Molecular phylogeny of Lymantriinae (Lepidoptera, Noctuoidea, Erebidae) inferred from eight gene regions

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Molecular phylogeny of Lymantriinae (Lepidoptera, Noctuoidea,
Erebidae) inferred from eight gene regions

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Running title: Molecular phylogeny of Lymantriinae

Abstract. In order to understand the evolutionary history of Lymantriinae and test the present higher-level classification, we performed the first broad-scale molecular phylogenetic analysis of the subfamily, based on 154 exemplars representing all recognized tribes and drawn from all major biogeographic regions. We used two mitochondrial genes (*cytochrome c oxidase subunit I* and *16S ribosomal RNA*) and six nuclear genes (*elongation factor-1 α* , *carbamoylphosphate synthase domain protein*, *ribosomal protein S5*, *cytosolic malate dehydrogenase*, *glyceraldehyde-3-phosphate dehydrogenase* and *wingless*). Data matrices (in total 5424 bp) were analysed by parsimony and model-based evolutionary methods (maximum likelihood and Bayesian inference). Based on the results of the analyses, we present a new phylogenetic classification for Lymantriinae composed of seven well-supported tribes, two of which are proposed here as new: Arctornithini, Leucomini, Lymantriini, Orgyiini, Nygmiini, Daplasini **trib. nov.** and Locharnini **trib. nov.**. We discuss the internal structure of each of these tribes and address some of the more complex problems with the genus-level classification, particularly within Orgyiini and Nygmiini.

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Introduction

The Noctuoidea are the largest superfamily of the Lepidoptera, containing just over a quarter of the known species: 42407 according to Nieukerken et al. (2011). As such, they have presented a formidable challenge to obtaining a satisfactory, predictive, hierarchic classification that reflects evolutionary history (Kitching, 1984; Kitching and Rawlins, 1998; Fibiger and Lafontaine, 2005; Lafontaine and Fibiger, 2006; Zahiri et al., 2011). As for most groups of organisms, early classifications developed in the 18th and 19th centuries primarily from regional treatments with a small amount of serendipitous input from collections made on global voyages, but the very high diversity of the noctuoids tended to inhibit attainment of a global consensus from these regional efforts well into the cladistic era, particularly between those of the Old and New Worlds (reviewed by Franclemont and Todd, 1983; Kitching, 1984; Fibiger and Hacker, 1991; Poole, 1995; Fibiger and Lafontaine, 2005). While cladistic methodology provided a means to revise groups that had been based on plesiomorphic characters (e.g. Noctuidae), the importance of taxon sampling soon became apparent (Hillis, 1996; Graybeal, 1998; Pollock et al., 2002; Zwickl and Hillis, 2002; Heath et al., 2008). Consequently, recent attempts based on multiple nuclear markers to reconstruct the evolutionary history of noctuoids and unify the classification have put strong emphasis on comprehensive taxon sampling in conjunction with targeting type-genera of family-level taxa (Mitchell et al., 2006; Regier et al., 2009; Zahiri et al., 2011, 2012). Despite these efforts, some large and economically important clades like the cosmopolitan tussock moths, variously treated at family or subfamily level (see

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below), were in these studies only partially included and are still lacking a higher-level classification based on a comprehensively sampled phylogenetic analysis. The present study aims to fill this gap motivated by the need to test and reconcile regional classifications and provide a phylogenetic framework for studies of host feeding evolution (foraging behaviour, host range), biogeographic history and diversification.

The subfamily Lymantriinae, commonly referred to as tussock moths, contains more than 2500 described species placed in approximately 360 genera, but the phylogenetic affinities within the group are very poorly understood. The subfamily is cosmopolitan in distribution with most species diversity in the Old World (Kitching and Rawlins, 1998). Species of the subfamily are predominantly arboreal defoliators in the larval stage and frequently polyphagous (Holloway, 1999). Some are major forest and agricultural pests such as *Lymantria dispar* Linnaeus (Gypsy Moth), *L. monacha* Linnaeus (Black Arches or Nun Moth), *Orgyia antiqua* Linnaeus (Vapourer or Rusty Tussock Moth), *O. pseudotsugata* McDunnough (Douglas-fir Tussock Moth), *Leucoma salicis* Linnaeus (White Satin Moth) and *Arna pseudoconspersa* Strand (Tea Tussock Moth) (Wallner, 1988; Chao, 2003; Pederson and Munson, 2006; Pogue and Schaefer, 2007; Ziemnicka, 2008; Uhlikova et al., 2011). The larvae of some species of the tribe Nygmiini like *Euproctis chrysorrhoea* Linnaeus (Brown-tail Moth) and *Sphrageidus similis* Fuessly (Yellow-tail Moth), possess urticating setae that can cause hazard to human health (Holloway et al., 1987; Common, 1990). The genus *Toxoproctis* Holloway is also notorious in this respect (Holloway, 1999). 154 species

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4 were listed as economically important by Zhang (1994), and over half the genera in
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6 which these are now placed are included in our analysis. This total represents about
7
8 10% of economically important Noctuoidea species, these representing a quarter of
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10 the total species of Lepidoptera listed by Zhang.
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14 Lymantriinae are clearly noctuid moths as they possess a metathoracic
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16 tympanum, which is considered a synapomorphy for the group. However, the
17
18 taxonomic rank of this group has varied in different noctuid classification systems. It
19
20 was traditionally assigned family rank on the basis of morphological characters
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22 (Miller, 1991; Scoble, 1992; Kitching and Rawlins, 1998; Fibiger and Lafontaine,
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24 2005), and was only recently downgraded to subfamily rank within the newly
25
26 established family Erebidae, owing to the support of molecular data (Lafontaine and
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28 Fibiger, 2006; Zahiri et al., 2011, 2012). The larvae have a single and eversible
29
30 mid-dorsal gland on each of the sixth and seventh abdominal segments; these glands
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32 are suggested to represent a apomorphy supporting the monophyly of Lymantriinae
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34 (Yela and Zahiri, 2011). Other distinctive features are: bipectinate antennae in the
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36 male with one to three spinules at the terminal of each branch; strongly reduced or
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38 absent proboscis; a prespiracular counter-tympanal hood; males with paired,
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prespiracular counter-tympanal hood, general similarities of the male genitalia structures, and the terminal spinules of the bipectinate male antennae, though such spinules only occur on some arctiines. A sister-group relationship of Lymantriinae and Pantheinae is the alternative hypothesis (Kuznetzov and Stekolnikov, 2004; Stekolnikov and Speidel, 2009), proposed on the basis of the following characters: the presence of secondary setae in first instars; the well-developed pupal cremaster; the interapophysal position of the retractor muscles of the apophyses of the ninth segment; the absence of depressor muscles of the anal papillae in the adult female terminalia.

However, the first hypothesis is not clearly supported by recent molecular studies (Zahiri et al., 2011, 2012). These indicate, but without strong support, a sister-group relationship within the highly diverse Erebidae between Lymantriinae and a clade consisting of Pangraptinae, Aganainae, Herminiinae and Arctiinae. The second hypothesis is rejected by the clear placement of Pantheinae in a relatively basal position within a more restricted concept of Noctuidae (Zahiri et al., 2013).

