Eyespots originated multiple times independently across the Lepidoptera

Brian Hanotte[1,*], Beatriz Willink[1,2], and Antónia Monteiro[1,*]

1) Department of Biological Sciences, National University of Singapore, Singapore

2) Department of Zoology, Stockholm University, Sweden

*Corresponding authors

Abstract

Eyespot color patterns often function as a defense against predators and in mate choice. In Nymphalid butterflies, eyespots have a single evolutionary origin close to the base of this clade, but eyespots are also present in many other lepidopteran lineages and may have multiple independent origins. Here we use phylogenetic comparative methods to investigate the evolution of eyespots across a multi-superfamily phylogeny of Lepidoptera, and to pinpoint lineages in which eyespots likely originated independently. We find a total of 28 separate origins of *Discal* eyespots (in the discal wing region) and 19 separate origins of *Marginal* eyespots (in the marginal wing region), including four separate instances where eyespots were preserved in most extant representatives of a species radiation. The first two eyespot radiations we observed are in the Nymphalidae, with a *Marginal* eyespot radiation occurring before a *Discal* one. While the remaining two eyespot radiations were observed in the Saturniidae, occurring in a reverse fashion, where a *Discal* eyespot radiation preceded a *Marginal* eyespot radiation. Even though eyespots do not appear to be homologous across Lepidoptera they may share a homologous gene-regulatory network. Our phylogenetic inference provides a roadmap for future developmental and functional studies addressing this hypothesis. This study therefore has implications for our understanding of the evolution of serial homologues and of convergent evolution of visual signals in insects.

Introduction

Lepidopteran wing color patterns have been a source of fascination and human inspiration for centuries (Hogue, 1987). While some of the classic early research focused on the adaptive role of general wing coloration, such as “industrial melanism” in moths (Kettlewell, 1973), other research

27 focused on the role of localized color patterns, such as eyespots (Blest, 1957). Eyespots consist of
28 more than one concentric ring of contrasting colored scales, often mimicking a vertebrate eye (Oliver
29 et al., 2014; Labanderia et al., 2016). These visually striking color patterns play roles in predator
30 deterrence, predator deflection, and mate selection (Breuker & Brakefield 2002; Stevens, 2005;
31 Robertson and Monteiro 2005; Vallin et al. 2007; Kodandaramaiah, 2011; Merilaita et al., 2011;
32 Prudic et al. 2012; Kodandaramaiah et al., 2013; Prudic et al., 2015; Mukherjee & Kodandaramaiah,
33 2015; Huq et al., 2019; Halali et al., 2019). Eyespots are thus adaptive, having evolved in several
34 clades of Lepidoptera, but their evolutionary history remains poorly understood.

35 Research on eyespot evolution to date has focused on nymphalid butterflies. Here eyespots develop
36 in between veins at the wing margins (Fig. 1a-b). Such *Marginal* eyespots evolved once in
37 Nymphalidae, shortly after the origin of the clade (Oliver et al., 2012 & 2014), and are therefore
38 considered homologous. Several moth lineages (e.g., Semanturidae, Saturniidae, Cambridae) also
39 exhibit *Marginal* eyespots, but their evolutionary history has not been investigated. In contrast to
40 *Marginal* eyespots, *Discal* eyespots are centered on cross veins or placed within the discal cell region
41 (Otaki., 2020; Fig. 1c-d). Across Lepidoptera, species may have *Marginal* eyespots, *Discal* eyespots, or
42 eyespots located on both wing regions (Fig. 2). Because these distinct wing regions express different
43 genes during development (Banerjee et al., 2023), the evolution of *Marginal* and *Discal* eyespots
44 might have occurred independently in each region (Fig. 1E). Alternatively, eyespots might have first
45 evolved on one wing region, and later evolved on the other region, with the order of these regions
46 potentially varying if there are multiple independent eyespot origins (Fig. 1e-g). By investigating the
47 evolution of eyespots across the Lepidoptera we aim to discover whether *Marginal* and *Discal*
48 eyespots are homologous or convergently evolved across the Lepidoptera.

49 Here we used modern phylogenetic methods to investigate the evolutionary origins of *Discal* and
50 *Marginal* eyespot across Lepidoptera. We first inferred a species-level phylogeny for Lepidoptera,
51 sampling up to 27 (5-24 fragments per species) molecular sequences in over 715 species. Our

52 phylogeny covers 90% of Lepidoptera families, allowing comparative inferences of eyespot evolution
53 in moths and butterflies. We then modeled evolutionary origins and losses of eyespots and inferred
54 ancestral states across the phylogeny. For each possible subtree with an ancestral eyespot origin, we
55 implemented a model comparison approach, based on marginal likelihood estimation, to quantify
56 support for eyespot homology among extant taxa. These analyses suggested differently ordered
57 sequences of eyespot evolution in the two main eyes-spot bearing radiations, the silkmoths
58 (Saturniidae) and the brush-footed butterflies (Nymphalidae). Our results demonstrate that eyespots
59 in the Lepidoptera have evolved multiple times, and that *Discal* and *Marginal* eyespots have evolved
60 in different temporal sequences in the main clades where they radiated (Nymphalidae and
61 Saturniidae). We also find that eyespots have evolved in a further 10 superfamilies and numerous
62 families across the Lepidopteran family tree. Finally, we find that eyespots across the lepidoptera are
63 more commonly observed in the *Discal* region (28 occurrences) than the *Marginal* region (19
64 occurrences) which was unexpected as most eyespot research is focused on *Marginal* eyespots
65 found in the Nymphalidae.

66 **Materials and methods**

67 Molecular data collection for phylogenetic tree construction

68 DNA sequence data for 645 species of Lepidoptera (moths and butterflies) and seven species of
69 Trichoptera (caddisflies, outgroup) were kindly provided by Professor Emeritus Charles Mitter
70 (University of Maryland, Table S1 & S2). Additional sequences for 70 species of Saturniidae
71 (silkmoths) were downloaded from NCBI (GenBank). The full dataset was composed of 27 protein-
72 coding genes (Table S2), with 5-24 fragments available across all species. Our taxonomic sampling
73 includes ~68% (90/133, Van Nieukerken et al., 2011) of all families and ~65% (28/43, Van Nieukerken
74 et al., 2011) of all superfamilies in the order Lepidoptera. This study focuses on the suborder Ditrysia,
75 which comprises ~98% of currently described lepidopterans. Of these, ~90% of families (90/100,
76 Reiger et al., 2009) and ~93-96% (28/29-30) of superfamilies (Van Nieukerken et al., 2011; Heikkla et

al., 2015; Mitter et al., 2017) are represented. We chose the Trichoptera for our outgroup because they are the closest extant relatives to the Lepidoptera (Mey et al., 2017), but distant enough to provide ingroup monophyly.

Sequence alignment and phylogenetic inference

DNA sequences were aligned via MAFFT v 7.490 (Katoh & Standley, 2013). A global alignment strategy with iterative refinement (G-INS-i) was employed to maximize alignment accuracy based on weighted sum-of-pairs and a consistency scores. The length of the final alignment, consisting of all 27 concatenated gene fragments, was 22,643 bp.

IQ-TREE v 1.6.12 (Nguyen et al., 2015, Kalyaanamoorthy et al., 2017 & Hoang et al., 2018) was used for phylogenetic inference under maximum likelihood. All genes were subject to a single substitution process automatically set by IQ-TREE,using ModelFinder (Kalyaanamoorthy et al., 2017). Substitutions followed a generalized time reversible (GTR) model, with estimated base frequencies. Rate variation among sites followed a gamma distribution containing 10 categories. Node support was estimated using ultra-fast bootstrap in UFBoot (Hoang et al., 2018) for 100,000 iterations. UFBoot is an efficient approximation to the traditional bootstrap method that is particularly well-suited for large datasets such as ours. After pruning the outgroup, our maximum likelihood tree was transformed into an ultrametric tree, with branch lengths scaled to time, using the ape package v 5.7-1 (Paradis & Schliep, 2019) in R v 4.3.0 (R Core Team 2023). For branch scaling, we used an age of ~290 Ma for the most recent common ancestor of Ditrysia, following the most recent dated phylogeny of Lepidoptera (Kawahara et al., 2019).

Image data collection

We scored images of each of the 715 species in our phylogeny for presence or absence of eyespot patterns (in any wing surface or sex). An eyespot pattern was identified as present only if it met three criteria: 1) it had at least two concentric rings of distinct colors, 2) the rings were circular or oblong in

101 shape, and 3) the color inside the internal ring differed from the color on the outside of both rings
102 (Fig. 3). To explore the sensitivity of our results to these conservative criteria, we repeated our main
103 comparative analyses under a more relaxed definition of eyespots, where criterion 2 was extended
104 to non-circular/oblong shapes (e.g., triangles, rectangles, teardrops, see Fig. S1 for examples).
105 Eyespots were further classified based on their locations on the wing surface. *Discal* eyespots
106 straddle the cross veins in the discal cell region or are found within and around the discal cell (Otaki
107 et al., 2020 & Figure 1), whereas *Marginal* eyespots are found in between longitudinal veins, at the
108 wing margins and within the discal cell of the wing (Fig. 1a-d).

109 We first queried a wide range of online databases for images of the type specimen of each of the
110 sampled species (Table S3, Supplementary data file 1). If not available, images of other (non-type)
111 specimens were collected from the same databases with a preference for museum specimens over
112 other specimens. In cases where sequence data was assigned to a particular subspecies, we
113 prioritized images of the same taxonomic rank when available. Ninety-six species included in our
114 data set lacked publicly available and reliably identified images. We photographed 81 of these
115 species at the Mcguire Center for Lepidoptera (MGCL, Florida Museum of Natural History, 3215 Hull
116 Rd, Gainesville, Fl 32611), using a Cannon D50 DSLR camera. We were unable to obtain images for 15
117 species (2%), which are treated as missing data in all comparative analyses.

118 <u>Modelling the origin and loss of eyespots in Lepidoptera</u>

119 RevBayes v 1.2.1 (Höhna et al., 2016) was used in this and subsequent analyses to model eyespot
120 evolution across Lepidoptera. RevBayes is an open-source software package designed for Bayesian
121 phylogenetic inference. It allows users to build probabilistic graphical models using an interactive
122 model-specification language.

123 Eyespots were modelled as a discrete trait with two states (presence/absence) with unequal
124 transition rates drawn from identical exponential priors. The rate parameters of these priors were set
125 to reflect an expectation of 10 events (10 eyespot gains and 10 eyespot losses) along the tree. Root

126 state frequencies were in turn drawn from a Dirichlet prior, assuming equal probability of presence
127 or absence of eyespots at the origin. Eyespot evolution was modelled separately using three
128 datasets: eyespot presence/absence irrespective of eyespot location on the wing, presence/absence
129 of *Marginal* eyespots, and presence/absence of *Discal* eyespots. For all three datasets, eyespots
130 could be located on any wing surface and either sex.

131 Each model was run for 100,000 iterations with an initial burn-in of 10,000, and tuning parameter
132 proposals every 1,000 iterations on two independent chains. Joint conditional ancestral states were
133 sampled every 100 iterations and plotted using RevGadgets v 1.1.1 (Tribble et al., 2023) in R. We
134 evaluated the convergence and stationarity of the MCMC chains for each model using the R package
135 Convenience v 1.0.0 (Fanreti et al., 2013)

136 Testing eyespot homology in selected clades

137 We next implemented a model testing approach to investigate eyespot homology among extant
138 species of Lepidoptera. We identified all subclades including three or more taxa bearing eyespots,
139 regardless of their location. If the most recent ancestor of these clades also displayed eyespots, it is
140 likely that eyespots in extant taxa are homologous. To test this hypothesis, we extracted all subclades
141 from the complete ultrametric phylogeny and applied in each case two alternative versions of the
142 discrete-trait model described above. In the first version (hereafter the multiple-origin model), we
143 set the root frequency of eyespot presence to zero, effectively constraining the common ancestor of
144 the subclade to lack eyespots. In the second version (the common-ancestor model), we instead
145 enforced a common ancestor with eyespots by setting the root frequency of eyespot presence to
146 one. We then compared the marginal likelihood (ML) of these alternative models using log 10 of the
147 raw Bayes factor using thresholds based on Jeffreys (1998). In our study, results above positive 0.1
148 were considered to show some support for an eyespot originating at a specific node. Results above
149 0.5 were considered to have strong support, results above 1.0 were considered to have very strong
150 support and results which were positive numbers but below 0.1 were considered to demonstrate

very weak support which wasn't worth mentioning. Finally negative results were considered to represent no support for an eyespot origin at a given node. These thresholds for the support of eyespots being present at a particular node were chosen due to the high number of negative values we obtained in our study (values above -1.0) which is indicative of a lack of support for a single origin of eyespots.

ML estimates gauge the fit of a model, including its priors, to the data, in this case, the phylogeny and presence or absence of eyespots in extant taxa. Because the two models being compared differ only in their prior assumptions about the character state at the root, their direct comparison serves as a statistical test of the support for eyespot presence in the most recent common ancestor of the clade. ML was estimated via the use of two sampling methods, steppingstone sampling (SS) and path sampling (PS, Lartillot and Philippe, 2006, Fan et al., 2011 & Xie et al., 2011). For both methods the power posterior analysis was split into 50 intervals between the prior and posterior and was run for 5,000 iterations with a burn-in of 5,000 generations. We repeated ML approximations for each subclade and eyespot dataset and confirmed that both PS and SS estimates were stable (i.e. differing by no more than 0.5 between independent runs of each set of power posteriors). The results of these analyses were summarized and plotted onto the phylogeny using the R packages phytools v1.9-16 (Revell, 2012), ggplot2 v3.4.3 (Wickham et al., 2016) and ggtree v3.9.0 (Yu et al., 2017 & 2018, Yu, 2020 & 2022 & Xu et al., 2022), followed by the online tool ITOL (2023).

