Manuscript Title

A comprehensive molecular phylogeny of Geometridae (Lepidoptera) with a focus on enigmatic small subfamilies

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Abstract

Our study aims to investigate the relationships of the major lineages within the moth family Geometridae, with a focus on the poorly studied Oenochrominae-Desmobathrinae complex, and to translate some of the results into a coherent subfamily and tribal level classification for the family. We analyzed a molecular dataset of 1206 Geometridae terminal taxa from all biogeographical regions comprising up to 11 molecular markers that included one mitochondrial (COI) and 10 protein-coding nuclear gene regions (Wingless, ArgK, MDH, RpS5, GAPDH, IDH, Ca-ATPase, Nex9, EF-1alpha, CAD). The molecular data set was analyzed using maximum likelihood as implemented in IQ-TREE and RAxML. We found high support for the traditional subfamilies Larentiinae, Geometrinae and Ennominae in their traditional scopes. Sterrhinae is monophyletic only if *Ergavia*, *Ametris* and *Macrotes*, which are currently placed in Oenochrominae, are formally transferred to Sterrhinae. Desmobathrinae and Oenochrominae are found to be polyphyletic. The concepts of Oenochrominae and Desmobathrinae required major revision and, after appropriate rearrangements, these groups also form monophyletic subfamily-level entities. Oenochrominae *s.str.* as originally conceived by Guenée is phylogenetically distant from *Epidesmia*. The latter is hereby described as the subfamily Epidesmiinae Murillo-Ramos, Sihvonen & Brehm, **subfam. nov.** Epidesmiinae are a lineage of “slender bodied Oenochrominae” that include the genera *Ecphyas* Turner, *Systatica* Turner, *Adeixis* Warren, *Dichromodes* Guenée, *Phrixocomes* Turner, *Abraxaphantes* Warren**,** *Epidesmia* Duncan [& Westwood] and *Phrataria* Walker. Archiearinae are monophyletic ~~when~~if *Dirce* and *Acalyphes* are formally transferred to Ennominae. We also found that many tribes were para- or polyphyletic and therefore propose tens of taxonomic changes at the tribe and subfamily levels. Archaeobalbini Viidalepp (Geometrinae) is raised from synonymy of Pseudoterpnini Warren to ~~the tribe~~tribal rank. Chlorodontoperini Murillo-Ramos, Sihvonen & Brehm, **trib. nov.** and Drepanogynini Murillo-Ramos, Sihvonen & Brehm, **trib. nov.** are described as new tribes in Geometrinae and Ennominae, respectively.

Keywords: Phylogeny, new subfamily, moths, Epidesmiinae, taxonomy.

Introduction

Geometridae are the second most species-rich family of Lepidoptera, with approximately 24,000 described species (Nieukerken et al., 2011, updated), found in all regions except Antarctica. The monophyly of Geometridae is well supported based on distinctive morphological characters (Cook & Scoble, 1992; Scoble, 1992; Minet & Scoble, 1999). In particular, adult members of the family possess paired tympanal organs at the base of the abdomen, while in ~~the ~~larvae~~,~~ the ventral prolegs are reduced to two pairs in almost all species, which causes the larvae to move in a looping manner (Minet & Scoble, 1999).

The phylogenetic relationships of the major subdivisions of Geometridae have been studied based on molecular data, which have contributed to the understanding of the evolutionary relationships within the family (Abraham et al., 2001; Yamamoto & Sota, 2007; Sihvonen et al., 2011). At ~~the ~~present, eight subfamilies are recognized in Geometridae (Sihvonen et al., 2011). Several recent studies have attempted to confirm the monophyly or clarify the taxonomy of most of these groups, for instance: Sterrhinae (Holloway, 1997; Hausmann, 2004; Sihvonen & Kaila, 2004; Õunap et al., 2008), Larentiinae (Holloway, 1997; Mironov, 2003; Viidalepp, 2006, 2011; Hausmann & Viidalepp, 2012; Õunap et al., 2016), Desmobathrinae (Holloway, 1996; Hausmann, 2001), Archiearinae (Hausmann, 2001; Young, 2006), Oenochrominae (Holloway, 1996; Scoble & Edwards, 1990; Cook & Scoble, 1992; Hausmann, 2001; Young, 2006), Geometrinae (Cook, 1993; Pitkin, 1996; Hausmann, 2001; Ban et al., 2018), Orthostixinae (Holloway, 1997) and Ennominae (Holloway, 1994; Pitkin, 2002; Beljaev, 2006; Young, 2006; Wahlberg et al., 2010; Õunap et al., 2011; Skou & Sihvonen, 2015; Sihvonen et al., 2015). An important shortcoming is that our understanding of geometrid systematics is biased towards the long-studied European fauna, whereas the highest diversity of this family is in the tropics, which is still largely unexplored (Brehm et al., 2016). Many species remain undescribed and there are many uncertainties in tribe and genus level classifications.

One of the most ~~complete~~comprehensive phylogenetic studies on Geometridae to date was published by Sihvonen et al. (2011). They analyzed a data set of 164 taxa and eight genetic markers, and the most species-rich subfamilies were recovered as monophyletic. However, the systematic positions of Oenochrominae and Desmobathrinae remained uncertain due to low taxon sampling, and the groups were suggested to be polyphyletic. Moreover, many geometrid genera remained unassigned to tribe.

This study is the first in a series of papers, which investigate the phylogenetic relationships of Geometridae on the basis of a sample with global coverage. Our dataset comprises 1206 terminal taxa of Geometridae with samples from all major biomes, using up to 11 molecular markers. Our paper includes an overview of the relationships of the major lineages within the family, with **particular focus** on defining the limits and finding the phylogenetic affinities of the subfamilies, **with a focus** on Oenochrominae and Desmobathrinae. Further papers in the series will focus on particular subfamilies and regions, and they will propose further formal taxonomic changes beyond those suggested in the present article: tribe and genus level relationships in Sterrhinae (Sihvonen et al., in prep), New World taxa (Brehm et al., in prep), Larentiinae (Õunap et al., in prep) and the Ennominae tribe Boarmiini (Murillo-Ramos et al., in prep).

A close relationship of Oenochrominae and Desmobathrinae has been proposed both in morphological (Meyrick, 1889; Cook & Scoble, 1992; Holloway, 1996) and in molecular studies (Sihvonen et al., 2011; Ban et al., 2018). In ~~the first~~early classifications, species of Desmobathrinae and Oenochrominae were included in the former family Monoctenidae. Meyrick (1889) diagnosed them on the basis of the position of the Rs veins in the hindwing ~~veins~~ and vein Sc+R1 ~~o~~in the forewing, which approximate to the upper margin of the cell from near its base to its middle ~~cell~~ or beyond (Scoble & Edwards, 1990). However, the classification proposed by Meyrick was not fully supported by subsequent taxonomic work (Scoble & Edwards, 1990; Cook & Scoble, 1992; Holloway, 1996). Unfortunately, Oenochrominae became a “trash bin” for geometrids that could not be placed in other subfamilies, including even Hedylidae, a family of moth-like butterflies (Scoble, 1992). Unsurprisingly, many taxa traditionally classified in Oenochrominae have recently been shown to be misplaced (Holloway, 1997; Staude, 2001; Sihvonen & Staude, 2011; Staude & Sihvonen, 2014). In Scoble & Edwards (1990), the family concept of Oenochrominae was restricted to the robust-bodied Australian genera, with one representative from the Oriental region. These authors were not able to find synapomorphies to define Monoctenidae *sensu* Meyrick, and referred back to the original grouping proposed by Guenée (1858). Scoble & Edwards (1990) defined a narrower group for Oenochrominae based on ~~the~~ male genitalia: The sclerotisation of the diaphragm dorsal to the anellus fuses with the transtilla to form a rigid plate. Cook & Scoble (1992) suggested that the circular form of the lacinia and its orientation parallel to the tympanum was apomorphic for these robust-bodied Oenochrominae.

In an extensive morphological study, Holloway (1996) revived the subfamily Desmobathrinae to include species with appendages and slender bodies previously assigned to Oenochrominae. According to Holloway (1996), Desmobathrinae comprises two tribes: Eumeleini and Desmobathrini. However, no synapomorphies were found to link Eumeleini and Desmobathrini. Holloway (1996) highlighted that the modification of the tegumen of the male genitalia ~~is~~was variable in both groups but that the reduction of cremastral spines in the pupa from eight to four in *Ozola* Walker, 1861 and *Eumelea* Duncan [& Westwood], 1841 provided evidence of a closer relationship between Eumeleini and Desmobathrini. The proposed classification is included in the “World list of family group names in Geometridae” (Forum Herbulot, 2007). Currently, 328 species (76 genera) are included in Oenochrominae, and 248 species (19 genera) are assigned to Desmobathrinae (Beccaloni et al., 2003; Sihvonen et al., 2011, 2015).

Most recent molecular phylogenies have shown Oenochrominae and Desmobathrinae taxa to be intermingled (Sihvonen et al., 2011; Ban et al., 2018), but taxon sampling was limited to eight and four species, respectively. The poor taxon sampling and the obviously unresolved relationships around the ~~O~~oenochromin~~ae~~e and d~~D~~esmobathrin~~ae~~e complex called for a sound phylogenetic study that clarifies the relationships of these poorly known taxa within Geometridae. We hypothesize that both Oenochrominae and Desmobathrinae are para- or polyphyletic assemblages, and our paper aims to establish a new concept in which all subfamilies of the Geometridae represent monophyletic entities. Our new study comprises 29 terminal taxa of Oenochrominae and 11 representatives of Desmobathrinae. Most species are distributed in the Australian and Oriental Region, but some also occur in other parts of the world.

