**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 subfamilial 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 includes 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 subfamilies Larentiinae, Geometrinae and Ennominae in their traditional scopes. Sterrhinae becomes monophyletic only if *Ergavia* Walker, *Ametris* Hübner and *Macrotes* Westwood, 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 *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 **stat. rev.** Viidalepp (Geometrinae) is raised from synonymy with Pseudoterpnini Warren to 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, loopers.

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## Introduction

Geometridae are the second most species-rich family of Lepidoptera, with approximately 24,000 described species (number updated by the authors from Nieukerken et al., 2011) 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 larvae the 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). Eight subfamilies are recognized in Geometridae (Sihvonen et al., 2011). Several recent molecular and morphological 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), but questions remain. 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 are still largely unexplored (Brehm et al., 2016). Many species remain undescribed and there are many uncertainties in the classification of tropical taxa.

One of the most comprehensive phylogenetic studies on Geometridae to date was published by Sihvonen et al. (2011). They analyzed a data set of 164 taxa and up to eight genetic markers, and the most species-rich subfamilies were confirmed as monophyletic. However, the systematic positions of Oenochrominae and Desmobathrinae remained uncertain due to low taxon sampling, and both subfamilies were suspected to be polyphyletic. Moreover, because of

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taxonomic uncertainty, many geometrid genera, especially among tropical taxa, remained unassigned to any tribe.

This study is the first in a series of papers that investigate the phylogenetic relationships of Geometridae on the basis of global sampling. Our dataset comprises 1192 terminal taxa of Geometridae and 14 outgroup taxa, 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 the particular aim of 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 will build upon the taxonomic changes proposed in the present article: e.g., relationships in Sterrhinae (Sihvonen et al., in prep), New World taxa (Brehm et al., submitted), Larentiinae (Õunap et al., in prep) and the ennomine tribe Boarmiini (Murillo-Ramos et al., in prep).

Oenochrominae and Desmobathrinae are considered the most controversial subfamilies in Geometridae. A close relationship of these subfamilies 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 early classifications, species of Desmobathrinae and Oenochrominae were included in the former family Monoctenidae (Meyrick, 1889). Meyrick diagnosed them on the basis of the position of the R veins in the hindwing and Sc+R1 in the forewing (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). Too often, Oenochrominae was used for geometrids that could not be placed in other subfamilies, and at some point, even included Hedylidae, the moth-butterflies (Scoble, 1992). Unsurprisingly, many taxa formerly 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. Scoble & Edwards were not able to find synapomorphies to define Monoctenidae *sensu* Meyrick, and referred back to the original grouping proposed by Guenée (1858). They restricted Oenochrominae to a core clade based on male genitalia: the diaphragm dorsal to the anellus is fused with the transtilla to form a rigid plate. Additionally, Cook & Scoble (1992) suggested that

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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) re-established 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 the two tribes. Holloway (1996) noted that the modification of the tegumen of the male genitalia 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 close relationship between Eumeleini and Desmobathrini. A proposed classification for ???? 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 to be intermingled (Sihvonen et al., 2011; Ban et al., 2018), but previous taxon sampling was limited to eight and four species, respectively. The poor taxon sampling and unresolved relationships around the oenochromine and desmobathrine complex called for additional phylogenetic study to clarify 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 study includes 29 terminal taxa of Oenochrominae and 11 Desmobathrinae, mostly from the Australian and Oriental Regions.

## Materials & Methods

### *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 terminal taxa in our study (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 be amplified successfully. A total of

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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-geometrid 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 emphasized type species or species similar to type species, judged by morphological characters and/or genetic similarity of DNA barcodes in order to better inform 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 appropriate literature, by comparing them with type material from different collections, museums and DNA barcode sequences. Moreover, we compiled an illustrated catalogue of all Archiearinae, Desmobathrinae and Oenochrominae taxa included in this study, to demonstrate their morphological diversity and to facilitate subsequent verification of our identifications. This catalogue contains images of all analysed specimens of the above-mentioned taxa as well as photographs of the respective type material (Supplemental data S2). Further taxa from other subfamilies 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 specimens could not yet be assigned to species, and their identifications are preliminary, particularly for (potentially undescribed) tropical species. Taxonomic data, voucher IDs, number of genes, current systematic placement, and references to relevant literature with regard to tribal assignment, are shown in Supplemental data S1.

