



Phylogeny and classification of Endromidae (Lepidoptera: Bombycoidea) based on mitochondrial genomes

Min Deng^{1,2}, Andreas Zwick³, Qi Chen¹, Cheng-Qing Liao¹, Wei Wang², Xing Wang², Guo-Hua Huang¹

¹ Hunan Provincial Key Laboratory for Biology and Control of Plant Diseases and Insect Pests, College of Plant Protection, Hunan Agricultural University, Changsha, Hunan 410128, China

² College of Science, Qiongtai Normal University, Haikou, Hainan 571100, China

³ CSIRO, Australian National Insect Collection, Canberra, ACT 2601, Australia

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Corresponding authors: Guo-Hua Huang (guohuahuang@hunau.edu.cn), Xing Wang (xingwanghjt@163.com)

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Abstract

The small, relict-like moth family Endromidae is well-established within the superfamily Bombycoidea, but relationships within the family have remained vague for the last decade, primarily due to very limited taxon sampling. This resulted in the explicit removal of all internal suprageneric classification by Zwick et al. (2011) when they synonymized Mirinidae and the bombycid subfamilies Oberthueriinae and Prismostictinae with Endromidae. Nucleotide and amino acid data sets of the 13 mitochondrial, protein-coding genes from representatives of 13 of the 16 accepted endromid genera were used to estimate phylogenetic relationships based on maximum likelihood and Bayesian inference methods. The results strongly support Endromidae as a monophyletic group and enable the establishment and diagnosis of four subfamilies (Endrominae, Mirininae **stat. rev.**, Oberthueriinae **stat. rev.** and Prismostictinae **stat. rev.**). Within subfamily Oberthueriinae, we establish three tribes: Oberthueriini **stat. rev.**, Andracini **tribe nov.** and Mustiliini **tribe nov.** We provide morphological diagnoses and a genus-level checklist for the three tribes. *Promustilia yajiangensis* Wang, X. & Zolotuhin, 2015 is transferred to *Mustilizans* as *M. yajiangensis* **comb. nov.** to establish reciprocal monophyly of the two genera, and *Andraca gongshanensis* is transferred to *Pseudandraca* as *P. gongshanensis* **comb. nov.** We also synonymize *Andraca* (*Chrypathemola*) **syn. nov.** with *Andraca* (*Andraca*), as the latter is deeply nested within the former.

Keywords

Endromidae, mitochondrial genome, phylogenetic analysis, revision

1. Introduction

The moth family Endromidae Boisduval, 1828 is relatively species poor (72 species) and occurs primarily in Asia, with just a single species extending into Europe. This species, the very distinct and widespread Palearctic species *Endromis versicolora* (Linnaeus, 1758), is placed in

the monobasic genus *Endromis* Ochsenheimer, 1810 and, for over a century, its own family Endromidae. It was regarded as an isolated taxon within the “Bombyces”, until Seitz (1911) tentatively included the then monobasic genus *Mirina* Staudinger, 1892. This action was followed

by Kuznetsov & Stekolnikov (1985), who studied the muscles of Bombycoidea. Shortly after, Kozlov (1985) erected the family Mirinidae Kozlov, 1985 for *Mirina*. The concept of two closely related yet distinct families was then generally accepted due to the clear differences in adult morphology, larval appearance and host plant usage (e.g., Kozlov 1985; Minet 1986, 1994; Lemaire and Minet 1998; Zolotuhin and Witt 2000).

The use of DNA sequence data has greatly contributed to the phylogenetic hypotheses and consequential changes in the classification of Bombycoidea. Based on five protein-coding nuclear genes, phylogenetic analyses of the ‘bombycoid complex’ grouped Endromidae, Mirinidae and the bombycid subfamilies Oberthueriinae Kuznetsov & Stekolnikov, 1985 and Prismostictinae Forbes, 1955 into a single clade (Regier et al. 2008). Zwick et al. (2011) robustly corroborated the above result with increased taxon and gene sampling (50 bombycoid taxa, up to 20 nuclear, protein-coding genes), and genetic variation within this clade was found to be less than in other bombycoid families. However, the internal branches between endromid genera were very short and taxon sampling was minimal with only four species, resulting in weak and sometimes conflicting statistical support for relationships within the clade. Consequently, Zwick et al. (2011) synonymized Mirinidae, Oberthueriinae and Prismostictinae with Endromidae, intentionally removing all suprageneric structure within Endromidae in recognition of the uncertain relationships and poor taxon sampling. Although the previous, independent systematic family status was preferred by many workers (e.g., Wang et al. 2011a; Zolotuhin and Than 2011; Zolotuhin 2012; Zolotuhin and Wang 2013), other authors agreed with the revised concept of Endromidae *sensu* Zwick et al. (2011) and followed or further supported it in their respective studies (e.g., Wang et al. 2011b; Regier et al. 2013; Hamilton et al. 2019; Wang et al. 2019). Similarly, the previous and clearly polyphyletic (Regier et al. 2008; Zwick, 2008; Zwick et al. 2011) concept of Bombycidae Latreille, [1802] *sensu* Minet (1994), which united Oberthueriinae, Prismostictinae, Bombycinae, Phiditiidae Minet, 1994 and Apatelodidae Neumoegen & Dyar, 1894, was retained by some authors as “Bombycidae *sensu lato*” (e.g., Zolotuhin 2007; Zolotuhin and Witt 2009; Zolotuhin and Tran 2011; Zolotuhin 2012; Zolotuhin and Wang 2013; Wang et al. 2015; Wu and Chang 2016).