Materials & Methods

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The

ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: Epidesmiinae subfam.nov. LSIDurn:lsid:zoobank.org:act:34D1E8F7-99F1-4914-8E12-0110459C2040, Chlorodontoperini trib.nov.LSIDurn:lsid:zoobank.org:act:0833860E-A092-43D6-B2A1-FB57D9F7988D, and Drepanogynini trib.nov., LSIDurn:lsid:zoobank.org:act:AA384988-009F-4175-B98C-6209C8868B93. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

Material acquisition, taxon sampling and species identification

In addition to 461 terminal taxa with published sequences (see Supplemental data S1), we included sequences from 745 new terminal taxa in our study. They were gathered from several museum collections and collectors, including most of the authors (Supplemental data S1). Representative taxa of all subfamilies recognized in Geometridae were included, except for the small subfamily Orthostixinae for which most molecular markers could not ~~successfully~~ be amplified. A total of 93 tribes are represented in this study following recent phylogenetic hypotheses and classifications (Sihvonen et al., 2011; Wahlberg et al., 2010; Sihvonen et al., 2015; Õunap et al., 2016; Ban et al., 2018). In addition, 14 non-~~G~~geometrid~~ae~~ species belonging to other families of Geometroidea were included as outgroups based on the hypothesis proposed by Regier et al. (2009; 2013). Where possible, two or more samples were included per tribe and genus, especially for species-rich groups that are widely distributed and in cases where genera were suspected to be poly- or paraphyletic. We preferred type species or species phylogenetically close to type species in order to ease subsequent taxonomic work, to favor nomenclatorial stability and to establish the phylogenetic position of genera unassigned to tribes.

Sampled individuals were identified by the authors using their complementary expertise and appropriate literature, and by comparing type material from different collections and museums. Moreover, we compiled an illustrated catalogue of all Archiearinae, Desmobathrinae and Oenochrominae taxa included in this study, to display the external diversity and to ~~allow~~facilitate subsequent verification of our identifications. This catalogue contains images of all analysed specimens as well as photographs of the respective type material (Supplemental data S2). Many further specimens will be illustrated in other papers (Brehm et al. in prep., Sihvonen et al. in prep., Õunap et al. in prep.) Some of the studied ~~individuals~~specimens could not yet be assigned to species, and their identifications are preliminary because of a lack of modern identification tools, particularly for (potentially undescribed) tropical species. Taxonomic data, voucher ID, number of genes, current systematic placement, and references to relevant literature where the tribal association is used, are shown in Supplemental data S1.

Molecular techniques

DNA was extracted from 1–3 legs preserved either in ethanol or dry. In a few cases, other sources of tissue, such as parts of larvae, were used. The remaining parts of specimens were preserved as vouchers and will ~~be~~ eventually be deposited in public museum collections. Genomic DNA was extracted and purified using a NucleoSpin® Tissue Kit (MACHERY-NAGEL), ~~according~~following ~~to~~ the manufacturer's protocol. DNA amplification and sequencing were carried out following protocols proposed by Wahlberg & Wheat (2008) and Wahlberg et al. (2016). PCR products were visualized on agarose gels. PCR products were cleaned enzymatically and sent to Macrogen Europe (Amsterdam) for Sanger sequencing. One mitochondrial (COI) and 10 protein-coding nuclear gene regions (Wingless, ArgK, MDH, RpS5, GAPDH, IDH, Ca-ATPase, Nex9, EF-1alpha, CAD) were sequenced. The final dataset had a concatenated length of 7665 bp with gaps. To check for potential misidentifications, DNA barcode sequences were compared to those in BOLD (Barcode of Life Data Systems, (http://www.barcodinglife.org/views/login.php) where references of more than 21,000 geometrid species are available, some 10,000 of them being reliably identified to Linnean species names (Ratnasingham & Hebert, 2007). GenBank accession numbers for sequences used in this study are provided in Supplemental data S1.

Alignment and cleaning sequences

Multiple sequence alignments were ~~done~~carried out in MAFFT as implemented in Geneious v.11.0.2 (Biomatters, http://www.geneious.com/) for each gene based on a reference sequence of Geometridae downloaded from the database VoSeq (Peña & Malm, 2012). ~~We used MAFFT algorithm as implemented in Geneious v.11.0.2 (Biomatters, http://www.geneious.com/).~~ The alignment~~s~~ ~~per~~of each gene w~~ere~~as carefully checked by eye relative to the reference sequence, taking into ~~consideration relevant~~account the respective genetic codes and reading frames, ~~relative to the reference sequence~~. Heterozygous positions were coded with IUPAC codes. Sequences with bad quality and ambiguities were removed from the alignments. Finally, aligned sequences were uploaded to VoSeq (Peña & Malm, 2012) and then assembled in a dataset comprising 1206 taxa. To check for possible errors in alignments~~ and~~, potentially contaminated or identical sequences and misidentifications, we constructed maximum likelihood trees for each gene. ~~With these trials, we also looked for identical sequences or misidentifications.~~ These ~~trial~~preliminary analyses were conducted using RAxML-HPC2 V.8.2.10 (Stamatakis, 2014) on the web-server CIPRES Science Gateway (Miller et al., 2010). After cleaning, the final data set included at least three genes per taxon except for *Oenochroma vinaria* (Guenée, 1858), *Acalyphes philorites* Turner, 1925, *Dirce lunaris* (Meyrick, 1890), *D. aesiodora* Turner, 1922, *Furcatrox australis* (Rosenstock, 1885), *Chlorodontopera mandarinata* (Leech, 1889), *Chlorozancla falcatus* (Hampson, 1895), *Pamphlebia rubrolimbraria* (Guenée, 1858) and *Thetidia albocostaria* (Bremer, 1864). For these taxa, included in studies by Young (2006) and Ban et al. (2018), only two markers were available.

Tree search strategies and model selection

We ran maximum likelihood analyses with a data set partitioned by gene and codon position using IQ-TREE V1.6.6 (Nguyen et al., 2015) and data partitioned by codon in RAxML (Stamatakis et al 2014). IQ-TREE is a stochastic algorithm suitable for analyzing big datasets (Nguyen et al., 2015). ~~Different~~Best-fitting substitution models were ~~determined implementing~~selected by ModelFinder, which is a model-selection method that incorporates a model of ~~free~~flexible rate heterogeneity across sites (Kalyaanamoorthy et al., 2017). ModelFinder implements a greedy strategy as implemented in PartitionFinder that starts with the full partitioned model and consequentially merges two partitions (TESTNEWMERGE option) until the model fit does not increase (Lanfear et al., 2012). After the best model ~~is~~has been found, IQ-TREE starts the tree reconstruction under the best model scheme. The phylogenetic analyses were carried out with the -*spp* option that allowed each partition to have its own evolutionary rate. The RAxML analysis was ~~implemented~~carried out on CIPRES using the GTR+GAMMA option with a data set partitioned by gene and codon position.

Support for nodes ~~were~~was evaluated with 1000 ultrafast bootstrap (UFBoot2) approximations (Hoang et al., 2017) in IQ-TREE, and rapid bootstrap (RBS) in RAxML (Stamatakis, 2008). Additionally, we implemented SH-like approximate likelihood ratio test (Guindon et al., 2010), which is considered to be a useful complement to bootstrap analysis. To reduce the risk of overestimating branch supports with UFBoot2 test, we implemented -*bnni* option, which optimizes each bootstrap tree using a hill-climbing nearest neighbor interchange (NNI) search. Trees were visualized and edited in FigTree v1.4.3 software (Rambaut, 2012). The final trees were rooted with species of the families Sematuridae, Epicopeiidae, Pseudobistonidae and Uraniidae following previous hypotheses proposed in Regier et al. (2009; 2013), Rajaei et al. (2015) and Heikkilä et al. (2015).

Results

Searching strategies and model selection

The results from ModelFinder suggested that each gene and codon position kept their own evolutionary model, i.e. no partitions were combined. Similarly, Akaike information criterion (AIC) and Bayesian information criterion (BIC) values showed best partition schemes for the data partitioned by codon position, with 33 partitions in total (evolutionary models are listed in Supplemental data S3). Topologies recovered by IQ-TREE and RAxML analyses resulted in trees with nearly identical patterns of relationships. Also, node support methods tended to agree on the support of nodes with strong phylogenetic signal. However, in most of the cases UFBoot2 from IQ-TREE showed higher support values compared to RBS in RAxML (RAxML tree with support values is showed in Supplemental data S4). UFBoot2 and SH-like performed similarly, with UFBoot2 showing slightly higher values, and both tend to show high support for the same nodes (Fig. 1). As noted by the authors of IQ-TREE, values of UF >= 95 and SH >= 80 indicate well-supported clades (Trifinopoulos & Minh, 2018).

General patterns in the phylogeny of Geometridae

Analyses of the dataset of 1206 terminal taxa, comprising up to 11 markers and an alignment length of 7665 bp recovered topologies with many well supported clades. About 20 terminal taxa were recovered as very similar genetically and they are likely to represent closely related species, subspecies or specimens of a single species. The examination of their taxonomic status is not the focus of this study, so the number of unique species in the analysis is slightly less than 1200. Our findings confirm the monophyly of Geometridae (values of UFBoot2, SH-like = 100) (Fig. 1). The general patterns in our phylogenetic hypotheses suggest that Sterrhinae are the sister group to the rest of Geometridae. This subfamily is recovered as monophyletic when three genera traditionally included in Oenochrominae are considered as belonging to Sterrhinae. Tribes in Sterrhinae, such as Cosymbiini and Timandriini were not recovered as monophyletic (Fig- 2). A detailed analysis, including formal changes to the classification of Sterrhinae, will be provided by Sihvonen et al. (in prep).

The monophyly of Larentiinae was established in previous studies (Sihvonen et al., 2011; Õunap et al., 2016) and our results are in full agreement with their hypotheses. However, our results do not support the sister relationship between Sterrhinae and Larentiinae found in the previous studies. In concordance with recent findings (Sihvonen et al., 2011; Õunap et al. 2016; Strutzenberger et al., 2017), we recover Dyspteridini as the sister group to the remaining Larentiinae (Fig. 3). Phylogenetic relationships within Larentiinae were treated in detail by Õunap et al. (2016). Further details of the analyses and changes to the classification of Larentiinae will be discussed by Brehm et al. (in prep) and Õunap et al. (in prep).