Results

Tree topology

The phylogeny constructed for this study contains 28 superfamilies, each containing 1 – 128 species in our samples (median = 14). The full list of superfamilies as well as the number of species representatives for each superfamily are outlined in Table S1 (Supplementary tables and figures). The topology of our tree is largely congruent with previous phylogenies (Heikkil et al., 2015; Mitter et al., 2017; Kawahara et al., 2019). Topological differences observed between this study and previous

176 ones involve species whose placement is phylogenetically uncertain (*incertae cedis*) or superfamilies
177 previously shown to require reclassification (Tineoidea or the Cossioidea-Sesioidea complex for
178 example; Mutanen et al., 2010; Bazinet et al., 2013; Reiger et al., 2013; Heikkil et al., 2015 Reiger et
179 al., 2015A; Mitter et al., 2017; Appendix 1). These differences in topology are unlikely to have a
180 significant impact on the main findings of this work, as they primarily nested within large clades
181 entirely lacking eyespots. A summary and discussion of novel species relationships identified in this
182 work can be found in the Supplementary Information (Appendix 1).

183 Ancestral state reconstructions and evolutionary rates

184 Our three ancestral state reconstructions (*Both*, *Marginal* and *Discal*) indicate that the common
185 ancestor, at the root of Lepidoptera did not have any eyespots (Fig. 4, Figs. S16 & S17). Eyespots thus
186 evolved multiple times in the history of Lepidoptera (Figs. 4 & 5). Nonetheless, eyespots may often
187 be evolutionarily short lived. Our results show a higher rate of eyespot losses than eyespot gains
188 regardless of eyespot type. The *Both* eyespot model (Fig. 4), *Marginal* eyespot model and *discal*
189 eyespot model all showing a higher rate of eyespot losses than gains (Fig. 4 & Fig. S16 & S17). To
190 explore the sensitivity of these results, we repeated all analyses under a more relaxed definition of
191 eyespots, where we also included non-circular/oblong shapes as eyespots. These results were
192 qualitatively similar to the results in our main analysis and are therefore presented in the
193 supplementary tables and figures section (Fig. S18).

194 Our ancestral state reconstructions are consistent with 28 independent Discal eyespot gains, and 19
195 independent Marginal eyespot gains across 12 superfamilies of Lepidoptera represented in this tree
196 (Figs. 4, 5, S16 & S17). In contrast, we did not find any eyespots in specimens sampled from 16
197 superfamilies: Cimelioidea, Thyridoidea, Copromorphoidea, Hyblaeoidea, Sesioidea, Gelechioidea,
198 Epermenioidea, Tortricoidea, Galacticoidea, Immoidea, Choreutoidea, Urodoidea, Pterophoroidea,
199 Gracillarioidea, Yponomeutoidea and Tineoidea). Most of the eyespots found in the remaining 12
200 superfamilies occur in the single species/genera sampled and are not present in sister lineages on

the tree. There are, however, two major independent radiations of Both Marginal and Discal eyespots found in the families Nymphalidae and Saturniidae, where Both eyespot types were retained in multiple members of these families after they originated (Fig. 5, Figs. S10 & S15).

Homology of eyespot radiations

To further investigate the ancestral nodes of independent eyespot origins, as suggested by our ancestral state reconstructions above, we contrasted the fit of a common-ancestor model *vs* a multiple-origin model, for the ancestor of each putative eyespot radiation. Our results using the combined eyespot data (i.e. all eyespots regardless of location), supported our earlier findings of eyespot bearing ancestors in Nymphalidae and Saturniidae (Table 1). By contrasting the results of analyses on the *Marginal* data and the *Discal* data, we inferred which eyespot location likely evolved first in each radiation (Fig. 1e-g). We were surprised to find that the area of the wing where eyespots first appeared was reversed between these two main clades. In nymphalids, the first eyespots appeared along the margin and were followed by *Discal* eyespots (Figs. 5, S10 & S15). The opposite was observed in saturniids, where *Discal* eyespots originated first followed by *Marginal* eyespots (Fig. 5. Figs. S10 & S15). *Discal* eyespots likely originated in the most recent common ancestor of all saturniids, while *Marginal* eyespots evolved within the Attacini tribe of the subfamily Saturniinae. In nymphalids, *Marginal* eyespots first evolved at the base of the sister lineage to the Libytheinae, and Discal eyespots followed in ancestors of Heliconiine and Nymphaline. We found that the Bayes Factor (BF) between our two sapling methods (PS & SS) was largely consistent between runs for the same taxa (Table 1). When the circular criteria for eyespot shape was relaxed (Fig. S18), we found some evidence for a more ancestral origin of Discal eyespots in the Saturniidae. The BF for this more relaxed model is available in the supplementary information (Fig. S18).

Table 1. Log 10 of the raw Bayes factor for each of our eyespot radiations identified in our tree. Values for both PS and SS sampling methods are provided.

Taxa (Family)	*Discal* PS	*Discal* SS	*Marginal* PS	*Marginal* SS	*Both* PS	*Both* SS
Saturniidae	0.146	0.145	0.110	0.104	0.247	0.253
Nymphalidae	0.127	0.126	0.131	0.126	0.150	0.132

223 To investigate the 27 other Discal and 18 other Marginal eyespot occurrences which were not part of
224 any eyespot radiation (Fig. 5), we investigated the occurrence of eyespots in up to 3 closely related
225 species. These closely related species did not feature on our tree and were limited from the genus to
226 the family level (Fig. S19). We found that many clades with eyespots that were represented by a
227 single species on our tree (Fig. 5) had several closely related species also baring eyespots (Fig. S19).
228 This suggests that these multiple clades represent separate, independent eyespot radiations (Fig. 5 &
229 Fig. S19).

230 **Discussion**

231 Our results show that eyespot evolution in Lepidoptera is diverse and complex. The majority of
232 eyespot research, up to now, has been conducted in a single clade (Nymphalidae), but here we
233 demonstrate that eyespots have evolved multiple times independently across the Lepidoptera,
234 including in many poorly known moth clades (Fig. 4 & Fig. 5). In our phylogeny, these clades are often
235 represented by a single species. However, we documented eyespots in close relatives to each of
236 these lineages (Fig. S19), suggesting eyespots have been preserved across additional radiations.
237 Future phylogenetic studies, with a denser taxonomic sampling, will be required to characterize the
238 evolutionary history of eyespots in these lesser-known clades. Nonetheless, our study strongly
239 suggests that eyespots are not homologous across the entire Lepidoptera.

240 The evolution of Marginal eyespots in the Nymphalidae has been studied before and we report
241 similar findings to these previous studies. Our findings align more closely with the 'early' model of
242 eyespot evolution first proposed by Oliver et al. (2012 & 2014), as opposed to the 'late' model that
243 became the preferred model (Oliver et al. 2014). In Both our analysis, and in the 'early' model,
244 eyespots were coded as being present or absent anywhere on the wing, whereas the 'late' model
245 preferred by Oliver et al., (2014) had increased resolution by scoring the presence of eyespots in
246 specific wing sectors. This late model brought the origin of eyespots to a node above the one
247 discovered here, to the base of the lineage that is sister to the Danainae. Despite minor conflict as to

248 when exactly *Marginal* eyespots first evolved, this and previous studies agree on a single and
249 relatively early origin of Marginalthese eyespots in Nymphalidae.

250 Nymphalid *Discal* eyespots and their evolutionary history have not been investigated before. Here
251 we presented a first estimate of *Discal* eyespot evolution in the nymphalidae, as Oliver et al., (2012 &
252 2014) did not study these *Discal* eyespots. *Discal* nymphalid eyespots appear to have evolved in two
253 separate clades and are not homologous across all species in the family Nymphalidae. Firstly, in the
254 closely related Nymphalidae subclades Heliconiine (Limenitidinae- *Limenitis arthemis*) and
255 Nymphaline (Apaturinae-*Asterocampa celtis*, Biblidinae-*Hamadryas arinome*, Melitaeini-P*hyciodes*
256 *phaon* & Nymphalini-*Vanessa carye*), we find that the *Discal* eyespot evolved once and then radiated
257 across several groups, making discal eyespots homologus across the Heliconiine and Nymphalini (Fig.
258 5 & Fig S10). The second instance of discal eyespot evolution which is not homologus to the other
259 Nymphalidae is *Neope goschkevitschii* (Satryinae, Nymphalidae. Figs. 2 & 5 & Figs. S10 & S19). *Neope*
260 *sp*. and closely related species within the Satryinae were found to have *Discal* eyespot patterns (Fig.
261 S19), upon our investigation of closely related species not featured on the tree and may represent a
262 unique *Discal* eyespot radiation within the Satyrinae (Fig. S19).

263 We provided the first examination of the evolution of eyespots (*Discal* and *Marginal*) in the
264 Saturniidae and demonstrate that *Discal* eyespots in the Saturniidae are homologus while *Marginal*
265 eyespots are not. We found that *Discal* eyespots likely originated in the most recent common
266 ancestor of all Saturniids, with *Discal* eyespots being present in 62% of the represented clades within
267 the family. Making discal eyespots homologus across the family Saturniidae. *Marginal* eyespots, on
268 the other hand, have evolved and radiated within the Attacini tribe of the subfamily Saturniinae. The
269 *Marginal* eyespot radiation observed within the Attacini includes species of the genus *Samia,*
270 *Callosamia, Epiphora & Hyalophora*. We also observed independent origins of *Marginal* eyespots
271 within the Saturniidae in three additional taxonomic groups, meaning that marginal eyespots in the
272 Saturniidae are not homologus. Two of the three representatives of these groups in our phylogeny

273 (*Copaxa multifenestrata*-tribe Saturniinae & subfamily Saturniinae and *Asthenidia transversaria*-
274 subfamily Oxytenninae) were found to have close relatives with Marginal eyespots suggesting
275 individual eyespot radiations within these taxa (Fig. 5 & Figs. S15A, S15C & S19). One species,
276 *Eupackardia calleta* (tribe Attacini, subfamily Saturniinae) is monotypic at the genus level and its
277 closest relatives are other Saturniidae of the tribe Attacini. Despite being in the Attacini, this species
278 is not picked up in our analysis as being part of the *Marginal* eyespot radiation associated with the
279 other Attacini in our study SS Log10 of BF = -0.123, PS Log 10 of BF = -0.130) (Fig. 5, Fig. S15A &
280 S15C). We therefore conclude that the marginal eyespot in this species likely evolved independently
281 to its congeners in the Attacini.

282 Our analyses revealed that eyespots appeared after each other (and in a different order in butterflies
283 and silk-moths). *Marginal* eyespots in Nymphalidae are considered serially homologous (Monteiro et
284 al., 2007 & Hombría 2011) but they appeared in a particular sequence on the wings. They first
285 originated in ventral hindwings, and millions of years later they appeared in forewings and dorsal
286 surfaces (Oliver 2014; Schachat et al 2015). *Discal* eyespots may be yet another instance of a serial
287 homolog, with a more distinct and central location on the wing. By statistically demonstrating that
288 eyespots, as a complex derived trait, can evolve in different locations on the wing in a different
289 sequence, we open the door to more in-depth developmental level studies that investigate how each
290 type of eyespot differentiates on the wing.

291 Although we demonstrate that nymphalid and saturniid eyespots evolved in lineages which are
292 currently understood to be ~110 million years apart (Kawahara et al., 2019) and are not
293 evolutionarily homologous, it is still possible that eyespots in these two superfamilies share the same
294 gene regulatory network (GRN). Previous research by Murugesan et al. (2022) found that an
295 appendage gene regulatory network was co-opted to build *Marginal* eyespots in *Bicyclus anynana*, a
296 nymphalid butterfly. We suggest that the co-option of the same GRN could have happened more
297 than once across the Lepidoptera. To test this, it will be important to characterize the *Marginal* and

298 *Discal* eyespot GRN in moth lineages and/or the *Discal* eyespot GRN in butterfly lineages, at the level
299 of gene expression. Early immunochemistry work in two saturniid species detected the presence of
300 two (nymphalid) eyespot marker proteins, Distal-less and Engrailed, in the moth *Discal* eyespots
301 (Monteiro et al. 2006). Stronger evidence for the use of the same appendage GRN in these Discal
302 moth eyespots may need to come from CRISPR knockouts of cis-regulatory elements belonging to
303 common eyespot and appendage genes, showing that Both appendages and eyespots are affected
304 (Murugesan et al. 2022).

305 Finally, while the focus of this work is on eyespot evolution, this phylogeny also provides evidence
306 supporting Both new and already established relationships among Lepidopteran lineages, including
307 at the superfamily level (Appendix 1). These insights can fuel future systematic research and further
308 comparative work on how wing color patterns, and other adaptive traits, evolve in the Lepidoptera.

309 **Acknowledgements:** We thank Dr Mark Willmott and Prof Akito Kawahara (MGCL) for hosting B.H. at
310 the MGCL and facilitating access to the collections; Prof emeritus Charles Mitter (University of
311 Maryland) for graciously sending us molecular sequence data for most specimens reanalyzed here;
312 Monteiro lab members for lively discussion, and Mr David Teo Yan Hua for expertise in PC
313 engineering and technological assistance. B.H was supported by a National Research Foundation
314 (NRF) Graduate Fellowship; B.W. was funded by an International Postdoc Grant from the Swedish
315 Research Council (VR; grant no. 2019-06444); and research was supported by a NRF Investigatorship
316 award (NRF-NRFI05-2019-0006) to A.M.

317 **Conflict of interest:** The authors declare no conflict of interests.

318 **References:**

319 Aarvik & Karisch in Aarvik L, Karisch T, plazi (2009). Revision of Multiquaestia, Karisch (Lepidoptera:
320 Tortricidae: Grapholitini). Plazi.org taxonomic treatments database. Checklist dataset
321 https://doi.org/10.5281/zenodo.274748 accessed via GBIF.org on 2023-02-22.

