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

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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.

1   **Manuscript Title**

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33 **Abstract**

34 Our study aims to investigate the relationships of the major lineages within the moth family

35 Geometridae, with a focus on the poorly studied Oenochrominae-Desmobathrinae complex, and

36 to translate some of the results into a coherent subfamilial and tribal level classification for the

37 family. We analyzed a molecular dataset of 1206 Geometridae terminal taxa from all

38 biogeographical regions comprising up to 11 molecular markers that includes one mitochondrial

39 (COI) and 10 protein-coding nuclear gene regions (wingless, *ArgK*, MDH, RpS5, GAPDH, IDH,

40 Ca-ATPase, Nex9, EF-1alpha, CAD). The molecular data set was analyzed using maximum

41 likelihood as implemented in IQ-TREE and RAxML. We found high support for the subfamilies

42 Larentiinae, Geometrinae and Ennominae in their traditional scopes. Sterrhinae becomes

43 monophyletic only if *Ergavia* Walker, *Ametris* Hübner and *Macrotes* Westwood, which are

44 currently placed in Oenochrominae, are formally transferred to Sterrhinae. Desmobathrinae and

45 Oenochrominae are found to be polyphyletic. The concepts of Oenochrominae and

46 Desmobathrinae required major revision and, after appropriate rearrangements, these groups also

47 form monophyletic subfamily-level entities. Oenochrominae *s.str.* as originally conceived by

48 Guenée is phylogenetically distant from *Epidesmia.* The latter is hereby described as the

49 subfamily Epidesmiinae Murillo-Ramos, Sihvonen & Brehm, **subfam. nov.** Epidesmiinae are a

50 lineage of "slender-bodied Oenochrominae" that include the genera *Ecphyas* Turner, *Systatica*

51 Turner, *Adeixis* Warren, *Dichromodes* Guenée, *Phrixocomes* Turner, *Abraxaphantes* Warren**,**

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53 *Dirce* and *Acalyphes* are formally transferred to Ennominae. We also found that many tribes

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56 with Pseudoterpnini Warren to tribal rank. Chlorodontoperini Murillo-Ramos, Sihvonen &

57 Brehm, **trib. nov.** and Drepanogynini Murillo-Ramos, Sihvonen & Brehm, **trib. nov.** are

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63 **Introduction**

64 Geometridae are the second most species-rich family of Lepidoptera, with approximately 24,000

65 described species (number from Nieukerken et al., 2011 updated by the authors) found in all

66 regions except Antarctica. The monophyly of Geometridae is well supported based on distinctive

67 morphological characters (Cook & Scoble, 1992; Scoble, 1992; Minet & Scoble, 1999). In

68 particular, adult members of the family possess paired tympanal organs at the base of the

69 abdomen, while in larvae the prolegs are reduced to two pairs in almost all species, which causes

70 the larvae to move in a looping manner (Minet & Scoble, 1999).

71 The phylogenetic relationships of the major subdivisions of Geometridae have been

72 studied based on molecular data, which have contributed to the understanding of the evolutionary

73 relationships within the family (Abraham et al., 2001; Yamamoto & Sota, 2007; Sihvonen et al.,

74 2011). Eight subfamilies are recognized in Geometridae (Sihvonen et al., 2011). Several recent

75 molecular and morphological studies have attempted to confirm the monophyly or clarify the

76 taxonomy of most of these groups, for instance: Sterrhinae (Holloway, 1997; Hausmann, 2004;

77 Sihvonen & Kaila, 2004; Õunap et al., 2008), Larentiinae (Holloway, 1997; Mironov, 2003;

78 Viidalepp, 2006, 2011; Hausmann & Viidalepp, 2012; Õunap et al., 2016), Desmobathrinae

79 (Holloway, 1996; Hausmann, 2001), Archiearinae (Hausmann, 2001; Young, 2006),

80 Oenochrominae (Holloway, 1996; Scoble & Edwards, 1990; Cook & Scoble, 1992; Hausmann,

81 2001; Young, 2006), Geometrinae (Cook, 1993; Pitkin, 1996; Hausmann, 2001; Ban et al.,

82 2018), Orthostixinae (Holloway, 1997) and Ennominae (Holloway, 1994; Pitkin, 2002; Beljaev,

83 2006; Young, 2006; Wahlberg et al., 2010; Õunap et al., 2011; Skou & Sihvonen, 2015;

84 Sihvonen et al., 2015), but questions remain. An important shortcoming is that our understanding

85 of geometrid systematics is biased towards the long-studied European fauna, whereas the highest

86 diversity of this family is in the tropics, which are still largely unexplored (Brehm et al., 2016).

87 Many species remain undescribed and there are many uncertainties in the classification of

88 tropical taxa.

89 One of the most comprehensive phylogenetic studies on Geometridae to date was

90 published by Sihvonen et al. (2011). They analyzed a data set of 164 taxa and up to eight genetic

91 markers, and the most species-rich subfamilies were confirmed as monophyletic. However, the

92 systematic positions of Oenochrominae and Desmobathrinae remained uncertain due to low

93 taxon sampling and genetic markers, and both subfamilies were suspected to be polyphyletic.

94   Moreover, because of taxonomic uncertainty, many geometrid genera, especially among tropical

95   taxa, remained unassigned to any tribe.

96   This study is the first in a series of papers that investigate the phylogenetic relationships

97   of Geometridae on the basis of global sampling. Our dataset comprises 1192 terminal taxa of

98   Geometridae and 14 outgroup taxa, with samples from all major biomes, using up to 11

99   molecular markers. Our paper includes an overview of the relationships of the major lineages

100 within the family, with the particular aim of defining the limits and finding the phylogenetic

101 affinities of the subfamilies, with a focus on Oenochrominae and Desmobathrinae. Further

102 papers in the series will focus on particular subfamilies and regions, and will build upon the

103 taxonomic changes proposed in the present article: e.g., relationships in Sterrhinae (Sihvonen et

104 al., in prep), New World taxa (Brehm et al., submitted), Larentiinae (Õunap et al., in prep) and

105 the ennomine tribe Boarmiini (Murillo-Ramos et al., in prep).

106   Oenochrominae and Desmobathrinae are considered the most controversial subfamilies in

107 Geometridae. A close relationship of these subfamilies has been proposed both in morphological

108 (Meyrick, 1889; Cook & Scoble, 1992; Holloway, 1996) and in molecular studies (Sihvonen et

109 al., 2011; Ban et al., 2018). In early classifications, species of Desmobathrinae and

110 Oenochrominae were included in the former family Monoctenidae (Meyrick, 1889). Meyrick

111 diagnosed them on the basis of the position of the R veins in the hindwing and Sc+R1 in the

112 forewing (Scoble & Edwards, 1990). However, the classification proposed by Meyrick was not

113 fully supported by subsequent taxonomic work (Scoble & Edwards, 1990; Cook & Scoble, 1992;

114 Holloway, 1996). Too often, Oenochrominae was used for geometrids that could not be placed in

115 other subfamilies, and at some point, even included Hedylidae, the moth-butterflies (Scoble,

116 1992). Unsurprisingly, many formerly classified in Oenochrominae have recently been shown to

117 be misplaced (Holloway, 1997; Staude, 2001; Sihvonen & Staude, 2011; Staude & Sihvonen,

118 2014). In Scoble & Edwards (1990), the family concept of Oenochrominae was restricted to the

119 robust-bodied Australian genera, with one representative from the Oriental region. Scoble &

120 Edwards (1990) were not able to find synapomorphies to define Monoctenidae *sensu* Meyrick,

121 and referred back to the original grouping proposed by Guenée (1858). They restricted

122 Oenochrominae to a core clade based on male genitalia: the diaphragm dorsal to the anellus is

123 fused with the transtilla to form a rigid plate. Additionally, Cook & Scoble (1992) suggested that

124   the circular form of the lacinia and its orientation parallel to the tympanum was apomorphic for

125   these robust-bodied Oenochrominae.

126   In an extensive morphological study, Holloway (1996) delimited the subfamily

127   Desmobathrinae to include species with appendages and slender bodies previously assigned to

128   Oenochrominae. According to Holloway (1996), Desmobathrinae comprises two tribes:

129   Eumeleini and Desmobathrini. However, no synapomorphies were found to link the two tribes.

130   Holloway (1996) noted that the modification of the tegumen of the male genitalia was variable in

131   both groups but that the reduction of cremastral spines in the pupa from eight to four in *Ozola*

132   Walker, 1861 and *Eumelea* Duncan [& Westwood], 1841 provided evidence of a close

133   relationship between Eumeleini and Desmobathrini. Currently, 328 species (76 genera) are

134   included in Oenochrominae, and 248 species (19 genera) are assigned to Desmobathrinae

135   (Beccaloni et al., 2003; Sihvonen et al., 2011, 2015).

136   Most recent molecular phylogenies have shown Oenochrominae and Desmobathrinae to

137   be intermingled (Sihvonen et al., 2011; Ban et al., 2018), but previous taxon sampling was

138   limited to eight and four species, respectively. The poor taxon sampling and unresolved

139   relationships around the oenochromine and desmobathrine complex called for additional

140   phylogenetic studies to clarify the relationships of these poorly known taxa within Geometridae.

141   We hypothesize that both Oenochrominae and Desmobathrinae are para- or polyphyletic

142   assemblages, and we address this hypothesis with 29 terminal taxa of Oenochrominae and 11

143   representatives of Desmobathrinae, mostly from the Australian and Oriental Regions.

144

145   **Material & Methods**

146   *Material acquisition, taxon sampling and species identification*

147   In addition to 461 terminal taxa with published sequences (see Supplemental data S1), we

148   included sequences from 745 terminal taxa in our study (Supplemental data S1). Representative

149   taxa of all subfamilies recognized in Geometridae were included, except for the small subfamily

150   Orthostixinae for which most molecular markers could not be amplified successfully. A total of

151   93 tribes are represented in this study following recent phylogenetic hypotheses and

152   classifications (Sihvonen et al., 2011; Wahlberg et al., 2010; Sihvonen et al., 2015; Õunap et al.,

153   2016; Ban et al., 2018). In addition, 14 non-geometrid species belonging to other families of

154   Geometroidea were included as outgroups based on the hypothesis proposed by Regier et al.

155   (2009; 2013). Where possible, two or more samples were included per tribe and genus,

156   especially for species-rich groups that are widely distributed and in cases where genera were

157   suspected to be poly- or paraphyletic. We emphasized type species or species similar to type

158   species, judged by morphological characters and/or genetic similarity of DNA barcodes in order

159   to better inform subsequent taxonomic work, to favor nomenclatorial stability and to establish

160   the phylogenetic positions of genera unassigned to tribes.

161   Sampled individuals were identified by the authors using appropriate literature, by

162   comparing them with type material from different collections, museums and DNA barcode

163   sequences. Moreover, we compiled an illustrated catalogue of all Archiearinae, Desmobathrinae

164   and Oenochrominae taxa included in this study, to demonstrate their morphological diversity and

165   to facilitate subsequent verification of our identifications. This catalogue contains images of all

166   analysed specimens of the above-mentioned taxa as well as photographs of the respective type

167   material (Supplemental data S2). Further taxa from other subfamilies will be illustrated in other

168   papers (Brehm et al. in prep., Sihvonen et al. in prep., Õunap et al. in prep.). Some of the studied

169   specimens could not yet be assigned to species, and their identifications are preliminary,

170   particularly for (potentially undescribed) tropical species. Taxonomic data, voucher IDs, number

171   of genes, current systematic placement, and references to relevant literature with regard to tribal

172   assignment, are shown in Supplemental data S1.

173

174   *Molecular techniques*

175

176   DNA was extracted from 1–3 legs of specimens either preserved in ethanol or dry. In a few

177   cases, other sources of tissue were used, such as parts of larvae. The remaining parts of

178   specimens were preserved as vouchers deposited in the collections of origin, both public and

179   private (eventually private material will be deposited in public museum collections). Genomic

180   DNA was extracted and purified using a NucleoSpin® Tissue Kit (MACHEREY-NAGEL),

181   following the manufacturer's protocol. DNA amplification and sequencing were carried out

182   following protocols proposed by Wahlberg & Wheat (2008) and Wahlberg et al. (2016). PCR

183   products were visualized on agarose gels. PCR products were cleaned enzymatically with

184   Exonuclease I and FastAP Thermosensitive Alkaline Phosphatase (ThermoFisher Scientific) and

185   sent to Macrogen Europe (Amsterdam) for Sanger sequencing. One mitochondrial (*cytochrome*

186 *oxidase subunit I,* COI) and 10 protein-coding nuclear gene regions, *carbamoylphosphate*

187 *synthetase* (CAD), *Ribosomal Protein S5* (RpS5), *wingless* (wgl), *cytosolic malate*

188 *dehydrogenase* (MDH), *glyceraldehydes-3-phosphate dehydrogenase* (GAPDH*), Elongation*

189 *factor 1 alpha* (EF-1alpha), *Arginine Kinase* (ArgK), *Isocitrate dehydrogenase* (IDH), *sorting*

190 *nexin-9-like* (Nex9), and *sarco/endoplasmic reticulum calcium ATPase* (Ca-ATPase), were

191 sequenced. To check for potential misidentifications, DNA barcode sequences were compared to

192 those in BOLD (Ratnasingham & Hebert 2007) where references of more than 21,000 geometrid

193 species are available, some 10,000 of them being reliably identified to Linnean species names

194 (Ratnasingham & Hebert, 2007). GenBank accession numbers for sequences used in this study

195 are provided in Supplemental data S1.

196

197 *Alignment and cleaning sequences*

198

199 Multiple sequence alignments were carried out in MAFFT as implemented in Geneious v.11.0.2

200 (Biomatters, http://www.geneious.com/) for each gene based on a reference sequence of

201 Geometridae downloaded from the database VoSeq (Peña & Malm, 2012). The alignment of

202 each gene was carefully checked by eye relative to the reference sequence, taking into account

203 the respective genetic codes and reading frames. Heterozygous positions were coded with

204 IUPAC codes. Sequences with bad quality were removed from the alignments. Aligned

205 sequences were uploaded to VoSeq (Peña & Malm, 2012) and then assembled into a dataset

206 comprising 1206 taxa. The final dataset had a concatenated length of 7665 bp including gaps. To

207 check for possible errors in alignments, potentially contaminated or identical sequences and

208 misidentifications, we constructed maximum likelihood trees for each gene. These preliminary

209 analyses were conducted using RAxML-HPC2 V.8.2.10 (Stamatakis, 2014) on the web-server

210 CIPRES Science Gateway (Miller et al., 2010). The final data set included at least three genes

211 per taxon except for *Oenochroma vinaria* (Guenée, 1858), *Acalyphes philorites* Turner, 1925,

212 *Dirce lunaris* (Meyrick, 1890), *D. aesiodora* Turner, 1922, *Furcatrox australis* (Rosenstock,

213 1885), *Chlorodontopera mandarinata* (Leech, 1889), *Chlorozancla falcatus* (Hampson, 1895),

214 *Pamphlebia rubrolimbraria* (Guenée, 1858) and *Thetidia albocostaria* (Bremer, 1864). For these

215 taxa, included in studies by Young (2006) and Ban et al. (2018), only two markers were

216 available. The final data matrix included 32% missing data.