With further studies on the phylogeny of Bombycoidea (Hamilton et al. 2019; Wang et al. 2019), the composition of Endromidae has gradually been clarified and stabilized. Hamilton et al. (2019) included nine genera of Endromidae, but even with up to 571 nuclear loci from anchored hybrid enrichment, relationships and statistical support within Endromidae varied depending on the type of data and method of analysis. The currently recognized endromid taxa are detailed in a global checklist of Bombycoidea (Kitching et al. 2018) and subsequent publications (Chandra et al. 2019; *Andraca yauichui* Wu & Chang, 2016 and *Mustilizans zolotuhini* Chandra, 2019). At present, a mere 72 species are recognized as valid in 16 genera, and three of these genera are monobasic (*Endromis*; *Prismostictoi-*

des Zolotuhin & Than Thieu, 2011; *Falcogona* Zolotuhin, 2007). However, no objective phylogeny-based subfamily or tribal classification exists for the genera of Endromidae, despite the very different appearances of the moths and caterpillars, which has led to their long taxonomic separation and hinders the recognition of natural relationships. These deep morphological differences, combined with very limited species diversity in most genera and restricted distributions, indicate a relictual nature of this family. Indeed, the Endromidae are the Asian representatives of a more inclusive relictual lineage, the “CAPOPEM” group of Regier et al. (2008), which includes additionally the monobasic Carthaeidae Common, 1966 in the SW corner of Australia, the small Austral-New Guinean family Anthelidae Turner, 1904 and the even smaller Neotropical family Phiditiidae Minet, 1994.

Several endromid genera (e.g., *Dalailama* Staudinger, 1896, *Sesquiluna* Forbes, 1955 and *Falcogona*) are rarely collected and underrepresented in collections, making it difficult to obtain comprehensive taxon sampling for molecular phylogenetic studies. DNA sequencing of old collection specimens helps to improve taxon sampling of rarely collected species (Zimmermann et al. 2008; Burrell et al. 2015), and mitochondrial (mt) genomes are particularly easy to obtain from strongly degraded DNA samples due to their high copy number (Duan et al. 2018). Furthermore, mt-genomes are characterized by a simple genetic structure, small size, strictly orthologous genes, reduced recombination and fast evolutionary rates (Zhang and Hewitt 1997; Boore 1999; Cameron 2014), which makes them attractive for some phylogenetic questions. Some studies found that mt-genomes were inadequate for resolving subfamily-level relationships, but given good taxon sampling, could resolve lower-level phylogenetic relationships (Nie et al. 2020; Ghanavi et al. 2022). In other studies, mt-genomes have proven a useful data source for taxonomic and phylogenetic studies of arthropods (e.g., Xiao et al. 2012; Cameron 2014; Wang et al. 2018; Chen et al. 2020; Bian et al. 2020; Jin et al. 2020a, b). In this study, we utilize mt-genomes of 13 of the 16 genera (80% of lineage diversity) to investigate the phylogeny of the family Endromidae and to revise its internal classification.

2. Material and methods

2.1. Taxon sampling and DNA extraction

The mt-genomes of 26 taxa of Endromidae, belonging to 13 genera in four subfamilies (Table S1), were newly sequenced for this study. Following collection, the three right legs or thorax of each specimen were preserved in absolute ethanol and then stored at -20°C . The remainders of all specimens are deposited as vouchers in the Insect Museum of Hunan Agricultural University, Changsha City, Hunan Province, China.

Total genomic DNA was extracted from the legs or thoracic tissue of each specimen using a TaKaRa MiniBEST Universal Genomic DNA Extraction Kit Ver.5.0 (Shiga Prefecture, Kusatsu City, Japan). Purified DNA was preserved at -20°C prior to sequencing.

2.2. Genome sequencing and assembly

Illumina TruSeq libraries with 350 bp insert size were prepared for each species, and these Whole Genome Shotgun libraries were sequenced by Novogene (Beijing, China) on the Illumina HiSeq platform with 150 bp paired-end reads. For each library, 6 Gbp of clean data were obtained after removing reads containing adaptor contamination, poly-Ns (>15 bp Ns), or >75 bp bases with quality scores ≤ 20 . Cleaned reads were assembled into contigs and scaffolds using IDBA (v1.1.3; Peng et al. 2010, 2011, 2012), with kmer values ranging between 60 and 160 bp. The mt-genomes were annotated with ORF finder (<https://www.ncbi.nlm.nih.gov/orffinder>) and compared against annotated sequences in NCBI using BLAST (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>). Then, the 22 tRNA and two rRNA sequences were annotated with MITOS web server (<http://mitos.bioinf.uni-leipzig.de/index.py>) (Bernt et al. 2013). The two rRNA subunits and all protein-coding genes (PCGs) were annotated by alignment with homologous genes from the same genus or subfamily using Geneious R8 (Kearse et al. 2012). MEGA 10.1.5 was used to calculate the AT and GC content and P-distances (Kumar et al. 2018). The annotated sequences of the 22 newly sequenced species are deposited in GenBank, and accession numbers (OQ472264–OQ472285) and the other 13 sequences, which are incomplete, can be accessed from Zenodo (<https://doi.org/10.5281/zenodo.7655269>). The collection data are detailed for all new endromid samples in Table S1.