322 Arias, M., Mappes, J., Desbois, C., Gordon, S., McClure, M., Elias, M., . . . Gomez, D. (2019).
323 Transparency reduces predator detection in mimetic clearwing butterflies. Functional Ecology, 33(6),
324 1110-1119.

325 Auguie B (2017). _gridExtra: Miscellaneous Functions for "Grid" Graphics_. R package version 2.3,
326 <https://CRAN.R-project.org/package=gridExtra>.

327 Banerjee, T. D., Murugesan, S. N., Connahs, H., & Monteiro, A. (2023). Spatial and temporal
328 regulation of Wnt signaling pathway members in the development of butterfly wing patterns. Science
329 Advances, 9(30), eadg3877.

330 Bazinet, A. L., Cummings, M. P., Mitter, K. T., & Mitter, C. W. (2013). Can RNA-Seq resolve the rapid
331 radiation of advanced moths and butterflies (Hexapoda: Lepidoptera: Apoditrysia)? An exploratory
332 study. PloS one, 8(12), e82615.

Bhardwaj, S., Jolander, L. S.-H., Wenk, M. R., Oliver, J. C., Nijhout, H. F., & Monteiro, A. (2020). Origin of the mechanism of phenotypic plasticity in satyrid butterfly eyespots. Elife, 9, e49544.

Blest, A. D. (1957). The function of eyespot patterns in the Lepidoptera. Behaviour, 209-256.

Brakefield, P. M. (2003). The power of evo-devo to explore evolutionary constraints: experiments with butterfly eyespots. Zoology, 106(4), 283-290.

Breuker, C. J., & Brakefield, P. M. (2002). Female choice depends on size but not symmetry of dorsal eyespots in the butterfly Bicyclus anynana. Proceedings of the Royal Society of London. Series B: Biological Sciences, 269(1497), 1233-1239.

Carter, D. J., & Hargreaves, B. (1986). A field guide to caterpillars of butterflies and moths in Britain and Europe: Collins.

Connahs, H., Rhen, T., & Simmons, R. B. (2016). Physiological perturbation reveals modularity of eyespot development in the painted lady butterfly, Vanessa cardui. PloS one, 11(8), e0161745.

D'Abrera, B. (1995). Saturniidae Mundi, Saturniid moths of the world part I. Keltern, Germany: Automeris press in association with Victoria Australia Melborne & London: Hill house.

D'Abrera, B. (2012). Saturniidae Mundi, Saturniid moths of the world part II. Victoria Australia, Melborne & London: Hill house.

D'Abrera, B. (1998). Saturniidae Mundi, Saturniid moths of the world part III. Keltern, Germany: Goecke & Evers in association with Victoria Australia Melborne & London: Hill house.

De Prins, J., & Kawahara, A. Y. (2012). Systematics, revisionary taxonomy, and biodiversity of Afrotropical Lithocolletinae (Lepidoptera: Gracillariidae). Zootaxa, 3594(1), 1–283-281–283.

De Prins W. & Steeman C. 2003–2023. *Catalogue of the Lepidoptera of Belgium*. Last accessed on the 22/02/2023. Available online at https://projects.biodiversity.be/lepidoptera

Epstein, M. E. (1996). Revision and phylogeny of the limacodid-group families, with evolutionary studies on slug caterpillars (Lepidoptera: Zygaenoidea).

Fabreti, L. Hoehna, S & Magee, A. (2023). _convenience: Convergence assessment for phylogenetic inference_. R package version 1.0.0.

Fan, Y., Wu, R., Chen, M.-H., Kuo, L., & Lewis, P. O. (2011). Choosing among partition models in Bayesian phylogenetics. Molecular biology and evolution, 28(1), 523-532.

Halali, D., Krishna, A., Kodandaramaiah, U., & Molleman, F. (2019). Lizards as predators of butterflies: shape of wing damage and effects of eyespots. The Journal of the Lepidopterists' Society, 73(2), 78-86.

Heikkilä, M., Kaila, L., Mutanen, M., Peña, C., & Wahlberg, N. (2012). Cretaceous origin and repeated tertiary diversification of the redefined butterflies. Proceedings of the Royal Society B: Biological Sciences, 279(1731), 1093-1099.

Heikkilä, M., Mutanen, M., Kekkonen, M., & Kaila, L. (2014). Morphology reinforces proposed molecular phylogenetic affinities: a revised classification for Gelechioidea (Lepidoptera). Cladistics, 30(6), 563-589.

Heikkilä, M., Mutanen, M., Wahlberg, N., Sihvonen, P., & Kaila, L. (2015). Elusive ditrysian phylogeny: an account of combining systematized morphology with molecular data (Lepidoptera). BMC Evolutionary Biology, 15(1), 1-27.

Hoang, D, T. Chernomor, O. Von Haeseler, A. Minh, B, Q & Vinh, L, S. (2018). UFBoot2: Improving the ultrafast bootstrap approximation. Mol. Biol. Evol., 35:518–522.

Hogue, C. L. (1987). Cultural entomology. Annual Review of Entomology, 32(1), 181-199.

Höhna, Landis, Heath, Boussau, Lartillot, Moore, Huelsenbeck, Ronquist. (2016). RevBayes: Bayesian phylogenetic inference using graphical models and an interactive model-specification language. Systematic Biology, 65:726-736.

Hombría, J. C.-G. (2011). Butterfly eyespot serial homology: enter the Hox genes. BMC biology, 9(1), 1-3.

Hsu Y-F, Powell JA (2005) Phylogenetic relationships within Heliodinidae and systematics of moths formerly assigned to Heliodines Stainton (Lepidoptera: Yponomeutoidea). University California Publications Entomology 124: 1–158.

Huq, M., Bhardwaj, S., & Monteiro, A. (2019). Male *Bicyclus anynana* butterflies choose females on the basis of their ventral UV-reflective eyespot centers. Journal of insect science, 19(1), 25.

Jeffreys, H. (1998). The theory of probability: OuP Oxford.

Kalyaanamoorthy, S. Minh, B, Q. Wong, T, K, F. Von Haeseler, A. & Jermiin, L, S. (2017). ModelFinder: Fast Model Selection for Accurate Phylogenetic Estimates, Nature Methods, 14:587–589.

Katoh, K. & Standley, D. M. (2013). MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. Molecular Biology and Evolution, 30(4), 772–780.

Kawahara, A., Ohshima, I., Kawakita, A., Regier, J., Mitter, C., Cummings, M., . . . Lopez-Vaamonde, C. (2011). Increased gene sampling provides stronger support for higher-level groups within gracillariid leaf mining moths and relatives (Lepidoptera: Gracillariidae). BMC Evol. Biol, 11, 182.

Kawahara, A. Y., & Rubinoff, D. (2012). Three new species of Fancy Case caterpillars from threatened forests of Hawaii (Lepidoptera, Cosmopterigidae, Hyposmocoma). ZooKeys(170), 1.

Kawahara, A. Y., & Breinholt, J. W. (2014). Phylogenomics provides strong evidence for relationships of butterflies and moths. Proceedings of the Royal Society B: Biological Sciences, 281(1788), 20140970.

Kawahara, A. Y., Plotkin, D., Espeland, M., Meusemann, K., Toussaint, E. F., Donath, A., . . . Dos Reis, M. (2019). Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. Proceedings of the National Academy of Sciences, 116(45), 22657-22663.

Kawahara, A. Y., Plotkin, D., Ohshima, I., LOPEZ-VAAMONDE, C., Houlihan, P. R., Breinholt, J. W., . . . Davis, D. R. (2017). A molecular phylogeny and revised higher-level classification for the leaf-mining moth family Gracillariidae and its implications for larval host-use evolution. Systematic Entomology, 42(1), 60-81.

Kawahara, A. Y., Storer, C., Carvalho, A. P. S., Plotkin, D. M., Condamine, F. L., Braga, M. P., . . . Lohman, D. J. (2023). A global phylogeny of butterflies reveals their evolutionary history, ancestral hosts and biogeographic origins. Nature Ecology & Evolution. doi:10.1038/s41559-023-02041-9

Kettlewell, H. (1973). The Evolution of Melanism: The Study of Recurring Necessity; with Special Reference to Industrial Melanism in the Lepidoptera. Clarendon Press, Oxford.

Kristensen, N. P., & Schmidt-Rhaesa, A. (1998). Volume 1: Evolution, Systematics, and Biogeography (Vol. 1): Walter de Gruyter.

Kodandaramaiah, U. (2011). The evolutionary significance of butterfly eyespots. Behavioral Ecology, 22(6), 1264-1271.

Kodandaramaiah, U., Lindenfors, P., & Tullberg, B. S. (2013). Deflective and intimidating eyespots: a comparative study of eyespot size and position in Junonia butterflies. Ecology and evolution, 3(13), 4518-4524.

Labandeira, C. C., Yang, Q., Santiago-Blay, J. A., Hotton, C. L., Monteiro, A., Wang, Y.-J., . . . Rose, T. R. (2016). The evolutionary convergence of mid-Mesozoic lacewings and Cenozoic butterflies. Proceedings of the Royal Society B: Biological Sciences, 283(1824), 20152893.

Lartillot, N., & Philippe, H. (2006). Computing Bayes factors using thermodynamic integration. Systematic biology, 55(2), 195-207.Miller, J. Y. (2008). Studies in the Castniidae. V. Description of a New Species of Zegara: Florida Museum of Natural History, University of Florida.

Merilaita, S., Vallin, A., Kodandaramaiah, U., Dimitrova, M., Ruuskanen, S., & Laaksonen, T. (2011). Number of eyespots and their intimidating effect on naive predators in the peacock butterfly. Behavioral Ecology, 22(6), 1326-1331.

Mey, W., Wichard, W., Müller, P., & Wang, B. (2017). The blueprint of the Amphiesmenoptera–Tarachoptera, a new order of insects from Burmese amber (Insecta, Amphiesmenoptera). Fossil Record, 20(2), 129-145.

Mitter, C., Davis, D. R., & Cummings, M. P. (2017). Phylogeny and evolution of Lepidoptera. Annual review of entomology.

Monteiro, A., Glaser, G., Stockslager, S., Glansdorp, N., & Ramos, D. (2006). Comparative insights into questions of Lepidopteran wing pattern homology. BMC Developmental Biology, 6(1), 1-13.

Monteiro, A., Chen, B., Scott, L. C., Vedder, L., Prijs, H. J., Belicha-Villanueva, A., & Brakefield, P. M. (2007). The combined effect of two mutations that alter serially homologous color pattern elements on the fore and hindwings of a butterfly. BMC genetics, 8, 1-10.

Monteiro, A. (2015). Origin, development, and evolution of butterfly eyespots. Annual review of entomology, 60, 253-271.

Mukherjee, R., & Kodandaramaiah, U. (2015). What makes eyespots intimidating–the importance of pairedness. BMC Evolutionary Biology, 15(1), 1-10.

Murugesan, S. N., Connahs, H., Matsuoka, Y., Das Gupta, M., Tiong, G. J., Huq, M., . . . Werner, T. (2022). Butterfly eyespots evolved via cooption of an ancestral gene-regulatory network that also patterns antennae, legs, and wings. Proceedings of the National Academy of Sciences, 119(8), e2108661119.

Mutanen, M., Wahlberg, N., & Kaila, L. (2010). Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. Proceedings of the Royal Society B: Biological Sciences, 277(1695), 2839-2848.

Nguyen, L, T. Schmidt, Heiko A. Haeseler, A & Minh, B, Q. (2015). IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies.

Oliver, J. C., Tong, X.-L., Gall, L. F., Piel, W. H., & Monteiro, A. (2012). A single origin for nymphalid butterfly eyespots followed by widespread loss of associated gene expression.

Oliver, J. C., Beaulieu, J. M., Gall, L. F., Piel, W. H., & Monteiro, A. (2014). Nymphalid eyespot serial homologues originate as a few individualized modules. Proceedings of the Royal Society B: Biological Sciences, 281(1787), 20133262.

Otaki, J. M. (2020). Morphological and spatial diversity of the discal spot on the hindwings of nymphalid butterflies: Revision of the nymphalid groundplan. Insects, 11(10), 654.

Paradis, E. & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35: 526-528.

Plummer, M. Best, N. Cowles, K. & Vines, K. (2006). CODA: Convergence Diagnosis and Output Analysis for MCMC, R News, vol 6, 7-11

R Core Team (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Regier, J. C., Zwick, A., Cummings, M. P., Kawahara, A. Y., Cho, S., Weller, S., . . . Parr, C. (2009). Toward reconstructing the evolution of advanced moths and butterflies (Lepidoptera: Ditrysia): an initial molecular study. BMC Evolutionary Biology, 9(1), 1-21.

Regier, J. C., Brown, J. W., Mitter, C., Baixeras, J., Cho, S., Cummings, M. P., & Zwick, A. (2012). A molecular phylogeny for the leaf-roller moths (Lepidoptera: Tortricidae) and its implications for classification and life history evolution. PLoS ONE, 7(4), e35574. (2012A)

Regier, J. C., Mitter, C., Mitter, K., Cummings, M. P., Bazinet, A. L., Hallwachs, W., . . . Zwick, A. (2017). Further progress on the phylogeny of Noctuoidea (Insecta: Lepidoptera) using an expanded gene sample. Systematic Entomology, 42(1), 82-93.

Regier, J. C., Mitter, C., Solis, M. A., Hayden, J. E., Landry, B., Nuss, M., . . . Cummings, M. P. (2012). A molecular phylogeny for the pyraloid moths (Lepidoptera: Pyraloidea) and its implications for higher-level classification. Systematic Entomology, 37(4), 635-656. (2012B)

Regier, J. C., Mitter, C., Zwick, A., Bazinet, A. L., Cummings, M. P., Kawahara, A. Y., . . . Davis, D. R. (2013). A large-scale, higher-level, molecular phylogenetic study of the insect order Lepidoptera (moths and butterflies). PLoS ONE, 8(3), e58568.