217

218   *Tree search strategies and model selection*

219   We ran maximum likelihood analyses with a data set partitioned by gene and codon position

220   using IQ-TREE V1.6.10 (Nguyen et al., 2015) and data partitioned by codon in RAxML

221   (Stamatakis et al 2014). Best-fitting substitution models were selected by ModelFinder, which is

222   a model-selection method that incorporates a model of flexible rate heterogeneity across sites

223   (Kalyaanamoorthy et al., 2017). ModelFinder implements a greedy strategy as implemented in

224   PartitionFinder that starts with the full partitioned model and consequentially merges partitions

225   (MFP+MERGE option) until the model fit does not increase (Lanfear et al., 2012). After the best

226   model has been found, IQ-TREE starts the tree reconstruction under the best model scheme. The

227   phylogenetic analyses were carried out with the *-spp* option that allowed each partition to have

228   its own evolutionary rate. The RAxML-HPC2 V.8.2.10 analysis was carried out on CIPRES

229   using the GTR+CAT option.

230   Support for nodes was evaluated with 1000 ultrafast bootstrap (UFBoot2) approximations

231   (Hoang et al., 2017) in IQ-TREE, and SH-like approximate likelihood ratio test (Guindon et al.,

232   2010). Additionally, we implemented rapid bootstrap (RBS) in RAxML (Stamatakis, 2008). To

233   reduce the risk of overestimating branch supports in UFBoot2 test, we implemented *-bnni* option,

234   which optimizes each bootstrap tree using a hill-climbing nearest neighbor interchange (NNI)

235   search. Trees were visualized and edited in FigTree v1.4.3 software (Rambaut, 2012). The final

236   trees were rooted with species of the families Sematuridae, Epicopeiidae, Pseudobistonidae and

237   Uraniidae following previous hypotheses proposed in Regier et al. (2009; 2013), Rajaei et al.

238   (2015) and Heikkilä et al. (2015).

239   *Taxonomic decisions*

240   The electronic version of this article in Portable Document Format (PDF) will represent a

241   published work according to the International Commission on Zoological Nomenclature (ICZN),

242   and hence the new names contained in the electronic version are effectively published under that

243   Code from the electronic edition alone. This published work and the nomenclatural acts it

244   contains have been registered in ZooBank. The ZooBank LSIDs (Life Science Identifiers) can be

245   resolved and the associated information viewed through any standard web browser by appending

246   the LSID to the prefix http://zoobank.org/. For this publication: LSIDurn:l

247   sid:zoobank.org:pub:662A9A18-B620-45AA-B4B1-326086853316. The online version of this

248   work is archived and available from the following digital repositories: PeerJ, PubMed Central

249   and CLOCKSS.

250

251   Results

252

253   *Searching strategies and model selection*

254

255   The ModelFinder analysis resulted in 26 partitions with associated best-fit models (Table 1). IQ-

256   TREE and RAxML analyses resulted in trees with nearly identical topology. Also, the different

257   methods of evaluating robustness tended to agree in supporting the same nodes. However, in

258   most of the cases UFBoot2 from IQ-TREE showed higher support values compared to RBS in

259   RAxML (RAxML tree with support values is shown in Supplemental data S3). SH-like and

260   UFBoot2 performed similarly, with UFBoot2 showing slightly higher values, and both tended to

261   show high support for the same nodes (Fig. 1). As noted by the authors of IQ-TREE, values of

262   SH >= 80 and UFBoot2 >= 95 indicate well-supported clades (Trifinopoulos & Minh, 2018).

263

264   *General patterns in the phylogeny of Geometridae*

265

266   Analyses of the dataset of 1206 terminal taxa, comprising up to 11 markers and an

267   alignment length of 7665 bp recovered topologies with many well-supported clades. About 20

268   terminal taxa are recovered as very similar genetically and they are likely to represent closely

269   related species, subspecies or specimens of a single species. The examination of their taxonomic

270   status is not the focus of this study, so the number of unique species in the analysis is slightly

271   less than 1200. Our findings confirm the monophyly of Geometridae (values of SH-like,

272   UFBoot2= 100) (Fig. 1). The general patterns in our phylogenetic hypotheses suggest that

273   Sterrhinae are the sister group to the rest of Geometridae. This subfamily is recovered as

274   monophyletic when three genera traditionally included in Oenochrominae are considered to

275   belong to Sterrhinae (see details below). Tribes in Sterrhinae, such as Timandriini,

276   Rhodometrini, Lythriini, Rhodostrophiini and Cyllopodini, are not recovered as monophyletic

277   (Fig. 2). A detailed analysis, including formal changes to the classification of Sterrhinae, will be

278   provided by Sihvonen et al. (in prep).

279   The monophyly of Larentiinae is established in previous studies (Sihvonen et al., 2011;

280   Õunap et al., 2016) and our results are largely in agreement with their hypotheses. However, our

281   results do not support the sister relationship between Sterrhinae and Larentiinae found in

282   previous studies. Rather, we find that Sterrhinae are the sister to the rest of Geometridae. Within

283   Larentiinae, in concordance with recent findings (Sihvonen et al., 2011; Õunap et al. 2016;

284   Strutzenberger et al., 2017), we find Dyspteridini as the sister group to the remaining Larentiinae

285   (Fig. 3). Phylogenetic relationships within Larentiinae were treated in detail by Õunap et al.

286   (2016). Further details of the analyses and changes to the classification of Larentiinae will be

287   discussed by Brehm et al. (submitted) and Õunap et al. (in prep).

288   Archiearinae are represented by more taxa than in a previous study (Sihvonen et al.,

289   2011). Archiearinae grouped as sister to Oenochrominae + Desmobathrinae complex+ *Eumelea*

290   + Geometrinae and Ennominae (Fig. 4). The monophyly of this subfamily is well supported

291   (values of SH-like, UFBoot2 = 100). However, as in the previous study (Sihvonen et al. 2011),

292   the Australian genera *Dirce* Prout, 1910 and *Acalyphes* Turner, 1926 are not part of Archiearinae

293   but can clearly be assigned to Ennominae. Unlike previously assumed (e.g., McQuillan &

294   Edwards 1994), the subfamily Archiearinae probably does not occur in Australia, despite

295   superficial similarities of *Dirce, Acalyphes* and Archiearinae.

296   Desmobathrinae were shown to be paraphyletic by Sihvonen et al. (2011). In our

297   analysis, the monophyly of this subfamily is not recovered either, as we find two genera

298   traditionally placed in Oenochrominae (i.e. *Zanclopteryx* Herrich-Schäffer, [1855] and *Racasta*

299   Walker, 1861) nested within Desmobathrinae (Fig. 4). We formally transfer these genera to

300   Desmobathrinae. In the revised sense, Desmobathrinae form a well-supported group with two

301   main lineages. One of them comprises *Ozola* Walker, 1861, *Derambila* Walker, [1863] and

302   *Zanclopteryx*. This lineage is sister to a well-supported clade comprising *Conolophia* Warren,

303   1894, *Noreia* Walker, 1861, *Leptoctenopsis* Warren, 1897, *Racasta*, *Ophiogramma* Hübner,

304   [1831], *Pycnoneura* Warren, 1894 and *Dolichoneura* Warren, 1894.

305   Oenochrominae in the broad sense are not a monophyletic group. However,

306   Oenochrominae *sensu stricto* (Scoble & Edwards, 1990) form a well-supported lineage

307   comprising two clades. One of them contains a polyphyletic *Oenochroma* with *O. infantilis*

308   Prout, 1910 being sister to *Dinophalus* Prout, 1910, *Hypographa* Guenée, [1858], *Lissomma*

309   Warren, 1905, *Sarcinodes* Guenée, [1858] and two further species of *Oenochroma*, including the

310   type species *O. vinaria* Guenée, [1858]. The other clade comprises *Monoctenia* Guenée, [1858],

311   *Onycodes* Guenée, [1858], *Parepisparis* Bethune-Baker, 1906, *Antictenia* Prout, 1910, *Arthodia*

312   Guenée, [1858], *Gastrophora* Guenée, [1858] and *Homospora* Turner, 1904 (Fig. 4). Most of the

313   remaining genera traditionally placed in Oenochrominae, including e.g. *Epidesmia* Duncan [&

314   Westwood], 1841, form a well-supported monophyletic clade that is sister to Oenochrominae *s.*

315   *str.* + *Eumelea ludovicata* + Geometrinae + Ennominae assemblage.

316   The genus *Eumelea* Duncan [& Westwood], 1841 has an unclear phylogenetic position in our

317   analyses. The IQ-TREE result suggests *Eumelea* to be sister to the subfamily Geometrinae (SH-

318   like = 93.6, UFBoot2 = 71, whereas RAxML recovered *Eumelea* in Ennominae as sister of

319   *Plutodes* Guenée, [1858] (RBS = 60).

320   The monophyly of Geometrinae is well supported (Fig. 5) and in IQ-TREE results

321   Geometrinae are recovered as the sister-taxon of *Eumelea*. The *Eumelea* + Geometrinae clade is

322   sister to Oenochrominae *s. str.* Although a recent phylogenetic study proposed several taxonomic

323   changes (Ban et al., 2018), the tribal composition in Geometrinae is still problematic. Many

324   tribes are recovered as paraphyletic. Our results suggest that *Ornithospila* Warren, 1894 and

325   *Agathia* Guenée, [1858] are the sister lineage to the rest of Geometrinae. *Chlorodontopera* is

326   placed as an isolated lineage sister to Aracimini, Neohipparchini, Timandromorphini, Geometrini

327   and Comibaenini which are recovered as monophyletic groups, respectively. Synchlorini are

328   nested within Nemoriini in a well-supported clade (support branch SH-like = 98.3, UFBoot2=

329   91, RBS = 93). The monophyly of Pseudoterpnini could not be recovered, instead this tribe splits

330   up into three well-defined groups. Several genera currently placed in Pseudoterpnini *s.l.* are

331   recovered as an independent lineage clearly separate from Pseudoterpnini *s.str.* (SH-like,

332   UFBoot2 = 100). *Xenozancla* Warren, 1893 is sister to a clade comprising Dysphaniini and

333   Pseudoterpnini *s.str.* Hemitheini *sensu* Ban et al. (2018) are recovered as a well-supported clade.

334   The African *Lophostola* Prout, 1912 and *Crypsiphona ocultaria* Meyrick, 1888 were resolved as

335   a single lineage, close to Hemitheini.

336   Ennominae are strongly supported as monophyletic in IQ-TREE analyses (SH-like = 100,

337   UFBoot2= 99) whereas in RAxML the monophyly is weakly supported (RBS = 63). Detailed

338   results concerning the classification, especially for the Neotropical taxa, will be presented by

339   Brehm et al. (submitted), but the main results are summarized here (Fig. 6). Very few tribes are

340   monophyletic according to the results of the present study. One group of Neotropical taxa

341   currently assigned to Gonodontini (unnamed E1), *Idialcis* Warren 1906 (unnamed clade E2),

342   Gonodontini s.str., Gnophini, Odontoperini, unnamed clade E3, Nacophorini, and Ennomini

343   (*sensu* Beljaev, 2008) group together (SH-like = 90.3, UFBoot2 = 87). Ennomini were sister to

344   this entire group. Campaeini is recovered as sister of Alsophilini + Wilemaniini and Colotoini. In

345   turn they are sister to a clade comprising a number of taxa. These include the New Zealand genus

346   *Declana* Walker, 1858 (unnamed E4) which appear as sister to a large complex including

347   *Acalyphes* Turner, 1926 + *Dirce* Prout, 1910, Lithinini, intermixed with some genera currently

348   placed in Nacophorini and Diptychini.

349   *Neobapta* Warren, 1904 and *Oenoptila* Warren, 1895 form an independent lineage

350   (unnamed E5) sister to Theriini, which in turn form a supported clade with *Lomographa*

351   (Baptini) (SH-like, UFBoot2 = 100). Likewise, we recovered *Erastria* Hübner, [1813] +

352   *Metarranthis* Warren, 1894 (unnamed E6) and *Plutodes* Guenée, [1858] + Palyadini. The IQ-

353   TREE analyses show Palyadini as a well-defined lineage, sister to *Plutodes*. However, in

354   RAxML analyses, *Eumelea* and *Plutodes* group together and Palyadini cluster with a group of

355   Caberini species. Apeirini formed a lineage with Hypochrosini, Epionini, *Sericosema* Warren,

356   1895 and *Ithysia* Hübner, [1825]. This lineage is in turn sister of African *Drepanogynis* Guenée,

357   [1858] which groups together with *Sphingomima* Warren, 1899, *Thenopa* Walker, 1855 and

358   *Hebdomophruda* Warren, 1897. Caberini are sister to an unnamed clade composed of *Trotogonia*

359   Warren, 1905, *Acrotomodes* Warren, 1895, *Acrotomia* Herrich-Schäffer, [1855] and *Pyrinia*

360   Hübner, 1818. Finally, our analyses recover a very large, well-supported clade comprising the

361   tribes Macariini, Cassymini, Abraxini, Eutoeini and Boarmiini (SH-like = 100, UFBoot2 = 99).

362   This large clade has previously been referred to informally as the "boarmiines" by Forbes (1948)

363   and Wahlberg et al. (2010). The tribe Cassymini is clearly paraphyletic: genera such as

364   *Cirrhosoma* Warren, 1905, *Berberodes* Guenée, 1858, *Hemiphricta* Warren, 1906 and

365   *Ballantiophora* Butler, 1881 currently included in Cassymini, cluster in their own clade together

366   with *Dorsifulcrum* Herbulot, 1979 and *Odontognophos* Wehrli, 1951. We were unable to include

367   Orthostixinae in the analyses, so we could not clarify the taxonomic position of this subfamily

368   with regard to its possible synonymy with Ennominae (Sihvonen et al., 2011).

369

370 **Discussion**

371

372 *Optimal partitioning scheme and support values*

373 The greedy algorithm implemented in ModelFinder to select the best-fitting partitioning scheme

374 combined the codon partitions into 26 subsets (Table 2). These results are not different from

375 previous studies that tested the performance of different data partitioning schemes and found that

376 in some cases partitioning by gene can result in suboptimal partitioning schemes and may limit

377 the accuracy of phylogenetic analyses (Rota, 2011; Lanfear et al., 2012). However, we note that

378 although the AIC and BIC values were lower when the data were partitioned by gene, the tree

379 topology recovered was nevertheless almost the same as when data were partitioned by codon

380 position, suggesting that much of the phylogenetic signal in the data is robust to partitioning

381 schemes. As would be expected, the analyses resulted in some disagreements between the

382 different measures of node support. Ultrafast bootstrap gave the highest support values, followed

383 by SH-like and finally standard bootstrap as implemented in RAxML gave the lowest. Although

384 support indices obtained by these methods are not directly comparable, differences in node

385 support of some clades can be attributed to the small number of markers, insufficient

386 phylogenetic signal or saturated divergence levels (Guindon et al., 2010).

387

388 *Current understanding of Geometridae phylogeny and taxonomic implications*

389

390 **Geometridae Leach, 1815**

391 The phylogenetic hypothesis presented in this study is by far the most comprehensive to date in

392 terms of the number of markers, sampled taxa, and geographical coverage. In total, our sample

393 includes 814 genera, thus representing 41% of the currently recognised Geometridae genera

394 (Scoble & Hausmann, 2007). Previous phylogenetic hypotheses were based mainly on the

395 European fauna and many clades were ambiguously supported due to low taxon sampling. The

396 general patterns of the phylogenetic relationships among the subfamilies recovered in our study

397 largely agrees with previous hypotheses based on morphological characters and different sets of

398 molecular markers (Holloway, 1997; Abraham, 2001; Yamamoto & Sota, 2007; Sihvonen et al.,

399 2011). However, the results of our larger dataset differ in many details and shed light on the

400 phylogenetic relationships of several, poorly resolved, small subfamilies.

401   Sterrhinae are recovered as the sister subfamily to the remaining Geometridae. This result

402   is not in concordance with Sihvonen et al. (2011), Yamamoto & Sota (2007) and Regier et al.