Lymantriinae stand out amongst Erebidae in having non-feeding adults, in contrast to other groups of large physical size such as Erebinae and Calpinae where adult feeding is commonplace (Zaspel et al., 2012; Holloway et al., 2013). Holloway et al. (2013) noted parallels between these extremes in Erebidae and the alternative life strategies for tropical big moths proposed by Janzen (1984) with a focus on the Bombycoidea. Non-feeders tend to be short-lived, sexually dimorphic, with males searching for relatively static females calling with pheromone plumes; oviposition is in masses, with larvae aposematic or cryptic, often with urticating spines. Feeders

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4 tend to be long-lived, with sexual dimorphism weak at most, both sexes being active,
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6 often migratory; they oviposit singly, and the larvae are generally unspined and
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8 cryptic. Janzen also noted general larval host plant differences between the two
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10 categories, with non-feeders favouring hosts with foliage low in nutrients but rich in
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12 phenolics, and feeders favouring nutrient-rich foliage that is low in phenolics but may
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14 contain toxic alkaloids.
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18 The classification within Lymantriinae remains quite fragmentary, and a
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20 comprehensive and global systematic study is still lacking. Ferguson (1978) treated
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22 Nearctic taxa of Lymantriidae (the previous concept as family-rank) as being within
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24 one single subfamily (Lymantriinae) that included two tribes, Lymantriini and
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26 Orgyiini, but felt that African and Indo-Australian taxa would probably represent
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28 additional subfamilies. Holloway (1999) followed Ferguson's concept of one
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30 subfamily, but recognized three additional tribes (Arctornithini, Leucomini and
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32 Nygmiini) based on Indo-Australian taxa. Benkhelil (1999) redefined Ferguson's
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34 Lymantriini and Orgyiini as two subfamilies mainly based on European taxa, with the
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36 genus *Euproctis* Hübner being transferred to Orgyiinae from Lymantriinae. More
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38 recently, Speidel and Witt (2011) supported Lymantriinae as a subfamily of Erebidae
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40 following the arrangement of Zahiri et al. (2011), and separated European
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42 Lymantriinae species into two tribes, Lymantriini and Orgyiini. These were further
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44 divided into five subtribes corresponding to five tribal groups of Holloway (1999):
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46 Lymantriini with Lymantriina, Arctornithina and Leucomina, and Orgyiini with
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48 Orgyiina and Nygmiina. However, Lafontaine and Schmidt (2013) commented that
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the concept of Orgyiini proposed by Speidel and Witt (2011) seemed not to be monophyletic. All of these studies are regional systematic overviews, and Neotropical taxa as well as the diverse African species have barely featured in the existing classification.

To date, little molecular information has been applied to elucidate the phylogenetic relationships within Lymantriinae. Mitchell et al. (2006) used two nuclear genes from a sample of four lymantriine genera, with the results indicating that *Euproctis* is more closely related to *Lymantria* Hübner than to *Orgyia* Ochsenheimer + *Dasychira* Hübner. Based on the five type genera representing separately the five lymantriine tribes of Holloway (1999) and the phylogenetic analysis of eight gene regions, Zahiri et al. (2011, 2012) proposed a phylogenetic hypothesis that Arctornithini are sister to the remaining four tribes, and that these are divided into two pairs: Orgyiini + Nygmiini and Lymantriini + Leucomini.

Here, we offer the first broad-scale molecular phylogenetic analyses of lymantriine moths using molecular data from eight gene regions to investigate the phylogenetic relationships and revise the existing classification within the subfamily.

Materials and Methods

Taxon Sampling

We selected 154 exemplars from 55 genera representing all the currently recognised lymantriine tribes and drawn from almost all biogeographic regions, together with 10 representatives of other Erebidae as outgroups. A list of taxa with the

localities, voucher codes and GenBank accession numbers is provided in Tables S1.

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from one or two legs of adults, dried or freshly preserved in 96% ethanol, using the TIANGEN™ DNA extraction kit (Beijing, China) or the QIAGEN DNeasy tissue extraction kit (Hilden, Germany) following the manufacturer's instructions. For molecular markers, we selected *cytochrome oxidase subunit I (COI)* and, *16S ribosomal RNA (16S rRNA)* from the mitochondrial genome, and *elongation factor-1 α (EF-1 α)*, *carbamoylphosphate synthase domain protein (CAD)*, *ribosomal protein S5 (RpS5)*, *cytosolic malate dehydrogenase (MDH)*, *glyceraldehyde-3-phosphate dehydrogenase (GAPDH)* and *wingless (WNT)* from the nuclear genome. All these markers have previously been found to be highly informative in phylogenetic analyses of Lepidoptera (Wahlberg and Zimmermann, 2000; Wahlberg et al., 2009; Zahiri et al., 2011, 2012, 2013). DNA amplification and sequencing protocols follow (Wahlberg and Wheat, 2008) and (Wang et al., 2014).

Sequence alignment

The sequences obtained were edited and aligned using BioEdit version 7.2.0 (Hall, 1999) or MEGA version 5.0 (Tamura et al., 2011), except that the *16S* was aligned with the online version of MAFFT (<http://mafft.cbrc.jp/alignment/server/>). For the *16S* sequences, ambiguously aligned regions were identified and excluded using Gblock version 0.91b (Castresana, 2000; Talavera and Castresana, 2007), with parameters allowing for smaller final blocks, gap positions within the final blocks and less strict flanking positions. Neighbor-joining and maximum-likelihood trees were

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separately constructed for each gene to reduce errors in alignments and avoid the risk of confusion during sequencing.

Phylogenetic analyses

The data were analyzed using non-model-based (Maximum parsimony, MP) and model-based (Maximum likelihood, ML; and Bayesian Inference, BI) phylogenetic methods. For MP analysis, we performed New Technology heuristic searches (Goloboff, 1999) developed for large datasets using a “driven search” until minimum length was hit 10 times by means of a combination of Tree Fusion, Ratchet, Tree Drifting and Sectorial searches under default parameters in the program TNT version 1.1 (Goloboff et al., 2008). All characters were treated as unordered and equally weighted. Nodal support for each clade was estimated by Bremer support (Bremer, 1988; Bremer, 1994) using a script (Pena et al., 2006). For the model-based analyses, we used two different partitioning strategies: by gene regions (eight partitions) and by codon positions separated by genome source (see Miller et al., 2009; seven partitions: the first, second and third positions for nuclear genes, same for mitochondrial COI, and with ribosomal 16S as a separate partition). GTR+G+I model was selected as the most appropriate model of sequence evolution for each gene and codon partition using the Akaike Information Criterion (AIC) implemented in MrModeltest2 (Nylander, 2004). However, MrModeltest only evaluates a subset of the 203 possible and reversible 4 by 4 substitution rate models. When evaluating all by using reversible-jump MCMC, commonly less complex models (3 or 4 rate parameters) than the GTR (6) are selected (Huelsenbeck et al, 2004). We therefore used the