Archiearinae are represented by more taxa than in a previous study (Sihvonen et al., 2011), and ~~it~~the subfamily is sister ~~of~~to Oenochrominae + Desmobathrinae complex + Geometrinae and Ennominae (Fig. 4). The monophyly of this subfamily is well supported (values of SH-like, UFBoot2 = 100). However, as in the previous study (Sihvonen et al. 2011), the Australian genera *Dirce* Prout, 1910 and *Acalyphes* Turner, 1926 are not part of Archiearinae but can clearly be assigned to Ennominae. Unlike previously assumed (e.g., McQuillan & Edwards 1994), the subfamily Archiearinae doesn’t occur in Australia, despite superficial similarities and the shared high-altitude distribution of *Dirce*, *Acalyphes* and Archiearinae.

Desmobathrinae were shown ~~as~~to be paraphyletic by Sihvonen et al. (2011). In our analysis, the monophyly of this subfamily is not recovered either, as we find three taxa traditionally placed in Oenochrominae~~,~~ (i.e. *Zanclopteryx* Herrich-Schäffer, [1855], *Nearcha*

Guest, 1887 and *Racasta* Walker, 1861) nested within Desmobathrinae (Fig. 4). We formally transfer these taxa to Desmobathrinae. In the revised sense, Desmobathrinae ~~are~~form a well-supported group with two main lineages. One of them comprises the genera *Ozola* Walker, 1861, *Derambila* Walker, [1863] and *Zanclopteryx*. This lineage is sister to a well-supported clade comprising *Conolophia* Warren, 1894, *Noreia* Walker, 1861, *Leptoctenopsis*, *Racasta*, *Ophiogramma* Hübner, [1831], *Pycnoneura* Warren, 1894 and *Dolichoneura* Warren, 1894. The genus *Eumelea* Duncan [& Westwood], 1841 has an unclear phylogenetic position in our analyses. The IQ-TREE result suggested this genus to be sister to the subfamily Geometrinae, whereas RAxML recovered *Eumelea* in Ennominae as the sister of *Plutodes* Guenée, [1858].

Oenochrominae in the broad sense are not a monophyletic group. However, Oenochrominae *sensu stricto* (Scoble & Edwards, 1990) form a well-supported lineage comprising two clades. One of them contains a polyphyletic *Oenochroma* with *O. infantilis* Prout, 1910 being sister to *Dinophalus* Prout, 1910, *Hypographa* Guenée, [1858], *Lissomma* Warren, 1905, *Sarcinodes* Guenée, [1858] and two further species of *Oenochroma*, including the type species *O. vinaria* Guenée, [1858]. The other clade comprises the genera *Monoctenia* Guenée, [1858], *Onycodes* Guenée, [1858], *Parepisparis* Bethune-Baker, 1906, *Antictenia* Prout, 1910, *Arthodia* Guenée, [1858], *Gastrophora* Guenée, [1858] and *Homospora* Turner, 1904 (Fig. 4). Most of the remaining genera traditionally placed in Oenochrominae, including e.g. *Epidesmia* Duncan [& Westwood], 1841, form a well-supported monophyletic clade that is sister to Oenochrominae *s. str*. + *Eumelea ludovicata* + Geometrinae + Ennominae assemblage. *Ergavia* Walker, 1866, *Ametris* Guenée, [1858] and *Macrotes* Westwood, 1841 form a monophyletic group within Sterrhinae (see also Sihvonen et al., 2011).

The monophyly of Geometrinae is well supported (Fig. 5) and it was recovered as the sister-taxon of *Eumelea*. The *Eumelea* + Geometrinae clade is sister to Oenochrominae *s. str*. Although a recent phylogenetic study proposed several taxonomic changes (Ban et al., 2018), the tribal composition in this subfamily is still problematic. Many tribes were recovered as paraphyletic, because their constituent genera were intermingled in the phylogenetic tree. Hemitheini *sensu* Ban et al. (2018) were recovered as a well-supported clade, which is sister to the rest of Geometrinae. In turn, the African genus *Lophostola* Prout, 1912 was resolved as sister to all other Hemitheini. The monophyly of Pseudoterpnini could not be recovered, instead this tribe splits up into three well-defined groups. *Crypsiphona ocultaria* Meyrick, 1888 is recovered as an isolated lineage, *Xenozancla* Warren, 1893 is sister to a clade comprising Dysphaniini and Pseudoterpnini *s.str.* In addition, several genera currently placed in Pseudoterpnini *s.l.* were recovered as an independent lineage clearly separate from Pseudoterpnini *s.str.* (SH-like = 86.3, UFBoot2 = 96). Ornithospilini and Agathiini clustered together but they were not sister to all Geometrinae as shown by Ban et al. (2018). Although there are no phylogenetic studies which investigate the relationship between *Ornithospila* Warren, 1894 and *Agathia* Guenée, [1858], our results suggested that these genera are sister clades. Aracimini, Neohipparchini, Timandromorphini, Geometrini and Comibaenini were recovered as monophyletic groups. Synchlorini were nested within Nemoriini in a well-supported clade (support branch SH-like = 99.8, UFBoot2 = 100, RBS = 93).

Ennominae are strongly supported as monophyletic in IQ-TREE analyses (UFBoot2, and SH-like = 100) whereas in RAxML the monophyly is weakly supported (RBS = 63). Detailed results concerning the classification, especially for the Neotropical taxa, will be presented by Brehm et al. (in prep.), but the main results are summarized here (Fig. 6). Very few tribes are monophyletic according to the results of the present study. One group of Neotropical taxa currently assigned to Gonodontini, Gnophini, Odontoperini~~,~~ and *Bryoptera* Guenée, [1858] + *Ectropis* Hübner, [1825], Nacophorini, and Ennomini (*sensu* Beljaev, 2008) grouped together in a large well-supported clade (SH-like = 96.6, UFBoot2 = 97). Ennomini were sister ~~of~~to th~~e~~ ~~whole~~is entire group. The New Zealand genus *Declana* Walker, 1858 appeared as an isolated lineage sister to Campaeini, which in turn is sister to Alsophilini + Wilemaniini + Colotoini. These groups are in turn the sister to *Grabiola* Taylor, 1904 +*Acalyphes* Turner, 1926 and a large complex including Lithinini, intermixed with some genera placed currently in Nacophorini and Diptychini. Theriini were recovered close to the genera *Erastria* Hübner, [1813] + *Metarranthis* Warren, 1894 and Palyadini + *Plutodes* Guenée, [1858]. The IQ-TREE analyses show Palyadini as a well-defined lineage, sister to *Plutodes*. However, in RAxML analyses *Eumelea* and *Plutodes* grouped together and Palyadini clustered with a group of Caberini species. The genera *Neobapta* Warren, 1904 and *Oenoptila* Warren, 1895 formed an independent lineage. Hypochrosini formed a lineage with Apeirini, Epionini, *Sericosema* Warren, 1895 and *Ithysia* Hübner, [1825]. This lineage is in turn the sister of the African *Drepanogynis* Guenée, [1858] which grouped together with the genera *Sphingomima* Warren, 1899, *Thenopa* Walker, 1855 and *Hebdomophruda* Warren, 1897. Caberini ~~came out~~was placed as the sister of an unnamed clade composed of *Trotogonia* Warren, 1905, *Acrotomodes* Warren, 1895, *Acrotomia* Herrich-Schäffer, [1855] and *Pyrinia* Hübner, 1818. Finally, our analyses recovered a very large well-supported clade comprising the tribes Macariini, Cassymini, Abraxini, Eutoeini and Boarmiini (SH-like and UFBoot2= 100). This large clade has previously been referred to informally as the “boarmiines” by Forbes (1948) and Wahlberg et al. (2010). The tribe Cassymini is clearly paraphyletic: genera such as *Cirrhosoma* Warren, 1905, *Berberodes* Guenée, 1858, *Hemiphricta* Warren, 1906 and *Ballantiophora* Butler, 1881 currently included in Cassymini, clustered in their own clade together with *Dorsifulcrum* Herbulot, 1979 and *Odontognophos* Wehrli, 1951, as sister to the Abraxini and Eutoeini complex. We were unable to include Orthostixinae in the analyses, so we could not clarify the taxonomic position of this subfamily with regard to the possible synonymy with Ennominae (Sihvonen et al., 2011).

Discussion

Optimal partitioning scheme and support values

The greedy algorithm implemented in ModelFinder to select the best-fitting partitioning scheme treated the partitions independently and failed to merge any data subsets. The results recovered highest values (AIC and BIC) for data partitioned by codon position. These results are not different from previous studies that tested the performance of different data partitioning schemes and found that in some cases partitioning by gene can result in suboptimal partitioning schemes and may limit the accuracy of phylogenetic analyses (Lanfear et al., 2012). However, we highlight that although the AIC and BIC values were lower in data partitioned by gene, the tree topology recovered was nevertheless almost the same as when data were partitioned by codon, suggesting that the phylogenetic signal in the data is robust to partitioning schemes. The analyses found some disagreements ~~in the methods implemented to evaluate~~between the different measures of node support. Ultrafast bootstrap gave the highest support values, followed by SH-like and finally standard bootstrap as implemented in RAxML gave the lowest. Although support indices obtained by these methods are not directly comparable, differences in node support of some clades can be attributed to the small number of markers, insufficient or saturated divergence levels (Guindon et al., 2010).

Current understanding of Geometridae phylogeny and taxonomic implications

Geometridae Leach, 1815

The phylogenetic hypothesis presented in this study is by far the most comprehensive to date in terms of the number of markers, sampled taxa, and geographical coverage. In total our sample includes 814 genera, thus representing 41% of the currently recognised Geometridae genera (Scoble & Hausmann, 2007). Previous phylogenetic hypotheses were based mainly on the European fauna and many clades were not unambiguously supported due to low taxon sampling. The general patterns of the phylogenetic relationships between the subfamilies recovered in this article largely agrees with previous hypotheses based on morphological characters and different sets of molecular markers (Holloway, 1997; Abraham, 2001; Yamamoto & Sota, 2007; Sihvonen et al., 2011). However, the results of our larger dataset differ in many details and shed~~s~~ light on the phylogenetic relationships of especially the poorly resolved small subfamilies.

