct and robust, and that 'known unknowns', when included, fall within these clades and tend to reinforce the well supported parts of their internal structure, rather than perturbing it (R. Zabiri *et al.* unpublished data).

In summary, we have shown that there are six strongly supported lineages in Noctuoidea that can be assigned family status. Four additional groups that we were unable to sample, Dilobinae, Cocytiinae, Eucocytiinae and Strepsimaninae, may prove to be further independent lineages. There are also a few genera of a similar nature that appear to be noctuid but have yet to be assigned to a family, such as *Kenguichardia*, *Plagerepne* and *Clytophylla* (Holloway *et al.* 2001; Holloway 2003). Within the newly

circumscribed families, Erebidae require much more attention; many traditional subfamilies and tribes (e.g. Calpinae and Chloephorinae of previous authors) were found to be polyphyletic, even with our limited sampling. The conclusion that the Euteliidae are not closely related to Erebidae was surprising and also needs further investigation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Phylogenetic tree from the maximum likelihood analysis of the all nuclear genes data set (the mitochondrial gene COI excluded). Support values are bootstrap values.

Appendix S2. Phylogenetic tree from the maximum likelihood analysis of the all gene regions together third codon positions excluded. Support values are bootstrap values.

Appendix S3. Phylogenetic trees from the maximum likelihood analysis of the single gene analyses. Support values are bootstrap values.

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