403   (2009), who found a sister group relationship between Sterrhinae and Larentiinae which in turn

404   were sister to the rest of Geometridae. Sihvonen et al. (2011) showed the Sterrhinae +

405   Larentiinae sister relationship with low support, while Yamamoto & Sota (2007) and Regier et

406   al. (2009) included only a few samples in their analyses. Our analyses include representatives

407   from almost all known tribes currently included in Sterrhinae and Larentiinae. The higher

408   number of markers, improved methods of analysis, the broader taxon sampling as well as the

409   stability of our results suggests that Sterrhinae are indeed the sister group to the remaining

410   Geometridae. Sterrhinae (after transfer of *Ergavia*, *Ametris* and *Macrotes*, see details below),

411   Larentiinae, Archiearinae, Geometrinae and Ennominae were highly supported as monophyletic.

412   Oenochrominae and Desmobathrinae formed polyphyletic and paraphyletic assemblages,

413   respectively. The monophylies of Oenochrominae and Desmobathrinae have long been

414   questioned. Morphological studies addressing Oenochrominae or Desmobathrinae have been

415   limited and the majority of genera have never been examined in depth. In addition, it has been

416   very difficult to establish the boundaries of these subfamilies on the basis of morphological

417   structures (Scoble & Edwards, 1990). Sihvonen et al. (2011) showed that neither Oenochrominae

418   nor Desmobathrinae were monophyletic, but these results were considered preliminary due to the

419   limited number of sampled taxa, and as a consequence no formal transfers were proposed.

420   The systematic status of Orthostixinae remains uncertain because it was not included in

421   our study. Sihvonen et al. (2011) included the genus *Naxa* Walker, 1856, formally placed in

422   Orthostixinae, and found it to be nested within Ennominae. However, only three genes were

423   successfully sequenced from this taxon, and its position in the phylogenetic tree turned out to be

424   highly unstable in our analyses. It was thus excluded from our dataset. *Orthostixis*

425   Hübner, [1823], the type genus of the subfamily, needs to be included in future analyses.

426

427   **Sterrhinae Meyrick, 1892**

428   We included 74 Sterrhinae taxa in our analyses, with all tribes recognized in Forum Herbulot

429   (2007) being represented. The recovered patterns generally agree with previous phylogenetic

430   hypotheses of the subfamily (Sihvonen, 2004, Sihvonen et al., 2011). The genera *Ergavia*

431   Walker, 1866, *Ametris* Guenée, [1858] and *Macrotes* Westwood, 1841, which currently are

432   placed in Oenochrominae were found to form a well-defined lineage within Sterrhinae with

433   strong support (SH-Like = 99 UFBoot2 = 100). These genera are distributed in the New World,

434   whereas the range of true Oenochrominae is restricted to the Australian and Oriental Regions.

435   Sihvonen et al. (2011) already found that *Ergavia* and *Afrophyla* Warren, 1895 belong to

436   Sterrhinae and suggested more extensive analyses to clarify the position of these genera, which

437   we did. *Afrophyla* was transferred to Sterrhinae by Sihvonen & Staude (2011) and *Ergavia,*

438   *Ametris* and *Macrotes* (plus *Almodes* Guenée, [1858]) will be transferred by Sihvonen et al. (in

439   prep.).

440   Cosymbiini, Timandrini, Rhodometrini and Lythriini are closely related as shown

441   previously (Sihvonen & Kaila, 2004; Õunap et al., 2008; Sihvonen et al., 2011). Cosymbiini

442   appear as sister to the Timandrini + *Traminda* Saalmüller, 1891 + *Pseudosterrha* Warren, 1888

443   and Rhodometrini + Lythriini clade. Lythriini are closely related to Rhodometrini as shown by

444   Õunap et al. (2008) with both molecular and morphological data. *Traminda* (Timandrini) and

445   *Pseudosterrha* (Cosymbiini) grouped together forming a lineage that is sister to the

446   Rhodometrini + Lythriini clade (Fig. 2).

447   Rhodostrophiini and Cyllopodini were recovered as polyphyletic with species of

448   Cyllopodini clustering within Rhodostrophiini. Similar results were recovered previously

449   (Sihvonen & Kaila, 2004; Sihvonen et al., 2011), suggesting that additional work is needed to be

450   done to clarify the status and systematic positions of these tribes. Sterrhini and Scopulini were

451   recovered as sister taxa as proposed by Sihvonen & Kaila (2004), Hausmann (2004), Õunap et al.

452   (2008) and Sihvonen et al. (2011). Our new phylogenetic hypothesis constitutes a large step

453   towards understanding the evolutionary relationships of the major lineages of Sterrhinae. Further

454   taxonomic changes and more detailed interpretation of the clades will be dealt with by Sihvonen

455   et al. (in prep.).

456

457   **Larentiinae Duponchel, 1845**

458   Larentiinae are a monophyletic entity (Fig. 3). In concordance with the results of Sihvonen et al.

459   (2011), Viidalepp (2011), Õunap et al. (2016) and Strutzenberger et al. (2017), Dyspteridini are

460   supported as sister to all other larentiines. Remarkably, *Brabirodes* Warren, 1904 forms an

461   independent lineage. Chesiadini are monophyletic and sister to all larentiines except

462　Dyspteridini, *Brabirodes* and Trichopterygini. These results do not support the suggestion by

463　Viidalepp (2006) and Sihvonen et al. (2011) that Chesiadini are sister to Trichopterygini.

464　　　　In our phylogenetic hypothesis, Asthenini are sister to the Perizomini + Melanthiini +

465　Eupitheciini clade. These results do not fully agree with Õunap et al. (2016) who found

466　Asthenini to be sister to all Larentiinae except Dyspteridini, Chesiadini, Trichopterygini and

467　Eudulini. However, our results do support the Melanthiini + Eupitheciini complex as a sister

468　lineage to Perizomini. Sihvonen et al. (2011) recovered Phileremini and Rheumapterini as well-

469　supported sister taxa. Our results suggest *Triphosa dubitata* Linnaeus 1758 (Triphosini) is sister

470　to Phileremini, with Rheumapterini sister to this clade. Cidariini were recovered as paraphyletic,

471　as the genera *Coenotephria* Prout, 1914 and *Lampropteryx* Stephens, 1831 cluster in a different

472　clade (unnamed clade L7) apart from the lineage comprising the type genus of the tribe, *Cidaria*

473　Treitschke, 1825. *Ceratodalia* Packard, 1876, currently placed in Hydriomenini and *Trichodezia*

474　Warren, 1895 nested within Cidariini. This result is not in concordance with Õunap et al. (2016),

475　who regarded this tribe to be monophyletic. Scotopterygini are sister to a lineage comprising

476　*Ptychorrhoe blosyrata* Guenée [1858], *Disclisioprocta natalata* (Walker, 1862) (placed in the

477　unnamed clade L8), Euphyiini, an unnamed clade L9 comprising the genera *Pterocypha,*

478　*Archirhoe* and *Obila*, Xanthorhoini and Cataclysmini. Euphyiini are monophyletic, but

479　Xanthorhoini are recovered as mixed with Cataclysmini. The same findings were shown by

480　Õunap et al. (2016), but no taxonomic rearrangements were proposed. Larentiini are

481　monophyletic and sister of Hydriomenini, Heterusiini, Erateinini, Stamnodini and some unnamed

482　clades (L11–14). Although with some differences, our results support the major phylogenetic

483　patterns of Õunap et al. (2016).

484　　　　Despite substantial progress, the tribal classification and phylogenetic relationships of

485　Larentiinae are far from being resolved (Õunap et al. 2016). Forbes (1948) proposed eight tribes

486　based on morphological information, Viidalepp (2011) raised the number to 23 and Õunap et al.

487　(2016) recovered 25 tribes studying 58 genera. Our study includes 23 of the currently recognized

488　tribes and 125 genera (with an emphasis on Neotropical taxa). However, the phylogenetic

489　position of many taxa remains unclear, and some tropical genera have not yet been formally

490　assigned to any tribe. Formal descriptions of these groups will be treated in detail by Brehm et al.

491　(submitted) and Õunap et al. (in prep).

492

493 **Archiearinae Fletcher, 1953**

494 The hypothesis presented in this study recovered Archiearinae as a monophyletic entity after

495 some taxonomic rearrangements are performed. This subfamily was previously considered as

496 sister to Geometrinae + Ennominae (Abraham et al., 2001), whereas Yamamoto & Sota (2007)

497 proposed them to be the sister-taxon to Orthostixinae + Desmobathrinae. Our findings agree with

498 Sihvonen et al. (2011) who recovered Archiearinae as the sister-taxon to the rest of Geometridae

499 excluding Sterrhinae and Larentiinae, although only one species was included in their study.

500 *Archiearis* Hübner, [1823] is sister to *Boudinotiana* Esper, 1787 and these taxa in turn are sister

501 to *Leucobrephos* Grote, 1874 (Fig. 4). The southern hemisphere Archiearinae require more

502 attention. Young (2006) suggested that two Australian Archiearinae genera, *Dirce* and

503 *Acalyphes*, actually belong to Ennominae. Our analyses clearly support this view and we

504 therefore propose to formally transfer *Dirce* and *Acalyphes* to Ennominae (all formal taxonomic

505 changes are provided in Table 2). Unfortunately, the South American Archiearinae genera

506 *Archiearides* Fletcher, 1953 and *Lachnocephala* Fletcher, 1953, and Mexican *Caenosynteles*

507 Dyar, 1912 (Pitkin & Jenkins 2004), could not be included in our analyses. These presumably

508 diurnal taxa may only be superficially similar to northern hemisphere Archiearinae as was the

509 case with Australian *Dirce* and *Acalyphes*.

510

511 **Desmobathrinae Meyrick, 1886**

512 Taxa placed in Desmobathrinae were formerly recognized as Oenochrominae genera with

513 slender appendages. Holloway (1996) revived Desmobathrinae from synonymy with

514 Oenochrominae and divided it into the tribes Eumeleini and Desmobathrini. Desmobathrinae

515 species have a pantropical distribution and they apparently (still) lack recognized morphological

516 apomorphies (Holloway, 1996). Our phylogenetic analysis has questioned the monophyly of

517 Desmobathrinae *sensu* Holloway because some species currently placed in Oenochrominae were

518 embedded within the group (see also Sihvonen et al., 2011), and also the phylogenetic position of

519 the tribe Eumeleini is unstable (see below). Desmobathrinae can be regarded as a monophyletic

520 group after the transfer of *Zanclopteryx, Nearcha* and *Racasta* from Oenochrominae to

521 Desmobathrinae, and the removal of Eumeleini (Table 2). Desmobathrinae as circumscribed here

522 are an independent lineage that is sister to all Geometridae except Sterrhinae, Larentiinae and

523 Archiearinae.

524   The monobasic Eumeleini has had a dynamic taxonomic history: *Eumelea* was

525   transferred from Oenochrominae *s.l.* to Desmobathrinae based on the pupal cremaster

526   (Holloway, 1996), whereas Beljaev (2008) pointed out that *Eumelea* could be a member of

527   Geometrinae based on the skeleto-muscular structure of the male genitalia. Molecular studies

528   (Sihvonen et al., 2011, Ban et al., 2018) suggested that *Eumelea* was part of Oenochrominae

529   *s.str.*, but these findings were not well-supported and no formal taxonomic changes were

530   proposed. Our analyses with IQTREE and RAxML recovered Eumeleini in two very different

531   positions, either as sister to Geometrinae (SH-like = 93.6, UFBoot2 = 71) (figs 4, 5), or as sister

532   of *Plutodes* in Ennominae (RBS = 60) (Supplemental data S3). The examination of

533   morphological details suggests that the position as sister to Geometrinae is more plausible:

534   hindwing vein M2 is present and tubular; anal margin of the hindwing is elongated; and large

535   coremata originate from the saccus (Holloway 1994, our observations). The morphology of

536   *Eumelea* is partly unusual, and for that reason we illustrate selected structures (Supplemental

537   data S4), which include for instance the following: antennae and legs of both sexes are very long;

538   forewing vein Sc (homology unclear) reaches wing margin; in male genitalia coremata are

539   extremely large and branched; uncus is cross-shaped (cruciform); tegumen is narrow and it

540   extends ventrally beyond the point of articulation with vinculum; saccus arms are extremely

541   long, looped; and vesica is with lateral rows of cornuti. However, the green geoverdin pigment

542   concentration of *Eumelea* is low in comparison to Geometrinae (Cook et al., 1994). We

543   tentatively conclude that *Eumelea* is probably indeed associated with Geometrinae. However,

544   since eleven genetic markers were not sufficient to clarify the phylogenetic affinities of *Eumelea*,

545   we provisionally place the genus as *incertae sedis* (Table 2).

546

547   **Oenochrominae Guenée, [1858]**

548   Oenochrominae has obviously been the group comprising taxa that could not easily be assigned

549   to other subfamilies. Out of the 76 genera currently assigned to Oenochrominae, our study

550   includes 25 genera (28 species). Three of these genera will be formally transferred to Sterrhinae

551   (Sihvonen et al. in prep.), three are here transferred to Desmobathrinae (see above, Table 2), and

552   eight are transferred to Epidesmiinae (see below). In agreement with Sihvonen et al. (2011),

553   Oenochrominae *s. str.* grouped together in a well-supported lineage. Genera of this clade can be

554   characterized as having robust bodies, and their male genitalia have a well-developed uncus and

555 gnathos, broad valvae and a well-developed anellus (Scoble & Edwards, 1990). Common host

556 plants are members of Proteaceae and Myrtaceae (Holloway, 1996). Our results strongly suggest

557 that the genus *Oenochroma* is polyphyletic: *O. infantilis* is sister to a clade including

558 *Dinophalus*, *Hypographa*, *Lissomma*, *Sarcinodes* and (at least) two species of *Oenochroma*. To

559 date, 20 species have been assigned to *Oenochroma* by Scoble (1999), and one additional species

560 was described by Hausmann et al. (2009), who suggested that *O. vinaria* is a species complex.

561 We agree with Hausmann et al. (2009), who pointed out the need for a major revision of

562 *Oenochroma*.

563   In our phylogenetic hypothesis, *Sarcinodes* is sister to *O. orthodesma* and *O. vinaria*, the

564 type species of *Oenochroma*. Although *Sarcinodes* and *Oenochroma* resemble each other in

565 external morphology, a sister-group relationship between these genera has not been hypothesized

566 before. The inclusion of *Sarcinodes* in Oenochrominae is mainly based on shared tympanal

567 characters (Scoble & Edwards, 1990). However, the circular form of the lacinia, which is an

568 apomorphy of Oenochrominae *s.str.* is missing or not apparent in *Sarcinodes* (Holloway, 1996).

569 In addition, *Sarcinodes* is found in the Oriental rather than in the Australian region, where all

570 *Oenochroma* species are distributed. A second clade of Oenochrominae *s.str.* comprises the

571 genera *Monoctenia*, *Onycodes*, *Parepisparis*, *Antictenia*, *Arhodia*, *Gastrophora* and *Homospora*,

572 which clustered together as the sister of *Oenochroma* and its relatives. These genera are widely

573 recognized in sharing similar structure of the male genitalia (Scoble & Edwards, 1990), yet their

574 phylogenetic relationships have never been tested. Young (2006) suggested the monophyly of

575 Oenochrominae *s.str.,* however, with a poorly resolved topology and low branch support. In her

576 study, *Parepisparis*, *Phallaria* and *Monoctenia* shared a bifid head, while in *Parepisparis* and

577 *Onychodes,* the aedeagus was lacking caecum and cornuti. Our analysis supports these

578 morphological similarities. *Monoctenia*, *Onycodes* and *Parepisparis* clustered together.