2.3. Phylogenetic analyses

Twelve publicly available mt-genomes were obtained from NCBI GenBank (<http://www.ncbi.nlm.nih.gov>), including nine ingroup species and three lasiocampid species used as outgroups. All mt-genome sequences were imported and standardized in Geneious R8. All PCGs were exported from Geneious R8. The 13 PCGs were aligned with the TranslatorX server (<http://www.translatorx.co.uk>) (Castresana 2000), with the “ALL”-parameter. Concatenation of single gene alignments was performed in Geneious R8, resulting in 2 datasets: 1) 13 protein-coding genes (13PCGs); 2) 13 PCGs as amino acids (13PCGs-AA). Partitionfinder 2.1.1 was used to search the optimal partitioning scheme and models for each data set. IQ-Tree (v1.5.5; Nguyen et al. 2016) was used to estimate a maximum likelihood (ML) tree with 1,000 non-parametric bootstrap replicates to estimate branch support. Nodes with a bootstrap percentage (BP) of at least 70% were considered well supported in the ML analyses (Hil-

lis et al. 1993). A Bayesian (BI) tree was calculated with MrBayes (v3.2.6) on XSEDE (<https://www.phylo.org/portal2/home.action>) (Nguyen et al. 2014; Ronquist et al. 2003), with the Markov Chain Monte Carlo analysis run for 10,000,000 generations, sampled every 1,000th generation and with a burn-in of 25%. Bayesian posterior probabilities (PP) > 0.95 were interpreted as strongly supported (Erixon et al. 2003). The phylogenetic trees were drawn using the software FigTree (v1.4.3; Rambaut 2016).

3. Results

3.1. Characteristics of endromid mt-genomes

Our study provides the first mt-genomes for six endromid genera, i.e., *Endromis*, *Mirina*, *Pseudandracra* Miyata, 1970, *Smerkata* Zolotuhin, 2007, *Dalailama* and *Promustilia* Zolotuhin, 2007. Most mt-genomes, except *Andracra lawa_21*, *Mustilizans dierli* and *Prismosticta tiretta_32*, used in this study comprised a total of 37 genes (13 PCGs, 22 tRNAs and 2 rRNAs), and the total length of all sequences ranges from an incomplete 6,350 bp (*Andracra lawa_21*) to 15,880 bp (*Andracra olivacea*–GD) (Figure S1). As is usual for the mt-genomes of Lepidoptera (Arnoldi et al. 2007; Yang et al. 2013; Amaral et al. 2016; Yuan et al. 2019), those of Endromidae have a significant bias towards adenine and thymine, ranging from 77.7% to 81.1% (average 79.8%; Table S2). For almost all samples, the AT-skew is greater than 0 and GC-skew is less than 0, except *Mirina confucius* Zolotuhin & Witt, 2000, which has a negative AT-skew (Table S2). Moreover, the uncorrected pairwise distance P (proportion of nucleotide sites at which two compared sequences are different) shows that the *COX1* gene, widely adopted as the DNA barcode marker, possesses the smallest amount of interspecies genetic variation, while ATP8 possesses the highest (Figure S2). The G + C content for each PCG reveals that ATP8 possesses the lowest G + C content, and ATP6 the highest (Figure S3).

3.2. Phylogenetic relationships among Endromidae

Based on the 13PCGs dataset, the two phylogenetic trees estimated with BI (Figure S4) and ML analyses (Figure S5) are almost identical. Only the relationships between the three clades of Oberthuriinae and the relationships between species of *Prismosticta* differ. And the Bayesian tree of the 13-PCGs data set is used to label the values of other trees. Statistical support (PP and BP) is strong for 34 of the 40 nodes, with weak support restricted to backbone nodes and within a clade of Oberthuriinae **stat. rev.** Within the limits of taxon sampling, the results strongly support the monophyly of the family Endromidae, as well as a division into four subfamilies, with Prismostictinae