### *Molecular techniques*

DNA was extracted from 1–3 legs of specimens either preserved in ethanol or dry. In a few cases, other sources of tissue were used, such as parts of larvae. The remaining parts of specimens were preserved as vouchers deposited in the collections of origin, both public and private (eventually private material will be deposited in public museum collections). Genomic DNA was extracted and purified using a NucleoSpin® Tissue Kit (MACHEREY-NAGEL), following the manufacturer's protocol. DNA amplification and sequencing were carried out following protocols

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proposed by Wahlberg & Wheat (2008) and Wahlberg et al. (2016). PCR products were visualized on agarose gels. PCR products were cleaned enzymatically with Exonuclease I and FastAP Thermosensitive Alkaline Phosphatase (ThermoFisher Scientific) 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 and CAD) were sequenced. To check for potential misidentifications, DNA barcode sequences were compared to those in BOLD (Ratnasingham & Hebert 2007) 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.

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### *Alignment and cleaning sequences*

Multiple sequence alignments were 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). The alignment of each gene was carefully checked by eye relative to the reference sequence, taking into account the respective genetic codes and reading frames. Heterozygous positions were coded with IUPAC codes. Sequences with bad quality were removed from the alignments. Aligned sequences were uploaded to VoSeq (Peña & Malm, 2012) and then assembled into a dataset comprising 1206 taxa. The final dataset had a concatenated length of 7665 bp including gaps. To check for possible errors in alignments, potentially contaminated or identical sequences and misidentifications, we constructed maximum likelihood trees for each gene. These preliminary analyses were conducted using RAxML-HPC2 V.8.2.10 (Stamatakis, 2014) on the web-server CIPRES Science Gateway (Miller et al., 2010). 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. The final data matrix included 32% missing data.

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*Tree search strategies and model selection*

We ran maximum likelihood analyses with a data set partitioned by gene and codon position using IQ-TREE V1.6.10 (Nguyen et al., 2015) and data partitioned by codon in RAxML (Stamatakis et al 2014). Best-fitting substitution models were selected by ModelFinder, which is a model-selection method that incorporates a model of 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 (MFP+MERGE option) until the model fit does not increase (Lanfear et al., 2012). After the best model 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-HPC2 V.8.2.10 analysis was carried out on CIPRES using the GTR+CAT option.

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Support for nodes was evaluated with 1000 ultrafast bootstrap (UFBoot2) approximations (Hoang et al., 2017) in IQ-TREE, and SH-like approximate likelihood ratio test (Guindon et al., 2010). Additionally, we implemented rapid bootstrap (RBS) in RAxML (Stamatakis, 2008). To reduce the risk of overestimating branch supports in 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).

*Taxonomic decisions*

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## Results

### *Searching strategies and model selection*

The best-fit partition model in ModelFinder resulted in merging the codon positions into 26 partitions. Similarly, Akaike information criterion (AIC) and Bayesian information criterion (BIC) values show best partition schemes for the data partitioned by codon position (evolutionary models are listed in Supplemental data S3). Topologies recovered by IQ-TREE and RAxML analyses result in trees with nearly identical topology. Also, the different support methods tend to agree in recovering same nodes with strong phylogenetic signal. However, in most of the cases UFBoot2 from IQ-TREE show higher support values compared to RBS in RAxML (RAxML tree with support values is showed in Supplemental data S4). SH-like and UFBoot2 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 SH >= 80 UFBoot2 >= 95 and 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 are 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 SH-like, UFBoot2 =