579 However, a close relationship of the genera *Antictenia*, *Arhodia*, *Gastrophora* and *Homospora*

580 has not been suggested before. Our analysis thus strongly supports the earliest definition of

581 Oenochrominae proposed by Guenée (1858), and reinforced by Cook & Scoble (1992).

582 Oenochrominae should be restricted to *Oenochroma* and related genera such as *Dinophalus*,

583 *Hypographa*, *Lissomma*, *Sarcinodes*, *Monoctenia*, *Onycodes*, *Parepisparis*, *Antictenia*, *Arhodia*,

584 *Gastrophora*, *Homospora*, *Phallaria* and *Palaeodoxa*. We consider that genera included in

585 Oenochrominae by Scoble & Edwards (1990), but recovered in a lineage separate from

586 *Oenochroma* and its close relatives in our study, belong to a hitherto unknown subfamily, which

587 is described below.

588

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

590 LSIDurn:lsid:zoobank.org:act:34D1E8F7-99F1-4914-8E12-0110459C2040

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

592 Material examined: Taxa included in the molecular phylogeny: *Ecphyas holopsara* Turner, 1929,

593 *Systatica xanthastis* Lower, 1894*, Adeixis griseata* Hudson 1903*, Dichromodes indicataria*

594 Walker 1866*, Phrixocomes* sp. Turner 1930*, Abraxaphantes perampla* Swinhoe 1890*, Epidesmia*

595 *chilonaria* Herrich-Schäffer [1855]*, Phrataria replicataria* Walker 1866.

596 Most of the slender-bodied Oenochrominae, excluded from Oenochrominae *s. str.* by Holloway

597 (1996), were recovered as an independent lineage (Fig. 4) that consists of two clades: *Ec.*

598 *holopsara* + *S. xanthastis* and *Ep. chilonaria* + five other genera. Branch support values from

599 IQ-TREE strongly support the monophyly of this clade (SH-like and UFBoot2 = 100), while in

600 RAxML the clade is moderately supported (RBS = 89). These genera have earlier been assigned

601 to Oenochrominae *s.l.* (Scoble & Edwards, 1990). However, we recovered the group as a well-

602 supported lineage independent from Oenochrominae *s. str.* and transfer them to Epidesmiinae,

603 subfam. n. (Table 2).

604 Phylogenetic position: Epidesmiinae is sister to Oenochrominae *s. str.* + *Eumelea* + Geometrinae

605 + Ennominae.

606 Short description of Epidesmiinae: Antennae in males unipectinate (exception: *Adeixis*), shorter

607 towards the apex. Pectination moderate or long. Thorax and abdomen slender (unlike in

608 Oenochrominae). Forewings with sinuous postmedial line and areole present. Forewings

609 planiform (with wings lying flat on the substrate) in resting position, held like a triangle, and

610 cover the hindwings.

611 Diagnosis of Epidesmiinae: The genera included in this subfamily form a strongly supported

612 clade with DNA sequence data from the following gene regions (exemplar *Epidesmia chilonaria*

613 Herrich-Schäffer, [1855]) ArgK (MK738299), Ca-ATPase (MK738690), CAD (MK738960),

614 COI (MK739187), EF1a (MK740168), GAPDH (MK740402), MDH (MK740974) and Nex9

615   (MK741433). A thorough morphological investigation of the subfamily, including diagnostic

616   characters, is under preparation.

617   Distribution: Most genera are distributed in the Australian region, with some species ranging into

618   the Oriental region. *Abraxaphantes* occurs exclusively in the Oriental region.

619

620   **Geometrinae Stephens, 1829**

621   The monophyly of Geometrinae is strongly supported, but the number of tribes included

622   in this subfamily is still unclear. Sihvonen et al. (2011) analyzed 27 species assigned to 11 tribes,

623   followed by Ban et al. (2018) with 116 species in 12 tribes. Ban et al. (2018) synonymized nine

624   tribes, and validated the monophyly of 12 tribes, with two new tribes Ornithospilini and

625   Agathiini being the first two clades branching off the main lineage of Geometrinae. Our study

626   (168 species) validates the monophyly of 13 tribes, eleven of which were defined in previous

627   studies: Hemitheini, Dysphaniini, Pseudoterpnini s.str., Ornithospilini, Agathiini, Aracimini,

628   Neohipparchini, Timandromorphini, Geometrini, Comibaeini, Nemoriini. One synonymization is

629   proposed: Synchlorini Ferguson, 1969 **syn. nov.** is synonymized with Nemoriini Gumppenberg,

630   1887. One tribe is proposed as new: Chlorodontoperini **trib. nov.**, and one tribe (Archaeobalbini

631   Viidalepp, 1981, **stat. rev.**) is raised from synonymy with Pseudoterpnini.

632   Ban et al. (2018) found that *Ornithospila* Warren, 1894 is sister to the rest of

633   Geometrinae, and *Agathia* Guenée, [1858] is sister to the rest of Geometrinae minus

634   *Ornithospila*. Although weakly supported, our results (with more species of *Agathia* sampled)

635   placed Ornisthospilini+Agathiini together and these tribes are the sister to the rest of

636   Geometrinae. *Chlorodontopera* is placed as an isolated lineage as shown by Ban et al. (2018).

637   Given that *Chlorodontopera* clearly forms an independent and well-supported lineage we

638   propose the description of a new tribe Chlorodontoperini.

639

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

641   LSIDurn:lsid:zoobank.org:act:0833860E-A092-43D6-B2A1-FB57D9F7988D

642   Type genus: *Chlorodontopera* Warren, 1893

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

644   *mandarinata* (Leech, 1889).

645   Some studies (Inoue, 1961; Holloway, 1996) suggested the morphological similarities of

646   *Chlorodontopera* Warren, 1893 with members of Aracimini. Moreover, Holloway (1996)

647   considered this genus as part of Aracimini. Our results suggest a sister relationship of

648   *Chlorodontopera* with a large clade comprising Aracimini, Neohipparchini, Timandromorphini,

649   Geometrini, Nemoriini and Comibaenini. Considering that our analysis strongly supports

650   *Chlorodontopera* as an independent lineage (branch support SH-like = 99 UFBoot2 = 100, RBS

651   = 99), we introduce the monobasic tribe Chlorodontoperini. This tribe can be diagnosed by the

652   combination of DNA data from six genetic markers (exemplar *Chlorodontopera discospilata*)

653   CAD (MG015448), COI (MG014735), EF1a (MG015329), GAPDH (MG014862), MDH

654   (MG014980) and RpS5 (MG015562). Ban et al. (2018) did not introduce a new tribe because the

655   relationship between *Chlorodontopera* and *Euxena* Warren, 1896 was not clear in their study.

656   This relationship was also been proposed by Holloway (1996) based on similar wing patterns.

657   Further analyses are needed to clarify the affinities between *Chlorodontopera* and *Euxena.*

658   The tribe Chlorodontoperini is diagnosed by distinct discal spots with pale margins on the

659   wings, which are larger on the hindwing; a dull reddish-brown patch is present between the

660   discal spot and the costa on the hindwing, and veins M3 and CuA1 are not stalked on the

661   hindwing (Ban et al., 2018). In the male genitalia, the socii are stout and setose and the lateral

662   arms of the gnathos are developed, not joined. Sternite 3 of the male has setal patches. Formal

663   taxonomic changes are listed in Table 2.

664   Aracimini, Neohipparchini, Timandromorphini, Geometrini and Comibaenini were recovered as

665   monophyletic groups. These results are in full agreement with Ban et al. (2018). However, the

666   phylogenetic position of *Eucyclodes* Warren, 1894 is uncertain (unnamed G2). The monophyly

667   of Nemoriini and Synchlorini is not supported. Instead, Synchlorini are nested within Nemoriini

668   (support branch SH-like = 98.3, UFBoot2 = 91, RBS = 93). Our findings are in concordance with

669   Sihvonen et al. (2011) and Ban et al. (2018), but our analyses included a larger number of

670   markers and a much higher number of taxa. Thus, we formally synonymize Synchlorini **syn.**

671   **nov.** with Nemoriini (Table 2).

672   The monophyly of Pseudoterpnini *sensu* Pitkin et al. (2007) could not be recovered.

673   Similar results were shown by Ban et al. (2018) who recovered Pseudoterpnini *s.l.* including all

674   the genera previously studied by Pitkin et al. (2007), forming a separate clade from

675   *Pseudoterpna* Hübner, [1823] + *Pingasa* Moore, 1887. Our results showed African *Mictoschema*

676 Prout, 1922 falling within Pseudoterpnini *s.str.*, and it is sister to *Pseudoterpna* and *Pingasa*. A

677 second group of Pseudoterpnini *s.l.* was recovered as an independent lineage clearly separate

678 from Pseudoterpnini *s.str.* (SH-like = 88.3, UFBoot2 = 64). Ban et al. (2018) did not introduce a

679 new tribe due to the morphological similarities and difficulty in finding apomorphies of

680 Pseudoterpnini *s.str*. In addition, their results were weakly supported. Considering that two

681 independent studies have demonstrated the paraphyly of Pseudoterpnini *sensu* Pitkin et al (2007),

682 we see no reason for retaining the wide concept of this tribe. Instead, we propose the revival of

683 the tribe status of Archaeobalbini.

684

685 Archaeobalbini Viidalepp, 1981, **status revised**

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

687 Type genus: *Archaeobalbis* Prout, 1912 (synonymized with *Herochroma* Swinhoe, 1893 in

688 Holloway (1996))

689 Material examined: *Herochroma curvata* Han & Xue, 2003*, H. baba* Swinhoe 1893*,*

690 *Metallolophia inanularia* Han & Xue, 2004*, M. cuneataria* Han & Xue, 2004*, Actenochroma*

691 *muscicoloraria* (Walker, 1862)*, Absala dorcada* Swinhoe, 1893*, Metaterpna batangensis* Hang

692 & Stüning, 2016*, M. thyatiraria* (Oberthür, 1913)*, Limbatochlamys rosthorni* Rothschild, 1894*,*

693 *Pachyodes pictaria* Moore, 1888*, Dindica para* Swinhoe, 1893*, Dindicodes crocina* (Butler,

694 1880)*, Lophophelma erionoma* (Swinhoe, 1893)*, L. varicoloraria* (Moore, 1868)*, L. iterans*

695 (Prout, 1926) and *Pachyodes amplificata* (Walker, 1862).

696

697 This lineage splits into four groups: *Herochroma* Swinhoe, 1893 + *Absala* Swinhoe, 1893 +

698 *Actenochroma* Warren, 1893 is the sister lineage of the rest of Archaeobalbini that were

699 recovered as three clades with unresolved relationships comprising the genera *Limbatochlamys*

700 Rothschild, 1894*, Psilotagma* Warren, 1894*, Metallolophia* Warren, 1895*, Metaterpna* Yazaki,

701 1992*, Dindica* Warren, 1893*, Dindicodes* Prout, 1912*, Lophophelma* Prout, 1912 and *Pachyodes*

702 Guenée, 1858. This tribe can be diagnosed by the combination of DNA data from six genetic

703 markers, see for instance *Pachyodes amplificata* CAD (MG015522), COI (MG014818), EF1a

704 (MG015409), GAPDH (MG014941), MDH (MG015057), and RpS5 (MG015638). Branch

705 support values in IQ-TREE confirm the monophyly of this clade (SH-like = 88.3, UFBoot2 =

706   64). GenBank accession numbers are shown in supplementary material. A morphological

707   diagnosis requires further research.

708   *Xenozancla* Warren, 1893 (unnamed G3) is sister to the clade comprising Dysphaniini

709   and Pseudoterpnini *s. str*. Sihvonen et al. (2011) did not include *Xenozancla* in their analyses and

710   suggested a sister relationship of Dysphaniini and Pseudoterpnini, but with low support.

711   According to Ban et al. (2018), *Xenozancla* is more closely related to Pseudoterpnini *s.str*. than

712   to Dysphaniini. However, due to low support, Ban et al. (2018) did not propose a taxonomic

713   assignment for *Xenozancla,* which is currently not assigned to a tribe. Although our IQ-TREE

714   results show that *Xenozancla* is sister to a clade comprising Dysphaniini and Pseudoterpnini *s*.

715   *str.*, the RAxML analysis did not recover the same phylogenetic relationships. Instead,

716   Dysphaniini + Pseudoterpnini *s.str*. are found to be sister taxa, but *Xenozancla* is placed close to

717   *Rhomborista monosticta* (Wehrli, 1924). As in Ban et al. (2018), our results do not allow us to

718   reach a conclusion about the phylogenetic affinities of these tribes, due to low support of nodes.

719   The Australian genus *Crypsiphona* Meyrick, 1888 (unnamed G4) was placed close to

720   Hemitheini. *Crypsiphona* has been assigned to Pseudoterpnini (e. g. Pitkin et al. 2007, Õunap &

721   Viidalepp 2009), but is recovered as a separate lineage in our tree. Given the isolated position of

722   *Crypsiphona*, the designation of a new tribe could be considered, but due to low support of nodes

723   in our analyses, further information (including morphology) is needed to confirm the

724   phylogenetic position of this genus. In our phylogenetic hypothesis, a large clade including the

725   former tribes Lophochoristini, Heliotheini, Microloxiini, Thalerini, Rhomboristini, Hemistolini,

726   Comostolini, Jodini and Thalassodini is recovered as sister to the rest of Geometrinae. These

727   results are in full agreement with Ban et al. (2018), who synonymized all of these tribes with

728   Hemitheini. Although the monophyly of Hemitheini is strongly supported, our findings

729   recovered only a few monophyletic subtribes. For example, genera placed in Hemitheina were

730   intermixed with those belonging to Microloxiina, Thalassodina and Jodina. Moreover, many

731   genera which were unassigned to tribe, were recovered as belonging to Hemitheini. Our findings

732   recovered *Lophostola* Prout, 1912 as sister to all Hemitheini. These results are quite different

733   from those found by Ban et al. (2018) who suggested Rhomboristina as being sister to the rest of

734   Hemitheini. In contrast, our results recovered Rhomboristina mingled with Hemistolina. These

735   different results are probably influenced by the presence of African and Madagascan *Lophostola*

736   in our analysis. We feel that the subtribe concept is not practical thus do not advocate its use in

737   geometrid classification.

738

739   **Ennominae Duponchel, 1845**

740   Ennominae are the most species-rich subfamily of geometrids. The loss of vein M2 on the

741   hindwing is probably the best apomorphy (Holloway, 1993), although this character does not

742   occur in a few ennomine taxa (Staude, 2001; Skou & Sihvonen, 2015). Ennominae are a

743   morphologically highly diverse subfamily, and attempts to find further synapomorphies shared

744   by all major tribal groups have failed.

745   The number of tribes as well as phylogenetic relationships among tribes are still debated

746   (see Skou & Sihvonen, 2015 for an overview). Moreover, the taxonomic knowledge of this

747   subfamily in tropical regions is still poor. Holloway (1993) recognized 21 tribes, Beljaev (2006)

748   24 tribes, and Forum Herbulot (2007) 27 tribes. To date, four molecular studies have

749   corroborated the monophyly of Ennominae (Yamamoto & Sota, 2007; Wahlberg et al., 2010;

750   Õunap et al., 2011, Sihvonen et al. 2011), with Young (2006) being the only exception who

751   found Ennominae paraphyletic. Moreover, three large-scale taxonomic revisions (without a

752   phylogenetic hypothesis) were published by Pitkin (2002) for the Neotropical region, Skou &

753   Sihvonen (2015) for the Western Palaearctic region, and Holloway (1994) for Borneo. More

754   detailed descriptions of taxonomic changes in Ennominae will be given by Brehm et al.