Regier, J. C., Mitter, C., Davis, D. R., Harrison, T. L., SOHN, J. C., Cummings, M. P., . . . Mitter, K. T. (2015). A molecular phylogeny and revised classification for the oldest ditrysian moth lineages (L epidoptera: T ineoidea), with implications for ancestral feeding habits of the mega-diverse D itrysia. Systematic Entomology, 40(2), 409-432.

Regier, J. C., Mitter, C., Solis, M. A., Hayden, J. E., Landry, B., Nuss, M., . . . Cummings, M. P. (2012). A molecular phylogeny for the pyraloid moths (Lepidoptera: Pyraloidea) and its implications for higher-level classification. *Systematic Entomology, 37*(4), 635-656.

Revell, L. J. (2012) phytools: An R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution, 3, 217-223.

Schachat, S. R., Oliver, J. C., & Monteiro, A. (2015). Nymphalid eyespots are co-opted to novel wing locations following a similar pattern in independent lineages. BMC evolutionary biology, 15(1), 1-9.

Sohn, J.-C., Regier, J. C., Mitter, C., Davis, D., Landry, J.-F., Zwick, A., & Cummings, M. P. (2013). A molecular phylogeny for Yponomeutoidea (Insecta, Lepidoptera, Ditrysia) and its implications for classification, biogeography and the evolution of host plant use. PLoS ONE, 8(1), e55066.

Sohn, J. C., Regier, J. C., Mitter, C., Adamski, D., LANDRY, J. F., Heikkilä, M., . . . Zwick, A. (2016). Phylogeny and feeding trait evolution of the mega-diverse Gelechioidea (Lepidoptera: Obtectomera): new insight from 19 nuclear genes. Systematic Entomology, 41(1), 112-132.

Sohn, J.-C., & Choi, S.-W. (2016). First report of Saridoscelinae (Lepidoptera, Yponomeutidae) in Korea with new records of Saridoscelis kodamai Moriuti from Korea and China. Korean journal of applied entomology, 55(4), 347-350.

Sondhi, S., Karmakar, T., Sondhi, Y., & Kunte, K. (2021). Moths of Tale Wildlife Sanctuary, Arunachal Pradesh, India with seventeen additions to the moth fauna of India (Lepidoptera: Heterocera). Tropical Lepidoptera Research, 1-53.

Stevens, M. (2005). The role of eyespots as anti-predator mechanisms, principally demonstrated in the Lepidoptera. Biological Reviews, 80(4), 573-588.

Tribble, C. May, M. Freyman, W. Landis, M. Ying, L. Barido-Sottani, J. Magee, A. Kopperud, B & Hohna, S. (2023). _RevGadgets: Visualization and Post-Processing of 'RevBayes' Analyses

Van Nieukerken, E., Kaila, L., Kitching, I., Kristensen, N., Lees, D., Minet, J., . . . Simonsen, T. (2011). Animal Biodiversity: an Outline of Higher-level Classification and Survey of Taxonomic Richness. Zootaxa (3148). In.Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Wickham, H. Hester, J. Chang, W & Bryan J (2022). _devtools: Tools to Make Developing R Packages Easier_. R package version 2.4.5, <https://CRAN.R-project.org/package=devtools>.

Wickham, H. Vaughan, D & Girlich M. (2023). _tidyr: Tidy Messy Data_. R package version 1.3.0, <https://CRAN.R-project.org/package=tidyr>.

Xie, W., Lewis, P. O., Fan, Y., Kuo, L., & Chen, M.-H. (2011). Improving marginal likelihood estimation for Bayesian phylogenetic model selection. Systematic biology, 60(2), 150-160.

Xu, S. Lin, L. Luo, X. Chen, M. Tang, W. Zhan, L. Dai, Z. Lam, T. Guan, Y. & Yu, G. (2022). Ggtree: A serialized data object for visualization of a phylogenetic tree and annotation data. iMeta 2022, 4(1):e56. doi:10.1002/imt2.56

Yu, G. (2020). Using ggtree to visualize data on tree-like structures. Current Protocols in Bioinformatics, 2020, 69:e96. doi: 10.1002/cpbi.96

Yu, G. (2022). Data Integration, Manipulation and Visualization of Phylogenetic Trees (1st edition). Chapman and Hall/CRC. doi:10.1201/9781003279242

Yu, G. Lam, T. Zhu, H. & Guan, Y. (2018). Two methods for mapping and visualizing associated data on phylogeny using ggtree. Molecular Biology and Evolution 2018, 35(2):3041-3043. doi: 10.1093/molbev/msy194

Yu, G. Smith, D. Zhu, H. Guan, & Y. Lam, T. (2017). ggtree: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. Methods in Ecology and Evolution 2017, 8(1):28-36. doi:10.1111/2041-210X.12628

Zahiri, R., Kitching, I. J., Lafontaine, J. D., Mutanen, M., Kaila, L., Holloway, J. D., & Wahlberg, N. (2011). A new molecular phylogeny offers hope for a stable family level classification of the Noctuoidea (Lepidoptera). Zoologica Scripta, 40(2), 158-173.

Zhang, L., & Reed, R. D. (2016). Genome editing in butterflies reveals that spalt promotes and Distal-less represses eyespot colour patterns. Nature communications, 7(1), 11769.

Websites:

Afro-Moths:

De Prins J. & De Prins W. 2011–2021. Afromoths, online database of Afrotropical moth species (Lepidoptera). World Wide Web electronic publication (http://www.afromoths.net) [last accessed on the 8/10/2022].

Bold V3 & V4:

Ratnasingham, S. & Hebert, P. D. N. (2007). BOLD: The Barcode of Life Data System (www.barcodinglife.org). Molecular Ecology Notes 7, 355-364. DOI: 10.1111/j.1471-8286.2006.01678.x

Ratnasingham S, Hebert P.D.N (2013). A DNA-Based Registry for All Animal Species: The Barcode Index Number (BIN) System. PLoS ONE 8(8): e66213. DOI:10.1371/journal.pone.0066213

Butterflies of America:

Warren, A. D., K. J. Davis, E. M. Stangeland, J. P. Pelham, K. R. Willmott & N. V. Grishin. (2023). Illustrated Lists of American Butterflies. Website version: [14-II-2023] last accessed on the 22/02/2023. Available at: http://www.butterfliesofamerica.com

Cornell university insect collection:

Cornell University insect collection (2023). A database of insect images and collections made available online by Cornell university. Last accessed on the 22/02/2023 and available at: https://cuic.entomology.cornell.edu/

CSIRO:

Australian moths online (CSIRO project, 2022). Online database of the Australian national museum, last accessed on the 16/11/2022 at: Australian Moths Online (csiro.au)

GBIF:

GBIF: The Global Biodiversity Information Facility (2022) What is GBIF? Available from https://www.gbif.org/what-is-gbif

Gracillariidae database:

De Prins J. & De Prins W. 2006–2022. Global Taxonomic Database of Gracillariidae (Lepidoptera). World Wide Web electronic publication (http://www.gracillariidae.net) [last accessed on the 22/02/2023].

Insecta Pro:

Insecta Pro (2022). A website which has a data base of many different species of Lepidoptera and other insects. Last accessed on the 18/08/2022 at: http://insecta.pro/

ITOL

iTOL(2023). Interactive Tree Of Life. Available at: https://itol.embl.de (Accessed: 6th January 2024)

Japanese moths:

Japanese moths.org (2023). A large website containing many Japanese moth species. Last accessed on the 22/02/2023. Available at: http://www.jpmoth.org

Lepi forum:

Lepi forum, a German Lepidopteran data base of online photos and other useful information about Lepidoptera. Last accessed on the 19/07/2022 and available at: https://lepiforum.org/

Moths Photographers group:

The website for the North American Moth photographers group based at the Mississippi entomological museum, part of Mississippi state university. Website was last accessed on the 16/08/2022 and is available at: Moth Photographers Group -- Main Menu (msstate.edu)

Moths of India:

Moths of India. (2023). An online database which holds the collection of many moths found in India. Last accessed on the 22/02/2023 and available at: Welcome to the Moths of India website! | Moths

Scan Bugs:

SCAN bugs. (2022). A image archive of insects from various institutions. Available at: http//:scan-bugs.org/portal/index.php. Last accessed on 02/08/2022.

Swedish museum of natural history:

Swedish museum of natural history. (2023). Available at Index of /en (nrm.se) Last accessed on 23/02/2023.

The museum of Shimane database:

The museum of Shimane database (2022). Database of Japanese Lepidoptera accessed on the 16/08/2022, last accessed at: http://museum-database.shimane-u.ac.jp/specimen/detail/502420180331122106

The Smithsonian Tropical Research Institute:

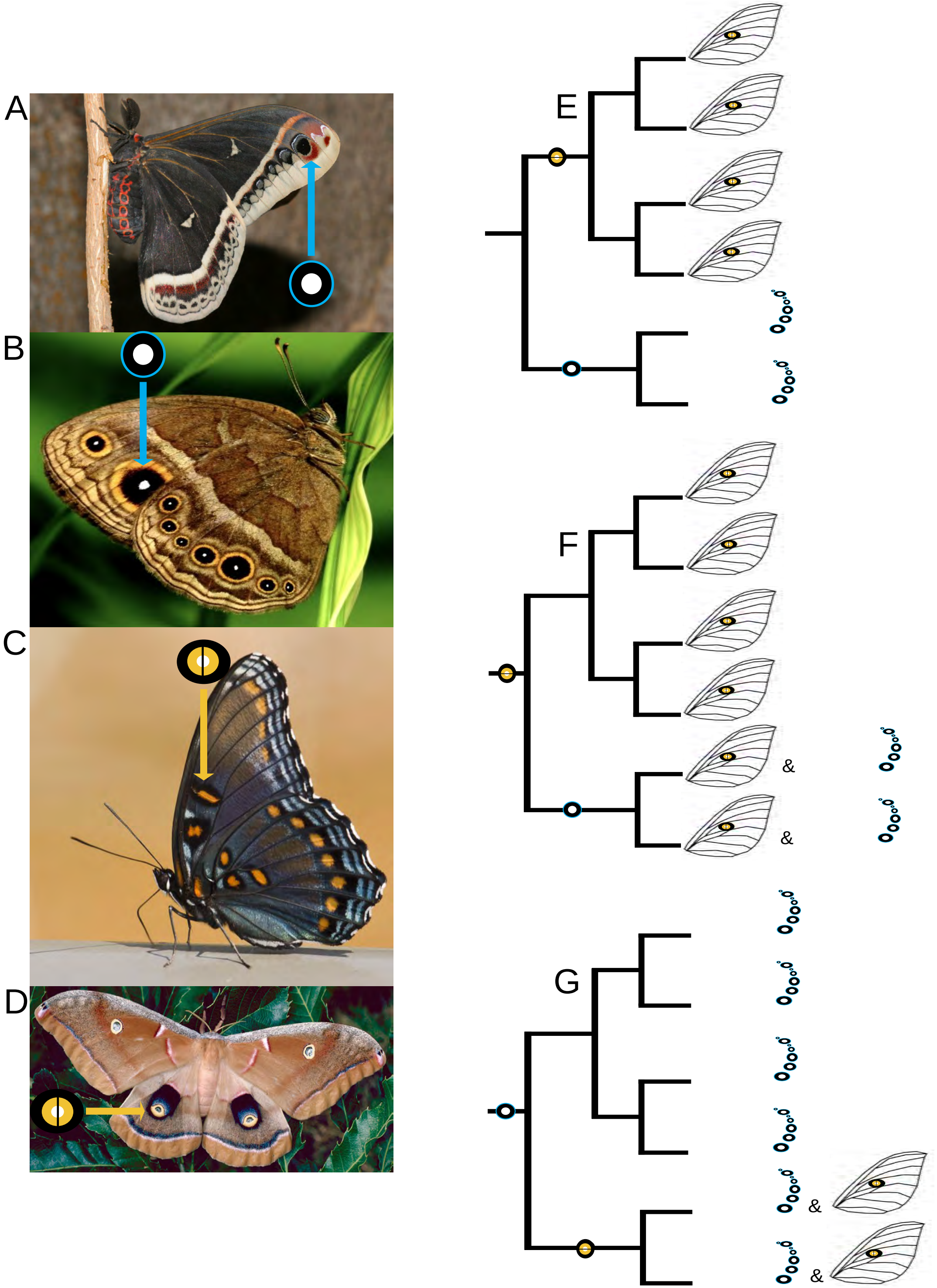
The Smithsonian Tropical Research Institute database. Last accessed on the 19/08/2022. Available at: Smithsonian Tropical Research Institute | (si.edu)

Taiwan encyclopedia of life:

Taiwan encyclopedia of life (2023). An online database of Taiwanese flora and fauna. Last accessed on the 22/02/2022 and available at: https://taieol.tw/

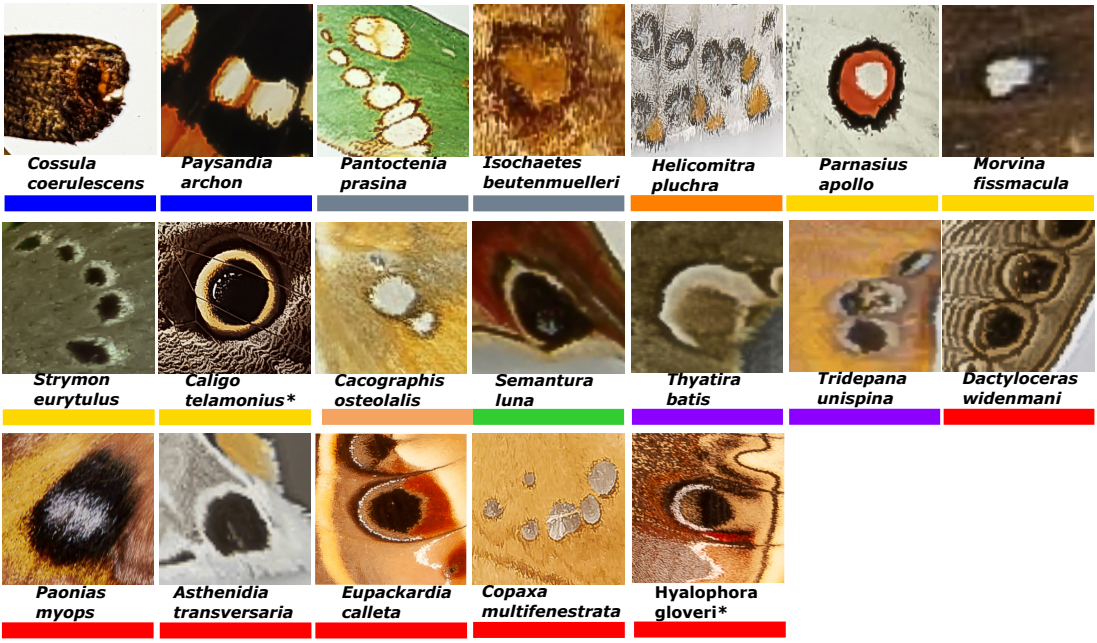
Places/Physical collections:

The Maguire Center for Lepidoptera (MGCL, 2022). Collections accessed in person 14.05.2022 to 04.06.2022. Hosted by Dr Keith Willmott (Director and curator) and Professor Akito Kawahara (Principal investigator and curator).