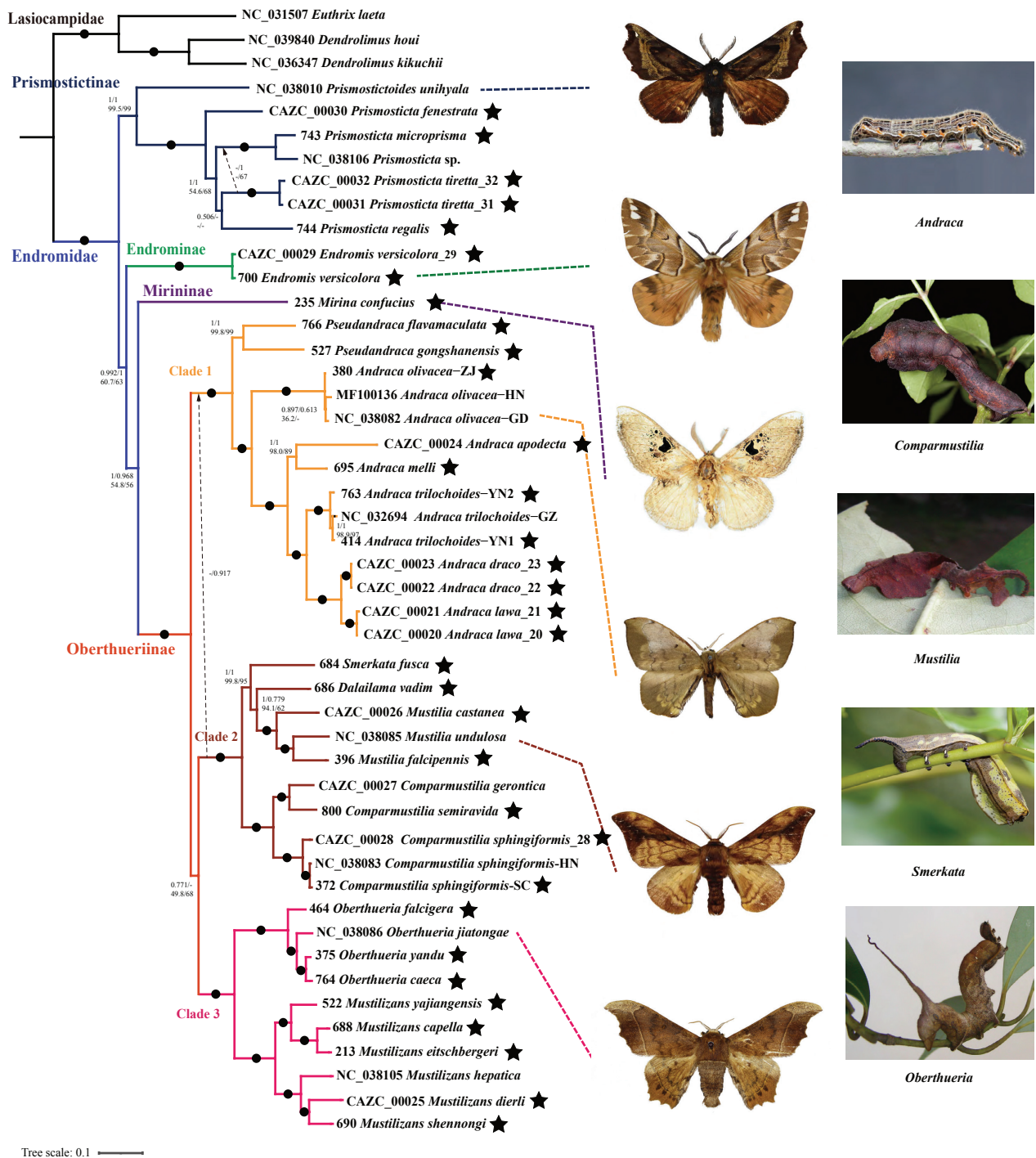


Figure 1. Phylogeny of Endromidae inferred from different data sets (13PCGs-AA, 13PCGs) using Bayesian inference and maximum likelihood analyses. Numbers above branches are posterior probabilities (BI PP), beneath which are bootstrap percentages (ML BP) for 1000 replicates; nodes with maximum support values are marked with a black dot instead. Dashed arrows (two in total) identify alternative topologies (relative to the topology shown) that receive at least 70% bootstrap support by one or more of the approaches. The asterisks indicate newly sequenced mitochondrial genomes.

stat. rev. sister to all other taxa (PP = 1, BP = 100%). The phylogenetic relationship between Endrominae and Mirininae **stat. rev.**, which are nested between the two other subfamilies, is strongly supported in the BI tree (PP = 0.992). Within Prismostictinae **stat. rev.**, the genera *Prismosticta* Butler, 1880 and *Prismostictoides* are sister to each other (PP = 1, BP = 99.5%). A distinct monophyletic group, subfamily Oberthueriinae **stat. rev.**, comprises three major, well-supported clades (PP = 1, BP = 100%).

Clade 1 includes the genera *Pseudandracra* Miyata, 1970 and *Andracra* Walker, 1865. In addition, *Andracra gongshanensis* and *Pseudandracra flavamaculata* are shown as sisters with strong support (PP = 1, BP = 99.8%). The clades (*Andracra apodecta* + *Andracra melli*) and (*Andracra trilochoides* + (*Andracra draco* + *Andracra lava*)) are grouped together (PP = 1, BP = 100%). Clade 2 includes four genera, with *Comparmustilia* Wang, X. & Zolotuhin, 2015 sister to the other genera. Clade 3 is divided into two

major groups comprising the monophyletic genus *Oberthueria* Kirby, 1892 (PP = 1, BP = 100%) and the genus *Mustilizans* Yang, 1995, which is a paraphyletic relative to the species *Promustilia yajiangensis* Wang, X. & Zolotuhin, 2015. The relationship of these three clades is shown as (Clade 1 + (Clade 2 + Clade 3)) (PP = 0.771, BP = 49.8). Although both methods of analysis of the different datasets resulted in largely congruent topologies, there are still obvious differences compared to the analysis results of the 13PCGs-AA dataset (BI in Figure S6, ML in Figure S7, and combined in Figure 1), which show the relationships of the three clades within Oberthueriinae as (Clade 3 + (Clade 1 + Clade 2)) in the BI tree (Figure S6) with good support (PP = 0.917).

4. Discussion

All the newly sequenced Endromidae mitochondrial genomes have the same gene order as in the other known Lepidoptera (Cao et al. 2012; Timmermans et al. 2014; Zou et al. 2017). The particularly low divergences among the *COXI* sequences indicate the genetic stability of the gene, which is used for species identification in many studies (e.g., Rodrigues et al. 2017; Liao et al. 2021).

Mitochondrial genomes are widely used for studying population genetics, comparative and evolutionary genomics, the reconstruction of phylogenetic relationships, and evolutionary biology (e.g., Boore 1999; Vilhelmsen 2019; Jin et al. 2020b; Quicke et al. 2020). Our analyses of mt-genomes resulted in ML and BI trees that overall differ very little from each other (only in the unstable position of three clades of Oberthueriinae). Furthermore, the study of Hamilton et al. (2019), which has by far the greatest nuclear gene sampling for nine of the 16 endromid genera, recovered exactly the same taxonomic groupings as our mt-genome analyses, albeit with greatly reduced taxon sampling (10 vs 35 endromid species). This congruence lends credibility to our results and the placement of the four additional genera *Prismostictoides*, *Smerkata*, *Dalailama* and *Promustilia*.

Endromid subfamilies

Our results are likewise in agreement with morphologically recognized group. Our analyses recovered both the family Endromidae and its four major lineages as monophyletic and strongly supported. These four lineages correspond to the morphologically recognized (sub)families that were synonymized with Endromidae (Zwick et al. 2011). Consequently, on this basis, we here re-instated these lineages as valid subfamilies: Endrominae, Mirininae **stat. rev.**, Oberthueriinae **stat. rev.** and Prismostictinae **stat. rev.** All the different data sets recovered the same topology as Hamilton et al. (2019), i.e., Prismostictinae + (Endrominae + (Mirininae + Oberthueriinae)).

Endrominae

Endrominae, which is just consisting of one species, has typical characteristics different from other endromid moths as follows: forewing with three triangular white spots, thorax and abdomen bright-colored (Figure 1. *Endromis*), uncus and valva tongue-shaped, and gnathos absent. Its larval host is also different from other endromid species, mainly feeding *Betula* sp., *Corylus* sp. *Cytisus* sp., *Quercus* spp. (Waring and Townsend 2003; Pérez et al. 2009).