Sterrhinae are recovered as the sister subfamily to the remaining Geometridae. This result is not in concordance with Sihvonen et al. (2011), Yamamoto & Sota (2007) and Regier et al. (2009), who found a sister group relationship between Sterrhinae and Larentiinae which in turn were sister to the rest of Geometridae. Sihvonen et al. (2011) showed these relationships with low support, while Yamamoto & Sota (2007) and Regier et al. (2009) included only a few samples in their analyses, which could have had an influence on the results. Our analyses include representatives from almost all known tribes currently included in Sterrhinae and Larentiinae. The higher number of markers, improved methods of analysis, the broader taxon sampling as well as the stability of our results suggests that Sterrhinae are indeed the sister group to the remaining Geometridae. Sterrhinae (after transfer of *Ergavia*, *Ametris* and *Macrotes*, see details below), Larentiinae, Archiearinae, Geometrinae and Ennominae were highly supported as monophyletic. Oenochrominae and Desmobathrinae formed polyphyletic and paraphyletic assemblages respectively. The monophylies of Oenochrominae and Desmobathrinae have always been questioned. Morphological studies addressing Oenochrominae or Desmobathrinae have been very limited and the majority of genera have never been examined in depth. In addition, it has been very difficult to establish the boundaries of these subfamilies only on the basis of morphological examination (Scoble & Edwards, 1990). Sihvonen et al. (2011) showed that neither Oenochrominae nor Desmobathrinae were monophyletic, but these results were considered preliminary due to the limited number of sampled taxa, and no formal transfers were proposed. To date, the phylogenetic positions of these subfamilies are not clear. The systematic status of Orthostixinae remains unclear because it was not included in our study. Sihvonen et al. (2011) included the genus *Naxa* Walker, 1856, formally placed in Orthostixinae, and found it to be nested within Ennominae. However, only three genes were successfully sequenced from this taxon, and its position in the phylogenetic tree turned out to be a highly unstable taxon in our analyses. It was thus excluded from our dataset. Without a doubt, *Orthostixis* Hübner, [1823], the type genus of the subfamily, needs to be included in future analyses.

Sterrhinae Meyrick, 1892

We included 74 Sterrhinae taxa in our analyses, with all tribes recognized in Forum Herbulot (2007) being represented. The recovered patterns generally agree with previous phylogenetic hypotheses of the subfamily (Sihvonen, 2004, Sihvonen et al., 2011). The genera *Ergavia*, *Ametris* and *Macrotes*, which currently are placed in Oenochrominae were found to form a well-defined lineage within Sterrhinae with strong support (SH-Like = 99 UFBoot2 = 100). These genera are distributed in the New World, whereas the range of true Oenochrominae is restricted to the Australian and Oriental region. Sihvonen et al. (2011) already found that *Ergavia* and *Afrophyla* Warren, 1895 belong to Sterrhinae and suggested more extensive analyses to clarify the position of these genera, which we did. *Afrophyla* was already transferred to Sterrhinae (Sihvonen & Staude, 2011) and *Ergavia*, *Ametris* and *Macrotes* (plus *Almodes* Guenée, [1858]) will be transferred by Sihvonen et al. (in prep.).

Cosymbiini, Timandrini, Rhodometrini and Lythriini are closely related as shown previously (Sihvonen & Kaila, 2004; Õunap et al., 2008; Sihvonen et al., 2011). Cosymbiini appear as sister to the Timandrini + Rhodometrini + Lythriini clade. Lythriini are closely related to Rhodometrini as shown by Õunap et al. (2008) with both molecular and morphological data. However, Timandrini was not the closest to Rhodometrini + Lythriini clade due to the phylogenetic position of *Traminda* Saalmüller, 1891 (Timandrini) and *Pseudosterrha* Warren, 1888 (Cosymbiini). These taxa grouped together forming a different lineage which is sister to Rhodometrini + Lythriini clade (Fig. 2).

Rhodostrophiini and Cyllopodini were recovered polyphyletic with species of Cyllopodini clustering within Rhodostrophiini. Similar results were recovered before (Sihvonen & Kaila, 2004; Sihvonen et al., 2011), suggesting that further work needs to be done to clarify the status and systematic position of these tribes. On the other hand, Sterrhini and Scopulini were recovered as sister taxa as proposed by Sihvonen & Kaila (2004); Hausmann (2004); Õunap et al. (2008) and Sihvonen et al. (2011). Our new phylogenetic hypothesis constitutes a large step towards understanding the evolutionary relationships of the major lineages of Sterrhinae. Further taxonomic changes and more detailed interpretation of the clades will be dealt with by Sihvonen et al. (in prep.).

Larentiinae Duponchel, 1845

Larentiinae are a monophyletic entity (Fig. 3). In concordance with the results of Sihvonen et al. (2011), Viidalepp (2011), Õunap et al. (2016) and Strutzenberger et al. (2017), Dyspteridini are placed as sister to all other larentiines. Such a systematic position is furthermore supported by the green coloration of the wings and the reduced size of the hindwings. Remarkably, *Brabirodes* Warren, 1904 forms an independent lineage. Chesiadini are monophyletic and sister to all larentiines except Dyspteridini, *Brabirodes* and Trichopterygini. These results do not support the suggestion by Viidalepp (2006) and Sihvonen et al. (2011) that Chesiadini are sister to Trichopterygini.

In our phylogenetic hypothesis, Asthenini are sister to the Perizomini + Melanthiini + Eupitheciini clade. These results do not fully agree with Õunap et al. (2016) who found Asthenini to be sister to all Larentiinae except Dyspteridini, Chesiadini, Trichopterygini and Eudulini. However, our results do support Melanthiini + Eupitheciini complex as a sister lineage ~~sister~~ to Perizomini. Sihvonen et al. (2011) recovered Phileremini and Rheumapterini as well-supported sister taxa. Our results suggest *Triphosa dubitata* Linnaeus 1758 as sister of Phileremini while Rheumapterini is the sister to this clade. Cidariini were recovered as polyphyletic, as the genera *Coenotephria* Prout, 1914 and *Lampropteryx* Stephens, 1831 cluster in a different clade apart from the lineage comprising the type genus of the tribe, *Cidaria* Treitschke, 1825. Also, *Ceratodalia* Packard, 1876, currently placed in Hydriomenini and *Trichodezia* Warren, 1895 were mixed in Cidariini. This result is not in concordance with Õunap et al. (2016), who found this tribe monophyletic. Scotopterygini were sister to a lineage comprising *Ptychorrhoe blosyrata* Guenée [1858], *Disclioprocta* sp, Euphyiini, an unnamed clade, Xanthorhoini and Cataclysmini. Euphyiini are monophyletic, but Xanthorhoini were recovered as mixed with

Cataclysmini. The same findings were shown by Õunap et al. (2016), but no taxonomic rearrangements were proposed. Larentiini are monophyletic and sister of Hererusiini, Hydriomenini, Erateinini, Stamnodini and some unnamed clades. Heterusiini are recovered as a polyphyletic group, while Erateinini are close to Stamnodini as proposed by Sihvonen et al. (2011). Although with some differences, our results support the major phylogenetic patterns of Õunap et al. (2016).

Despite substantial progress, the tribal classification and phylogenetic relationships of Larentiinae are far from being sufficiently resolved (Õunap et al. 2016). Forbes (1948) proposed eight tribes based on morphological information, Viidalepp (2011) raised the number to 23 and Õunap et al. (2016) recovered 25 tribes studying 58 genera. Our study includes 23 tribes and 125 genera (with a focus on Neotropical taxa). However, the phylogenetic position of many taxa remains unclear, and many tropical genera have not yet been formally assigned to any tribe. Formal descriptions of these groups will be treated in detail by Brehm et al. (in prep) and Õunap et al (in prep).

Archiearinae Fletcher, 1953

The hypothesis presented in this study recovered Archiearinae as a monophyletic entity if some taxonomic rearrangements are done. This subfamily was previously considered as sister to Geometrinae + Ennominae (Abraham et al., 2001), whereas Yamamoto & Sota (2007) proposed them as the sister-taxon to Orthostixinae + Desmobathrinae. Our findings agree with Sihvonen et al. (2011) who recovered Archiearinae as the sister-taxon to the rest of Geometridae excluding Sterrhinae and Larentiinae, although only one species was included in their study. *Archiearis* Hübner, [1823] is sister to *Boudinotiana* Esper, 1787 and these taxa in turn are sister to *Leucobrephos* Grote, 1874 (Fig. 4). The southern hemisphere Archiearinae require more attention. Young (2006) suggested that two Australian Archiearinae genera, *Dirce* and *Acalyphes*, actually belong to Ennominae. Our analyses clearly support this view and we therefore propose to formally transfer *Dirce* and *Acalyphes* to Ennominae (all formal taxonomic changes are provided in Table 1). Unfortunately, the South American Archiearinae genera *Archiearides* Fletcher, 1953 and *Lachnocephala* Fletcher, 1953, and Mexican *Caenosynteles* Dyar, 1912 (Pitkin & Jenkins 2004), could not be included in our analyses. The position in Archiearinae requires further study.

These presumably diurnal taxa may only be superficially similar to northern hemisphere Archiearinae as was the case with Australian *Dirce* and *Acalyphes*.

Desmobathrinae Meyrick, 1886

Taxa placed in Desmobathrinae were formerly recognized as Oenochrominae genera with slender appendages. Holloway (1996) revived this subfamily from synonymy with Oenochrominae and divided it into the tribes Eumeleini and Desmobathrini. Desmobathrinae species have a pantropical distribution and they apparently (still) lack recognized morphological apomorphies (Holloway, 1996). Our phylogenetic analysis has questioned the monophyly of Desmobathrinae *sensu* Holloway because some species currently placed in Oenochrominae were embedded within the group (see also Sihvonen et al., 2011), and also the phylogenetic position of the tribe Eumeleini is unstable (see below). Desmobathrinae can be regarded as a monophyletic group in our study, after the transfer of *Zanclopteryx, Nearcha* and *Racasta* from Oenochrominae to Desmobathrinae, and the removal of Eumeleini (Table 1). Desmobathrinae as circumscribed here are an independent lineage that is sister to all Geometridae except Sterrhinae, Larentiinae and Archiearinae.