755   (submitted) and Murillo-Ramos et al. (in prep.). We here discuss general patterns and give

756   details for taxonomic acts not covered in the other two papers.

757   Our findings recover Ennominae as a monophyletic entity, but results were not highly

758   supported in RAxML (RBS = 67) results compared to IQ-TREE (SH-Like =100, UFBoot2 = 99).

759   The lineage comprising Geometrinae and Oenochrominae is recovered as the sister clade of

760   Ennominae. In previous studies, Wahlberg et al. (2010) sampled 49 species of Ennominae,

761   Õunap et al. (2011) sampled 33 species, and Sihvonen et al. (2011) 70 species including up to

762   eight markers per species. All these studies supported the division of Ennominae into

763   "boarmiine" and "ennomine" moths (Holloway, 1994). This grouping was proposed by Forbes

764   (1948) and Holloway (1994), who suggested close relationships between the tribes Boarmiini,

765   Macariini, Cassymini and Eutoeini based on the bifid pupal cremaster and the possession of a

766   fovea in the male forewing. The remaining tribes were defined as "ennomines" based on the loss

767   of a setal comb on male sternum A3 and the presence of a strong furca in male genitalia. Both

768   Wahlberg et al. (2010) and Sihvonen et al. (2011) found these two informal groupings to be

769   reciprocally monophyletic.

770   In our analyses, 653 species with up to 11 markers were sampled, with an emphasis on

771   Neotropical taxa, which so far had been poorly represented in the molecular phylogenetic

772   analyses. Our results recovered the division into two major subclades, a core set of ennomines in

773   a well-supported clade, and a poorly supported larger clade that includes the "boarmiines"

774   among four other lineages usually thought of as "ennomines". The traditional "ennomines" are

775   thus not found to be monophyletic in our analyses, questioning the utility of such an informal

776   name. Our phylogenetic hypothesis supports the validation of numerous tribes proposed

777   previously, in addition to several unnamed clades. We validate 23 tribes (Forum Herbulot, 2007;

778   Skou & Sihvonen, 2015): Gonodontini, Gnophini, Odontoperini, Nacophorini, Ennomini,

779   Campaeini, Alsophilini, Wilemaniini, Prosopolophini, Diptychini, Theriini, Plutodini, Palyadini,

780   Hypochrosini, Apeirini, Epionini, Caberini, Macariini, Cassymini, Abraxini, Eutoeini and

781   Boarmiini. We hereby propose one new tribe: Drepanogynini **trib. nov.** (Table 2). Except for the

782   new tribe, most of the groups recovered in this study are in concordance with previous

783   morphological classifications (Holloway, 1993; Beljaev, 2006, 2016; Forum Herbulot, 2007;

784   Skou & Sihvonen, 2015).

785   Five known tribes and two further unnamed lineages (E1, E2 in figure 6) form the core

786   Ennominae: Gonodontini, Gnophini, Odontoperini, Nacophorini and Ennomini. Several

787   Neotropical clades that conflict with the current tribal classification of Ennominae will be

788   described as new tribes by Brehm et al. (submitted). Gonodontini and Gnophini are recovered as

789   sister taxa. Gonodontini was defined by Forbes (1948) and studied by Holloway (1994), who

790   showed synapomorphies shared by *Gonodontis* Hübner, [1823], *Xylinophylla* Warren, 1898 and

791   *Xenimpia* Warren, 1895. Our results recovered the genus *Xylinophylla* as sister of *Xenimpia* and

792   *Psilocladia* Warren, 1898. *Psilocladia* is an African genus currently unassigned to tribe (see

793   Sihvonen et al., 2015 for details). Considering the strong support and that the facies and

794   morphology are somewhat similar to other analysed taxa in Gonodontini, we formally include

795   *Psilocladia* in Gonodontini (Table 2). Gnophini are monophyletic and we formally transfer the

796   African genera *Oedicentra* Warren, 1902 and *Hypotephrina* Janse, 1932, from unassigned to

797   Gnophini (Table 2). The total number of species, and number of included genera in Gnophini are

798 still uncertain (Skou & Sihvonen, 2015). Based on morphological examination, Beljaev (2007,

799 2016) treated Angeronini as a synonym of Gnophini. The costal projection on male valva bearing

800 a spine or group of spines was considered as a synapomorphy of the group. Using molecular

801 data, Yamamoto & Sota (2007) showed a close phylogenetic relationship between *Angerona*

802 Duponchel, 1829 (Angeronini) and *Chariaspilates* Wehrli, 1953 (Gnophini). Similar results were

803 shown by Sihvonen et al. (2011) who recovered *Angerona* and *Charissa* Curtis, 1826 as sister

804 taxa, and our results also strongly support treating Angeronini as synonym of Gnophini.

805   Holloway (1993) suggested close affinities among Nacophorini, Azelinini and

806 Odontoperini on the basis of larval characters. In a morphology-based phylogenetic study, Skou

807 & Sihvonen (2015) suggested multiple setae on the proleg on A6 of the larvae as a

808 synapomorphy of the group. Our results also support a close relationship of Nacophorini,

809 Azelinini and Odontoperini. These clades will be treated in more detail by Brehm et al.

810 (submitted).

811   Following the ideas of Pitkin (2002), Beljaev (2008) synonymized the tribes

812 Ourapterygini and Nephodiini with Ennomini. He considered the divided vinculum in male

813 genitalia and the attachment of muscles *m*3 as apomorphies of the Ennomini, but did not provide

814 a phylogenetic analysis. Sihvonen et al. (2011) supported Beljaev's assumptions and recovered

815 *Ennomos* Treitschke, 1825 (Ennomini), *Ourapteryx* Leach, 1814 (Ourapterygini) and *Nephodia*

816 Hübner, [1823] (Nephodiini) as belonging to the same clade. Our comprehensive analysis

817 confirms those previous findings and we agree with Ennomini as the valid tribal name for this

818 large clade.

819   Campaeini, Alsophilini, Wilemaniini and Prosopolophini grouped together in a well-

820 supported clade (SH-like = 100, UFBoot2 = 99). Previous molecular analyses have shown an

821 association of Colotoini [= Prosopolophini] and Wilemaniini (Yamamoto & Sota, 2007;

822 Sihvonen et al., 2011), although no synapomorphies are known to support synonymization (Skou

823 & Sihvonen, 2015). The Palaearctic genera *Compsoptera* Blanchard, 1845, *Apochima* Agassiz,

824 1847, *Dasycorsa* Prout, 1915, *Chondrosoma* Anker, 1854 and *Dorsispina* Nupponen &

825 Sihvonen, 2013, are potentially part of the same complex (Skou & Sihvonen, 2015, Sihvonen

826 pers. obs.), but they were not included in the current study. Campaeini is a small group including

827   four genera with Oriental, Palaearctic and Nearctic distribution, apparently closely related to

828   Alsophilini and Prosopolophini, but currently accepted as a tribe (Forum Herbulot, 2007;

829   Sihvonen & Skou, 2015). Our results support the close phylogenetic affinities among these

830   tribes, but due to the limited number of sampled taxa, we do not propose any formal changes.

831   The genus *Declana* Walker, 1858 is recovered as an isolated clade sister to Diptychini.

832   This genus is endemic to New Zealand, but to date has not been assigned to tribe. According to

833   our results, *Declana* could well be defined as its own tribe. However, the delimitation of this

834   tribe is beyond the scope of our paper and more genera from Australia and New Zealand should

835   first be examined. A close relationship between Nacophorini and Lithinini was suggested by

836   Pitkin (2002), based on the similar pair of processes of the anellus in the male genitalia. Pitkin

837   also noted a morphological similarity in the male genitalia (processes of the juxta) shared by

838   Nacophorini and Diptychini. In a study of the Australasian fauna, Young (2008) suggested the

839   synonymization of Nacophorini and Lithinini. This was further corroborated by Sihvonen et al.

840   (2015) who found that Diptychini were nested within some Nacophorini and Lithinini. However,

841   none of the studies proposed formal taxonomic changes because of limited taxon sampling. In

842   contrast, samples in our analyses cover all biogeographic regions and the results suggest that true

843   Nacophorini is a clade which comprises almost exclusively New World species. This clade is

844   clearly separate from Old World "nacophorines" (cf. Young, 2003) that are intermixed with

845   Lithinini and Diptychini. We here formally transfer Old World nacophorines to Diptychini and

846   synonymize Lithinini **syn. nov.** with Diptychini (Table 2). Further formal taxonomic changes in

847   the Nacophorini complex are provided by Brehm et al. (submitted).

848   *Theria* Hübner, [1825], the only representative of Theriini in this study, clustered

849   together with *Lomographa* Hübner, [1825] (Baptini in Skou & Sihvonen, 2015)*,* in a well-

850   supported clade, agreeing with the molecular results of Sihvonen et al. (2011). The placement of

851   *Lomographa* in Caberini (Rindge, 1979; Pitkin, 2002) is not supported by our study nor by that

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

853   show that one Neotropical and one Palaearctic *Lomographa* species indeed group together. Our

854   results show that Caberini are not closely related to the Theriini + Baptini clade, unlike in earlier

855   morphology-based hypotheses (Rindge, 1979; Pitkin 2002). Morphologically, Theriini and

856   Baptini are dissimilar, therefore we recognize them as valid tribes (see description and

857   illustrations in Skou & Sihvonen, 2015).

858   According to our results, 11 molecular markers were not enough to infer phylogenetic

859   affinities of Plutodini (represented by one species of *Plutodes*). Similar results were found by

860   Sihvonen et al. (2011), who in some analyses recovered *Plutodes* as sister of *Eumelea*. Our

861   analyses are congruent with those findings. IQ-TREE results suggest that *Plutodes* is sister to

862   Palyadini, but RAxML analyses recovered *Eumelea* as the most probable sister of *Plutodes*.

863   Given that our analyses are not in agreement on the sister-group affinities of *Plutodes*, we do not

864   make any assumptions about its phylogenetic position. Instead we emphasize that further work

865   needs to be done to clarify the phylogenetic positions of *Plutodes* and related groups.

866   Hypochrosini is only recovered in a well-defined lineage if the genera *Apeira* Gistl, 1848

867   (Apeirini), *Epione* Duponchel, 1829 (Epionini), *Sericosema* (Caberini), *Ithysia* (Theriini),

868   *Capasa* Walker, 1866 (unassigned) and *Omizodes* Warren, 1894 (unassigned) were transferred to

869   Hypochrosini. Skou & Sihvonen (2015) already suggested a close association of Epionini,

870   Apeirini and Hypochrosini. We think that synonymising these tribes is desirable. However, due

871   to the limited number of sampled taxa we do not propose any formal changes until more data

872   becomes available. We do suggest, however, formal taxonomic changes for the genera *Capasa*

873   and *Omizodes* from unassigned to Hypochrosini (Table 2).

874   The southern African genus *Drepanogynis* is paraphyletic and has earlier been classified

875   as belonging in Ennomini, and later in Nacophorini (Krüger 2002). In our phylogeny, it is

876   intermixed with the genera *Sphingomima* Warren, 1899, and *Thenopa* Walker, 1855.

877   *Hebdomophruda errans* Prout, 1917 also clusters together with these taxa, apart from other

878   *Hebdomophruda* Warren, 1897 species, which suggests that this genus is polyphyletic. These

879   genera form a clade sister to the lineage that comprises several Hypochrosini species.

880   Considering that our analysis strongly supports this clade, we place *Thenopa*, *Sphingomina* and

881   *Drepanogynis* in a tribe of their own.

882

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

884   LSIDurn:lsid:zoobank.org:act:AA384988-009F-4175-B98C-6209C8868B93

885   Type genus: *Drepanogynis* Guenée, [1858]

886

887   The African genera *Thenopa*, *Sphingomima* and *Drepanogynis* appear as a strongly supported

888   lineage (SH-like, UFBoot2 and RBS = 100). Krüger (1997, p. 259) proposed "Boarmiini and

889   related tribes as the most likely sister group" for *Drepanogynis*, whereas more recently

890   *Drepanogynis* was classified in the putative southern hemisphere Nacophorini (Krüger, 2014;

891   Sihvonen et al., 2015). In the current phylogeny, *Drepanogynis* is isolated from Nacophorini

892   *sensu stricto* and from other southern African genera that have earlier been considered to be

893   closely related to it (Krüger 2014 and references therein). The other southern African genera

894   appeared to belong to Diptychini in our study. The systematic position of *Drepanogynis*

895   *tripartita* (Warren, 1898) has earlier been analysed in a molecular study (Sihvonen et al., 2015).

896   The taxon grouped together with the Palaearctic species of the tribes Apeirini, Theriini, Epionini

897   and putative Hypochrosini. Sihvonen et al. (2015) noted that *Argyrophora trofonia* (Cramer,

898   [1779]) (representing *Drepanogynis* group III *sensu* Krüger, 1999) and *Drepanogynis tripartita*

899   (representing *Drepanogynis* group IV *sensu* Krüger, 2002) did not group together, but no formal

900   changes were proposed. Considering that the current analysis strongly supports the placement of

901   *Drepanogynis* and related genera in an independent lineage, and the aforementioned taxa in the

902   sister lineage (Apeirini, Theriini, Epionini and putative Hypochrosini) have been validated at

903   tribe-level, we place *Drepanogynis* and related genera in a tribe of their own.

904   Material examined and taxa included: *Drepanogynis mixtaria* Guenée, [1858], *D.*

905   *tripartita*, *D. determinata* (Walker, 1860), *D. arcuifera* Prout, 1934, *D. arcuatilinea* Krüger,

906   2002, *D. cnephaeogramma* (Prout, 1938), *D. villaria* (Felder & Rogenhofer, 1875),

907   "*Sphingomima*" *discolucida* Herbulot, 1995 (genus combination uncertain, see taxonomic notes

908   below), *Thenopa diversa* Walker, 1855, "*Hebdomophruda*" *errans* Prout, 1917 (genus

909   combination uncertain, see taxonomic notes below).

910   Taxonomic notes: We choose *Drepanogynis* Guenée, [1858] as the type genus for

911   Drepanogynini, although it is not the oldest valid name (ICZN Article 64), because extensive

912   literature has been published on *Drepanogynis* (Krüger 1997, 1998, 1999, 2014), but virtually

913   nothing exists on *Thenopa,* except the original descriptions of its constituent species. Current

914   results show the urgent need for more extensive phylogenetic studies within Drepanogynini.

915   *Thenopa* and *Sphingomima* are embedded within *Drepanogynis*, rendering it paraphyletic, but

916   our taxon coverage is too limited to propose formal changes in this species-rich group.

917   Drepanogynini, as defined here, are distributed in sub-Saharan Africa. *Drepanogynis sensu*

918   Krüger (1997, 1998, 1999, 2014) includes over 150 species and it ranges from southern Africa to

919   Ethiopia (Krüger 2002, Vári et al. 2002), whereas the genera *Sphingomima* (10 species) and

920   *Thenopa* (4 species) occur in Central and West Africa (Scoble 1999). *Sphingomima* and *Thenopa*

921   are externally similar, so the recovered sister-group relationship in the current phylogeny

922   analysis was anticipated. In the current analysis, *Hebdomophruda errans* Prout, 1917 is isolated

923   from other analysed *Hebdomophruda* species (the others are included in Diptychini),

924   highlighting the need for additional research. Krüger (1997, 1998) classified the genus

925   *Hebdomophruda* into seven species groups on the basis of morphological characters, and *H.*

926   *errans* group is one of them (Krüger 1998). We do not describe a new genus for the taxon

927   *errans*, nor do we combine it with any genus in the Drepanogynini, highlighting its uncertain

928   taxonomic position (*incertae sedis*) pending more research. In the current analysis, *Sphingomima*

929   *discolucida* Herbulot, 1995 is transferred from unassigned tribus combination to Drepanogynini,

930   but as the type species of *Sphingomima* (*S. heterodoxa* Warren, 1899) was not analysed, we do

931   not transfer the entire genus *Sphingomima* into Drepanogynini. We highlight the uncertain

932   taxonomic position of the taxon *discolucida*, acknowledging that it may eventually be included

933   again in *Sphingomima* if the entire genus should be transferred to Drepanogynini.