reversible-jump MCMC setting across model space in MrBayes 3.2 (Ronquist et al, 2011) but implemented the suggested gamma-distributed rate variation across sites (G) and the proportion of invariant sites (I). Based on Bayes factor tests on initial BI analyses, we decided to use the partitioning scheme by gene regions. Partitions were allowed to evolve at different rates and all other parameters of the model (4x4 substitution rate matrix, state frequencies, among site rate variation and proportion of invariant sites) except branch length and topology were unlinked and estimated separately for each partition. The BI analysis was executed using MrBayes version 3.2.2 (Ronquist et al., 2012) on CIPRES Science Gateway (Miller et al., 2010), with the default parameters and four independent runs for 50000000 generations, each with one cold chain, sampled every 1000th generation, and three heated chains. Mixing, convergence and a suitable burn-in were assessed with the statistics provided by the program and with Tracer v. 1.6 (Rambaut et al., 2014), Post burn-in samples from the four runs were merged prior to the calculation of a majority-rule consensus tree. ML analysis was carried out with the web-server RAxML (Stamatakis et al., 2008) on CIPRES, using 1000 bootstrap replicates. Due to the debate about the correlation between parameters I and G (see Kelchner & Thomas, 2007; Ren et al, 2005; Zahiri et al 2010) and whether G adequately models also invariant sites in the absence of I, we ran ML analysis under both GTR+G and GTR+I+G for each partition. This merely affected a few poorly supported nodes and we report only on the result from the analysis using GTR+G.

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Results

The analyses of this study are based on the sequence data from two mitochondrial gene regions (670 bp of *COI* and 596 bp of *16S*) and six nuclear gene regions (820 bp of *CAD*, 1240 bp of *EF-1a*, 691 bp of *GAPDH*, 407 bp of *MDH*, 600 bp *RPS5* and 400 bp of *WNT*). The final aligned data matrix contained 5424 nucleotide sites, of which 193 for the *16S* gene were excluded from subsequent analyses due to alignment ambiguities. Some genes failed to amplify for some taxa (Table S1).

The three phylogenetic analyses (MP, ML and BI) of the combined datasets for eight gene regions yield very similar topologies (Fig. 1, Fig. S1), and the monophyly of Lymantriinae is strongly supported by the model-based analyses (BP=99, PP=1.00). All the topologies are characterized by seven major clades, although there are slight differences in the most parsimonious topological arrangement (Fig. S1). In the classification below we give the seven clades tribe status, two of which are proposed as new tribes. The tribes are Daplasini **trib. nov.**, Arctornithini, Locharnini **trib. nov.**, Leucomini, Lymantriini, Orgyiini and Nygmiini.

Daplasini are fully supported by our analyses as a monophyletic clade consisting of a single genus *Daplasa* Moore (PP=1.00; BP=100; BS=10). The Arctornithini clade is highly supported by the model-based analyses (PP=1.00; BP=94). *Carriola* Swinhoe, *Topomesoides* Strand and *Sitvia* Walker, with their type species sampled, render the genus *Arctornis* Germar paraphyletic with good support; the first two share its morphological features, but the status of *Sitvia* requires further

study. MP analysis suggests that an African taxon *Crorema ?jordani* Collenette could also be included in Arctornithini, with only moderate support (BS=6), but the model-based analyses assign it to Lymantriini.

The monophyly of the Locharnini clade is well supported by the Bayesian analysis (PP=0.96). Within the clade, the African genus *Euproctoides* Bethune-Baker, four Oriental genera *Locharna* Moore+*Kuromondokuga* Kishida+*Ramadra* Nye+*Pida* Walker and species currently misplaced in *Numenes* Walker and *Dasychira* come out as a strongly supported subclade (PP=1.00; BP=100; BS=9), in which *Dasychira pilodes* Collenette, *Ramadra calligramma* Walker and *Numenes patrana* Moore form a clade with *Pida*, and *Numenes albofascia* Leech and *N. separata* Leech are assigned to *Kuromondokuga*. The subclade appears as sister to a pairing of the African genus *Ruanda* Strand and the New World tropical genus *Eloria* Walker in the model-based analyses, but the latter two genera are not associated with the rest of Locharnini in the MP analysis.

The Leucomini clade is composed of *Leucoma* Hübner, *Perina* Walker and *Ivela* Swinhoe with high support in ML and BI analyses (PP=1.00; BP=90). The genus *Leucoma* is found to be polyphyletic, as *L. sericea* Moore and *L. chrysoscela* Collenette form an assemblage together with *Perina* and *Ivela*. The parsimony consensus tree also includes an African genus *Olapa* Walker, but with very low support (BS=2).

Lymantriini are redefined to accommodate two African genera (*Olapa*, *Crorema* Walker), three New World ones (*Sarsina* Walker, *Caviria* Walker+*Thagona* Möschler),

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an Oriental clade (*Imaus* Moore+*Cispia* Walker+*Dura* Moore) and *Lymantria* on the basis of the model-based analyses. The Bayesian tree provides strong support for the monophyly of Lymantriini (PP=1.00). The genus *Parocneria* Dyar is associated with *Lymantria* with high support (PP=1.00), but its position is unresolved with regard to *Lymantria* species.

The Oriental genus *Ilema* Moore and three African genera *Aroa* Walker, *Hemerophanes* Collenette and *Mylantria* Aurivillius constitute basal clades within Orgyiini, but the precise relationships lack good support. The remainder of the Orgyiini clade is strongly supported as a monophyletic group (PP=1.00; BP=72; BS=16). However, some current generic concepts within the group are polyphyletic. For example, the type species of *Aroa*, *A. discalis* Walker, is the species that is sister to *Hemerophanes*, while two Oriental exemplars, *A. substrigosa* Walker and an unidentified taxon, are grouped as sister to *Pantana* Walker with full support (PP=1.00; BP=100; BS=36) and are therefore not congeneric with the type. *Olene inclusa* Walker appears as sister to the members of *Orgyia*, but *O. dudgeoni* Swinhoe pairs with a representative of *Telochurus* Maes. The two *Dasychira* species are scattered across the distal clades of Orgyiini; a clade with four *Orgyia* species, including the type species *O. antiqua*, is strongly supported (PP=1.00; BP=100; BS=17).