Mirininae **stat. rev.**

Mirininae **stat. rev.** is consisting of only one genus, *Mirina*, which was been controversial. Some scholars considered that it should be a separate family (Minet 1994; Zolotuhin and Witt 2000; Huang and Wang 2003; Regier 2008; Zolotuhin et al. 2011), but others recognized that it should belong to the family Endromidae (Zwick et al. 2008; Zwick et al. 2011). Although *Mirina* and *Endromis* are different from larval morphology, host and adult appearance (Zolotuhin and Witt 2000), subsequent molecular phylogenetic studies had continued to find good support for Endromidae *sensu* Zwick et al. (2011). And then they were listed in the family Endromidae in the global checklist of the Bombycoidea (Kitching et al. 2018). In this paper, their relationships had been supported based on anchored hybrid enrichment (Hamilton et al. 2019) and showed as Endrominae nest to Mirininae.

Prismostictinae **stat. rev.**

The subfamily Prismostictinae **stat. rev.**, which is sister to a clade comprising all the other subfamilies, consists of only two morphologically similar genera, *Prismosticta* and *Prismostictoides*. The monobasic genus *Prismostictoides*, with the type species *Prismosticta unihyala* Chu & Wang, 1993, was separated from *Prismosticta* based on a broad postmedial line and broad, dark yellow submarginal band on the forewing upperside, uncus with a long uncuslike projection arising from the base of uncus, and valva asymmetrical. Otherwise, the two genera are rather similar and share a characteristic transparent spot near the apex of the forewing (Zolotuhin and Tran 2011; Wang et al. 2015), which might be used to diagnose the subfamily. Our molecular data place *Prismostictoides* as sister to the five sampled species of *Prismosticta*.

Oberthueriinae **stat. rev.**

Oberthueriinae **stat. rev.**, the largest subfamily of Endromidae, is divided into three major clades that are strongly supported as monophyletic groups. Based on our results, we treat these clades as three tribes: Andracini **tribe nov.** (Clade 1), Mustiliini **tribe nov.** (Clade 2) and Oberthueriini Kuznetsov & Stekolnikov, 1985 **stat. rev.** (Clade 3). The sister relationship between *Andraca* and *Pseudandraca* in Andracini **tribe nov.** is consistent with findings of previous studies (Wang et al. 2012, 2015;

Hamilton et al. 2019). The genus *Pseudandraca* was distinguished from *Andraca*, the type genus of Andracini, based on forewing pattern and male genital structures (Zolotuhin and Witt 2009; Wang et al. 2012). However, our phylogenetic analysis results indicate that *Andraca gongshanensis* should be transferred to *Pseudandraca* as *Pseudandraca gongshanensis* **comb. nov.** The two subgenera of *Andraca*, *Andraca* (*Andraca*) Walker, 1865 and *Andraca* (*Chrypathemola*) Zolotuhin, 2012, were established based on the structure of the uncus in male genitalia. However, none of our analyses support the distinction of these two subgenera. The two representatives of *Andraca* (*Andraca*), *A. (A.) lawa* and *A. (A.) draco*, are deeply nested within *Andraca* (*Chrypathemola*) and therefore we here synonymize *Andraca* (*Chrypathemola*) **syn. nov.** with *Andraca* (*Andraca*).

Previously, *Mustilia* Walker, 1865 had been split into six separate genera (Zolotuhin 2007; Wang et al. 2005), i.e., *Mustilia*, *Comparmustilia*, *Mustilizans*, *Promustilia*, *Smerkata* and *Falcogona*, but not all of these belong in the tribe Mustiliini **tribe nov.** Within this tribe, the genera *Mustilia* and *Comparmustilia* were recovered as sister taxa in previous studies (Wang et al. 2019; Hamilton et al. 2019). However, the inclusion of the newly sequenced genera *Smerkata* and *Dalailama* provides a more comprehensive and different picture, with these two genera nested between *Comparmustilia* and *Mustilia*, and *Dalailama* being sister to *Mustilia*.

Our analyses place three genera in the tribe Oberthueriini, i.e., *Oberthueria*, *Mustilizans* and *Promustilia*, of which the latter two were previously included in *Mustilia*. The genus *Oberthueria* is monophyletic, with strong statistical support for the three species included in this study, and the six currently recognized species are morphologically very similar and show only moderate differences in *COXI* barcode sequences (Zolotuhin and Wang 2013). In contrast, our results demonstrate clearly the paraphyly of the genus *Mustilizans* relative to the species *Promustilia yajiangensis*. Because our study lacks the type species of *Promustilia*, we do not, at this time, wish to synonymize *Promustilia* with *Mustilizans*. Instead, we transfer *P. yajiangensis* to *Mustilizans* as *M. yajiangensis* **comb. nov.** and retain *Promustilia* as a valid genus for the time being. The separation of *Promustilia* from *Mustilizans* is doubtful as the morphologies of *P. andracoides* (Zolotuhin, 2007) and *M. yajiangensis* **comb. nov.** are very similar, and the former also shares a similar bifid uncus and flat, apically blunt valva with *Mustilizans* (Zolotuhin 2007; Zolotuhin and Witt 2009; Wang et al. 2015). More detailed future studies should be undertaken to provide further molecular and morphological data to elucidate the relationships of these two genera.

Unfortunately, specimens of the remaining three endromid genera, *Falcogona*, *Sesquiluna* and *Theophoba* Fletcher & Nye, 1982 were unavailable to us and we lack mt-genomes for them. Based on similarities in adult morphology, such as eyes surrounded by setae, completely pectinate antennae and similar size, we tentatively include *Sesquiluna* and *Theophoba* in subfamily Prismostictinae **stat. rev.**, as postulated by Wang et al. (2015).