The monobasic Eumeleini (comprising only the genus *Eumelea*) has had a dynamic taxonomic history: *Eumelea* was transferred from Oenochrominae *s.l.* to Desmobathrinae based on the pupal cremaster (Holloway, 1996), whereas Beljaev (2008) pointed out that *Eumelea* could be a member of Geometrinae based on the skeleto-muscular structure of the male genitalia. Molecular studies (Sihvonen et al., 2011, Ban et al., 2018) suggested that *Eumelea* was part of Oenochrominae *s.str.*, but these findings were not well-supported and no formal taxonomic changes were proposed. Our analyses with IQTREE and RAxML recovered Eumeleini in two very different positions, either as sister to Geometrinae (SH-like = 92, UFBoot2 = 98) rather than belonging to Desmobathrinae (figs 4, 5), or as sister of *Plutodes* in Ennominae (RBS = 60) (Supplemental data S4). The examination of morphological details suggests that the position as sister to Geometrinae is more plausible: hindwing vein M2 is present and tubular; anal margin of the hindwing is elongated; and large coremata originate from saccus (Holloway 1994, our observations). The morphology of *Eumelea* is partly unusual, and for that reason we illustrate selected structures (Supplemental data S5), which include for instance the following: antennae and legs of both sexes are very long; forewing vein Sc (homology unclear) reaches wing margin;

in male genitalia coremata are extremely large and branched; uncus is cross-shaped (cruciform); tegumen is narrow and it extends ventrally beyond the point of articulation with vinculum; saccus arms are extremely long, looped; and vesica is with lateral rows of cornuti. However, the green geoverdin pigment concentration of *Eumelea* is low in comparison to Geometrinae (Cook et al., 1994). We tentatively conclude that *Eumelea* is probably indeed associated with Geometrinae. However, since eleven genetic markers were not sufficient to clarify the phylogenetic affinities of *Eumelea*, we provisionally place the genus as *incertae sedis* (Table 1).

Oenochrominae Guenée, [1858]

Oenochrominae has obviously been the group comprising taxa that could not easily be assigned to other subfamilies. Out of the 76 genera currently assigned to Oenochrominae, our study includes 25 genera (28 species). Three of these genera will be formally transferred to Sterrhinae (Sihvonen et al. in prep.), two are here transferred to Desmobathrinae (see above, Table 1), and eight are transferred to Epidesmiinae (see below). In agreement with Sihvonen et al. (2011), Oenochrominae *s. str.* grouped together in a well-supported lineage. Genera of this clade can be characterized as having robust bodies, and their male genitalia have a well-developed uncus and gnathos, broad valvae and a well-developed anellus (Scoble & Edwards, 1990). Common host plants are members of Proteaceae and Myrtaceae (Holloway, 1996). Our results strongly suggest that the genus *Oenochroma* is polyphyletic: *O. infantilis* is sister to a clade including *Dinophalus*, *Hypographa*, *Lissomma*, *Sarcinodes* and (at least) two species of *Oenochroma*. To date, 20 species have been assigned to *Oenochroma* by Scoble (1999), and one additional species was described by Hausmann et al. (2009), who suggested that *O. vinaria* is a species complex. We agree with Hausmann et al. (2009), who pointed out the need of major revision and taxonomic definition of *Oenochroma*.

In our phylogenetic hypothesis, *Sarcinodes* is sister to *O. orthodesma* and *O. vinaria*, the type species of *Oenochroma*. Although *Sarcinodes* and *Oenochroma* resemble each other in external morphology, a sister-group relationship between these genera has not been hypothesized before. The inclusion of *Sarcinodes* in Oenochrominae is mainly based on shared tympanal characters (Scoble & Edwards, 1990). However, the circular form of the lacinia, which is an apomorphy of Oenochrominae *s.str.* is missing or not apparent in *Sarcinodes* (Holloway, 1996). In addition, *Sarcinodes* is found in the Oriental rather than in the Australian region, where all

Oenochroma species are distributed. A second clade of Oenochrominae *s.str*. comprises ~~of~~ the genera *Monoctenia*, *Onycodes*, *Parepisparis*, *Antictenia*, *Arhodia*, *Gastrophora* and *Homospora*, which clustered together as the sister~~s~~ of *Oenochroma* and its relatives. These genera are widely recognized in sharing similar structure of male genitalia (Scoble & Edwards, 1990), yet their phylogenetic relationships have never been tested. Young (2006) suggested the monophyly of Oenochrominae *s.str*., however, with a poorly resolved topology and low branch support. In her study, *Parepisparis*, *Phallaria* and *Monoctenia* shared a bifid head, while in *Parepisparis* and *Onychodes*, the aedeagus was lacking caecum and cornuti. Our analysis supports these morphological similarities. ***Monoctenia, Onycodes* and *Parepisparis* clustered together** However, a close relationship of the genera *Antictenia*, *Arhodia*, *Gastrophora* and *Homospora* has not been suggested before. Our analysis thus strongly supports the earliest definition of Oenochrominae proposed by Guenée (1858), and reinforced by Cook & Scoble (1992). Oenochrominae should be restricted to *Oenochroma* and related genera such as *Dinophalus*, *Hypographa*, *Lissomma*, *Sarcinodes*, *Monoctenia*, *Onycodes*, *Parepisparis*, *Antictenia*, *Arhodia*, *Gastrophora*, *Homospora*, *Phallaria* and *Palaeodoxa*. We consider that genera included ~~to~~in Oenochrominae by ~~(~~Scoble & Edwards~~,~~ (1990), but recovered in a ~~separate~~ lineage ~~apart~~separate from *Oenochroma* and its close relatives in our study, belong to a hitherto unknown subfamily, which is described below.

Epidesmiinae Murillo-Ramos, Brehm & Sihvonen **new subfamily**

Type genus: *Epidesmia* Duncan [&Westwood], 1841.

Material examined: Taxa included in the molecular phylogeny: *Ecphyas* Turner, 1929, *Systatica* Turner, 1904, *Adeixis* Warren, 1987, *Dichromodes* Guenée, 1858, *Phrixocomes* Turner, 1930, *Abraxaphantes* Warren, 1894, *Epidesmia* Duncan [& Westwood], 1841, and *Phrataria* Walker, [1863].

Most of the slender-bodied Oenochrominae, excluded from Oenochrominae *s. str*. by Holloway (1996), were recovered as an independent lineage (Fig. 4) that consists of two clades: *Ecphyas* + *Systatica* and *Epidesmia* + five other genera. Branch support values ~~in the~~from IQ-TREE strongly support the monophyly of this clade (UFBoot2~~,~~ and SH-like = 100), while in RAxML ~~it~~the clade is moderately supported (RBS = 89). These genera have earlier been assigned to Oenochrominae *s.l.* (Scoble & Edwards, 1990). However, we recovered the group as a well-supported lineage independent from Oenochrominae *s. str.* and transfer them to Epidesmiinae, subfam. n. (Table 1). Phylogenetic position: Epidesmiinae is sister to Oenochrominae *s. str.* + *Eumelea* + Geometrinae + Ennominae.

Short description of Epidesmiinae: Antennae in males unipectinate (exception: *Adeixis*), towards apex shorter towards the apex. Pectination moderate or long. Thorax and abdomen slender (unlike in Oenochrominae). Forewings with sinuous postmedial line and areole present. Forewings planiform (with wings lying flat on the substrate) in resting position, held like a triangle, and cover the hindwings.

Diagnosis of Epidesmiinae: The genera included in this subfamily form a strongly supported clade with DNA sequence data from the following gene regions (exemplar *Epidesmia chilonaria* Herrich-Schäffer, [1855]) ArgK (GB Accession number), Ca-ATPase (GB Accession number), CAD (GB Accession number), COI (GB Accession number), EF1a (GB Accession number), GAPDH (GB Accession number), MDH (GB Accession number) and Nex9 (GB Accession number). **(note to the editor: GB accession numbers will be provided on acceptance)**. A thorough morphological diagnosis requires further research.

Distribution: Most genera are distributed in the Australian region, with range of some extending to the Orient as well, and *Apraxaphantes* is the only genus that occurs exclusively in the Oriental region

Geometrinae Stephens, 1829

The monophyly of Geometrinae is strongly supported, but the number of tribes included in this subfamily is still unclear. Sihvonen et al. (2011) analyzed 27 species assigned to 11 tribes, followed by Ban et al. (2018) with 116 species in 12 tribes. Ban et al. (2018) synonymized nine tribes, and validated the monophyly of 12 tribes, with two new tribes Ornithospilini and Agathiini being the first two clades branching off the main lineage of Geometrinae. Our study (168 species) validates the monophyly of 13 tribes, eleven of which were defined in previous studies: Hemitheini, Dysphaniini, Pseudoterpnini *s.str.*, Ornithospilini, Agathiini, Aracimini, Neohipparchini, Timandromorphini, Geometrini, Comibaeini, Nemoriini. One synonymization is proposed: Synchlorini Ferguson, 1969 **syn. nov.** is synonymized with Nemoriini. One further tribe is proposed as new: Chlorodontoperini **trib. nov.**, and one tribe (Archaeobalbini Viidalepp, 1981, **stat. rev.**) is raised from synonymy of Pseudoterpnini to tribe status.