A
B
C
D
E
F
G
&
&
&
&

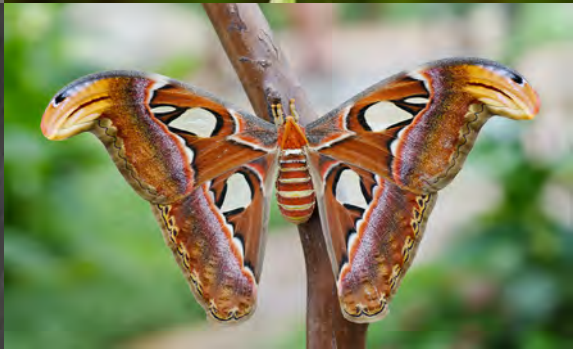
Discal

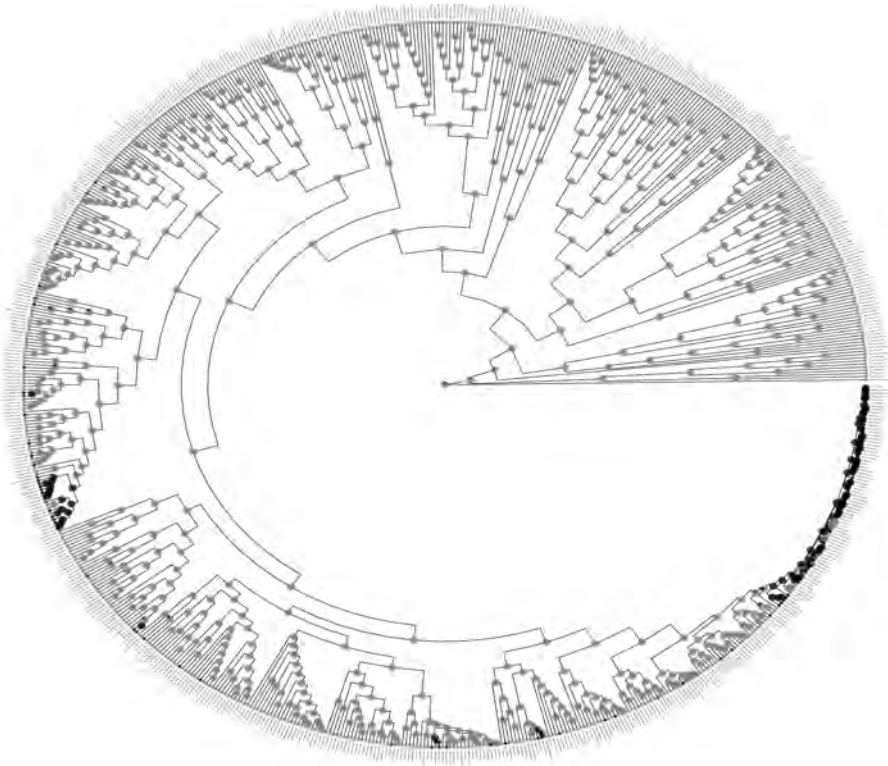
Marginal

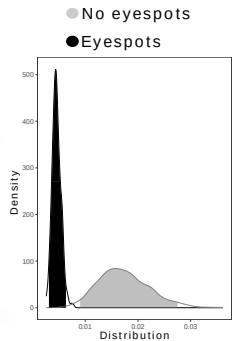


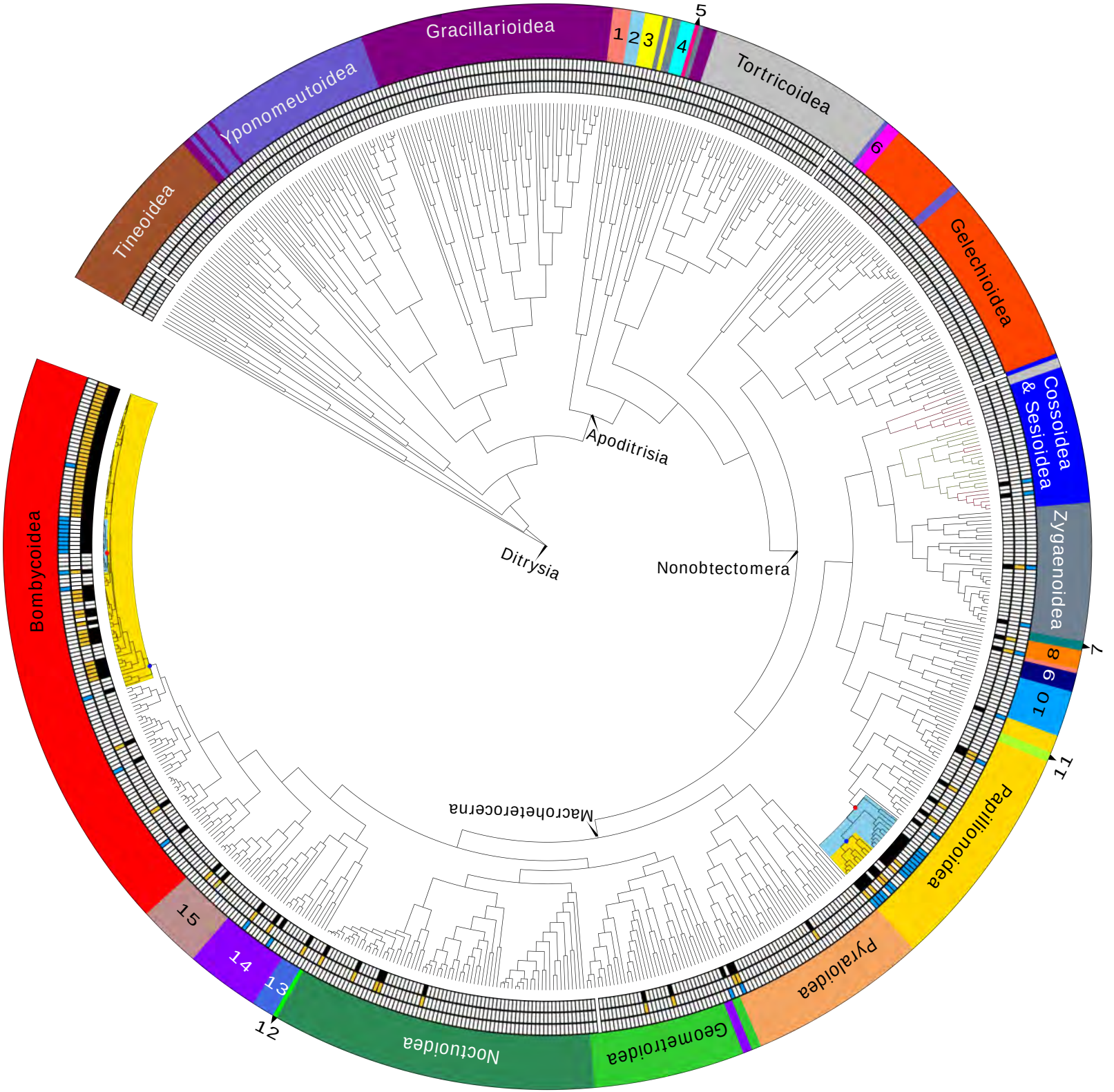
Key

- Cossoidea
- Zygaenoidea
- Calliduloidea
- Papilionoidea
- Pyraloidea
- Geometroidea
- Noctuoidea
- Mimallonoidea
- Drepanoidea
- Lasiocampoidea
- Bombycoidea






No eyespots
Eyespots
Density
500
400
300
200
100
0
0.01
0.02
0.03
Distribution


Gracillarioidea
Yponomeutoidea
Tineoidea
Tortricoidea
Gelechioidea
Cossoidea & Sesioidea
Zygaenoidea
Papilionoidea
Pyraloidea
Geometroidea
Noctuoidea
Bombycoidea
Apoditrisia
Ditrysia
Nonobtectomera
Macroheterocerna
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

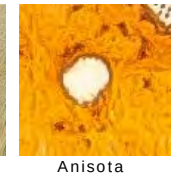
Discal eyespots in the Saturniidae

Actias isis

Actias luna

Aguila tau

Actias selene

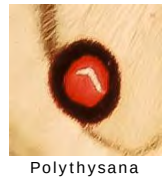

Anisota stigma

Gonimbrasia macrothyris

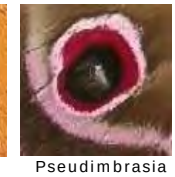
Erythromeris flexilineata

Saturnia walteorium

Graellsia isabellae


Polythysana apollina

Opodiphthera eucalypti


Pseudimbrasia deyrollei

Saturnia galbania

Loepa sikkima

Gonimbrasia tyrrhea

Hemileuca nevadensis

Saturnia albofasciata

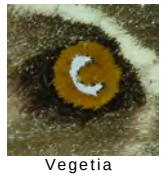
Saturnia nassegi

Rhodina fugnax

Eacles imperialis

Orthorene verana

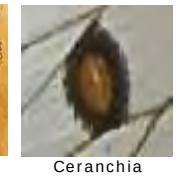
Epiphora mythimnia


Vegetia ducalis

Eubergia caisa

Antheraea youngi

Copaxa multifenestrata


Ceranchia apollina

Antheraea raffrayi

Antheraea pakustadorum

Antheraea pernyi

Antheraea larissa

Antheraea polyphemus

Antheraea rosemariae

Antheraea paphia

Saturnia caecigena

Antherina suraka

Antheraea yamamaii

Antheraea helferi

Antheraea roylii

Heniocha apollina

Argema mimosae

Saturnia mendocino

Antheraea lampei

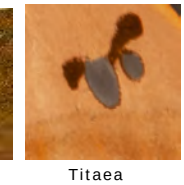
Cricula elaezia

Antheraea jana

Antheraea godmani

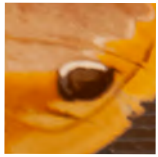
Bunaea alcinoe

Antheraea kelimutuensis

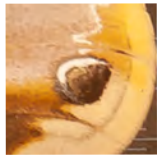

Titaea tamerlan

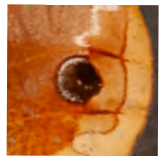
Marginal eyespots in the Saturniidae

Epiphora mythimnia


Samia cynthia

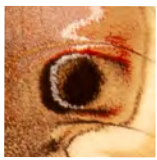
Samia luzonica


Samia ricini


Callosamia angulifera

Callosamia prometha

callosamia securifera


Hyalophora cecropia

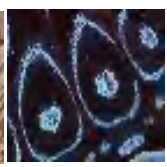
Hyalophora euryalus

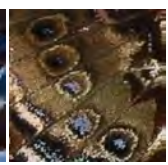
Hyalophora gloveri

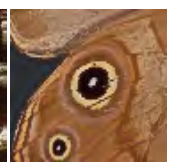
Marginal eyespots in the Nymphalidae

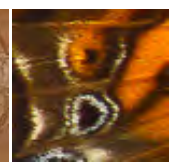
caligo telamonius

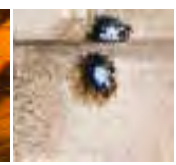
Asterocampa celtis

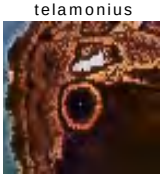

Hamadryas arinome


Hypanartia godmani


Lethe sicelis

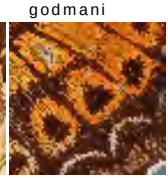

Marpesia petreus


Archeoprepona demophon


Manataria hercyna

Mycalesis gotama

Neope goschkevitschii


Phyciodes phaon

Pierella luna

Vanessa carye

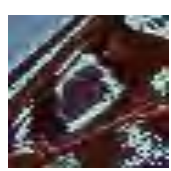
Taygetis andromeda

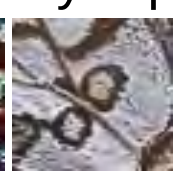
Discal eyespots in the Nymphalidae

Limenitis arthemis

Vanessa carye

Phyciodes phaon


Hamadryas arinome


Asterocampa celtis

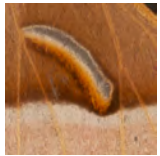
Eyespot like patterns in the Saturniidae