Our results robustly recover the monophyly of the Nygmiini clade (PP=1.00; BP=99), but confirm that *Euproctis* and possibly *Nygmia* Hübner are polyphyletic groups. In Nygmiini, *Albarracina* Staudinger is the most basal taxon followed by the

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4 *Bembina* Walker+ *Lacida* Walker pair in both model-based trees, but this trio is
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6 broken up in the parsimony consensus tree. *Somena* Walker+*Kidokuga* Kishida and
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8 *Orvasca* Walker+*Sphrageidus* Maes form a strongly supported clade (PP=1.00;
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10 BP=100; BS=29). *Arna* Walker is a sister group to *Artaxa* Walker (PP=1.00; BP=99;
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12 BS=28), with *Euproctis kanshireia* Wileman, *E. cryptosticta* Collenette and *E. sp3*
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14 included in the latter genus (PP=0.97; BS=6).
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19 Resolution of the inter-tribal relationships within Lymantriinae remains limited
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21 in our analyses. Daplasini are found at the sister position to all other lymantriine
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23 lineages in the BI and MP trees, but branch off after Arctornithini in the ML tree.
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25 The model-based analyses indicated that Locharnini form the sister-group to a large
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27 clade formed by Leucomini+Lymantriini (PP=1.00; BP=84) and
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29 Orgyiini+Nygmiini (PP=0.99; BP=66), but this lacks good support, while the MP
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31 analysis suggests that Locharnini branch off after Daplasini, followed by Orgyiini,
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33 with the remaining four tribes forming a polychotomy.
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40 Discussion

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43 The multi-gene phylogeny in this study, with extensive taxon sampling, recovers
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45 seven major lymantriine lineages that we define here as tribes, five of which are
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47 roughly concordant with the previous morphology-based concepts of five tribes
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49 recognized by Holloway (1999). With regard to the phylogenetic relationships among
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51 these five lineages, our results from the model-based analyses indicate that
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53 Arctornithini are a sister group to Orgyiini + Nygmiini together with Lymantriini +
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Leucomini, supporting the findings of Zahiri et al. (2010, 2012) which however dealt with higher taxonomic levels and sampled only a single species per tribe. The seven proposed tribes will be discussed in the following sections.

Tribe Arctornithini

Morphologically, the signum of the female genitalia is a broad, sparsely but uniformly scobinate plate, which has been thought to be an apomorphic character of Arctornithini (Holloway, 1999). Speidel and Witt (2011) downgraded this tribe to subtribe, placing it in their redefined Lymantriini based on larval characters. This taxonomic arrangement, however, is not supported by our molecular evidence, as Arctornithini appear in a more basal position in our phylogeny. Larval morphology in *Arctornis* has been found to be strikingly variable in Malaysian species in the form and distribution of hair-tufts (H. S. Barlow, pers. comm.).

Holloway (1999) originally proposed the tribe Arctornithini to accommodate two genera, *Arctornis* and *Carriola*. He mentioned that the two genera share many genital features. He also discussed the similarity of another unplaced genus, *Sitvia*, to *Arctornis* in some features of the genitalia and pupae. The Asian monotypic genus *Topomesoides* was previously assigned by Chao (2003) to his Orgyiinae concept, but the male genitalia of this genus illustrated by him show the definitive features of those of *Arctornis*. In this study, we found that *Carriola*, *Topomesoides* and *Sitvia* Walker (represented by their type species) fell within *Arctornis* with very strong support, and thus transfer them to that genus (**syns. nov.**), though the morphological justification for this in the case of *Sitvia* is weaker.

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4 *Arctornis diaphora* has undergone a series of taxonomic changes after it was
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6 described by Collenette (1934) in *Leucoma* and then transferred to *Redoa* Walker, a
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8 synonym of *Arctornis* established by Holloway (1999). This species was then placed
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10 in *Carriola* by Chao (2003), but with illustration of male genitalia that differ
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12 strikingly from those of *Arctornis*. Thus, *A. diaphora*, with distinct male genital
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14 characters and unusual discal spots on the hindwing similar to those of the forewing,
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16 has little in common with the species of *Arctornis*, and thus stands apart within
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18 Arctornithini. The basal phylogenetic position of this species in our analyses suggests
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20 that it needs further study, particularly with regard to the female.
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26 The tribe has the highest species richness in the Oriental tropics, attenuating
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28 eastwards to New Guinea, and has been recorded feeding on a wide range of plant
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30 families. The genus *Arctornis* shows particular affinity for the Dipterocarpaceae at
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32 the larval stage, which may explain the conspicuous radiation of this group in
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34 Southeast Asian forests that are dominated by this plant family (Holloway, 1999; H.
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36 S. Barlow, unpublished).
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41 *Tribe Daplasini* Holloway and Wang, **trib. nov.**
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44 *Type-genus: Daplasa* Moore. Description: An areole is present in the forewing
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46 venation, with R5 branching from Rs more distally than R2. M3 and CuA1 separate in
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48 the hindwing. Male abdomen has tymbals. Uncus bifid, Aedeagus bulbous at base,
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50 with a single, needle-like cornutus.
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54 Daplasini are proposed here as a new, currently monobasic (type genus *Daplasa*)
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56 tribe. *Daplasa* was previously included by Chao (2003) as a genus in his concept of
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Orgyiinae, on the basis of having an areole in the forewing. In our phylogeny, the Daplasini exemplars (two rather different species, including the type species, of *Daplasa*) formed a distinct group that fell into a basal position in the Lymantriinae clade. The aedeagus has a bulbous base and single, needle-like cornutus, which could offer an autapomorphy for this tribe. Also the uncus consists of two widely separated processes as in some Nygmiini, but the wing venation is plesiomorphic relative to that of nygmiines as described by Holloway (1999), who placed two related Bornean species, *lyclene* Swinhoe and *albolyclene* Holloway, under “*Euproctis*” in the tribe Nygmiini, but these now appear to be Daplasini and should be transferred to *Daplasa*, **combs nov.** The venation features that set them apart from typical nygmiines are that R5 branches from Rs more distally than R2, rather than more basally, in the forewing, and M3 and CuA1 are separate in the hindwing, rather than stalked. The tribe is currently restricted to the Oriental Region and exhibits two distinct forewing pattern types: the typical one of *irrorata* Moore with diffuse, oblique banding; the more sharply marked *blacklinea* Chao type with a black postmedial and tornal streak, and a basal ring of red or yellow spots. The latter includes species such as *variegata* Moore and *lyclene* where the male has a dark suffusion to the forewing, and the female is white as in both sexes of *blacklinea* and *albolyclene* (*postincisa* Moore may be the female of *variegata*). The female genitalia of the latter group have a long ductus bursae with a prominent sclerotized collar distally, and a flat, somewhat ovate and marginally dentate signum in the corpus bursae. All members of the second group are here formally transferred to *Daplasa*, **combs nov.**

Tribe *Locharnini* Holloway and Wang, **trib. nov.**

Type-genus: *Locharna* Moore. Description: Adults usually show obvious sexual dimorphism. Forewing venation has an areole from which R2 branches off near the apex, R5 somewhat connate or slightly stalked with R3+4. Rs stalked with M1 in the hindwing. Tymbals are present in the male abdomen. Male genitalia have apically sclerotized valves.