934

935   Diagnosis: Drepanogynini can be diagnosed by the combination of DNA data with up to 11

936   genetic markers (exemplar *Drepanogynis mixtaria* Guenée, [1858]) ArgK (MK738841), COI

937   (MK739615), EF1a (MK739960), IDH (MK740862), MDH (MK741181), Nex9 (MK741630),

938   RpS5 (MK741991) and Wingless (MK742540). In the light of our phylogenetic results, the

939   *Drepanogynis* group of genera, as classified earlier (Krüger 2014), is split between two unrelated

940   tribes (Drepanogynini and Diptychini). More research is needed to understand how other

941   *Drepanogynis* species and the *Drepanogynis* group of genera *sensu* Krüger (1997, 1998, 1999,

942   2014) (at least 11 genera), should be classified.

943   Boarmiini are the sister group to a clade that comprises Macariini, Cassymini, Abraxini

944   and Eutoeini. We found that many species currently assigned to Boarmiini are scattered

945   throughout Ennominae. Boarmiini *s. str.* are strongly supported but are technically not

946   monophyletic because of a large number of genera which need to be formally transferred from

947   other tribes to Boarmiini (see Brehm et al., submitted for Neotropical taxa and Murillo-Ramos et

948 al., in prep. for other taxa). The results are principally in concordance with Jiang et al. (2017),

949 who supported the monophyly of Boarmiini but with a smaller number of taxa.

950   The divided valva in male genitalia was suggested as a synapomorphy of Macariini +

951 Cassymini + Eutoeini by Holloway (1994). In addition, he proposed the inclusion of Abraxini in

952 Cassymini. Although our findings support a close relationship, this group requires more study

953 and a more extensive sampling effort. Similar findings were provided by Jiang et al. (2017) who

954 suggested more extensive sampling to study the evolutionary relationships of these tribes.

955

956 **Orthostixinae Meyrick, 1892**

957   Orthostixinae were not included in our study. Sihvonen et al. (2011) showed this

958 subfamily as deeply embedded within Ennominae, but unfortunately it was not represented by

959 the type genus of the tribe. These results agree with Holloway (1996) who examined *Orthostixis*

960 Hübner, [1823] and suggested the inclusion in Ennominae despite the full development of

961 hindwing vein M2, the presence of a forewing areole and the very broad base of the tympanal

962 ansa. We sampled the species *Naxa textilis* (Preyer, 1884) and *Orthostixis cribraria* (Hübner,

963 1796), but only three and one marker were successfully sequenced for these samples,

964 respectively. We included these species in the preliminary analyses but results were so unstable

965 that we excluded them from the final analysis. Further research including fresh material and

966 more genetic markers are needed to investigate the position of Orthostixinae conclusively.

967

968 **Conclusions**

969 This study elucidated important evolutionary relationships among major groups within

970 Geometridae. The monophyly of the subfamilies and the most widely accepted tribes were

971 tested. We found strong support for the traditional concepts of Larentiinae, Geometrinae and

972 Ennominae. Sterrhinae also becomes monophyletic when *Ergavia*, *Ametris* and *Macrotes*,

973 currently placed in Oenochrominae, are formally transferred to Sterrhinae. The concepts of

974 Oenochrominae and Desmobathrinae required major revision and, after appropriate

975 rearrangements, these groups also form monophyletic subfamily-level entities. Archiearinae are

976 monophyletic with the transfer of *Dirce* and *Acalyphes* to Ennominae. We treat Epidesmiinae as

977 a new subfamily.

978   This study proposes the recognition of eight monophyletic geometrid subfamilies. Many

979 geometrid tribes were recovered para- or polyphyletic. We attempted to address the needed

980 taxonomic changes, in order to favor taxonomic stability of the subfamilies and many tribes,

981 even if in an interim way, to allow other researchers to use an updated higher-taxonomic

982 structure that better reflects our current understanding of geometrid phylogeny. Although we

983 included a large number of new taxa, in our study, many clades remain poorly represented. This

984 is particularly true for taxa from tropical Africa and Asia. tribes in special need of reassessment

985 include Eumeleini, Plutodini, Eutoeini, Cassymini and Abraxini. We hope the phylogenetic

986 hypotheses shared here will open new paths of inquiry across Geometridae. Morphological

987 synapomorphies have not yet been identified for many of the re- and newly defined higher taxa

988 circumscribed by our 11-gene data set. Likewise, there is great need, across the family, to begin

989 the work of mapping behavioral and life history attributes to the clades identified in this work.

990

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1217

Figure 1(on next page)

Evolutionary relationships in major groups of the family Geometridae.

Numbers above branches are SH-aLRT support (%) / ultrafast bootstrap support, UFBoot2(%), for nodes to the right of the numbers. Values of SH >= 80 and UFBoot2>= 95 indicate well-supported clades (Trifinopoulos & Minh, 2018). *Formal taxonomic treatment will be dealt with in Sihvonen et al. in prep. § Epidesmiinae **subfam. nov.** See Oenochrominae section for more details.

100/100 — Sematuridae

99.2/92

GB_Geo_019_UN_Gen_sp — Unnamed

92.6/71

PseBi1_PSEUDOB_*Pseudobiston pinratanai* — Pseudobistonidae

26.9/40

100/100 — Epicopeiidae

98.7/97 — Uraniidae

99.2/92

99.2/98 — Sterrhinae+Oenochrominae*

100/100

100/100 — Larentiinae

74.5/87

100/100 — Archiearinae

99.5/100

99/98 — Desmobathrinae+Oenochrominae

81/77

100/100 — Epidesmiinae §

100/99

100/92 — Oenochrominae *s.str.*

89.9/84

MM13433_DESM_*Eumelea ludovicata inc. sed.*

93.6/71

100/100 — Geometrinae

38.1/69

100/99 — Ennominae

0.2

Figure 2(on next page)

Evolutionary relationships of the subfamily Sterrhinae.

Numbers above branches are SH-aLRT support (%) / ultrafast bootstrap support, UFBoot2(%), for nodes to the right of the numbers. Values of SH >= 80 and UFBoot2>= 95 indicate well-supported clades (Trifinopoulos & Minh, 2018). *Formal taxonomic treatment will be dealt with in Sihvonen et al. in prep.

Figure 3 (on next page)

Evolutionary relationships of the subfamily Larentiinae.

Numbers above branches are SH-aLRT support (%) / ultrafast bootstrap support, UFBoot2(%), for nodes to the right of the numbers. Values of SH >= 80 and UFBoot2>= 95 indicate well-supported clades (Trifinopoulos & Minh, 2018).

Sematuridae
Unnamed
Pseudobistonidae

Epicopeiidae
Uraniidae
Sterrhinae+Oenochrominae*

Larentiinae

Archiearinae

Other Geometridae subfamilies

Figure 4(on next page)

Phylogenetic relationships of the subfamilies Archierinae, Desmobathrinae, Epidesmiinae subfam. nov., Oenochrominae.

Numbers above branches are SH-aLRT support (%) / ultrafast bootstrap support, UFBoot2(%), for nodes to the right of the numbers. Values of SH >= 80 and UFBoot2>= 95 indicate well-supported clades (Trifinopoulos & Minh, 2018). Taxonomic changes are indicated by a symobolized arrow >.

Sematuridae
Unnamed
Pseudobistonidae
Epicopeiidae
Uraniidae
Sterrhinae+Oenochrominae*
Larentiinae

Archiearinae

Desmobathrinae+Oenochrominae

Epidesmiinae §

Oenochrominae s.str.

Geometrinae
Ennominae

0.2

Figure 5(on next page)

Evolutionary relationships of the subfamily Geometrinae.

Numbers above branches are SH-aLRT support (%) / ultrafast bootstrap support, UFBoot2(%), for nodes to the right of the numbers. Values of SH >= 80 and UFBoot2>= 95 indicate well-supported clades (Trifinopoulos & Minh, 2018).Taxonomic changes are indicated by a symobolized arrow >.

Desmobathrinae+Oenochrominae
Epidesmiinae §
Oenochrominae s.str.

MM13433 DESM *Eumelea ludovicata*

IOZ_LEP_M_10737 ORNI *Ornithospila esmeralda*
IOZ_LEP_M_21569 ORNI *Ornithospila submonstrans*
Ornithospilini

V8 AGAT *Agathia confuscata*
USNM703073 AGAT *Agathia kuehni*
MM14745 AGAT *Agathia sp*
IOZ_LEP_M_13655 AGAT *Agathia gemma*
IOZ_LEP_M_11632 AGAT *Agathia carissima*
IOZ_LEP_M_13320 AGAT *Agathia visenda*
Agathiini

IOZ_LEP_M_6623 UN>CHLO *Chlorodontopera discospilata*
IOZ_LEP_M_16463 UN>CHLO *Chlorodontopera mandarinata*
Chlorodontoperini **trib.nov.**

IOZ_LEP_M_13773 ARAC *Paramaxates taiwana*
IOZ_LEP_M_13974 ARAC *Paramaxates vagata*
IOZ_LEP_M_8087 ARAC *Dooabia puncticostata*
IOZ_LEP_M_21881 ARAC *Dooabia viridata*
MM13434 ARAC *Aracima serrata*
Aracimini

IOZ_LEP_M_20637 NEO *Chlororithra fea*
4939 NEO *Chlororithra missioniaria*
IOZ_LEP_M_16577 NEO *Neohipparchus vallata*
IOZ_LEP_M_17085 NEO *Chloroglyphica glaucochrista*
NJ13771 NEO *Chloroglyphica sp*
Neohipparchini

IOZ_LEP_M_16532 UN *Iotaphora iridicolor*
IOZ_LEP_M_17032 UN *Iotaphora admirabilis*
Unnamed G1

MM13435 TIMANDRO *Timandromorpha discolor*
IOZ_LEP_M_8133 TIMANDRO *Timandromorpha discolor*
IOZ_LEP_M_17041 TIMANDRO *Timandromorpha enervata*
IOZ_LEP_M_871 TIMANDRO *Timandromorpha olivaria*
Timandromorphini

IOZ_LEP_M_10550 GEOM *Mixochlora vittata*
IOZ_LEP_M_20201 GEOM *Chlorozancla falcatus*
IOZ_LEP_M_13704_GEOM *Tanaorhinus kina*
NJ17078_GEOM *Tanaorhinus kina*
IOZ_LEP_M_9212 GEOM *Geometra fragilis*
IOZ_LEP_M_14347 GEOM *Geometra sinoisaria*
IOZ_LEP_M_16551_GEOM *Geometra smaragdus*
IOZ_LEP_M_1650T_GEOM *Geometra glaucaria*
IOZ_LEP_M_16429_GEOM *Geometra euryagyia*
IOZ_LEP_M_16550_GEOM *Geometra symaria*
MM01146_GEOM *Geometra papilionaria*
IOZ_LEP_M_16545 GEOM *Tanaorhinus luteivirgatus*
IOZ_LEP_M_10029 GEOM *Tanaorhinus viridiluteata*
IOZ_LEP_M_4682 GEOM *Geometra ussuriensis*
IOZ_LEP_M_17065 GEOM *Geometra sponsaria*
IOZ_LEP_M_16499 GEOM *Geometra neovalida*
IOZ_LEP_M_16498 GEOM *Geometra valida*
IOZ_LEP_M_16552 GEOM *Geometra albovenaria*
Geometrini

IOZ_LEP_M_190 COMI *Protuliocnemis castalaria*
MM00223 UN *Argyrorapha moderata*
IOZ_LEP_M_18920 COMI *Linguisaccus subhyalina*
Hes467 COMI *Thetidia undulilinea*
IOZ_LEP_M_14403 COMI *Comibaena auromaculata*
IOZ_LEP_M_5262 COMI *Comibaena nigromacularia*
MM14710 COMI *Comibaena bajularia*
MM14751 COMI *Comibaena attenuata*
Hes427 COMI *Comibaena nr flavitaenia*
IOZ_LEP_M_4409 COMI *Thetidia albocostaria*
IOZ_LEP_M_11258 COMI *Thetidia chlorophyllaria*
EO0329 COMI *Thetidia smaragdaria*
Comibaenini

IOZ_LEP_M_4692 NEMO>UN *Eucyclodes aphrodite*
IOZ_LEP_M_4786 NEMO>UN *Eucyclodes difficta*
Unnamed G2

CNC541241 SYNC>NEMO *Synchlora aerata*
AH3854 SYNC>NEMO *Synchlora gerularia*
CNC580945 NEMO *Nemoria bistriaria*
gb_ID_15177 NEMO *Rhodochlora roseipalpis* group
gb_ID_15101 NEMO *Lissochlora latuta*
gb_ID_17689 NEMO *Nemoria nr nigrisquama*
gb_ID_17533 NEMO *Chavarriella nr fallax*
gb_ID_49457 NEMO *Hyalochlora nadia*
AH7057_NEMO *Nemoria nr erina*
gb_ID_17183 NEMO *Pyrochlora rhanis*
Pe_Geo_0004 UN *Hydata* sp
GB_Geo_030 UN *Hydata* sp
Pe_Geo_3043 UN *Hydata* sp
gb_ID_17485 NEMO *Phrudocentra affinis*
IZBE0121639 NEMO *Assachlora julietae*
Br_Geo_0070 UN *Tachyphyle acuta*
gb_ID_19233 NEMO *Tachychlora nr amilletes*
gb_ID_49684_NEMO *Neagathia corruptata*
CNC573668 NEMO *Dichorda iridaria*
AK_Geo_CR_0003 NEMO *Dichorda obliquata*
Nemoriini=Synchlorini

IOZ_LEP_M_8109 PSEU>ARCH *Herochroma curvata*
IOZ_LEP_M_9394 PSEU>ARCH *Herochroma baba*
IOZ_LEP_M_8194 PSEU>ARCH *Absala dorcada*
IOZ_LEP_M_9019 PSEU>ARCH *Actenochroma muscicoloraria*
IOZ_LEP_M_14105 PSEU>ARCH *Metallolophia inanularia*
IOZ_LEP_M_20202 PSEU>ARCH *Metallolophia cuneataria*
IOZ_LEP_M_14603 PSEU>ARCH *Metaterpna batangensis*
IOZ_LEP_M_16584 PSEU>ARCH *Metaterpna thyatiraria*
IOZ_LEP_M_16511 PSEU>ARCH *Limbatochlamys rosthorni*
IOZ_LEP_M_13684 PSEU>ARCH *Psilotagma pictaria*
IOZ_LEP_M_4175 PSEU>ARCH *Psilotagma decorata*
IOZ_LEP_M_1312 PSEU>ARCH *Dindica para*
IOZ_LEP_M_2263 PSEU>ARCH *Dindicodes crocina*
IOZ_LEP_M_10848 PSEU>ARCH *Lophophelma erionoma*
IOZ_LEP_M_15933 PSEU>ARCH *Pachyodes amplificata*
IOZ_LEP_M_13670 PSEU>ARCH *Lophophelma varicoloraria*
IOZ_LEP_M_4620 PSEU>ARCH *Lophophelma iterans*
Archaeobalbini **stat.rev.**