Callosamia angulifera

Callosamia promethea

Callosamia securifera

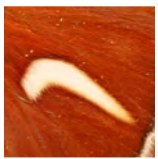
Samia cynthia


Samia luzonica

Samia ricini

Eupackardia calleta

Hyalophora cercopia


Hyalophora euryalus

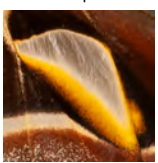
Hyalophora gloveri

Attacus lorquini

Attacus atlas

Attacus ceaser

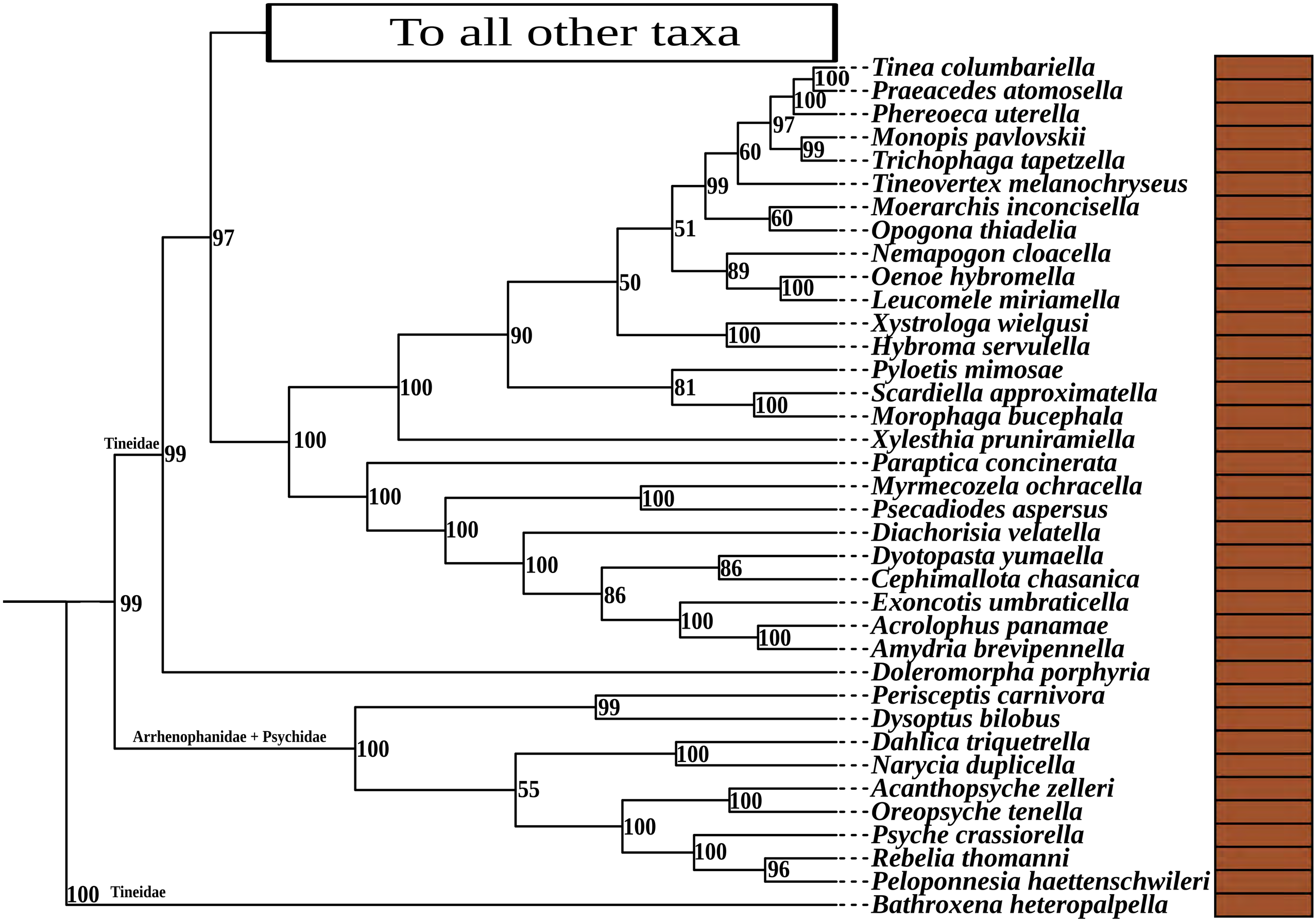
Coscinocera hercules

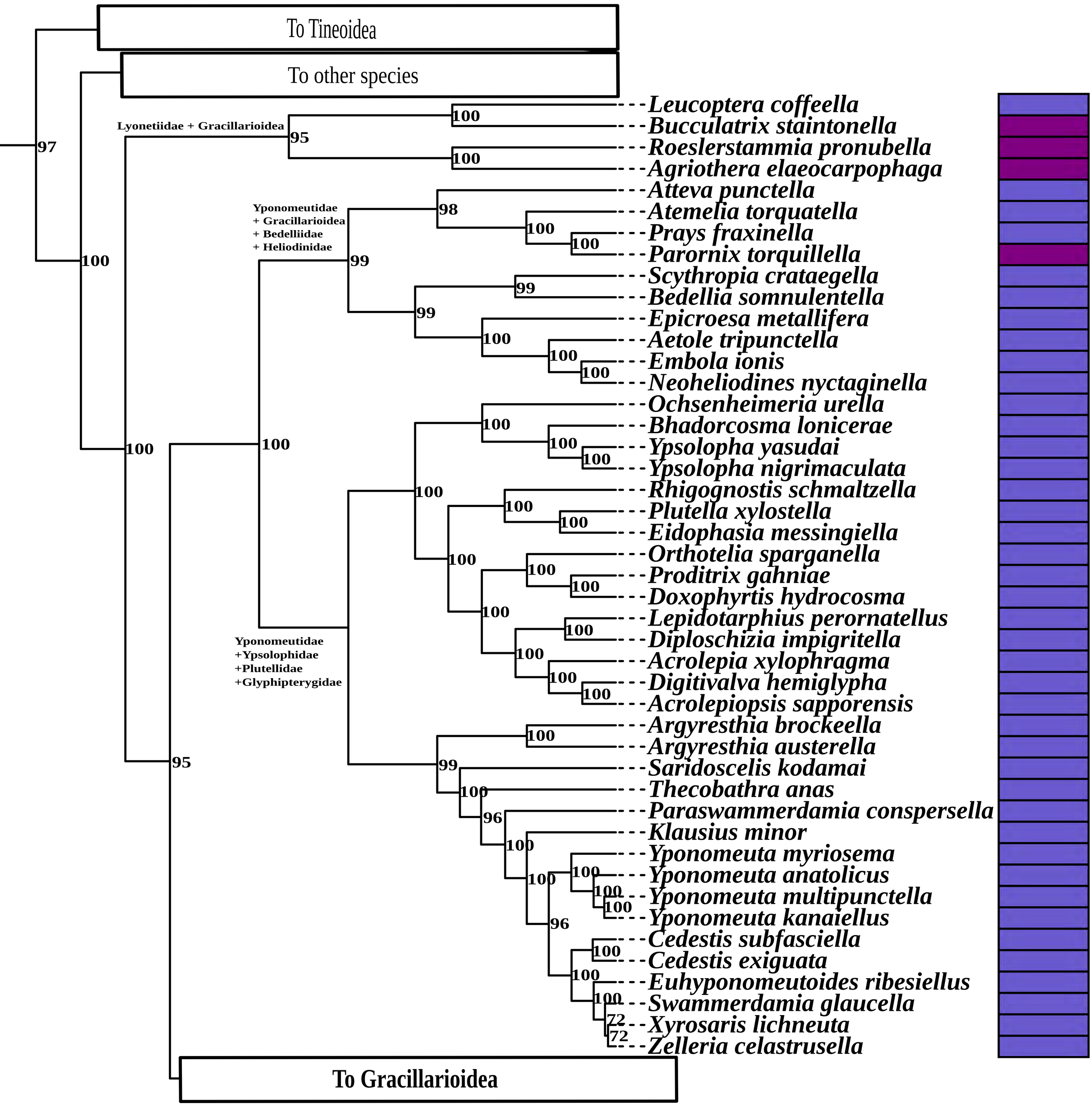

Archaeoattacus edwardsii

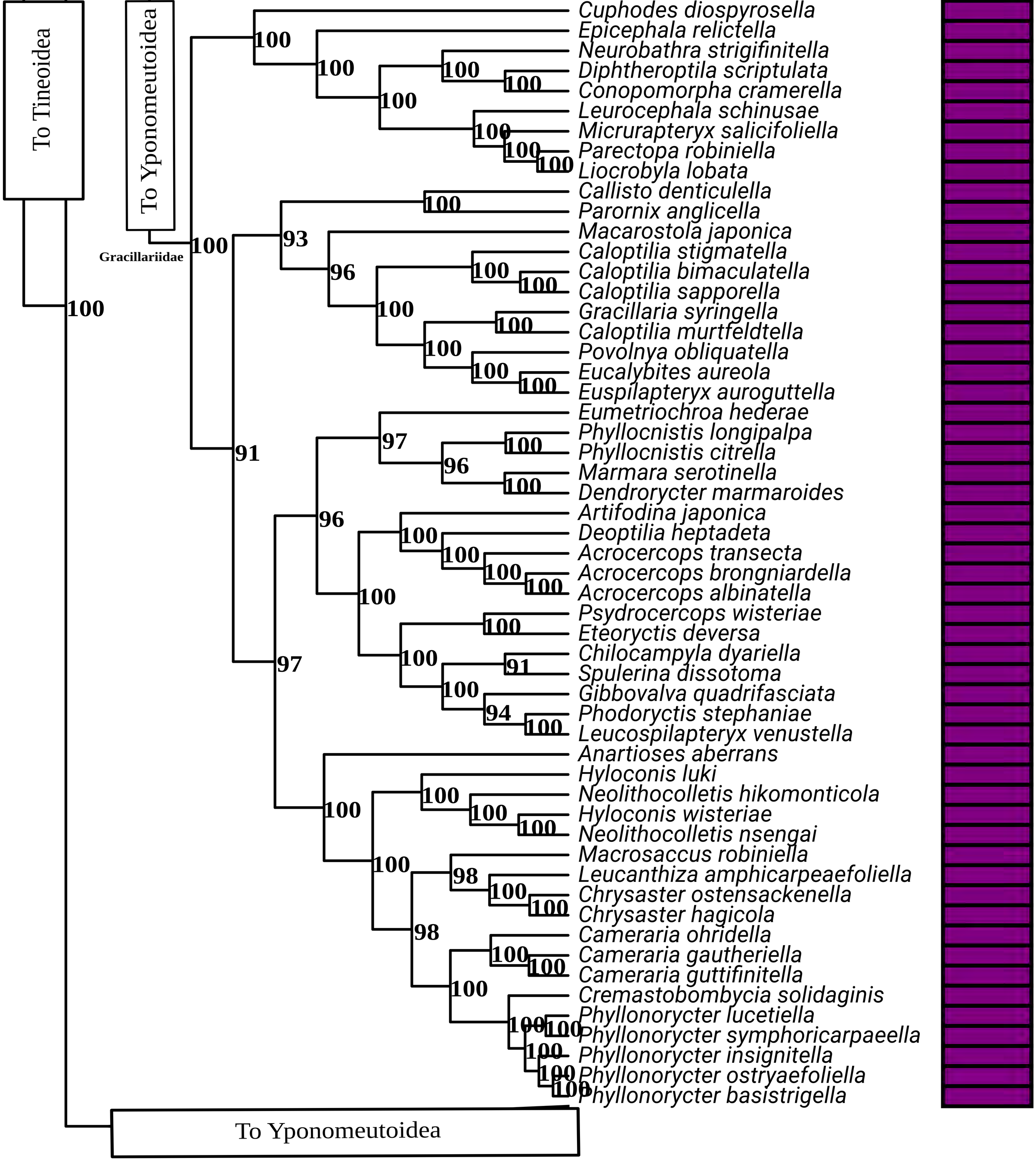
Rothschildia forbesi

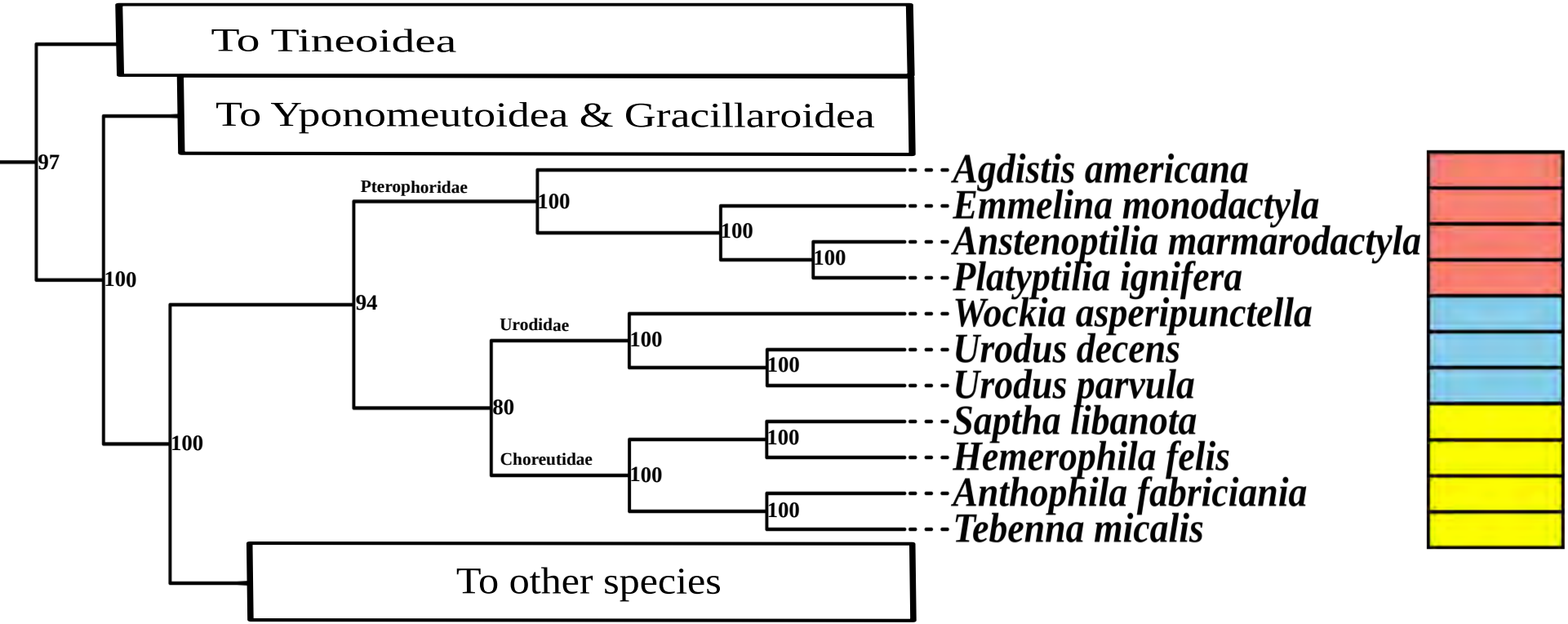
Rothschildia oriaba

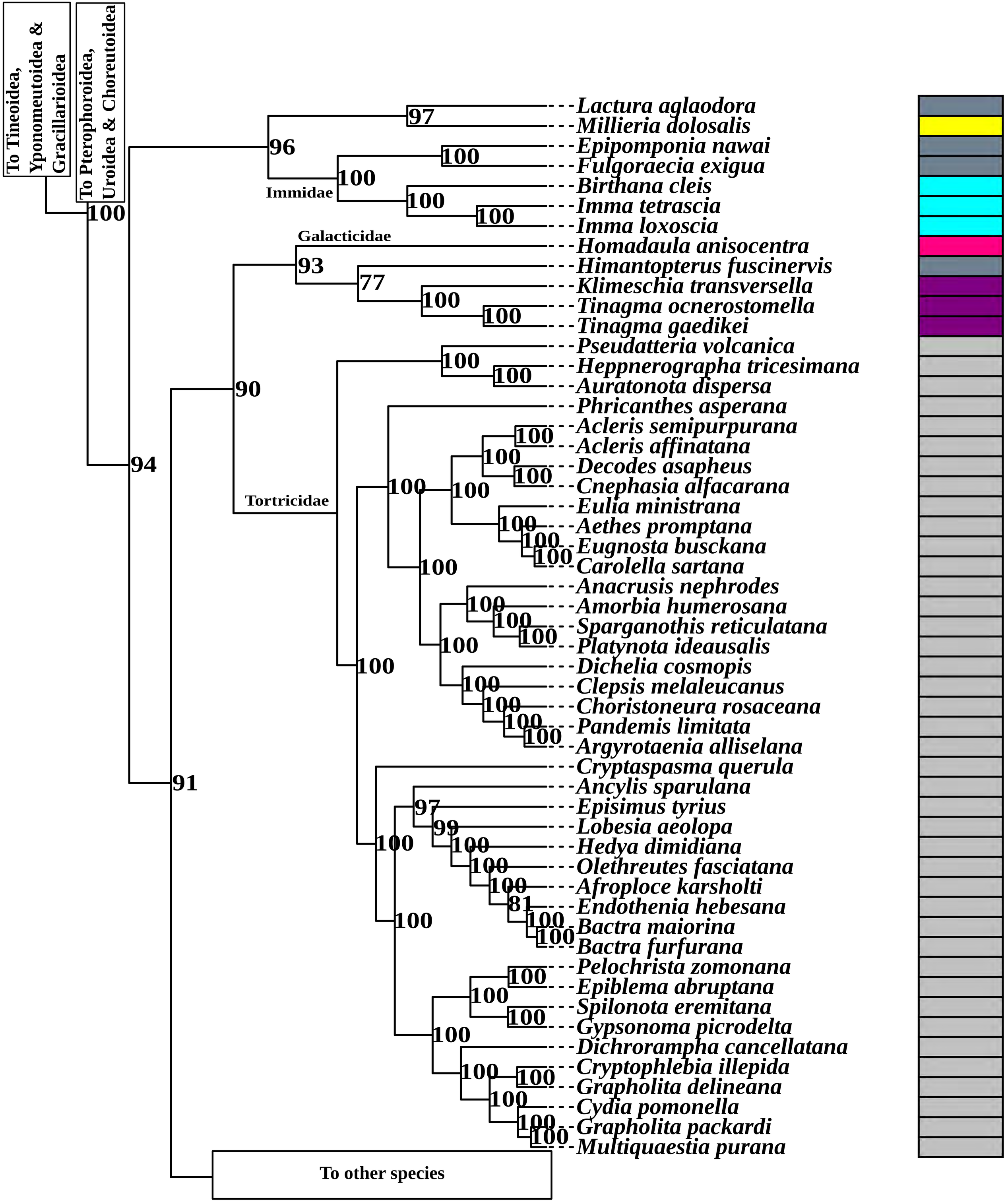
Holocerina smilax

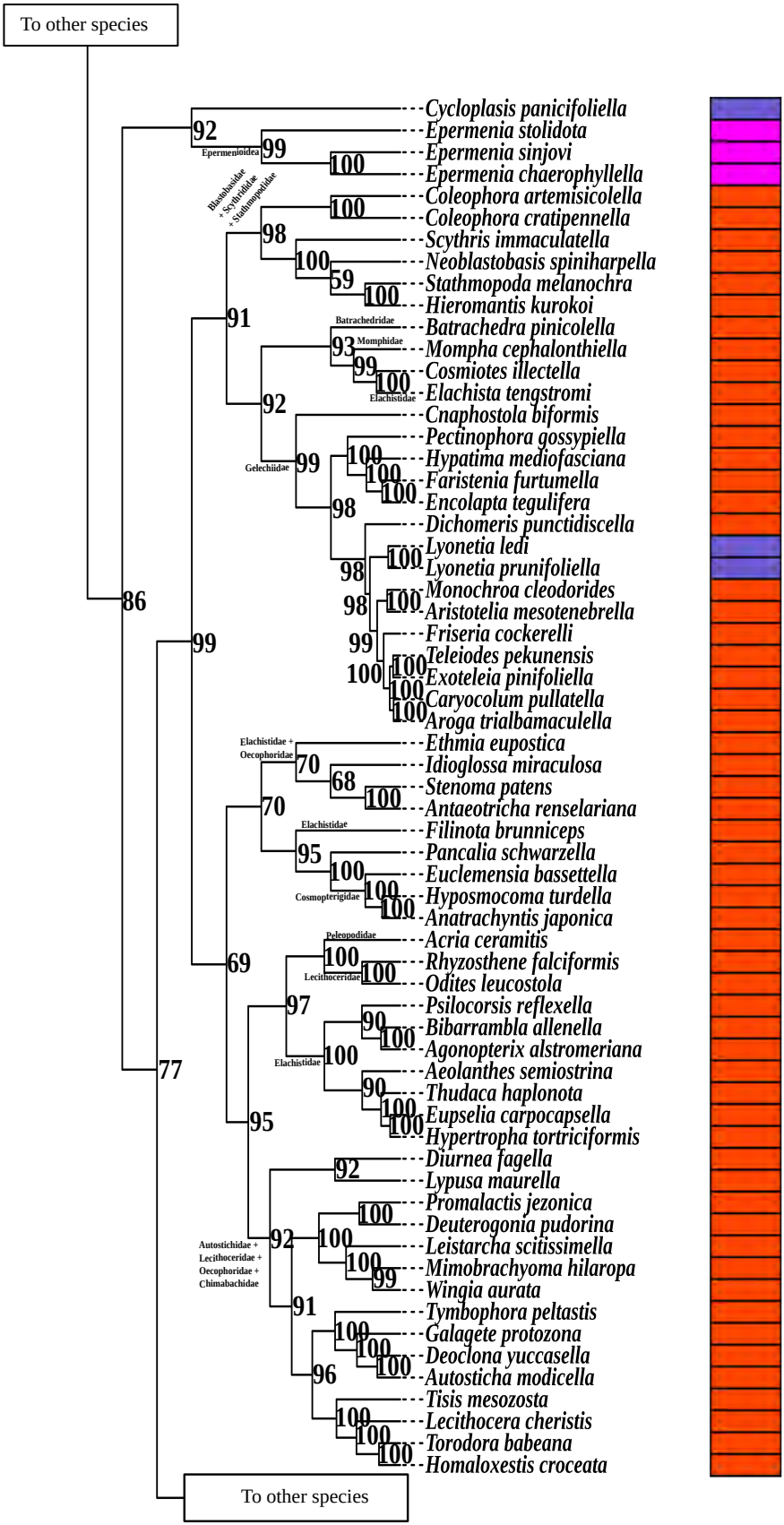

To all other taxa
Tineidae
Arrhenophanidae + Psychidae
Tineidae
Tinea columbariella
Praeacedes atomosella
Phereoeca uterella
Monopis pavlovskii
Trichophaga tapetzella
Tineovertex melanochryseus
Moerarchis inconcisella
Opogona thiadelia
Nemapogon cloacella
Oenoe hybromella
Leucomele miriamella
Xystrologa wielgusi
Hybroma servulella
Pyloetis mimosae
Scardiella approximatella
Morophaga bucephala
Xylesthia pruniramiella
Paraptica concinerata
Myrmecozela ochracella
Psecadiodes aspersus
Diachorisia velatella
Dyotopasta yumaella
Cephimallota chasanica
Exoncotis umbraticella
Acrolophus panamae
Amydria brevipennella
Doleromorpha porphyria
Perisceptis carnivora
Dysoptus bilobus
Dahlica triquetrella