In our phylogenetic hypothesis, a large clade including the former tribes Lophochoristini, Heliotheini, Microloxiini, Thalerini, Rhomboristini, Hemistolini, Comostolini, Jodini and Thalassodini is recovered as sister to the rest of Geometrinae. These results are in full agreement with Ban et al. (2018), who synonymized all of these tribes with Hemitheini. Although the monophyly of Hemitheini is strongly supported, our findings recovered only a few monophyletic subtribes. For example, genera placed in Hemitheina were intermixed with those belonging to Microloxiina, Thalassodina and Jodina. Moreover, many genera which were unassigned to tribe, were recovered as belonging to Hemitheini. Our findings recovered *Lophostola* Prout, 1912 as sister to all Hemitheini. These results are quite different from those found by Ban et al. (2018) who suggested Rhomboristina as being sister to the rest of Hemitheini. In contrast, our results recovered Rhomboristina mingled with Hemistolina. These different results are probably influenced by the presence of African and Madagascan *Lophostola* in our analysis. We feel that the concept of subtribe is not practical at this point in time and thus do not advocate its use in ~~G~~geometrid~~ae~~ classification.

The Australian genus *Crypsiphona* Meyrick, 1888 is sister to all tribes included in Geometrinae except Hemitheini. *Crypsiphona* has been assigned to Pseudoterpnini (e. g. Pitkin et al. 2007, Õunap & Viidalepp 2009), but is recovered as a separate lineage in our tree. Given the isolated position of *Crypsiphona*, the designation of a new tribe could be considered, but due to low support of branches in our analyses, further information (including morphology) is needed to confirm the phylogenetic position of this genus. *Xenozancla* Warren, 1893 is placed as sister to the clade comprising Dysphaniini and Pseudoterpnini *s. str.*. Sihvonen et al. (2011) did not include *Xenozancla* in their analyses and suggested the sister relationships of Dysphaniini and Pseudoterpnini but with low support. According to Ban et al. (2018), *Xenozancla* is more closely related to Pseudoterpnini *s.str*. rather than to Dysphaniini. However, due to low support of clades, Ban et al. (2018) did not propose a taxonomic assignment to *Xenozancla*, which is currently not assigned to a tribe. Although our IQ-TREE results show that *Xenozancla* is sister of clade comprising Dysphaniini and Pseudoterpnini *s. str.*, the RAxML analysis did not recover the same phylogenetic relationships. Instead, Dysphaniini + Pseudoterpnini *s.str*. are found to be sister to each other, but *Xenozancla* is placed close to *Rhomborista monosticta* (Wehrli, 1924). As in Ban et al. (2018), due to low support of nodes, we cannot reach ~~to~~ any conclusion about the phylogenetic affinities of these tribes based on our results due to low support of nodes.

The monophyly of Pseudoterpnini *sensu* Pitkin et al. (2007) could not be recovered. Same results were shown by Ban et al. (2018) who recovered Pseudoterpnini *s.l.* including all the genera previously studied by Pitkin et al. (2007)~~ and~~, forming a separate clade from *Pseudoterpna* Hübner, [1823]+ *Pingasa* Moore, 1887. Our results showed the African *Mictoschema* Prout, 1922 falling within Pseudoterpnini *s.str.*, and it is sister to *Pseudoterpna* and *Pingasa*. A second group of Pseudoterpnini *s.l.* was recovered as an independent lineage clearly separate from Pseudoterpnini *s.str.* (SH-like = 86.3, UFBoot2 = 96). Ban et al. (2018) did not introduce a new tribe due to the morphological similarities and difficulty in finding apomorphies of Pseudoterpnini *s.str*. In addition, their results were weakly supported. Considering that two independent studies have demonstrated the paraphyly of Pseudoterpnini *sensu* Pitkin et al (2007), we see no reason for retaining the wide concept of this tribe. Instead we propose the revival of the tribe status of Archaeobalbini and the description of a new tribe Chlorodontoperini, which removes paraphyly from the clades in question.

Archaeobalbini Viidalepp, 1981, **status revised**

(original spelling: Archeobalbini, justified emendation in Hausmann (1996))

Type genus: *Archaeobalbis* Prout, 1912 (synonymized with *Herochroma* Swinhoe, 1893 in Holloway (1996))

Material examined: *Herochroma curvata* Han & Xue, 2003, *H. baba* Swinhoe 1893, *Metallolophia inanularia* Han & Xue, 2004, *M. cuneataria* Han & Xue, 2004, *Actenochroma muscicoloraria* (Walker, 1862), *Absala dorcada* Swinhoe, 1893, *Metaterpna batangensis* Hang & Stüning, 2016, *M. thyatiraria* (Oberthür, 1913), *Limbatochlamys rosthorni* Rothschild, 1894, *Pachyodes pictaria* Moore, 1888, *Dindica para* Swinhoe, 1893, *Dindicodes crocina* (Butler, 1880), *Lophophelma erionoma* (Swinhoe, 1893), *L. varicoloraria* (Moore, 1868), *L. iterans* (Prout, 1926) and *Pachyodes amplificata* (Walker, 1862).

This lineage splits into four groups: *Herochroma* Swinhoe, 1893 + *Absala* Swinhoe, 1893 + *Actenochroma* Warren, 1893 is the sister lineage of the rest of Archaeobalbini that were recovered as a polytomic bunch of three clades ~~conforming~~comprising the genera

Limbatochlamys Rothschild, 1894, *Psilotagma* Warren, 1894, *Metallolophia* Warren, 1895, *Metaterpna* Yazaki, 1992, *Dindica* Warren, 1893, *Dindicodes* Prout, 1912, *Lophophelma* Prout, 1912 and *Pachyodes* Guenée, 1858. This tribe can be diagnosed by the combination of DNA data from six genetic markers, see for instance *Pachyodes amplificata* (CAD, COI, EF1a, GAPDH, MDH RpS5) shown in supplementary material. Branch support values in IQ-TREE strongly confirm the monophyly of this clade (SH-like = 86.3, UFBoot2 = 96). GenBank accession numbers are shown in supplementary material. A morphological diagnosis requires further research.

Chlorodontoperini Murillo-Ramos, Sihvonen & Brehm, **new tribe**

Type genus: *Chlorodontopera* Warren, 1893

Material examined: Taxa in the molecular phylogeny: *C. discospilata* (Moore, 1867) and *C. mandarinata* (Leech, 1889).

Some studies (Inoue, 1961; Holloway, 1996) suggested the morphological similarities of *Chlorodontopera* Warren, 1893 with members of Aracimini. Moreover Holloway (1996) considered this genus as part of Aracimini. Our results suggest a sister relationship of *Chlorodontopera* with Aracimini rather than the inclusion in the tribe as well as the sister relationship with a large lineage comprising the rest of Geometrinae. Considering that our analysis strongly supports *Chlorodontopera* as an independent lineage (branch support SH-like = 99 UFBoot2 = 100, RBS = 99), we introduce the monobasic tribe Chlorodontoperini. This tribe can be diagnosed by the combination of DNA data from six genetic markers (exemplar *Chlorodontopera discospilata*) CAD (MG015448), COI (MG014735), EF1a (MG015329), GAPDH (MG014862), MDH (MG014980) and RpS5 (MG015562). Ban et al. (2018) did not introduce a new tribe because the relationship between *Chlorodontopera* and *Euxena* Warren, 1896 was not clear in their study. This relationship was also been proposed by Holloway (1996) based on similar wing patterns. Further analyses are needed to clarify the affinities between *Chlorodontopera* and *Euxena*.

The tribe Chlorodontoperini is diagnosed by distinct discal spots with pale margins on the wings, which are larger on the hindwing; a dull reddish-brown patch is present between the discal spot and the costa on the hindwing, and veins M3 and CuA1 are not stalked on the hindwing

(Ban et al., 2018). In the male genitalia, the socii are stout and setose and the lateral arms of the gnathos are developed, not joined. Sternite 3 of the male has setal patches. Formal taxonomic changes are listed in Table 1.

Aracimini, Neohipparchini, Timandromorphini, Geometrini and Comibaenini were recovered as monophyletic groups. These results are in full agreement with Ban et al. (2018). However, the phylogenetic position of *Eucyclodes* Warren, 1894 is ~~not clear~~uncertain. This genus is placed as sister of Comibaenini (support branch SH-like = 32.4, UFBoot2 = 100, RBS = 67). The monophyly of Nemoriini and Synchlorini is not supported. Instead, Synchlorini are nested within Nemoriini (support branch SH-like = 99.8, UFBoot2 = 100, RBS = 93). Our findings are in concordance with Sihvonen et al. (2011) and Ban et al. (2018), but our analyses included a larger number of markers and a much higher number of taxa. Thus, we formally synonymize Synchlorini **syn. nov.** with Nemoriini (Table 1).

Ennominae Duponchel, 1845

Ennominae are the most species-rich subfamily of geometrids. The loss of vein M2 on the hindwing is probably the best apomorphy (Holloway, 1993), although this character does not occur in a few ennomine taxa (Staude, 2001; Skou & Sihvonen, 2015). Ennominae are a morphologically highly diverse subfamily, and attempts to find further synapomorphies shared by all major tribal groups have failed.

The number of tribes as well as phylogenetic relationships among tribes are still debatable (see Skou & Sihvonen, 2015 for an overview). Moreover, the taxonomic knowledge of this subfamily in tropical regions is still poor. Holloway (1993) recognized 21 tribes, Beljaev (2006) 24 tribes, and Forum Herbulot (2007) 27 tribes. To date, five molecular studies have corroborated the monophyly of Ennominae (Young, 2006; Yamamoto & Sota, 2007; Wahlberg et al., 2010; Õunap et al., 2011, Sihvonen et al. 2011) with no conflicting evidence ever presented, with Young (2006) being the only exception who found a paraphyletic Ennominae. Moreover, three large-scale taxonomic revisions (without a phylogenetic hypothesis) were published by Pitkin (2002) for the Neotropical region, Skou & Sihvonen (2015) for the Western Palaearctic region, and Holloway (1994) for Borneo. More detailed descriptions of taxonomic changes in Ennominae will be given by Brehm et al. (in prep) and Murillo-Ramos et al. (in prep), here we discuss general patterns and give details for taxonomic acts not covered in the other two papers.