IOZ_LEP_M_20204 UN *Xenozancla versicolor*
Unnamed G3

IOZ_LEP_M_11834 DYSPH *Dysphania militaris*
MM14748_DYSPH *Dysphania malayanus*
Dysphaniini

AH7532_PSEU *Pseudoterpna coronillaria*
PS236 PSEU *Mictoschema swierstrai*
SH0387 PSEU *Pingasa commutata*
IOZ_LEP_M_12816 PSEU *Pingasa rufofasciata*
USNM459884 PSEU *Pingasa chlora*
Pseudoterpnini

MM07510 PSEU>UN *Crypsiphona ocultaria*
Unnamed G4

Hes525 UN *Lophostola nr annuligera*
Hes631 UN *Lophostola cara*
IOZ_LEP_M_8321 HEMIT *Rhomborista monosticta*
GB_Geo_083 LOPH *Lophochorista nr curtifascia*
PS258 UN *Rhadinomphax divincta*
PS263 UN *Adicocrita discerpta*
AH3 HELI *Petovia marginata*
Hes696 HEMIT *Prasinocyma albisticta*
SH0416 HEMIT *Prasinocyma adornata*
SH2010 HEMIT *Prasinocyma nr adornata*
Hes632 HEMIT *Prasinocyma bongaensis*
SH0424 HEMIT *Prasinocyma pedicata*
SH1018 HEMIT *Prasinocyma nr baumgaertneri*
SH1029 HEMIT *Prasinocyma nr nereis*
SH1107 HEMIT *Prasinocyma nr fusca*
SH1136 HEMIT *Prasinocyma delicataria*
AH2 UN>HEMIT *Antharmostes papilio*
USNM205989 UN>HEMIT *Agathiopsis maculata*
IOZ_LEP_M_30131 HEMIT *Episothalma robustaria*
AH3607 MICR *Microloxia ruficornis*
V5 MICR *Mixocera albistrigata*
IOZ_LEP_M_17096 HEMIT *Thalera suavis*
MM11574 THALE *Thalera fimbrialis*
CNC535710 HEMIT *Xerochlora viridipallens*
gb_ID_17715 HEMIT *Chloropteryx nr opalaria*
IOZ_LEP_M_12730 HEMIT *Chlorissa amphitritaria*
IOZ_LEP_M_14087 HEMIT *Chlorissa distinctaria*
MJ150406.515 HEMIT *Pamphlebia rubrolimbraria*
Hes754 HEMIT *Phaiogramma faustinata*
SH4727 UN *Metallochlora misera*
IOZ_LEP_M_4125 HEMIT *Hemithea aestivaria*
MM10876 HEMIT *Hemithea aestivaria*
IOZ_LEP_M_8537 HEMIT *Hemithea krakenaria*
MM13439 HIER *Hierochthonia semitaria*
bo_chi_433 LOPH *Anomphax gnoma*
gb_ID_17778 RHOM *Oospila lacteguttata*
R207 UN> HEMIT *Ctenoberta nr abanga*
IOZ_LEP_M_13377 HEMIS *Hemistola tenuilinea*
AH3830 HEMIS *Hemistola chrysoprasaria*
IOZ_LEP_M_16582 HEMIS *Hemistola parallelaria*
Hes605 UN> HEMI *Comostolopsis sp SH01*
SH0406 UN> HEMI *Comostolopsis nr rubristicta*
SH1070 UN> HEMI *Comostolopsis stillata*
AH7829 COMO *Comostola leucomerata*
IOZ_LEP_M_14286 COSMO *Comostola sp_1*
IOZ_LEP_M_18569 COSMO *Comostola sp_2*
IOZ_LEP_M_1001 HEMIT *Ecchloropsis xenophyes*
IOZ_LEP_M_10853 HEMIT *Maxates acutissima*
IOZ_LEP_M_4549 HEMIT *Maxates grandificaria*
IOZ_LEP_M_10642 HEMIT *Maxates thetydaria*
IOZ_LEP_M_13845 HEMIT *Berta apopempta*
IOZ_LEP_M_8977 HEMIT *Berta chrysolineata*
IOZ_LEP_M_4580_HEMIT *Jodis lactearia*
EO0077 JODI *Jodis lactearia*
MM06428 JODI *Jodis putata*
GEOM>HEMI *Albinospila spAAB0430*
USNM494496a GEOM>HEMI *Oenospila spAAB6770*
USNM507892
USNM500740 JODI *Jodis albiflusa*
IOZ_LEP_M_21715 HEMIT *Aporandria specularia*
IOZ_LEP_M_11070 HEMIT *Thalassodes immissaria*
IOZ_LEP_M_14099 THALA *Pelagodes antiquadraria*
R106 THALA *Thalassodes quadraria*
IOZ_LEP_M_21386 THALA *Orothalassodes pervulgatus*
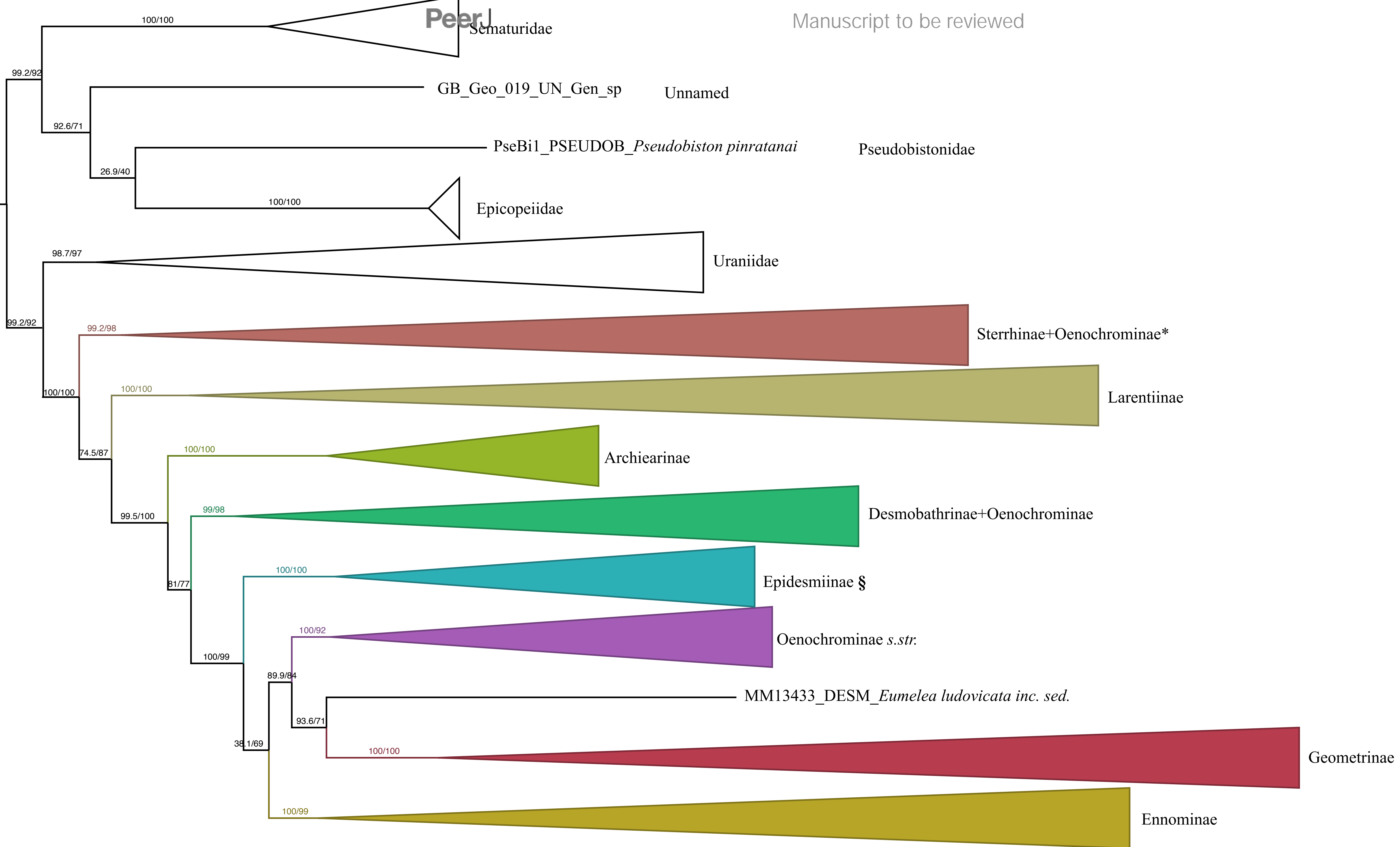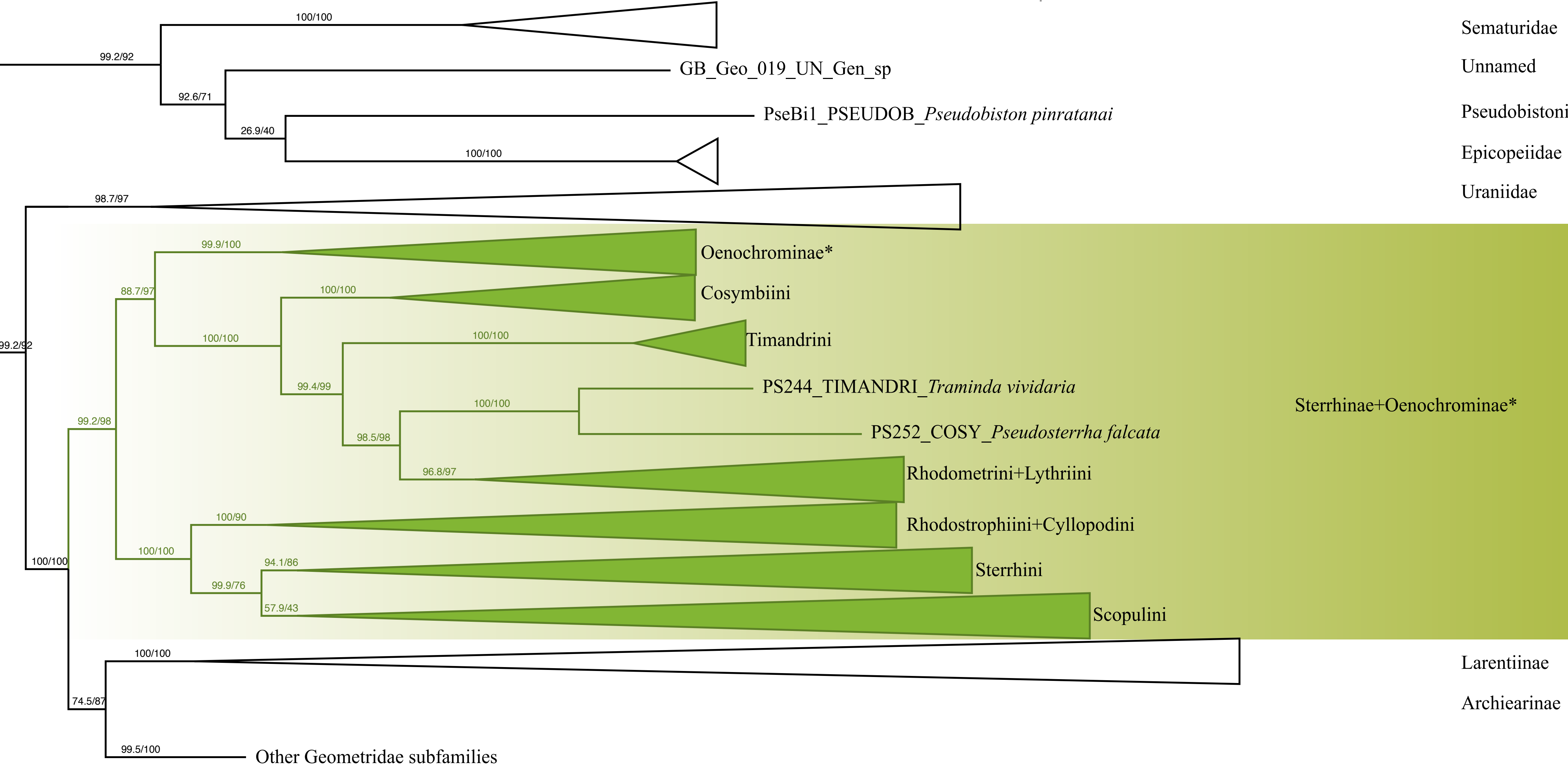Hemitheini

Ennominae

0.2

Figure 6(on next page)

Evolutionary relationships of the subfamily Ennominae.