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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 to belong to Sterrhinae (see details below). Tribes in Sterrhinae, such as Timandriini, Rhodometrini, Lythriini, Rhodostrophiini and Cyllopodini, are 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 is established in previous studies (Sihvonen et al., 2011; Õunap et al., 2016) and our results are largely in agreement with their hypotheses. However, our results do not support the sister relationship between Sterrhinae and Larentiinae found in previous studies. Rather, we find that Sterrhinae are the sister to the rest of Geometridae. Within Larentiinae, in concordance with recent findings (Sihvonen et al., 2011; Õunap et al. 2016; Strutzenberger et al., 2017), we find 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. (submitted) and Õunap et al. (in prep).

Archiearinae are represented by more taxa than in a previous study (Sihvonen et al., 2011). Archiearinae grouped as sister to Oenochrominae + Desmobathrinae complex+ *Eumelea* + 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 does probably not occur in Australia, despite superficial similarities of *Dirce, Acalyphes* and Archiearinae.

Desmobathrinae were shown 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] and *Racasta* Walker, 1861) nested within Desmobathrinae (Fig. 4). We formally transfer these taxa to Desmobathrinae. In the revised sense, Desmobathrinae form a well-supported group with two main lineages. One of them comprises *Ozola* Walker, 1861, *Derambila* Walker, [1863] and *Zanclopteryx*. This lineage is sister to a well-supported clade comprising *Conolophia* Warren, 1894, *Noreia* Walker, 1861,

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*Leptoctenopsis*, *Racasta*, *Ophiogramma* Hübner, [1831], *Pycnoneura* Warren, 1894 and *Dolichoneura* Warren, 1894.

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 *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.

The genus *Eumelea* Duncan [& Westwood], 1841 has an unclear phylogenetic position in our analyses. The IQ-TREE result suggests *Eumelea* to be sister to the subfamily Geometrinae (SH-like = 93.6, UFBoot2 = 71, whereas RAxML recovered *Eumelea* in Ennominae as sister of *Plutodes* Guenée, [1858] (RBS = 60).

The monophyly of Geometrinae is well supported (Fig. 5) and in IQ-TREE results Geometrinae are 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 Geometrinae is still problematic. Many tribes are recovered as paraphyletic. *Ornithospila* Warren, 1894 and *Agathia* Guenée, [1858], our results suggest are the sisters to the rest of Geometrinae, *Chlorodontopera* is placed as an isolated lineage sister of Aracimini, Neohipparchini, Timandromorphini, Geometrini and Comibaenini which are recovered as monophyletic groups. Synchlorini are nested within Nemoriini in a well-supported clade (support branch SH-like = 98.3, UFBoot2 = 91, RBS = 93). The monophyly of Pseudoterpnini could not be recovered, instead this tribe splits up into three well-defined groups. Several genera currently placed in Pseudoterpnini *s.l.* are recovered as an independent lineage clearly separate from Pseudoterpnini *s.str.* (SH-like, UFBoot2 = 100). *Xenozancla* Warren, 1893 is sister to a clade comprising Dysphaniini and Pseudoterpnini *s.str.* Hemitheini *sensu* Ban et al.

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(2018) are recovered as a well-supported clade. The African *Lophostola* Prout, 1912 and *Crypsiphona ocultaria* Meyrick, 1888 were resolved as a single lineages, close to Hemitheini.

Ennominae are strongly supported as monophyletic in IQ-TREE analyses (SH-like = 100, and UFBoot2) 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. (submitted), 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 (unnamed E1), *Idialcis* Warren 1906 (unnamed clade E2), Gonodontini s.str., Gnophini, Odontoperini, unnamed clade E3, Nacophorini, and Ennomini (*sensu* Beljaev, 2008) group together (SH-like = 90.3, UFBoot2 = 87). Ennomini were sister to this entire group. Campaeini is recovered as sister of Alsophilini + Wilemaniini and Colotoini. In turn, they are sister to the New Zealand genus *Declana* Walker, 1858 (unnamed E4), which appeared as an isolated lineage sister to *Acalyphes* Turner, 1926 + *Dirce* Prout, 1910 and a large complex including Lithinini, intermixed with some genera currently placed in Nacophorini and Diptychini.