Narycia duplicella
Acanthopsyche zelleri
Oreopsyche tenella
Psyche crassiorella
Rebelia thomanni
Peloponnesia haettenschwileri
Bathroxena heteropalpella

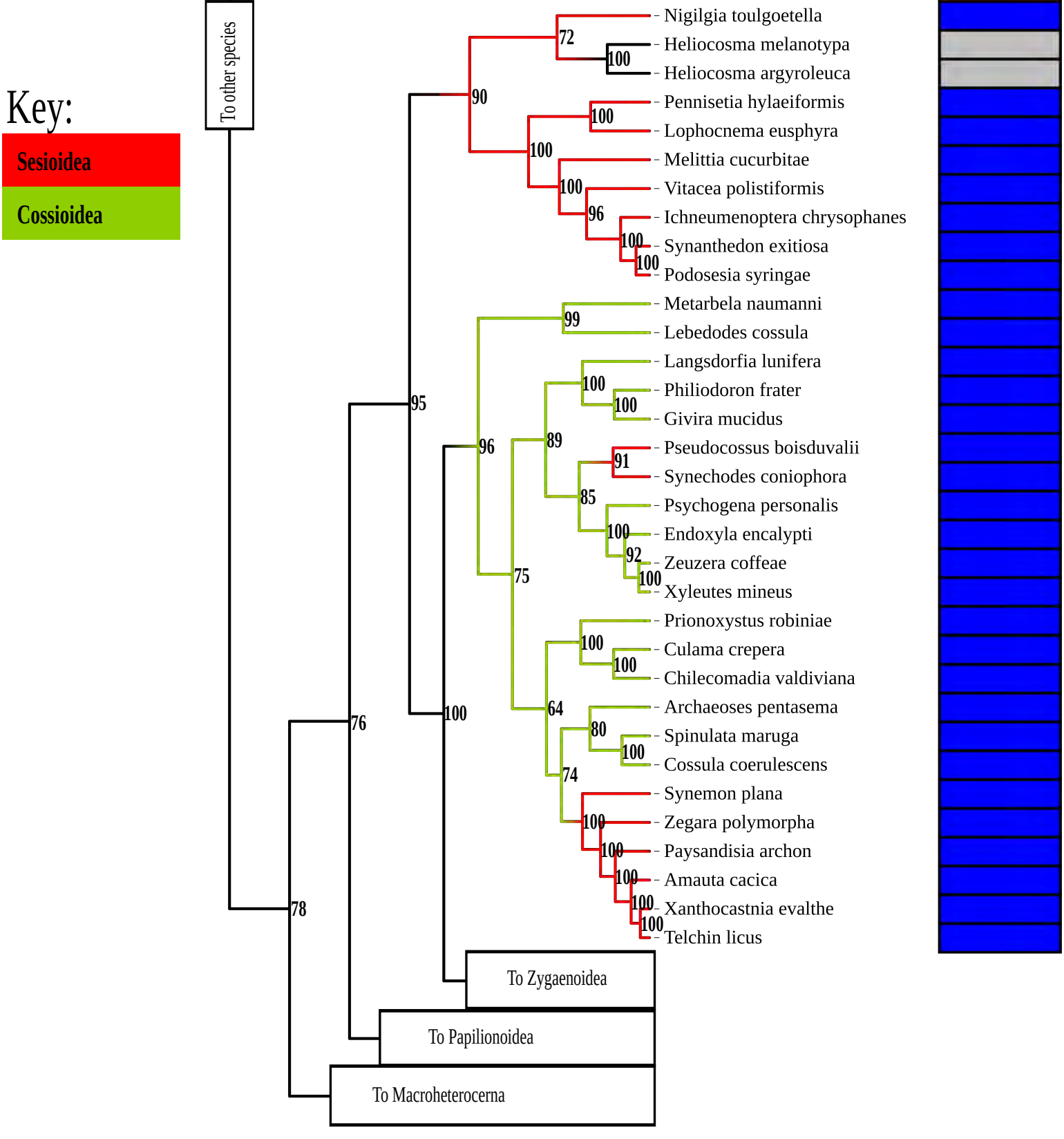

To Tineoidea
To other species
Lyonetiidae + Gracillarioidea
Yponomeutidae
+ Gracillarioidea
+ Bedelliidae
+ Heliodinidae
Yponomeutidae
+Ypsolophidae
+Plutellidae
+Glyphipterygidae
To Gracillarioidea
Leucoptera coffeella
Bucculatrix staintonella
Roeslerstammia pronubella
Agriothera elaeocarpophaga
Atteva punctella
Atemelia torquatella
Prays fraxinella
Parornix torquillella
Scythropia crataegella
Bedellia somnulentella
Epicroesa metallifera
Aetole tripunctella
Embola ionis
Neoheliodines nyctaginella
Ochsenheimeria urella
Bhadorcosma lonicerae
Ypsolopha yasudai
Ypsolopha nigrimaculata
Rhigognostis schmaltzella
Plutella xylostella
Eidophasia messingiella
Orthotelia sparganella
Proditrix gahniae
Doxophyrtis hydrocosma
Lepidotarphius perornatellus
Diploschizia impigritella
Acrolepia xylophragma
Digitivalva hemiglypha
Acrolepiopsis sapporensis
Argyresthia brockeella
Argyresthia austerella
Saridoscelis kodamai
Thecobathra anas
Paraswammerdamia conspersella
Klausius minor
Yponomeuta myriosema
Yponomeuta anatolicus
Yponomeuta multipunctella
Yponomeuta kanaiellus
Cedestis subfasciella
Cedestis exiguata
Euhyponomeutoides ribesiellus
Swammerdamia glaucella
Xyrosaris lichneuta
Zelleria celastrusella