On the basis of our results, we erect the *Locharnini* as a new tribe, represented by two sublineages. One comprises two genera, *Ruanda* (Africa) and *Eloria* (Neotropics), and the other one encompasses the remainder of the sampled *Locharnini*. However, a sister relationship between the two sublineages is not well supported in our analyses. Therefore we tentatively incorporate both in this tribe until their phylogenetic structure is better resolved, but typify the tribe on *Locharna* in the larger and more cohesive sublineage. The tribe retains a more plesiomorphic condition, such as forewing venation with an areole. Species in the typical sublineage tend to have a short, robust uncus and relatively simple, apically sclerotized valves in the male genitalia. The type genus and two other Oriental genera, *Pida* and *Kuromondokuga*, are strikingly sexually dimorphic (Chao, 2003), and our results suggest that other taxa sequenced could be incorporated within one or the other of these genera, as follows:

Numenes was classified in *Orgyiini* by Holloway (1999), with the suggestion that placement of some Chinese species in this genus was problematic, as their male genitalia features were quite different from those of the type species *N.siletti* Walker.

Our phylogeny indicates that *Numenes* is not a monophyletic group, even within Locharnini. This supports the morphological evidence, although no member of the typical group was available for sequencing. Here we transfer *N. patrana* to the genus *Pida* **comb. nov.**, which then also includes *Dasychira pilodes* **comb. nov.** and *Ramadra calligramma* **comb. nov.**, bringing *Ramadra* (= *Mardara* [praeocc.]) into synonymy with *Pida*, **syn. nov.** We transfer *N. albofascia* and *N. separata* into *Kuromondokuga* **combs nov.**, a genus segregated by Kishida (2011) from *Pida*.

Tribe *Leucomini*

Members of the tribe Leucomini were morphologically defined by Holloway (1999) as sharing pronounced asymmetry in the male genitalia, though this feature is not seen in the type species of *Leucoma*. *Leucoma* currently consists of a group of many satiny white species with a reddish-orange tinge to the forelegs, and has been suggested to be paraphyletic (Holloway, 1999). This is confirmed by our molecular phylogeny, indicating that further revision of this genus is needed, possibly with revival of current synonyms such as *Charala* Moore (type species *sericea*) and *Candidata* Toxopeus (type species *subargentea* Felder). *Leucoma* ranges from the Palaearctic to Africa, New Guinea and Australia, with the highest species diversity in the Oriental tropics. *Perina* is an Oriental genus that displays extreme sexual dimorphism, the much smaller males being black with transparent areas in the wings; the larvae have only been recorded feeding on *Ficus* Röding (Moraceae). The Asian genus *Ivela*, now included in Leucomini, shares the definitive male genital characters with the other genera of the tribe.

Tribe *Lymantriini*

The tribe *Lymantriini* was defined by Ferguson (1978) by the following features: adults lack an accessory cell (areole) in the forewing and the larvae do not have hair pencils or dense dorsal tufts on the first four abdominal segments. The tribe was subsequently redefined by Holloway (1999), with diagnostic features such as forewing facies with zig-zag or lunulate fasciation, a V-shaped discal spot and an orbicular spot. Speidel and Witt (2011) proposed a broader concept of this tribe that includes three subtribes (*Lymantriina*, *Arctornithina* and *Leucomina*), on the basis of larval characters that they considered to be apomorphic as follows: seta L1 replaced by a verruca in a postero-dorsal position from the spiracle; verrucas L2 and L3 approximate to each other on abdominal segments 1 to 6. This concept is not supported by our results, so we follow Holloway's (1999) taxonomic treatment, but add two African genera (*Olapa* and *Crorema*), three New World genera (*Caviria*, *Thagona* and *Sarsina*) and the genus *Cispia* to *Lymantriini*. The tribe thus has a global distribution, but still with its greatest diversity in the Oriental Region; this picture may change as further African genera are sequenced.

The genus *Lymantria* is the most species rich genus, and there is sexual dimorphism in size and pattern. In our phylogeny, the internal structure within the genus accords quite closely with the morphological subgeneric phylogeny suggested by Schintlmeister (2004), except for the pairing of *Parocneria* with *Lymantria*. However, many of the subgenera remain to be sequenced. Sutrisno (2014) also noted extensive, but not complete, support for the subgenera of Schintlmeister (2004) in his

analysis of COI gene data from a sample of just over 40 *Lymantria* species.

Tribe *Orgyiini*

Orgyiini are most clearly defined by the dorsal brushes on the first four larval abdominal segments (Holloway, 1999). The presence of an areole in the forewing was another diagnostic character suggested for this tribe by Ferguson (1978), but this feature is also found in Daplasini, Arctornithini and Locharnini, so is probably plesiomorphic.

The African sister genera *Aroa* and *Hemerophanes* and the genus *Ilema*, sharing the above larval features, are included as basal lineages in Orgyiini in our phylogeny, but lack good support for the precise positions. Further sampling is therefore needed to clarify their taxonomic placement.

Holloway (1982) revived the genus *Calliteara* Butler from synonymy with *Dasychira* and divided it into seven species groups. The monophyly of this genus is moderately supported by our analyses, with the African genus *Griveaudyria* Viette placed as sister to it. A high proportion of the species is montane, and all are robust with relatively narrow forewings. The larva is typically orgyiine, but with an additional, shorter, dorsal brush on the eighth segment, a feature also seen in *Ilema* and *Cifuna* Walker.

Our results provide strong support for the sister relationship of *Laelia* Stephens and *Pantana*, with *Aroa substrigosa* transferred here to the latter genus, **comb. nov.**. Both genera were discussed by Holloway (1999). Their larvae are considered to be specialists on Poaceae and Cyperaceae, and the adults are day-flying (Schaefer,

1988). *Psalis pennatula* Fabricius (see below) also shows some preference for Poaceae.

The genus *Dasychira* as historically defined was thought to be a very complex group (Schaefer, 1988); this is further confirmed by our study, though *Calliteara* had already been excluded, as noted above. The type species, *D. tephra* Hübner, was considered by Ferguson (1978) to be part of an exclusively North American group and he suggested that *Dasychira* should be restricted to this group. It is placed in our study as sister to *Cifuna*. This pair is one of three subclades of a well supported distal clade of the Orgyiini that is sister to the African genus *Neomardara* Hering. Many generic names are represented in this clade, often by their type species, including *Orgyia*, leading Holloway (1999) to attempt to find an acceptable classification that excluded *Dasychira* and retained *Orgyia*, but in the process he broadened the concept of *Olene* Hübner to include the species *dudgeoni*. Our results indicate this to have been a mistake because *dudgeoni* is placed in the most basal subclade, but the more typical *Olene inclusa* is part of the third subclade that also includes *Psalis* Hübner, *Teia* Walker and a quartet of *Orgyia* species. The basal subclade includes a species thought to be a *Telochurus* and *Dasychira glaucozona* Collenette as well as *dudgeoni*. The oldest generic name available for this subclade is *Pseudodura* Strand, based on a current junior synonym of *dudgeoni*. More extensive sampling will be needed across this complex to resolve the generic classification satisfactorily.

Tribe Nygmiini

The tribe Nygmiini was described by Holloway (1999), comprising 16 genera.