*Neobapta* Warren, 1904 and *Oenoptila* Warren, 1895 formed an independent lineage (unnamed E5) sister to Theriini, which form a supported clade with *Lomographa* (Baptini). Likewise, we recovered *Erastria* Hübner, [1813] + *Metarranthis* Warren, 1894 (unnamed E6) and *Plutodes* Guenée, [1858] + Palyadini. The IQ-TREE analyses show Palyadini as a well-defined lineage, sister to *Plutodes*. However, in RAxML analyses, *Eumelea* and *Plutodes* group together and Palyadini cluster with a group of Caberini species. Apeirini formed a lineage with Hypochrosini, Epionini, *Sericosema* Warren, 1895 and *Ithysia* Hübner, [1825]. This lineage is in turn sister of African *Drepanogynis* Guenée, [1858] which groups together with *Sphingomima* Warren, 1899, *Thenopa* Walker, 1855 and *Hebdomophruda* Warren, 1897. Caberini are sister to an unnamed clade composed of *Trotogonia* Warren, 1905, *Acrotomodes* Warren, 1895, *Acrotomia* Herrich-Schäffer, [1855] and *Pyrinia* Hübner, 1818. Finally, our analyses recover a very large, well-supported clade comprising the tribes Macariini, Cassymini, Abraxini, Eutoeini and Boarmiini (SH-like= 100 and UFBoot2=99). 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, cluster in their

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own clade together with *Dorsifulcrum* Herbulot, 1979 and *Odontognophos* Wehrli, 1951. We were unable to include Orthostixinae in the analyses, so we could not clarify the taxonomic position of this subfamily with regard to its 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 parsed the codon positions into 26 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 note that although the AIC and BIC values were lower when the data were partitioned by gene, the tree topology recovered was almost the same as when data were partitioned by codon, suggesting that much of the phylogenetic signal in the data is robust to partitioning schemes. As would be expected, the analyses yielded 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 data presented in this study are 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

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patterns of the phylogenetic relationships among the subfamilies recovered in our study 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 light on the phylogenetic relationships of several, 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. 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 long been questioned. Morphological studies addressing Oenochrominae or Desmobathrinae have been 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 on the basis of morphological structures (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 as a consequence no formal transfers were proposed. ~~To date, the phylogenetic positions of these subfamilies have been unclear.~~

The systematic status of Orthostixinae remains uncertain 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 highly unstable in our analyses. It was thus excluded from our dataset. *Orthostixis* Hübner, [1823], the type genus of the subfamily, needs to be included in future analyses.

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## 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* Walker, 1866, *Ametris* Guenée, [1858] and *Macrotes* Westwood, 1841, 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 Regions. 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 transferred to Sterrhinae by 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 + *Traminda* Saalmüller, 1891 + *Pseudosterrha* Warren, 1888 and Rhodometrini + Lythriini clade. Lythriini are closely related to Rhodometrini as shown by Õunap et al. (2008) with both molecular and morphological data. While *Traminda* (Timandrini) and *Pseudosterrha* (Cosymbiini) grouped together forming a different lineage that is sister to Rhodometrini + Lythriini clade (Fig. 2).

Rhodostrophiini and Cyllopodini were recovered as polyphyletic with species of Cyllopodini clustering within Rhodostrophiini. Similar results were recovered previously (Sihvonen & Kaila, 2004; Sihvonen et al., 2011), suggesting that additional work is needed to clarify the status and systematic positions of these tribes. 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 are ongoing.