Our findings recover Ennominae as a monophyletic entity, but results were not highly supported in RAxML (RBS = 67) results compared to IQ-TREE (UFBoot2 and SH-Like = 100). The lineage comprising Geometrinae and Oenochrominae is recovered as the sister clade of Ennominae. In previous studies, Wahlberg et al. (2010) sampled 49 species of Ennominae, Õunap et al. (2011) sampled 33 species, and Sihvonen et al. (2011) 70 species including up to eight markers per species. All these studies supported the division of Ennominae into "boarmiine" and "ennomine" moths (Holloway, 1994). This grouping was proposed by Forbes (1948) and Holloway (1994), who suggested close relationships between the tribes Boarmiini, Macariini, Cassymini and Eutoeini based on the bifid pupal cremaster and the possession of a fovea in the male forewing. The remaining tribes were defined as "ennomines" based on the loss of a setal comb on male sternum A3 and the presence of a strong furca in male genitalia. Both Wahlberg et al. (2010) and Sihvonen et al. (2011) found these two informal groupings to be reciprocally monophyletic.

In our analyses, 653 species with up to 11 markers were sampled, with an emphasis on Neotropical taxa which so far had been poorly represented in the molecular phylogenetic analyses. Our results recovered the division into two major subclades, a core set of ennomines in a well-supported clade, and a poorly supported larger clade that includes the "boarmiines" among four other lineages usually thought of as "ennomines". The traditional "ennomines" are thus not found to be monophyletic in our analyses, questioning the utility of such an informal name. Our phylogenetic hypothesis supports the validation of numerous tribes earlier proposed, in addition to several unnamed clades. We validate 23 tribes (Forum Herbulot, 2007; Skou & Sihvonen, 2015): Gonodontini, Gnophini, Odontoperini, Nacophorini, Ennomini, Campaeini, Alsophilini, Wilemaniini, Prosopolophini, Diptychini, Theriini, Plutodini, Palyadini, Hypochrosini, Apeirini, Epionini, Caberini, Macariini, Cassymini, Abraxini, Eutoeini and Boarmiini. We hereby propose one new tribe: Drepanogynini **trib. nov.** (Table 1). Except for the new tribe, most of the groups recovered in this study are in concordance with previous morphological classifications (Holloway, 1993; Beljaev, 2006, 2016; Forum Herbulot, 2007; Skou & Sihvonen, 2015).

Five known tribes and two further unnamed lineages form the core Ennominae: Gonodontini, Gnophini, Odontoperini, Nacophorini and Ennomini. Several Neotropical clades that conflict with the current tribal classification of Ennominae will be described as new tribes by Brehm et al (in prep). Gonodontini and Gnophini are recovered as sister taxa. Gonodontini was defined by Forbes (1948) and studied by Holloway (1994), who showed synapomorphies shared by *Gonodontis* Hübner, [1823], *Xylinophylla* Warren, 1898 and *Xenimpia* Warren, 1895. Our results recovered the genus *Xylinophylla* as sister of *Xenimpia* and *Psilocladia* Warren, 1898. *Psilocladia* is an African genus currently unassigned to tribe (see Sihvonen et al., 2015 for details). Considering the strong support and that the facies and morphology are somewhat similar to other analysed taxa in Gonodontini, we formally include *Psilocladia* in Gonodontini (Table 1). Gnophini are a well-defined assemblage and we formally transfer the African genera *Oedicentra* Warren, 1902 and *Hypotephrina* Janse, 1932, from unassigned to Gnophini (Table 1). The total number of species, and number of included genera in Gnophini are still uncertain (Skou & Sihvonen, 2015). Based on morphological examination, Beljaev (2007, 2016) treated Angeronini as a synonym of Gnophini. The costal projection on male valva bearing a spine or group of spines was considered as a synapomorphy of the group. Using molecular data, Yamamoto & Sota (2007) showed ~~the~~a close phylogenetic relationship between *Angerona* Duponchel, 1829 (Angeronini) and *Chariaspilates* Wehrli, 1953 (Gnophini). Similar results were shown by Sihvonen et al. (2011) who recovered *Angerona* and *Charissa* Curtis, 1826 as sister taxa, and our results also strongly support treating Angeronini as synonym of Gnophini.

Holloway (1993) suggested close affinities among Nacophorini, Azelinini and Odontoperini on the basis of larval characters. In a morphology-based phylogenetic study, Skou & Sihvonen (2015) suggested multiple setae on the proleg on A6 of the larvae as a synapomorphy of the group. Our results also supported a close relationship of Nacophorini, Azelinini and Odontoperini. These clades will be treated in more detail by Brehm et al. (in prep.).

Following the ideas of Pitkin (2002), Beljaev (2008) synonymized the tribes Ourapterygini and Nephodiini with Ennomini. He considered the divided vinculum in male genitalia and the attachment of muscles *m*3 as apomorphies of the Ennomini, but did not provide a phylogenetic analysis. Sihvonen et al. (2011) supported Beljaev's assumptions and recovered *Ennomos* Treitschke, 1825 (Ennomini), *Ourapteryx* Leach, 1814 (Ourapterygini) and *Nephodia* Hübner, [1823] (Nephodiini) as belonging to the same clade. Our comprehensive analysis confirms those previous findings and we agree with Ennomini as valid tribal name for this large clade.

The genus *Declana* Walker, 1858 is recovered as an isolated clade sister to a complex lineage comprising Campaeini, Alsophilini, Wilemaniini and Prosopolophini. This genus is endemic to New Zealand, but to date has not been assigned to any tribe. According to our results, *Declana* could well be defined as its own tribe. However, the delimitation of this tribe is beyond the scope of our paper and more genera from Australia and New Zealand should first be examined.

Campaeini, Alsophilini, Wilemaniini and Prosopolophini grouped together in a well-supported clade (SH-like and UFBoot2 = 100). Previous molecular analyses have shown an association of Colotoini [= Prosopolophini] and Wilemaniini (Yamamoto & Sota, 2007; Sihvonen et al., 2011), although no synapomorphies are known to support synonymization (Skou & Sihvonen, 2015). The Palaearctic genera *Compsoptera* Blanchard, 1845, *Apochima* Agassiz, 1847, *Dasycorsa* Prout, 1915, *Chondrosoma* Anker, 1854 and *Dorsispina* Nupponen & Sihvonen, 2013, are potentially part of the same complex (Skou & Sihvonen, 2015, Sihvonen pers. obs.), but they were not included in the current study. Campaeini is a small group including four genera with Oriental, Palaearctic and Nearctic distribution, apparently closely related to Alsophilini and Prosopolophini, but currently accepted as a tribe (Forum Herbulot, 2007; Sihvonen & Skou, 2015). Our results support the close phylogenetic affinities among these tribes, but due to the limited number of sampled taxa, we do not propose any formal changes.

A close relationship between Nacophorini and Lithinini was suggested by Pitkin (2002), based on the similar pair of processes of the anellus in the male genitalia. Pitkin also noted a morphological similarity in the male genitalia (processes of the juxta) shared by Nacophorini and Diptychini. In a study of the Australasian fauna, Young (2008) suggested the synonymization of Nacophorini and Lithinini. This was further corroborated by Sihvonen et al. (2015) who found that Diptychini were nested within some Nacophorini and Lithinini. However, none of the studies proposed formal taxonomic changes because of limited taxon sampling. In contrast, samples in our analyses cover all biogeographic regions and the results suggest that the true Nacophorini is a clade which comprises almost exclusively New World species. This clade is clearly separate from

Old World “nacophorines” (cf. Young, 2003) that are intermixed with Lithinini and Diptychini. We here formally transfer Old World nacophorines to Diptychini and synonymize Lithinini **syn. nov.** with Diptychini (Table 1). Further formal taxonomic changes in the Nacophorini complex are provided by Brehm et al. (in prep.).

Theria Hübner, [1825], the only representative of Theriini in this study, clustered together with *Lomographa* Hübner, [1825] (Baptini in Skou & Sihvonen, 2015), in a well-supported clade, agreeing with the molecular results of Sihvonen et al. (2011). The placement of *Lomographa* in Caberini (Rindge, 1979; Pitkin, 2002) is not supported by our study nor by that of ~~by~~ Sihvonen et al. (2011). The monophyly of *Lomographa* has not been tested before, but we show that the Neotropical and Palaearctic *Lomographa* species indeed group together. Our results show that Caberini are not closely related to the Theriini + Baptini clade, unlike in the earlier morphology-based hypotheses (Rindge, 1979; Pitkin 2002). Morphologically, Theriini and Baptini are dissimilar, therefore we recognize them as valid tribes (see description and illustrations in Skou & Sihvonen, 2015).

According to our results, 11 molecular markers were not enough to infer phylogenetic affinities of Plutodini (represented by one species of *Plutodes*). Similar results were found by Sihvonen et al. (2011), who in some analyses recovered *Plutodes* as sister of *Eumelea*. Our analyses are ~~in concordance~~congruent with those findings, IQ-TREE results suggested that *Plutodes* i~~a~~s sister to Palyadini, but RAxML analyses recovered *Eumelea* as the most probable sister of *Plutodes*. Given that our analyses were not in agreement about the sister-group affinities of *Plutodes*, we do not make any assumptions ~~to~~about its ~~the~~ phylogenetic position. Instead we emphasize that further work~~s~~ needs to be done to clarify the phylogenetic positions of *Plutodes* and related groups.

Hypochrosini is only recovered in a well-defined lineage ~~only~~ if the genera *Apeira* Gistl, 1848 (Apeirini), *Epione* Duponchel, 1829 (Epionini), *Sericosema* (Caberini), *Ithysia* (Theriini), *Capasa* Walker, 1866 (unassigned) and~~,~~ *Omizodes* Warren, 1894 (unassigned) would be transferred to Hypochrosini. Skou & Sihvonen (2015) already suggested a close association of Epionini, Apeirini and Hypochrosini. We think that ~~the~~ synonymi~~zation~~sing ~~of~~ these tribes is desirable. However, due to the limited number of sampled taxa we do not propose any formal changes until more data will become available. We do suggest, however, formal taxonomic changes of the genera *Capasa* and *Omizodes* from unassigned to Hypochrosini (Table 1).