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Most of these genera were segregated from the old concept of *Euproctis*. Kishida (2011) recognized another distinct genus, *Kidokuga*. Speidel and Witt (2011) transferred *Albarracina* to *Nygmiini*, a move supported by our analyses. The tribe is best defined by possession of a strong corethrogyne on an expanded seventh segment of the female. Holloway (1999) also noted characters that might be definitive as discussed earlier in relation to *Daplasini*; an areole is absent from most genera, another potential apomorphy. Our phylogeny with 13 genera sampled strongly supports the monophyly of the tribe, agreeing with the previous morphological classification.

In our results, the old broad concept of *Euproctis* remains extremely polyphyletic, and is in great need of revision, though the results do provide some reassurance that recent attempts to identify valid generic concepts within the *Euproctis* complex have some validity whilst at the same time emphasizing the scale of the task remaining.

The revival of the genus *Bembina* by Holloway (1999) is supported, but it is paired with *Lacida*; these genera do not appear to be close morphologically, with *Bembina* lacking tymbals and both genera having distinctive male genitalia.

The next large clade is well supported but mixes many species currently in *Euproctis* with representatives of *Micromorphe* Felder, *Somena*+*Kidokuga* and *Orvasca*+*Sphrageidus*, this last quartet sharing loss of vein M2 in the hindwing (Holloway, 1999).

Somena and *Kidokuga* form a well-supported lineage. The type species of both genera share a bicornute signum in bursa of the female, providing morphological

support for the lineage, although their male genitalia structures show great differences (Kishida, 2011; Wang et al., 2011).

The lineage of *Orvasca* and *Sphrageidus* is also well supported. *Orvasca* has a major representation in Australia, referred to under *Chionophasma* Butler by Common (1990), and many of the smaller species in New Guinea and the south-west Pacific may also be referable to this genus (Holloway, 1999). *Orvasca dolichocera* Collenette in our analysis is an example of this from Vanuatu.

Also in this clade, the four Oriental species, *E. singapura* Swinhoe, *E. pyraustis* Meyrick, *E. fumea* Chao and *E. seitzi* Strand, share similar male genitalia structures, with the following diagnostic features: broadly bifid uncus, rather square valves and single cornutus in the aedeagus vesica (Schintlmeister, 1994; Chao, 2003). They form a well-supported clade (PP=1.00; BP=100), which may represent a potential genus. Some allies such as *E. wilemani* Collenette and *E. subfasciata* Walker were noted by Holloway (1999).

All representatives of *Nygmia* sequenced except one are recovered in the next clade with moderate support. Probably many of the groups of larger species in Australasia will be found to belong here, as Holloway (1999) transferred several species to *Nygmia* from that region that typified some of the major species complexes.

The most distal clade in the Nygmiini, itself well supported, has three well-supported subclades. The first suggests a sister-relationship between *Arna* Walker and *Artaxa*. However, *E. kanshireia*, *E. cryptosticta* and *E. sp3* are mixed in the genus *Artaxa*.

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The second includes a representative of *Toxoproctis* Holloway, counter to the suggestion by Holloway (1999) that this genus might be related to *Sphrageidus*. This subclade also includes species such as *E. collenettei* Chao and *E. montis* Leech that have similar male genitalia to *Choerotricha biflava* Holloway (Holloway, 1999; Chao, 2003). Three of the four the African *Euproctis* sequenced fall into this clade as a trio that forms a sister group to the species just mentioned. The fourth, tentatively identified as *E. putris* Hering, occupies a basal position in the next clade.

The third subclade includes the type species of *Euproctis*, *chrysorrhoea*, paired with the Palearctic *E. karghalica* Wileman.

Nygmiini occur in the Old World with major higher level diversity in the Oriental tropics, but have yet to be identified in the New World. Most species appear to be polyphagous, although there are indications of some specialization on Loranthaceae by species groups in *Nygmia* (Holloway et al., 2001).

Biogeography

To conclude, we place these revised and globally based tribal concepts within Lymantriinae in a biogeographic context. All seven tribes are found in the Oriental Region, Daplasini uniquely so.

Arctornithini are highly diverse in the Oriental Region but extend into tropical Australasia and the Palearctic. Leucomini are similar but relatively less diverse in the Oriental Region. The type genus and species, *Leucoma salicis*, extends to the Nearctic. The status of both tribes in Africa is unclear, but the genus *Leucoma* as

currently constituted is represented by several species there.

Locharnini are more widespread, with significant pattern at a higher taxonomic level. The type lineage is restricted to the Oriental Region, but has a sister-genus in Africa. This group is in turn sister to a small but intriguing lineage of two genera: the African *Ruanda* and the Neotropical *Eloria*.

Lymantriini are the only other tribe to include Neotropical genera: *Caviria*, *Sarsina* and *Thagona*. Otherwise, this tribe is widespread and diverse in the Old World, more so in the tropics. One species, *Lymantria dispar*, occurs in the Nearctic as an introduction.

Nygmiini are essentially an Old World group with only the type species of *Euproctis* and *Sphrageidus* extending to the Nearctic. Again, the greatest diversity is Oriental, but the group is relatively rich in Australasia, and there appear to be distinct lineages in Africa.

Orgyiini have a similar distribution to Nygmiini but with a significant Nearctic representation consisting of the genus *Dasychira* and several species of *Orgyia*, one of which extends to Central America. Only Nygmiini and Orgyiini extend into the Pacific, but not further than Fiji and New Caledonia.

The lowest diversity at all levels appears to be in the New World, with little overlap between the Nearctic and the Neotropics. The genus *Desmoloma* Felder is of interest in the latter, as DNA barcoding results suggest that it is distinct from genera assigned in this analysis to the Locharnini and Lymantriini (Data from <http://www.boldsystems.org>). There are still a few unsequenced Oriental genera

unplaced to tribe (Holloway, 1999), and there are many genera in Africa left to sequence; it is therefore possible that the synopsis above will see changes as these gaps are filled.

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Figure

Fig. 1. Majority rule consensus tree from the BI analysis of the full dataset. Posterior probabilities from BI analysis and bootstrap support values from the ML analysis are indicated at the nodes as PP/BP.

Supplementary Information

Fig. S1. Strict consensus of 4 equally parsimonious trees from the combined dataset of all eight genes (length 29824 CI 0.145 RI 0.542). Numbers given above branches are Bremer support values.

Table. S1. List of taxa with voucher codes and Genbank accession numbers (TS refers to Type species).

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Fig.1. Majority rule consensus tree from the BI analysis of the full dataset. Posterior probabilities from BI analysis and bootstrap support values from the ML analysis are indicated at the nodes as PP/BP.

Fig. S1. Strict consensus of 4 equally parsimonious trees from the combined dataset of all eight genes (length 29824 CI 0.145 RI 0.542). Numbers given above branches are Bremer support values.

Table S1. List of taxa with voucher codes and Genbank accession numbers (TS refers to Type species).