The genus *Falcogona* is difficult to place phylogenetically because of some significant morphological differences, especially the very long and strongly modified cuiller (Zolotuhin et al. 2007). In other characteristics, such as wing shape, the short and broad gnathos, and the tubular phallus (Zolotuhin et al. 2007; Wang et al. 2015), *Falcogona* is rather similar to *Smerkata*. Consequently, we tentatively include *Falcogona* in the tribe Mustiliini **tribe nov.** The phylogenetic relationships among these and related genera should also be investigated in future studies.

Taxonomy of Oberthueriinae

Oberthueriini Kuznetsov & Stekolnikov, 1985 stat. rev.

Type genus. *Oberthueria* Kirby, 1892

Diagnosis. Members of this tribe share the following characters: 1) forewings long and narrow; 2) labial palpi of moderate length, about 2/3 of the vertical diameter of the compound eye; 3) distal half of antenna devoid of well-developed rami (Figure 2). In addition, the larvae also bear some distinct characters, such as a hairless body, moderately wider expansion of the thoracic tergites, and an extremely long anal horn (Figure 1: *Oberthueria*).

Notes. Zolotuhin (2007) treated *Promustilia* as a subgenus of *Mustilizans*, before Wang et al. (2015) raised it to full genus level when they described *Promustilia yajiangensis*. Although *P. yajiangensis* is here transferred to *Mustilizans* to ensure monophyly of that genus, *Promustilia* is retained as a distinct genus as the type species, *Mustilizans* (*Promustilia*) *andracoides*, was not included in this study. If not even synonymous, *Mustilizans* and *Promustilia* are closely related, and *Promustilia* is here included in Oberthueriini **stat. rev.**

Oberthueria Kirby, 1892

Oberthueria Kirby, 1892, Syn. Cat. Lepid. Het., 1: 720. Type species: *Euphranor caeca* Oberthür, 1880, by monotypy

Oberthueria Staudinger, 1892, in Romanoff, Mém. Lépid.: 337. Type species: *Euphranor caeca* Oberthür, 1880, by monotypy (a junior homonym and junior objective synonym of *Oberthueria* Kirby, 1892)

Oberthüria: Staudinger, 1892, in Romanoff, Mémoires sur les lépidoptères (Mém. Lépid.) 6: 337. (incorrect original spelling)

Euphraor: Kirby, 1892, Syn. Cat. Lepid. Het. 1: 720 (incorrect subsequent spelling)

Euphranor Oberthür, 1880, Etudes d'Entomologie (Étud. ent.) 5: 40. Type species: *Euphranor caeca* Oberthür, 1880, by monotypy (a junior homonym of *Euphranor* Herrich-Schäffer, 1855 (Lepidoptera, Saturniidae))

Mustilizans Yang, 1995

Mustilizans Yang, 1995, Insects of Baishanzu Mountain, Eastern China: 355. Type species: *Mustilizans drepaniformis* Yang, 1995, by original designation

Promustilia Zolotuhin, 2007

Promustilia Zolotuhin, 2007, Neue ent. Nachr. 60: 199. Originally erected as a subgenus of *Mustilizans* Yang, 1993. Type species: *Mustilizans (Promustilia) andracoides* Zolotuhin, 2007, by original designation

Mustiliini tribe nov.

Type genus. *Mustilia* Walker, 1865

Diagnosis. Mustiliini tribe nov. is similar to Oberthueriini stat. rev. in having narrow forewings and the distal half of the antenna with underdeveloped rami, but it can be easily distinguished by particularly short or completely reduced labial palpi. Larvae of this tribe also possess a hairless body, but the thoracic tergites are laterally strongly expanded, and the anal horn is relatively long and stout (Figure 1: *Comparmustilia*, *Mustilia* and *Smerkata*).

Notes. Based on the above morphological characteristics, we here establish the new tribe Mustiliini tribe nov., which is also supported by molecular data. Although we lack molecular data for *Falcogona*, it is included in this tribe because of its similarity in habitus and male genital structures to *Smerkata*.

Comparmustilia Wang, X. & Zolotuhin, 2015

Comparmustilia Wang, X. & Zolotuhin, 2015, Zootaxa, 3989: 79. Type species: *Mustilia sphingiformis* Moore, 1879, by present designation

Smerkata Zolotuhin, 2007

Smerkata Zolotuhin, 2007, Neue ent. Nachr. 60: 193. Originally proposed as a subgenus of *Mustilia* Walker, 1865. Type species: *Mustilia phaeopera* Hampson, 1910, by original designation

Dalailama Staudinger, 1896

Dalailama Staudinger, 1896, Dt. ent. Z. Iris 8 (2): 303. Type species: *Dalailama bifurca* Staudinger, 1896, by monotypy
Dailalama: Staudinger, 1901, Cat. Lepid. palaeart. Faunengeb. (1): 128. Incorrect subsequent spelling
Deilelamia: Pagenstecher, 1909, Geschichte eur. Schmett.: 433. Incorrect subsequent spelling

Mustilia Walker, 1865

Mustilia Walker, 1865, List Specimens lepid. Insects Colln Br. Mus. 32: 580. Type species: *Mustilia falcipennis* Walker, 1865, by monotypy

Falcogona Zolotuhin, 2007

Falcogona Zolotuhin, 2007, Neue ent. Nachr. 60: 199. Type species: *Falcogona gryphea* Zolotuhin, 2007, by original designation

Andracini tribe nov.