Numbers above branches are SH-aLRT support (%) / ultrafast bootstrap support, UFBoot2(%), for nodes to the right of the numbers. Values of SH >= 80 and UFBoot2>= 95 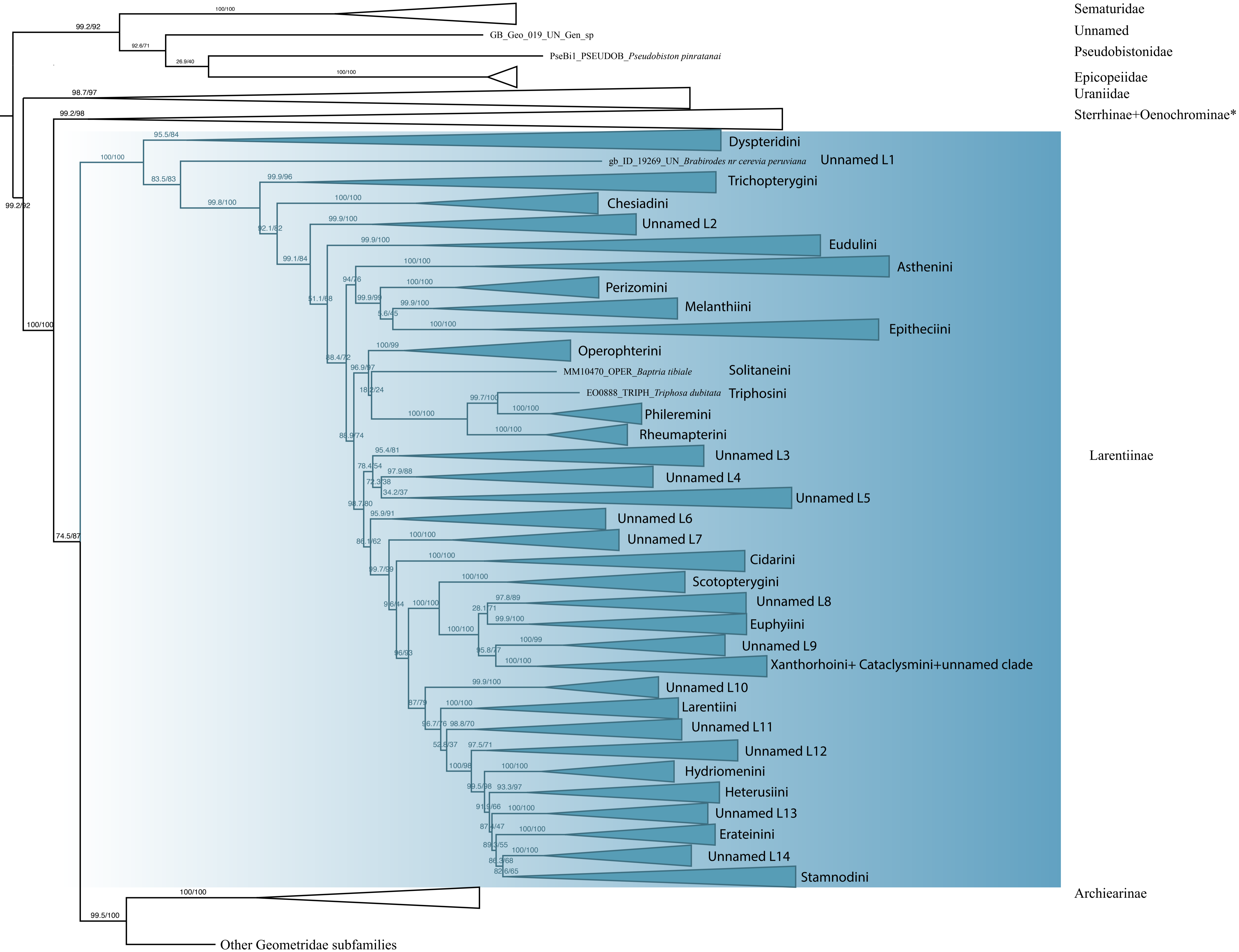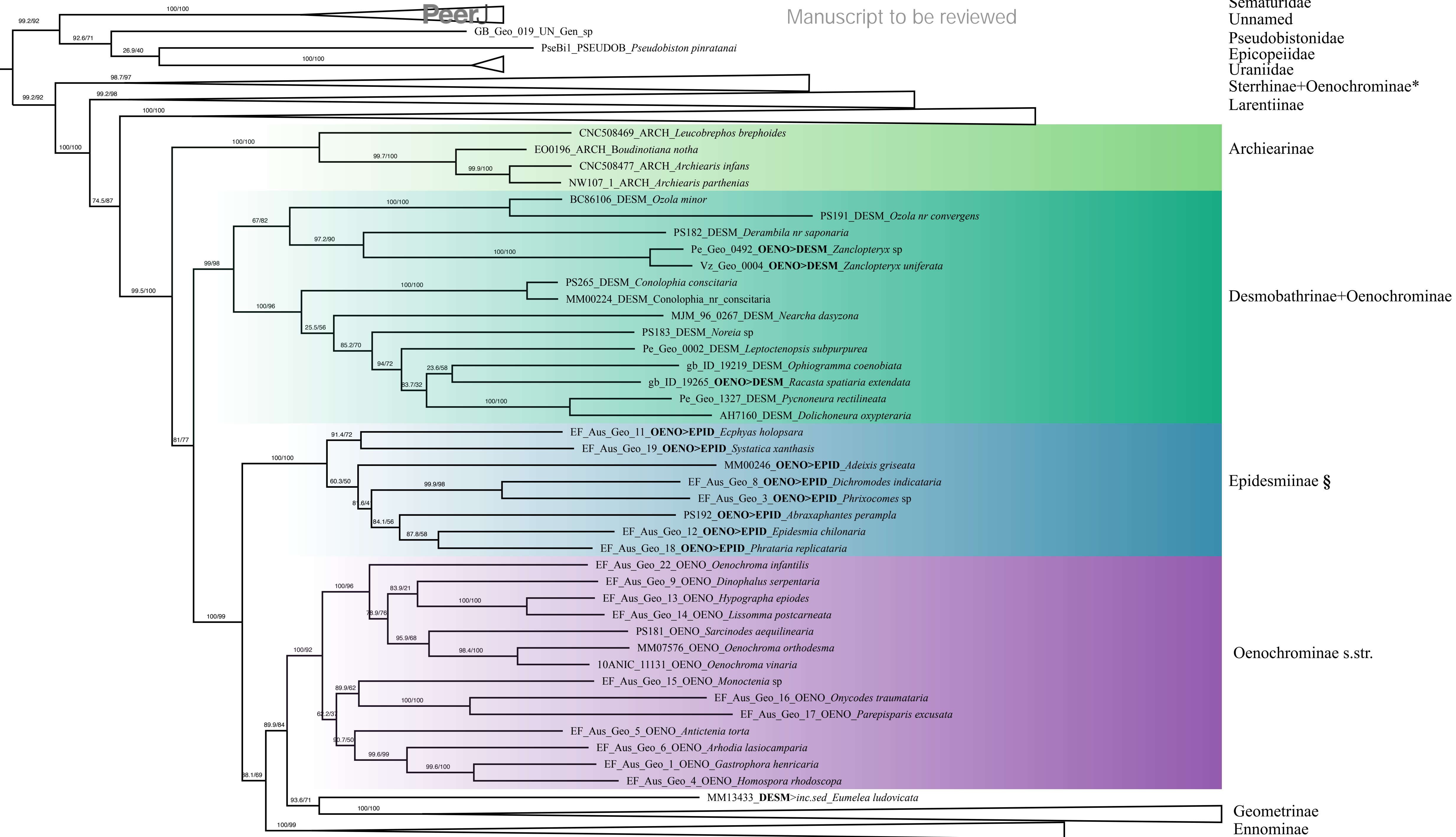indicate well-supported clades (Trifinopoulos & Minh, 201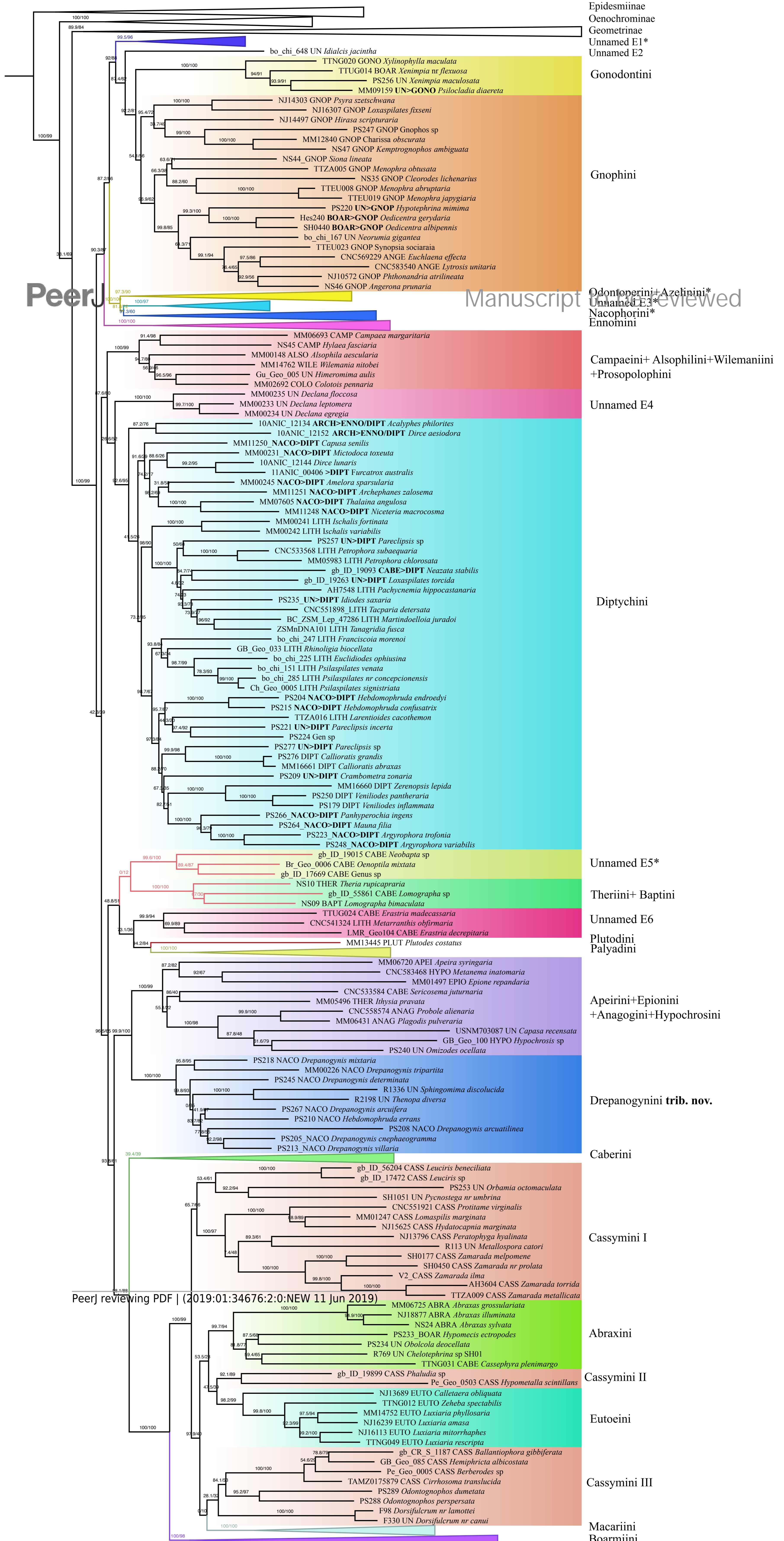8).Taxonomic changes are indicated by a symobolized arrow >.* Formal taxonomic treatment will be dealt with in Brehm et al. submitted.

Table 1(on next page)

Evolutionary models recovered in ModelFinder

Evolutionary models	Codon position	Data type
SYM+R5	ArgK_pos1	Nuclear
SYM+R4	ArgK_pos2_Ca-ATPase_pos2	Nuclear
GTR+F+R6	ArgK_pos3	Nuclear
GTR+F+R5	Ca-ATPase_pos1_IDH_pos1	Nuclear
SYM+I+G4	Ca-ATPase_pos3	Nuclear
SYM+I+G4	CAD_pos1	Nuclear
K3P+I+G4	CAD_pos2	Nuclear
GTR+F+R7	CAD_pos3	Nuclear
TIM2+F+I+G4	COI_pos1	Mitochondrial
K2P+R8	COI_pos2_MDH_pos2_RpS5_pos2_WntGeo_pos2	Mitochondrial/Nuclear
GTR+F+ASC+R10	COI_pos3	Mitochondrial
TIM2e+R10	EF1a_pos1	Nuclear
TIM+F+I+G4	EF1a_pos2	Nuclear
SYM+R10	EF1a_pos3_GAPDH_pos3_RpS5_pos3	Nuclear
TVM+F+I+G4	GAPDH_pos1	Nuclear
SYM+I+G4	GAPDH_pos2	Nuclear
GTR+F+R4	IDH_pos2	Nuclear
SYM+R6	IDH_pos3	Nuclear
GTR+F+I+G4	MDH_pos1	Nuclear
SYM+I+G4	MDH_pos3	Nuclear
SYM+I+G4	Nex9_pos1	Nuclear
K3P+I+G4	Nex9_pos2	Nuclear
GTR+F+R6	Nex9_pos3	Nuclear
SYM+I+G4	RpS5_pos1	Nuclear
GTR+F+I+G4	WntGeo_pos1	Nuclear
SYM+R7	WntGeo_pos3	Nuclear

1

Table 2(on next page)

Summary of formally proposed taxonomic changes.

1

Transfer from Archiearinae to Ennominae
Acalyphes Turner, 1926, to Ennominae: Diptychini
Dirce Prout, 1910, to Ennominae: Diptychini

Transfer from Oenochrominae to Desmobathrinae:
Desmobathrini Meyrick, 1886
Nearcha Guest, 1887
Racasta Walker, 1861
Zanclopteryx Herrich-Schäffer, [1855]

Transfer from Oenochrominae to Epidesmiinae:
Abraxaphantes Warren, 1894
Adeixis Warren 1987
Dichromodes Guenée [1858]
Ecphyas Turner, 1929
Epidesmia Duncan [& Westwood], 1841
Phrixocomes Turner, 1930
Phrataria Walker, [1863]
Systatica Turner, 1904

New tribe combinations Ennominae
Psilocladia Warren, 1898, from unassigned to Gonodontini
Oedicentra Warren, 1902, from Boarmiini to Gnophini
Hypotephrina Janse, 1932, from unassigned to Gnophini
Capusa Walker, 1857, from Nacophorini to Diptychini
Mictodoca Meyrick, 1892, from Nacophorini to Diptychini
Furcatrox McQuillan, 1996, from Nacophorini to Diptychini
Amelora Guest, 1897, from Nacophorini to Diptychini
Archephanes Turner, 1926, from Nacophorini to Diptychini
Thalaina Walker, 1855, from Nacophorini to Diptychini
Niceteria Turner, 1929, from Nacophorini to Diptychini
Neazata Warren, 1906 from Caberini to Diptychini
Idiodes Guenée, [1858] from unassigned to Diptychini
Panhyperochia Krüger, 2013, from Nacophorini to Diptychini
Mauna Walker, 1865, from Nacophorini to Diptychini
Pareclipsis Warren, 1894, from unassigned to Diptychini
Crambometra Prout, 1915, from unassigned to Diptychini
Hebdomophruda Warren, 1897, from Nacophorini to Diptychini
Pareclipsis Warren, 1894, from unassigned to Diptychini

Capasa Walker 1866, from unassigned to Hypochrosini
Omizodes Warren, 1894, from unassigned to Hypochrosini
Metallospora Warren, 1905, from unassigned to Cassymini
Obolcola Walker, 1862, from unassigned to Abraxini
Chelotephrina Fletcher, 1958 from unassigned to Abraxini
Cassephyra Holloway, 1993 from Cassymini to Abraxini
Thenopa Walker, 1855 from unassigned to Drepanogynini
Drepanogynis Guenée, [1858] from Nacophorini to Drepanogynini

New tribe combinations Geometrinae
Agathiopsis Warren 1896, from unassigned to Hemitheini
Albinospila Holloway 1996, from Geometrini to Hemitheini
Antharmostes Warren 1899, from unassigned to Hemitheini
Ctenoberta Prout 1915, from unassigned to Hemitheini
Comostolopsis Warren 1902, from unassigned to Hemitheini
Oenospila Swinhoe 1892, from Geometrini to Hemitheini

New and upgraded tribes in Geometrinae	Included taxa
Archaeobalbini, **stat. rev.**	Type genus: *Herochroma* Swinhoe, 1893 (syn. *Archaeobalbis* Prout, 1912). Other included genera: *Pachyodes* <u>Guenée</u>, [1858]; *Metallolophia* Warren, 1895; *Actenochroma* Warren, 1893; *Absala* Swinhoe 1893; *Metaterpna* Yazaki, 1992; *Limbatochlamys* Rothschild, 1894; *Psilotagma* Warren, 1894; *Dindica* Warren, 1893; *Dindicodes* <u>Prout</u>, 1912; *Lophophelma* Prout, 1912.
Chlorodontoperini, Murillo-Ramos, Sihvonen & Brehm, **trib. nov.**	Type genus: *Chlorodontopera* Warren, 1893. Species included: *C. discospilata* (Moore, 1867); *C. mandarinata* (Leech, 1889); *C. chalybeata* (Moore, 1872); *C. taiwana* (Wileman, 1911).

New tribe in Ennominae	Included taxa
Drepanogynini, Murillo-Ramos, Sihvonen & Brehm, **trib. nov.**	Type genus: *Drepanogynis* Guenée, [1858]. Other included genera: *Thenopa* Walker, 1855. Species included, genus combination uncertain (*incertae sedis*): *"Sphingomima" discolucida* Herbulot, 1995 (transferred from unassigned to Drepanogynini); *"Hebdomophruda" errans* Prout, 1917 (transferred from Nacophorini to Drepanogynini).

Synonymized tribes	Valid tribe
Lithinini Forbes, 1948, **syn. nov.**	Diptychini Janse, 1933 (Ennominae)
Synchlorini Ferguson, 1969 **syn. nov.**	Nemoriini Gumppenberg, 1887 (Geometrinae)
Incertae sedis	
Eumelea Duncan [& Westwood], 1841	
Hebdomophruda errans Prout, 1917	

2

3