Subfamily	Tribe	genus	species	Locality	Voucher codes	Type Status	COI	16S	EF1-a	wingless	RPS5	MDH	GAPDH	CAD
Calpinae	Calpini	Calyptra	thalictri	Finland	MM00963	TS								
Erebinae	Catocalini	Catocala	sponsa	Finland	MM04358									
Aganainae		Mecodina	praecipua	China	RZ268									
Aganainae	Aganaini	Peridrome	orbicularis	Malaysia	RZ280	TS								
Aganainae	Aganaini	Asota	caricae	Thailand	MM00145	TS								
Arctiinae	Lithosiini	Brunia	antica	China	RZ28	TS								
Arctiinae	Arctiini	Arctia	caja	Finland	MM03713	TS								
Arctiinae	Syntomini	Syntomis	phegea	Hungary	RZ8	TS								
Arctiinae	Spilosomini	Estigmene	tenuistrigata	Zambia	T1									
Arctiinae	Spilosomini	Spilosomina	sp	Ghana	M5									
Lymantriinae	Arctornithini	Carriola	ecnomoda	Malaysia	H379	TS								
Lymantriinae	Arctornithini	Carriola	ecnomoda*		NSGJZ006	TS								
Lymantriinae	Arctornithini	Arctornis	diaphora	China	H209									
Lymantriinae	Arctornithini	Arctornis	sp1	China	H148									
Lymantriinae	Arctornithini	Arctornis	discirufa	Brunei	S93									
Lymantriinae	Arctornithini	Arctornis	sp2	Thailand	H392									
Lymantriinae	Arctornithini	Arctornis	phrika	Brunei	S88									
Lymantriinae	Arctornithini	Arctornis	gracilis	China	H220									
Lymantriinae	Arctornithini	Arctornis	rutila	Brunei	S89									
Lymantriinae	Arctornithini	Arctornis	1-nigrum	China	H164	TS								
Lymantriinae	Arctornithini	Arctornis	nivea	China	A99									
Lymantriinae	Arctornithini	Arctornis	sp3	Thailand	H391									

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7	Lymantriinae	Arctornithini	Arctornis	sp4		NSGJZ004	
8	Lymantriinae	Arctornithini	Arctornis	sp5	Japan	RZ89	
9	Lymantriinae	Arctornithini	Arctornis	submarginata	China	H372	
10	Lymantriinae	Arctornithini	Arctornis	sp6	China	H149	
11	Lymantriinae	Arctornithini	Sitvia	denudata	Malaysia	H382	TS
12	Lymantriinae	Arctornithini	Topomesoides	jonasi	China	H348	TS
13	Lymantriinae	Daplasini	Daplasa	irrorata	China	H229	TS
14	Lymantriinae	Daplasini	Daplasa	blacklinea	China	H166	
15	Lymantriinae	Locharnini	Ruanda	aetheria	S. Sudan	M11	TS
16	Lymantriinae	Locharnini	Eloria	onaba	Costa Rica	10-SRNP-72499	
17	Lymantriinae	Locharnini	Eloria	torrida	Costa Rica	11-SRNP-35118	
18	Lymantriinae	Locharnini	Euproctoides	acrisia	Zambia	M1	
19	Lymantriinae	Locharnini	Locharna	strigipennis	China	H159	TS
20	Lymantriinae	Locharnini	Kuromondokuga	niphonis	China	H167	TS
21	Lymantriinae	Locharnini	Numenes	albofascia	China	H190	
22	Lymantriinae	Locharnini	Numenes	separata	China	H347	
23	Lymantriinae	Locharnini	Numenes	patrana	China	H3	
24	Lymantriinae	Locharnini	Ramadra	calligramma	China	H4	TS
25	Lymantriinae	Locharnini	Pida	minensis	China	H114	
26	Lymantriinae	Locharnini	Pida	apicalis	China	H205	TS
27	Lymantriinae	Locharnini	Dasychira	pilodes	China	H370	
28	Lymantriinae	Leucomini	Leucoma	costalis	China	H373	
29	Lymantriinae	Leucomini	Leucoma	sp	China	H377	
30	Lymantriinae	Leucomini	Leucoma	salicis	China	H351	TS
31	Lymantriinae	Leucomini	Leucoma	salicis*	Finland	MM06740	TS
32	Lymantriinae	Leucomini	Leucoma	sericea	China	H120	
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Lymantriinae	Leucomini	Leucoma	chrysoscela	Vietnam	S83	
Lymantriinae	Leucomini	Ivela	sp	China	H340	
Lymantriinae	Leucomini	Ivela	auripes	China	H49	TS
Lymantriinae	Leucomini	Perina	nuda	China	H181	TS
Lymantriinae	Lymantriini	Olapa	? tavetensis	Zimbabwe	M6	
Lymantriinae	Lymantriini	Caviria	regina	Costa Rica	12-SRNP-41748	
Lymantriinae	Lymantriini	Thagona	tibialis	Costa Rica	07-SRNP-58990	
Lymantriinae	Lymantriini	Thagona	errans	Costa Rica	11-SRNP-3924	
Lymantriinae	Lymantriini	Imaus	munda	Laos	HS01	
Lymantriinae	Lymantriini	Cispia	lunata	China	H125	
Lymantriinae	Lymantriini	Dura	ippoline	China	H121	TS
Lymantriinae	Lymantriini	Dura	ippoline*	Laos	HS6	TS
Lymantriinae	Lymantriini	Crorema	? jordani	S. Sudan	M10	
Lymantriinae	Lymantriini	Sarsina	purpurascens	Costa Rica	11-SRNP-72098	
Lymantriinae	Lymantriini	Parocneria	nigriplagiata	China	H60	
Lymantriinae	Lymantriini	Lymantria	furvinis	China	H62	
Lymantriinae	Lymantriini	Lymantria	fergusoni	China	H124	
Lymantriinae	Lymantriini	Lymantria	grisea	China	H6	
Lymantriinae	Lymantriini	Lymantria	tortivalvula	China	H269	
Lymantriinae	Lymantriini	Lymantria	sp1	Madagascar	SM01	
Lymantriinae	Lymantriini	Lymantria	mathura	China	H122	
Lymantriinae	Lymantriini	Lymantria	beatrice	Thailand	H401	
Lymantriinae	Lymantriini	Lymantria	hauensteini	China	H361	
Lymantriinae	Lymantriini	Lymantria	sp2	Madagascar	S01	
Lymantriinae	Lymantriini	Lymantria	dispar	Turkey	S04	TS
Lymantriinae	Lymantriini	Lymantria	schaeferi	China	H317	