Type genus. *Andraca* Walker, 1865

Diagnosis. Morphological synapomorphies supporting the monophyly of Andracini tribe nov. are the relatively broad forewings, the very long labial palpi (longer than the vertical diameter of the compound eye), and underdeveloped rami over the distal 1/3 of the antenna (Figure 2). The larvae of this tribe share non-expanded thoracic tergites, a very short or completely absent anal horn, and the body in most species is densely covered with short hairs (Figure 1: *Andraca*).

Notes. *Pseudandraca* was established by Miyata (1970) with the type species *Andraca gracilis* Butler, 1885 based on a boot-shaped sacculus in the male genitalia. Wang et al. (2015) added *Andraca flavamaculata* Yang, 1995. Our molecular results also support these two genera as sister taxa. *Andraca* had been considered to have two subgenera (Zolotuhin 2012), but our analyses recover the subgenus *Chrypathemola* syn. nov. as a synonym of *Andraca*. The species *Pseudandraca gongshanensis* comb. nov. has a complex wing pattern, a relatively straight phallus and a foot-shaped apex of the valva, which are all characteristics shared with *Pseudandraca* (Figure 3).

Andraca Walker, 1865

Andraca Walker, 1865, List Specimens lepid. Insects Colln Br. Mus. 32: 581. Type species: *Andraca bipunctata* Walker, 1865, by monotypy
Pseudoeupterote Shiraki, 1911, Catalogue Insectorum Noxiarum Formosarum: 48. Type species: *Oreta theae* Matsumura, 1909, by monotypy

Pseudandraca Miyata, 1970

Pseudandraca Miyata, 1970, Tinea. 8: 190. Type species: *Andraca gracilis* Butler, 1885, by original designation

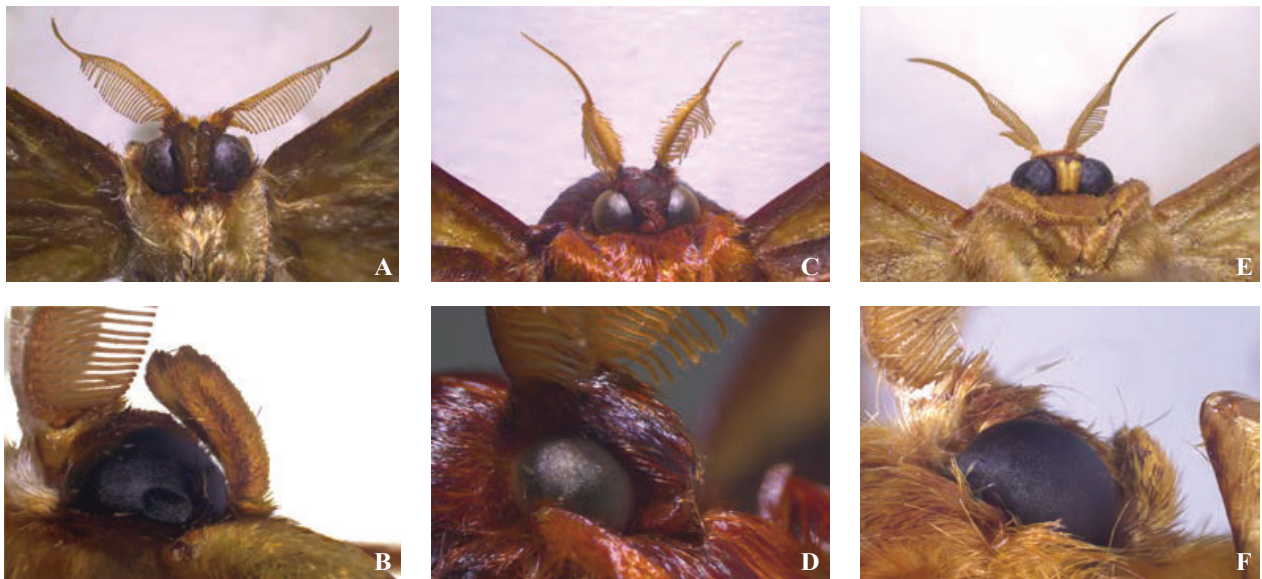


Figure 2. Cephalic characters of Oberthueriinae. **A, B** *Andraca olivacea*; **C, D** *Mustilia undulosa*; **E, F** *Oberthueria jiatongae*.)