## Larentiinae Duponchel, 1845

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Larentiinae are a monophyletic entity (Fig. 3). Partly in concordance with the results of Sihvonen et al. (2011), Viidalepp (2011), Õunap et al. (2016) and Strutzenberger et al. (2017), Dyspteridini are supported as sister to all other larentiines. 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 the Melanthiini + Eupitheciini complex as a sister lineage to Perizomini. Sihvonen et al. (2011) recovered Phileremini and Rheumapterini as well-supported sister taxa. Our results suggest *Triphosa dubitata* (Triphosini) Linnaeus 1758 is sister to Phileremini, with Rheumapterini sister to this clade. Cidariini were recovered as paraphyletic, as the genera *Coenotephria* Prout, 1914 and *Lampropteryx* Stephens, 1831 cluster in a different clade (unnamed clade L7) apart from the lineage comprising the type genus of the tribe, *Cidaria* Treitschke, 1825. *Ceratodalia* Packard, 1876, currently placed in Hydriomenini and *Trichodezia* Warren, 1895 nested within Cidariini. This result is not in concordance with Õunap et al. (2016), who regarded this tribe to be monophyletic. Scotopterygini are sister to a lineage comprising *Ptychorrhoe blosyrata* Guenée [1858], *Disclisioprocta* *natalata* (Walker, 1862) (placed in unnamed clade L8), Euphyiini, an unnamed clade L9 comprising the genera *Pterocypha*, *Archirhoe* and *Obila*, Xanthorhoini and Cataclysmini. Euphyiini are monophyletic, but Xanthorhoini are 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 Hydriomenini, Heterusiini, Erateinini, Stamnodini and some unnamed clades (L11-14). 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 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 of the currently recognized tribes and 125 genera (with an emphasis on Neotropical taxa). However, the phylogenetic

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position of many taxa remains unclear, and many tropical genera have not yet been formally assigned to a tribe. Formal descriptions of these groups will be treated in detail by Brehm et al. (submitted) and Õunap et al. (in prep).

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### Archiearinae Fletcher, 1953

The hypothesis presented in this study recovered Archiearinae as a monophyletic entity if some taxonomic rearrangements are performed. 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

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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 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 = 93.6, UFBoot2 = 71) 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).

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### Oenochrominae Guenée, [1858]

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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 the genera *Monoctenia*, *Onycodes*, *Parepisparis*, *Antictenia*, *Arhodia*, *Gastrophora* and *Homospora*, which clustered together as the sister 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,

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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 in Oenochrominae by Scoble & Edwards (1990), but recovered in a lineage 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**

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

Material examined: Taxa included in the molecular phylogeny: *Ecphyas holopsara* Turner, 1929, *Systatica xanthastis* Lower, 1894, *Adeixis griseata* Hudson 1903, *Dichromodes indicataria* Walker 1866, *Phrixocomes* sp. Turner 1930, *Abraxaphantes perampla* Swinhoe 1890, *Epidesmia chilonaria* Herrich-Schäffer [1855], *Phrataria replicataria* Walker 1866.

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: *Ec. holopsara* + *S. xanthastis* and *Ep. chilonaria* + five other genera. Branch support values from IQ-TREE strongly support the monophyly of this clade (SH-like and UFBoot2 = 100), while in RAxML 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.

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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 (MK738299), Ca-ATPase (MK738690), CAD (MK738960), COI (MK739187), EF1a (MK740168), GAPDH (MK740402), MDH (MK740974) and Nex9 (MK741433). A thorough morphological investigation of the subfamily, including diagnostic characters, is under preparation (Murillo-Ramos et al.).

Distribution: Most genera are distributed in the Australian region, with some species ranging into the Oriental region. *Abraxaphantes* 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 Gumppenberg, 1887. One tribe is proposed as new: Chlorodontoperini **trib. nov.**, and one tribe (Archaeobalbini Viidalepp, 1981, **stat. rev.**) is raised from synonymy with Pseudoterpnini.