Lymantriinae	Lymantriini	Lymantria	concolor	China	H37	
Lymantriinae	Lymantriini	Lymantria	dissoluta	China	H127	
Lymantriinae	Lymantriini	Lymantria	similis	China	H58	
Lymantriinae	Lymantriini	Lymantria	monacha	Finland	MM01048	
Lymantriinae	Orgyiini	Hemerophanes	diatoma	Zambia	M7	
Lymantriinae	Orgyiini	Aroa	discahis	Zambia	M2	TS
Lymantriinae	Orgyiini	Mymantria	xanthospila	Uganda	T8	TS
Lymantriinae	Orgyiini	Griveaudyria	?cangia	Zambia	M4	
Lymantriinae	Orgyiini	Calliteara	taiwana	China	H218	
Lymantriinae	Orgyiini	Calliteara	complicata	China	H291	
Lymantriinae	Orgyiini	Calliteara	angulata	China	H112	
Lymantriinae	Orgyiini	Calliteara	wolongensis	China	H248	
Lymantriinae	Orgyiini	Calliteara	contexta	China	H161	
Lymantriinae	Orgyiini	Calliteara	grotei	China	H135	
Lymantriinae	Orgyiini	Calliteara	melli	China	H29	
Lymantriinae	Orgyiini	Laelia	coenosa	China	H14	TS
Lymantriinae	Orgyiini	Laelia	umbrina	China	H20	
Lymantriinae	Orgyiini	Laelia	umbrina*	China	H111	
Lymantriinae	Orgyiini	Aroa	sp	China	S25	
Lymantriinae	Orgyiini	Aroa	substrigosa	China	H134	
Lymantriinae	Orgyiini	Pantana	sinica	China	H34	
Lymantriinae	Orgyiini	Pantana	sinica*	China	H162	
Lymantriinae	Orgyiini	Pantana	visum	Thailand	H390	
Lymantriinae	Orgyiini	Pantana	sp	Vietnam	S11	
Lymantriinae	Orgyiini	Neomardara	africana	Zambia	T2	TS
Lymantriinae	Orgyiini	Dasychira	tephra	USA	BIUG01420-B05	TS

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Lymantriinae	Orgyiini	Dasychira	glaucozona	China	H25	
Lymantriinae	Orgyiini	Psalis	pennatula	Thailand	H385	
Lymantriinae	Orgyiini	Telochurus	sp	China	H52	
Lymantriinae	Orgyiini	Olene	dudgeoni	China	H63	
Lymantriinae	Orgyiini	Olene	inclusa	China	H131	
Lymantriinae	Orgyiini	Cifuna	locuples	China	H47	TS
Lymantriinae	Orgyiini	Teia	parallela	China	H349	
Lymantriinae	Orgyiini	Orgyia	osseata	Brunei	S28	
Lymantriinae	Orgyiini	Orgyia	postica	Vietnam	S22	
Lymantriinae	Orgyiini	Orgyia	antiqua	Finland	RZ130	
Lymantriinae	Orgyiini	Orgyia	povera	Costa Rica	12-SRNP-13137	
Lymantriinae	Orgyiini	Ilema	jankowskii	China	H26	
Lymantriinae	Orgyiini	Ilema	catocaloides	China	H160	
Lymantriinae	Orgyiini	Ilema	costalis	China	H200	TS
Lymantriinae	Orgyiini	Ilema	anaha	Vietnam	S07	
Lymantriinae	Nygmiini	Albarracina	warionis	Morocco	M8	
Lymantriinae	Nygmiini	Bembina	isabellina	Malaysia	H383	
Lymantriinae	Nygmiini	Lacida	vertiginosa	Laos	S51	
Lymantriinae	Nygmiini	Lacida	sp	Thailand	H389	
Lymantriinae	Nygmiini	Micromorphe	linta	Malaysia	H381	TS
Lymantriinae	Nygmiini	Somena	scintillans	China	H141	TS
Lymantriinae	Nygmiini	Kidokuga	piperita	China	H367	TS
Lymantriinae	Nygmiini	Kidokuga	sp	China	H368	
Lymantriinae	Nygmiini	Sphrageidus	sp	Madagascar	S34	
Lymantriinae	Nygmiini	Sphrageidus	similis	China	H46	TS
Lymantriinae	Nygmiini	Orvasca	subnotata	China	H110	TS

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7	Lymantriinae	Nygmiini	Orvasca	dolichocera	Vanuatu	S56	
8	Lymantriinae	Nygmiini	Arna	bicostata	China	H74	
9	Lymantriinae	Nygmiini	Arna	bipunctapex	China	H139	TS
10	Lymantriinae	Nygmiini	Artaxa	digramma	China	H142	
11	Lymantriinae	Nygmiini	Artaxa	angulata	China	H67	
12	Lymantriinae	Nygmiini	Artaxa	rubiginosa	Vietnam	S62	
13	Lymantriinae	Nygmiini	Toxoproctis	croceola	China	H158	
14	Lymantriinae	Nygmiini	Nygmia	quadrangularis	China	H137	
15	Lymantriinae	Nygmiini	Nygmia	marginata	China	H371	
16	Lymantriinae	Nygmiini	Nygmia	uniformis	China	H145	
17	Lymantriinae	Nygmiini	Nygmia	javana	China	H386	
18	Lymantriinae	Nygmiini	Nygmia	staudingeri	China	H192	
19	Lymantriinae	Nygmiini	Nygmia	plana	China	H138	
20	Lymantriinae	Nygmiini	Nygmia	plana*	China	RZ34	
21	Lymantriinae	Nygmiini	Nygmia	inornata	China	H136	
22	Lymantriinae	Nygmiini	Euproctis	sp1	Thailand	H388	
23	Lymantriinae	Nygmiini	Euproctis	sp2	Thailand	H402	
24	Lymantriinae	Nygmiini	Euproctis	singapura	Vietnam	S47	
25	Lymantriinae	Nygmiini	Euproctis	pyraustis	China	H375	
26	Lymantriinae	Nygmiini	Euproctis	fumea	China	H374	
27	Lymantriinae	Nygmiini	Euproctis	seitzii	China	H113	
28	Lymantriinae	Nygmiini	Euproctis	falvotriangulata	China	H261	
29	Lymantriinae	Nygmiini	Euproctis	callichalena	China	H369	
30	Lymantriinae	Nygmiini	Euproctis	kanshireia	China	H346	
31	Lymantriinae	Nygmiini	Euproctis	sp3	China	H2	
32	Lymantriinae	Nygmiini	Euproctis	cryptosticta	China	H144	
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Lymantriinae	Nygmiini	Euproctis	? aureoplaga	Madagascar	S50	
Lymantriinae	Nygmiini	Euproctis	molunduana	Uganda	M3	
Lymantriinae	Nygmiini	Euproctis	? ionthada	Uganda	M9	
Lymantriinae	Nygmiini	Euproctis	montis	China	H350	
Lymantriinae	Nygmiini	Euproctis	collenettei	China	H353	
Lymantriinae	Nygmiini	Euproctis	? putris	Zambia	T10	
Lymantriinae	Nygmiini	Euproctis	karghalica	China	H352	
Lymantriinae	Nygmiini	Euproctis	chrysorrhoea	Sweden	H380	TS
Lymantriinae	Nygmiini	Euproctis	conistica	China	H76	
Lymantriinae	Nygmiini	Euproctis	yunnanpina	China	A102	
Lymantriinae	Nygmiini	Euproctis	magna	China	HS31	
Lymantriinae	Nygmiini	Euproctis	?serulla	China	H23	