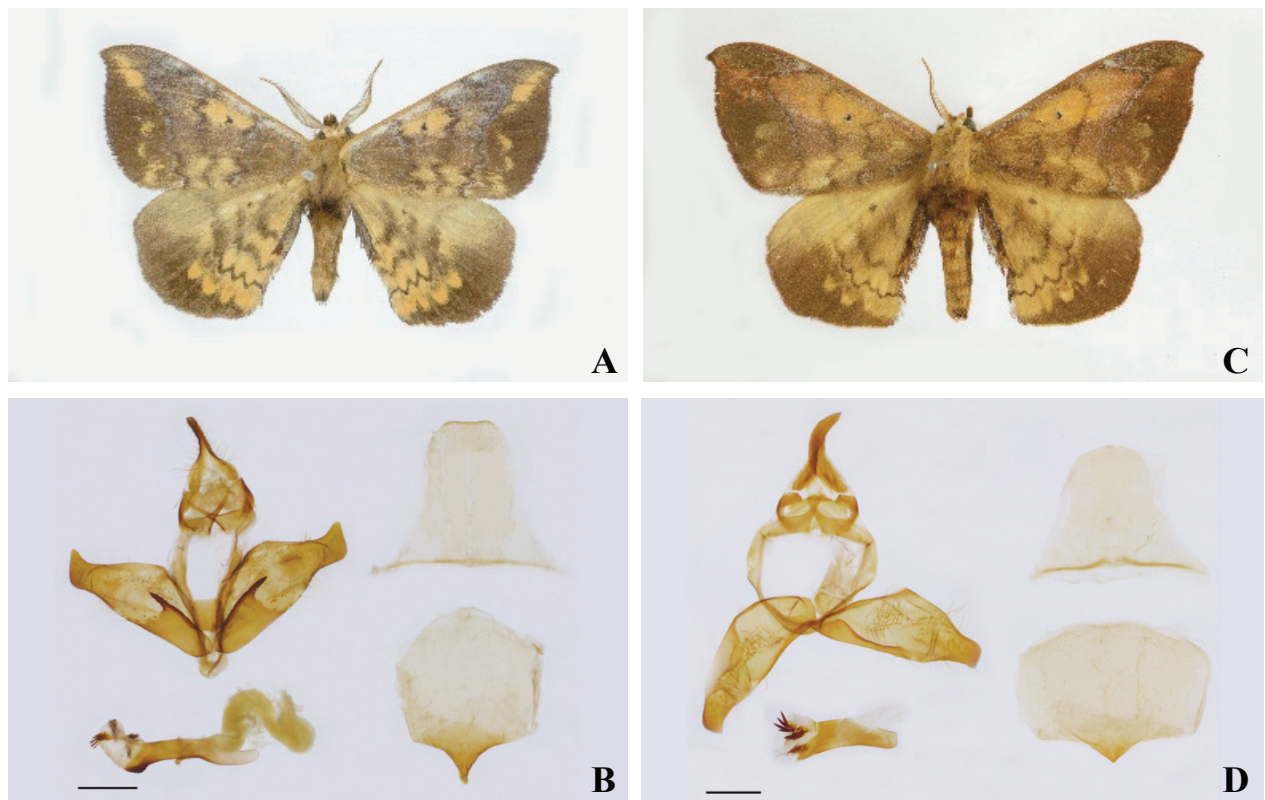


Figure 3. *Pseudandraca* adult and male genitalia. **A, B** *Pseudandraca flavamaculata*; **C, D** *P. gongshanensis* **comb. nov.**

5. Data availability statement

The complete sequences were uploaded to the NCBI (GenBank accession numbers: OQ472264–OQ472285). The incomplete sequences provided in this article can be accessed from Zenodo, DOI: <https://doi.org/10.5281/zenodo.7655269>

6. Conflict of Interest

The authors have no conflicts of interests to declare.

7. Authors' contributions

M.D. was responsible for drafting the manuscript, as well as the acquisition, analysis and interpretation of data. A.Z. provided part molecular sequences and contributed to the conception and design of the current study. Q.C. analyzed and interpreted the data. W.W. made suggestions and revised the manuscript. X.W. confirmed the insect species and revised the manuscript. G.-H.H. helped perform the analysis with constructive discussions and provided financial support. All authors read and approved the final manuscript.

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9. References

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Supplementary material 1

Table S1

Authors: Deng M, Zwick A, Chen Q, Liao CQ, Wang W, Wang X, Huang GH (2023)

Data type: .docx

Explanation note: List of taxa (genera and species) examined for the study and sources of information.

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Link: <https://doi.org/asp.81.e90721.suppl1>

Supplementary material 2

Table S2

Authors: Deng M, Zwick A, Chen Q, Liao CQ, Wang W, Wang X, Huang GH (2023)

Data type: .docx

Explanation note: The characteristics of the mitochondrial genomes of Endromidae.

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Link: <https://doi.org/asp.81.e90721.suppl2>

Supplementary material 3

Figure S1

Authors: Deng M, Zwick A, Chen Q, Liao CQ, Wang W, Wang X, Huang GH (2023)

Data type: .pdf

Explanation note: Characters of thirty-five newly sequenced endromid species' mitochondrial genomes. Gene names are annotated using standard abbreviations; single letters are IUPAC amino acid abbreviations.

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Link: <https://doi.org/asp.81.e90721.suppl3>

Supplementary material 4

Figure S2

Authors: Deng M, Zwick A, Chen Q, Liao CQ, Wang W, Wang X, Huang GH (2023)

Data type: .pdf

Explanation note: Boxplot showing P-distances between all 47 samples for each of the 13 genes analyzed. Outlier values are depicted as points outside of the box.

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Link: <https://doi.org/asp.81.e90721.suppl4>

Supplementary material 5

Figure S3

Authors: Deng M, Zwick A, Chen Q, Liao CQ, Wang W, Wang X, Huang GH (2023)

Data type: .pdf

Explanation note: Boxplot showing the GC-ratios of all 47 samples for each of the 13 genes analyzed. Outlier values are depicted as points outside of the box.

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Link: <https://doi.org/asp.81.e90721.suppl5>

Supplementary material 6

Figure S4

Authors: Deng M, Zwick A, Chen Q, Liao CQ, Wang W, Wang X, Huang GH (2023)

Data type: .pdf

Explanation note: Bayesian inference phylogram constructed with the 13PCGs data set of Endromidae.

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Link: <https://doi.org/asp.81.e90721.suppl6>

Supplementary material 7

Figure S5

Authors: Deng M, Zwick A, Chen Q, Liao CQ, Wang W, Wang X, Huang GH (2023)

Data type: .pdf

Explanation note: Maximum likelihood phylogram constructed with the 13PCGs data set of Endromidae.

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Link: <https://doi.org/asp.81.e90721.suppl7>

Supplementary material 8

Figure S6

Authors: Deng M, Zwick A, Chen Q, Liao CQ, Wang W, Wang X, Huang GH (2023)

Data type: .pdf

Explanation note: Bayesian inference phylogram constructed with the 13PCGs-AA data set of Endromidae.

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Link: <https://doi.org/asp.81.e90721.suppl8>

Supplementary material 9

Figure S7

Authors: Deng M, Zwick A, Chen Q, Liao CQ, Wang W, Wang X, Huang GH (2023)

Data type: .pdf

Explanation note: Maximum likelihood phylogram constructed with the 13PCGs-AA data set of Endromidae.

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