Although there are no phylogenetic studies which investigate the relationships between *Ornithospila* Warren, 1894 and *Agathia* Guenée, [1858], our results suggest Ornisthospilini+Agathiini are sister clades. This tribes are the sisters to the rest of Geometrinae. *Chlorodontopera* is placed as an isolated lineage as shown by Ban et al. (2018). Given that Chlorodontopera is clearly forming an independent and well-supported lineage we propose the description of a new tribe Chlorodontoperini.

Chlorodontoperini Murillo-Ramos, Sihvonen & Brehm, **new tribe**
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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 uncertain (unnamed G2). 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 = 98.3, UFBoot2 = 91, RBS = 93). Our findings are in concordance with Sihvonen et al. (2011) and Ban et al. (2018), but our analyses included a larger

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number of markers and a much higher number of taxa. Thus, we formally synonymize Synchlorini **syn. nov.** with Nemoriini (Table 1).

The monophyly of Pseudoterpnini *sensu* Pitkin et al. (2007) could not be recovered. Similar results were shown by Ban et al. (2018) who recovered Pseudoterpnini *s.l.* including all the genera previously studied by Pitkin et al. (2007), forming a separate clade from *Pseudoterpna* Hübner, [1823] + *Pingasa* Moore, 1887. Our results showed 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 = 88.3, UFBoot2 = 64). 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.

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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 comprising the genera *Limbatochlamys* Rothschild, 1894, *Psilotagma* Warren, 1894, *Metallolophia* Warren, 1895, *Metaterpna* Yazaki,

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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 = 88.3, UFBoot2 = 64). GenBank accession numbers are shown in supplementary material. A morphological diagnosis requires further research.

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*Xenozancla* Warren, 1893 (unnamed G3) is sister to the clade comprising Dysphaniini and Pseudoterpnini *s. str*. Sihvonen et al. (2011) did not include *Xenozancla* in their analyses and suggested a sister relationship 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 taxa, 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 a conclusion about the phylogenetic affinities of these tribes based on our results.

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The Australian genus *Crypsiphona* Meyrick, 1888 (unnamed G4) placed close to *Lophostola* and 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. 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

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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 subtribe concept is not practical thus do not advocate its use in geometrid classification.

**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, four molecular studies have corroborated the monophyly of Ennominae (Yamamoto & Sota, 2007; Wahlberg et al., 2010; Õunap et al., 2011, Sihvonen et al. 2011), with Young (2006) being the only exception who found Ennominae paraphyletic. 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. (submitted) and Murillo-Ramos et al. (in prep.). We here 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 (SH-Like = 100 UFBoot2=99). 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

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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 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

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"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 (E1, E2 in figure 6) 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 (submitted). 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

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*Psilocladia* in Gonodontini (Table 1). Gnophini are are monophyletic 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 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.

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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 support a close relationship of Nacophorini, Azelinini and Odontoperini. These clades will be treated in more detail by Brehm et al. (submitted).

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 the valid tribal name for this large clade.

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Campaeini, Alsophilini, Wilemaniini and Prosopolophini grouped together in a well-supported clade (SH-like = 100 and UFBoot2= 99). 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,

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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.

The genus *Declana* Walker, 1858 is recovered as an isolated clade sister to to Diptychini, including *Acalyphes* and *Dirce*. This genus is endemic to New Zealand, but to date has not been assigned to 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.

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 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. (submitted).

*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 Sihvonen et al. (2011). The monophyly of *Lomographa* has not been tested before, but we show

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**Moved up [7]:** 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. ¶

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that one Neotropical and one Palaearctic *Lomographa* species indeed group together. Our results show that Caberini are not closely related to the Theriini + Baptini clade, unlike in 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 congruent with those findings. IQ-TREE results suggest that *Plutodes* is sister to Palyadini, but RAxML analyses recovered *Eumelea* as the most probable sister of *Plutodes*. Given that our analyses are not in agreement about the sister-group affinities of *Plutodes*, we do not make any assumptions about its phylogenetic position. Instead we emphasize that further work needs to be done to clarify the phylogenetic positions of *Plutodes* and related groups.