The southern African genus *Drepanogynis* is paraphyletic and has earlier been classified as belonging in Ennomini, and later in Nacophorini (Krüger 2002). In our phylogeny, it is intermixed with the genera *Sphingomima* Warren, 1899, and *Thenopa* Walker, 1855. *Hebdomophruda errans* Prout, 1917 also clustered together with these taxa ~~also~~, apart from other *Hebdomophruda* Warren, 1897 species, which suggests that this genus is polyphyletic. These genera form a clade sister to the lineage that comprises several Hypochrosini species. Considering that our analysis strongly supports this clade, we place *Thenopa*, *Sphingomina* and *Drepanogynis* in a tribe of their own.

Drepanogynini Murillo-Ramos, Sihvonen & Brehm **new tribe**

Type genus: *Drepanogynis* Guenée, [1858]

The African genera *Thenopa*, *Sphingomima* and *Drepanogynis* appeared as a strongly supported lineage (RBS, SH-like and UFBoot2 = 100). Krüger (1997, p. 259) proposed "Boarmiini and related tribes as the most likely sister group" for *Drepanogynis*, whereas more recently *Drepanogynis* was classified in the putative southern hemisphere Nacophorini (Krüger, 2014; Sihvonen et al., 2015). In the current phylogeny, *Drepanogynis* is isolated from Nacophorini *sensu stricto* and from other southern African genera that have earlier been considered to be closely related to it (Krüger 2014 and references therein). The other southern African genera appeared as belonging to Diptychini in our study. The systematic position of *Drepanogynis tripartita* (Warren, 1898) has earlier been analysed in a molecular study (Sihvonen et al., 2015). The taxon grouped together with the Palearctic species of the tribes Apeirini, Theriini, Epionini and putative Hypochrosini. Sihvonen et al. (2015) noted that *Argyrophora trofonia* (Cramer, [1779]) (representing *Drepanogynis* group III *sensu* Krüger, 1999) and *Drepanogynis tripartita* (representing *Drepanogynis* group IV *sensu* Krüger, 2002) did not group together, but no formal changes were proposed. Considering that the current analysis strongly supports the placement of *Drepanogynis* and related genera in an independent lineage, and the aforementioned taxa in the sister lineage (Apeirini, Theriini, Epionini and putative Hypochrosini) have been validated at tribe-level, we place *Drepanogynis* and related genera in a tribe of their own.

Material examined and taxa included: *Drepanogynis mixtaria* Guenée, [1858], *D. tripartita*, *D. determinata* (Walker, 1860), *D. arcuifera* Prout, 1934, *D. arcuatilinea* Krüger, 2002, *D. cnephaeogramma* (Prout, 1938), *D. villaria* (Felder & Rogenhofer, 1875), "*Sphingomima" discolucida* Herbulot, 1995 (genus combination uncertain, see taxonomic notes below), *Thenopa diversa* Walker, 1855, *"Hebdomophruda" errans* Prout, 1917 (genus combination uncertain, see taxonomic notes below).

Taxonomic notes: We choose *Drepanogynis* Guenée, [1858] as the type genus for Drepanogynini, although it is not the oldest valid name (ICZN Article 64), because extensive literature has been published on *Drepanogynis* (Krüger 1997, 1998, 1999, 2014), but virtually nothing exists on *Thenopa*, except the original descriptions of its constituent species. Current results show the urgent need for more extensive phylogenetic studies within Drepanogynini. *Thenopa* and *Sphingomima* are embedded within *Drepanogynis*, ~~making~~rendering it paraphyletic, but our taxon coverage is too limited to propose formal changes in this species-rich group. Drepanogynini, as defined here, are distributed in sub-Saharan Africa. *Drepanogynis sensu* Krüger (1997, 1998, 1999, 2014) includes over 150 species and it ranges from southern Africa to Ethiopia (Krüger 2002, Vári et al. 2002), whereas the genera *Sphingomima* (10 species) and *Thenopa* (4 species) occur in Central and West Africa (Scoble 1999). *Sphingomima* and *Thenopa* are externally similar, so the recovered sister-group relationship in the current phylogeny analysis ~~is~~was anticipated. In the current analysis *Hebdomophruda errans* Prout, 1917 is isolated from other analysed *Hebdomophruda* species (the others are included in Diptychini), highlighting the need for additional research. Krüger (1997, 1998) classified the genus *Hebdomophruda* into seven species groups on the basis of morphological characters, and *H. errans* group is one of them (Krüger 1998). We do not describe a new genus for the taxon *errans*, nor do we combine it with any genus in the Drepanogynini, highlighting its uncertain taxonomic position (*incertae sedis*) ~~waiting for~~pending more research. In the current analysis *Sphingomima discolucida* Herbulot, 1995 is transferred from unassigned tribus combination to Drepanogynini, but ~~because~~as the type species of *Sphingomima* (*S. heterodoxa* Warren, 1899) was not analysed, we do not transfer the entire genus *Sphingomima* into Drepanogynini. We highlight the uncertain taxonomic position of the taxon *discolucida*, acknowledging that it may eventually be ~~combined back to~~included again in *Sphingomima* if the entire genus ~~is~~should get transferred ~~in~~to Drepanogynini.

Diagnosis. Drepanogynini can be diagnosed by the combination of DNA data with up to 11 genetic markers (exemplar *Drepanogynis mixtaria* Guenée, [1858]) ArgK (GB Accession number), Ca-ATPase (GB Accession number), CAD (GB Accession number), COI (GB Accession number), EF1a (GB Accession number), GAPDH (GB Accession number), IDH (GB Accession number), MDH (GB Accession number), Nex9 (GB Accession number), RpS5 (GB Accession number) and Wingless (GB Accession number). In the light of our phylogenetic results, the *Drepanogynis* group of genera, as classified earlier (Krüger 2014), is split between two unrelated tribes (Drepanogynini and Diptychini). More research is needed to understand how other *Drepanogynis* species and the *Drepanogynis* group of genera *sensu* Krüger (1997, 1998, 1999, 2014) (at least 11 genera), should be classified.

Boarmiini are the sister group to a clade that comprises Macariini, Cassymini, Abraxini and Eutoeini. We found that many species currently assigned to Boarmiini are scattered throughout Ennominae. Boarmiini *s. str.* are strongly supported but are technically ~~is~~ not monophyletic because of a large number of genera which need to be formally transferred from other tribes to Boarmiini (see Brehm et al., in prep. for Neotropical taxa and Murillo-Ramos et al., in prep. for other taxa). The results are principally in concordance with Jiang et al. (2017), who supported the monophyly of Boarmiini but with a smaller number of taxa.

The divided valva in male genitalia was suggested as a synapomorphy of Macariini + Cassymini + Eutoeini by Holloway (1994). In addition, he proposed the inclusion of Abraxini in Cassymini. Our findings support Holloway's suggestions; Cassymini is recovered as polyphyletic and Abraxini and Eutoeini were found to be sister taxa. Synonymization of Eutoeini and Cassymini with Abraxini should be considered in future studies, but the support ~~indices~~values of the basal branches are too low in our hypothesis to draw final conclusions. Similar findings were provided by Jiang et al. (2017) who suggested more extensive sampling to study the evolutionary relationships of these tribes.

Orthostixinae Meyrick, 1892

Orthostixinae were not included in our study. Sihvonen et al. (2011) showed this subfamily as deeply embedded within Ennominae, but unfortunately it was not represented by the type genus of the tribe. These results agree with Holloway (1996) who examined *Orthostixis* Hübner, [1823] and suggested the inclusion in Ennominae despite the full development of hindwing vein M2, the presence of a forewing areole and the very broad base of the tympanal ansa. We sampled the species *Naxa textilis* (Preyer, 1884) and *Orthostixis cribraria* (Hübner, 1796) but, only three and one marker were successfully sequenced ~~from~~ for these samples, respectively. We included these species in the preliminary analyses but results were so unstable that we excluded them from the final analysis. Further research including fresh material and more genetic markers are needed to investigate the position of Orthostixinae conclusively.

Conclusions

This study elucidated some of the evolutionary relationships of the major groups within Geometridae. The monophyly of the subfamilies and the most widely accepted tribes was tested. We found high support for the subfamilies Larentiinae, Geometrinae and Ennominae in their traditional scopes. Sterrhinae also becomes monophyletic when *Ergavia*, *Ametris* and *Macrotes*, currently placed in Oenochrominae, are formally transferred to Sterrhinae. The concepts of Oenochrominae and Desmobathrinae required major revision and, after appropriate rearrangements, these groups will also form monophyletic subfamily-level entities. Archiea~~e~~rinae are monophyletic with the transfer of *Dirce* and *Acalyphes* to Ennominae. We separated Epidesmiinae as a new subfamily. As a result, this study proposes a higher level classification of Geometridae comprising 8 monophyletic subfamilies. Moreover, we found that many tribes in the different subfamilies were para- or polyphyletic. We attempted to address the needed taxonomic changes, in order to favor taxonomic stability of the subfamilies and many tribes, even if in an interim way, to allow applied researchers to use an updated higher taxonomic structure that better reflects our current understanding of geometrid phylogeny. Further papers will be added to this work and will provide a large number of ~~further~~additional taxonomic changes in the Geometridae (see Introduction). Despite our efforts to include a very large number of new taxa to be analyzed in our study, we acknowledge that many clades are still strongly under-represented. This is particularly true for taxa from tropical Africa and Asia, and more detailed phylogenetic studies are required including e.g. the tribes Eumeleini, Plutodini, Eutoeini, Cassymini and Abraxini. A better taxon sampling in these regions will allow to draw better conclusions about phylogeny and subsequent classification to reflect it. For th~~is~~ese tax~~on~~a and many tribes – old and new – we encourage morphological studies that attempt to find more apomorphies and that include a broader range of taxa.

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