Hypochrosini is only recovered in a well-defined lineage if the genera *Apeira* Gistl, 1848 (Apeirini), *Epione* Duponchel, 1829 (Epionini), *Sericosema* (Caberini), *Ithysia* (Theriini), *Capasa* Walker, 1866 (unassigned) and *Omizodes* Warren, 1894 (unassigned) were transferred to Hypochrosini. Skou & Sihvonen (2015) already suggested a close association of Epionini, Apeirini and Hypochrosini. We think that synonymising 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).

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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 clusters together with these taxa, 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**

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Type genus: *Drepanogynis* Guenée, [1858]

The African genera *Thenopa*, *Sphingomima* and *Drepanogynis* appear as a strongly supported lineage (SH-like UFBoot2, and RBS = 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.

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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.

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*Thenopa* and *Sphingomima* are embedded within *Drepanogynis*, 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 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*) pending more research. In the current analysis, *Sphingomima discolucida* Herbulot, 1995 is transferred from unassigned tribus combination to Drepanogynini, but 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 included again in *Sphingomima* if the entire genus should get transferred 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 (MK738841), COI (MK739615), EF1a (MK739960), IDH (MK740862), MDH (MK741181), Nex9 (MK741630), RpS5 (MK741991) and Wingless (MK742540). 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 not

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monophyletic because of a large number of genera which need to be formally transferred from other tribes to Boarmiini (see Brehm et al., submitted 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. Although our findings support a close relationship, this group requires more study and a more extensive sampling effort. Similar findings were provided by Jiang et al. (2017) who suggested more extensive sampling to study the evolutionary relationships of these tribes.

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**Deleted:** Holloway's suggestions; Cassymini is recovered as polyphyletic and Abraxini and Eutoeini as sister taxa. Synonymization of Eutoeini and Cassymini with Abraxini should be considered in future studies, but the support values of the basal branches are too low in our hypothesis to draw final conclusions. Similar findings were

### 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 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 important evolutionary relationships among major groups within Geometridae. The monophyly of the subfamilies and the most widely accepted tribes were tested. We found strong support for the traditional concepts of Larentiinae, Geometrinae and Ennominae. Sterrhinae also becomes monophyletic when *Ergavia*, *Ametris* and *Macrotes*, currently placed in Oenochrominae, are 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. Archiearinae

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are monophyletic with the transfer of *Dirce* and *Acalyphes* to Ennominae. We treat Epidesmiinae as a new subfamily.

This study proposes the recognition of eight monophyletic geometrid subfamilies. Many geometrid tribes were recovered as 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 other 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 additional taxonomic changes in the Geometridae (see Introduction).~~ Although we included a large number of new taxa in our study, many clades remain poorly represented. This is particularly true for taxa from tropical Africa and Asia. Tribes in special need of reassessment include Eumeleini, Plutodini, Eutoeini, Cassymini and Abraxini. ~~Denser taxon sampling will ensure more robust phylogenetic conclusions towards a natural classification.~~ We hope the phylogenetic hypotheses shared here will open new paths of inquiry across the Geometridae. Morphological synapomorphies have not yet been identified for many of the re- and newly defined higher taxa circumscribed by our 11-gene data set. Likewise, there is great need, across the family, to begin the work of mapping behavioral and life history attributes to the clades identified in this work.

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**Page 12: [4] Commented [WD9]** **Wagner, David** **5/22/19 3:49:00 AM**

How supported?  Weakly? Strongly?  Or just say ,” “formed a clade,” if the support is of average strength (deleting the word supported).

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Elements of a series that contain commas should be separated with semi-colons.

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