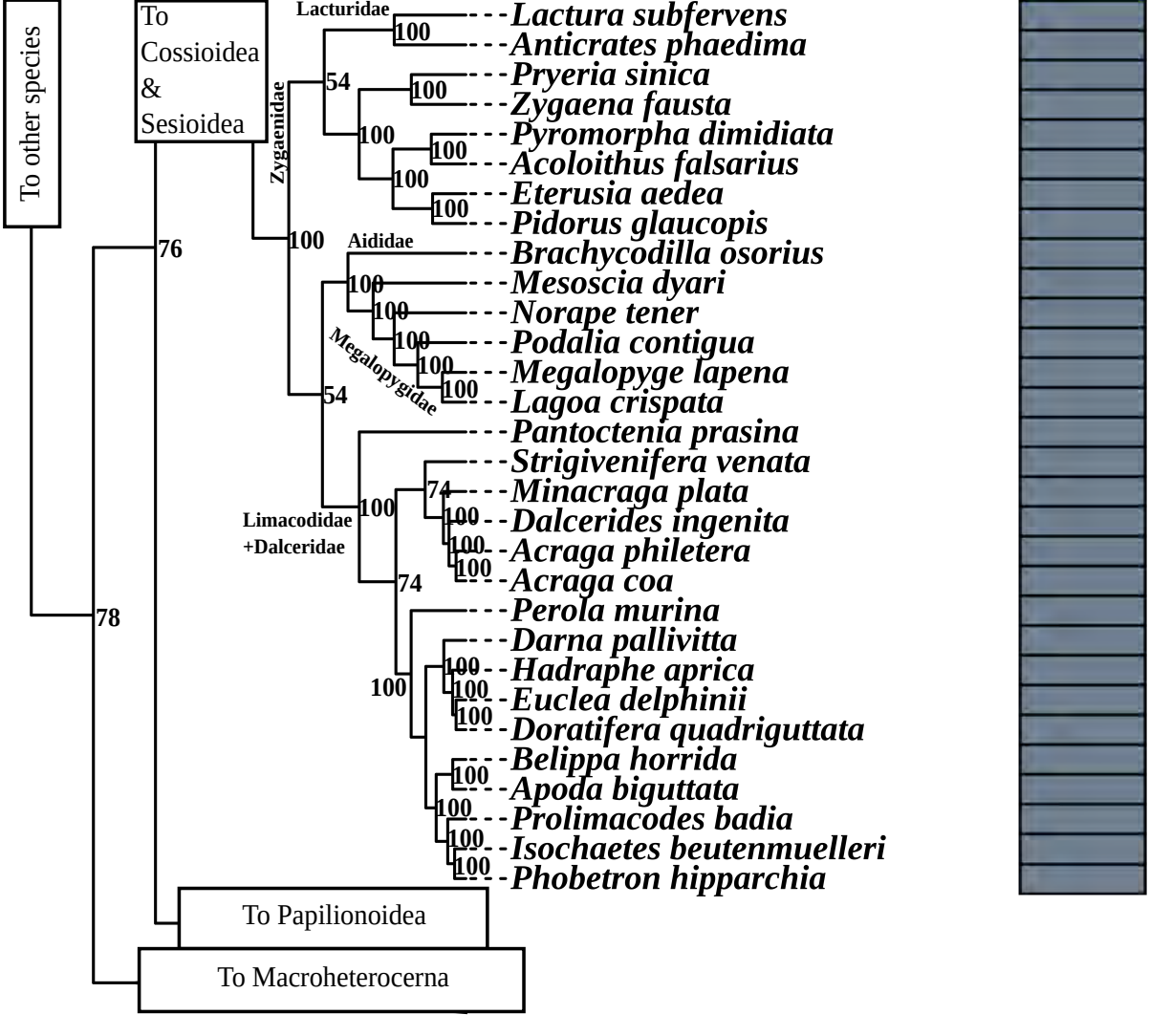

To Tineoidea
To Yponomeutoidea
Gracillariidae
100
100
100

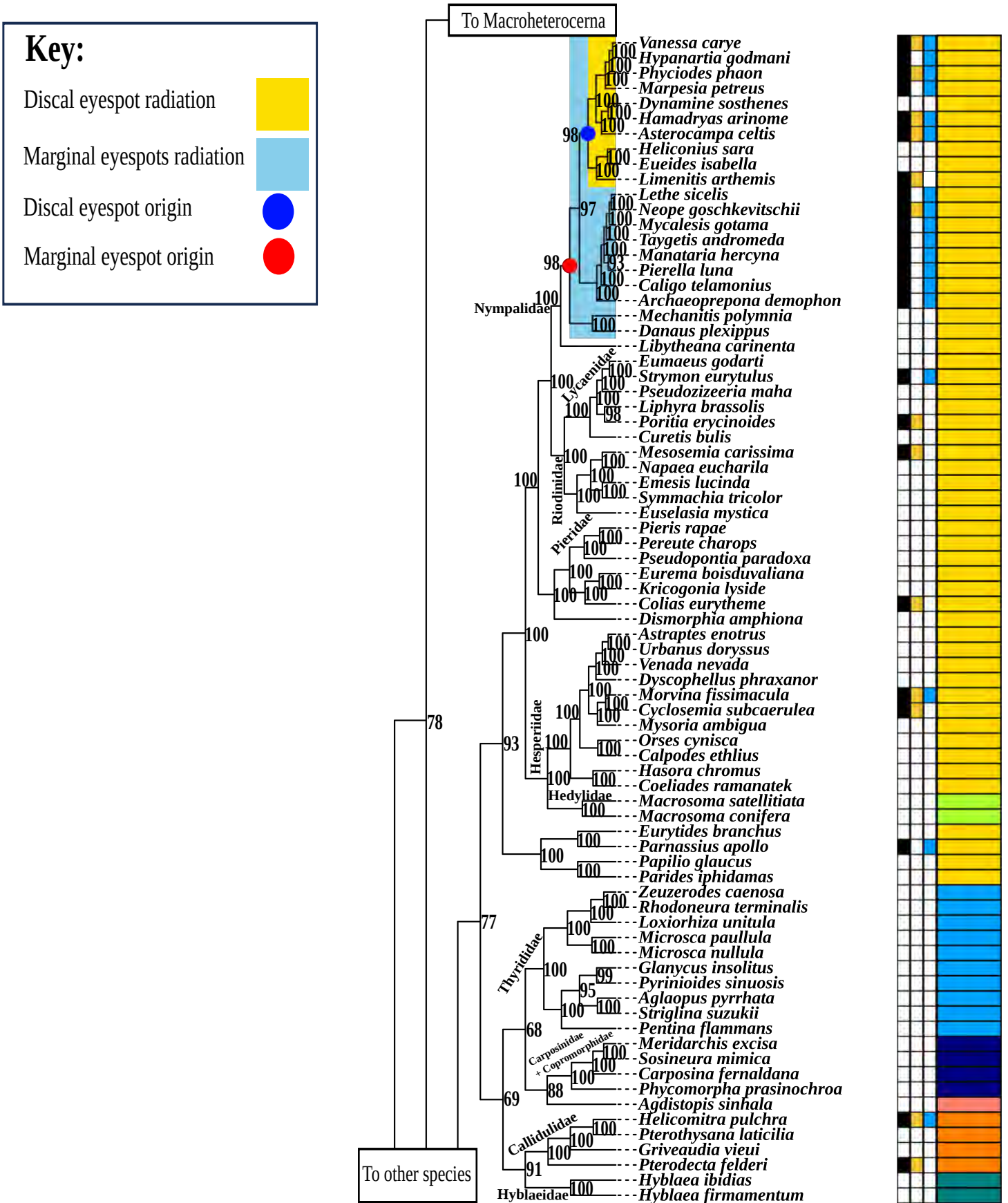

To Tineoidea
To Yponomeutoidea & Gracillaroidea
97
100
100
94
Pterophoridae
100
100
100
Urodidae
100
100
80
Choreutidae
100
100
100
Agdistis americana
Emmelina monodactyla
Anstenoptilia marmarodactyla
Platyptilia ignifera
Wockia asperipunctella
Urodus decens
Urodus parvula
Saptha libanota
Hemerophila felis
Anthophila fabriciania
Tebenna micalis
To other species

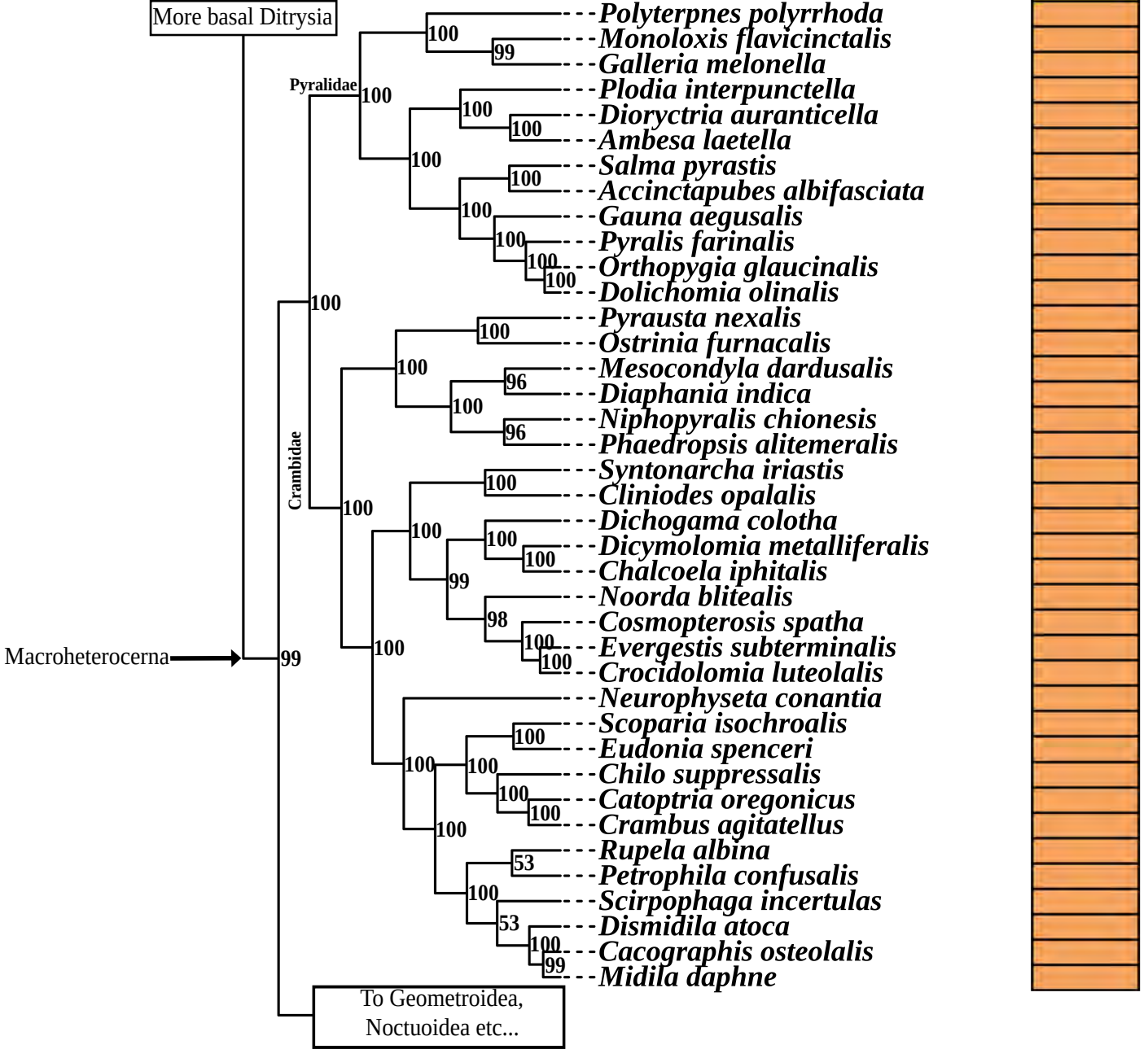

To Tineoidea, Yponomeutoidea & Gracillarioidea
To Pterophoroidea, Uroidea & Choreutoidea
Immidae
Galacticidae
Tortricidae
To other species
Lactura aglaodora
Millieria dolosalis
Epipomponia nawai
Fulgoraecia exigua
Birthana cleis
Imma tetrascia
Imma loxoscia
Homadaula anisocentra
Himantopterus fuscinervis
Klimeschia transversella
Tinagma ocnerostomella
Tinagma gaedikei
Pseudatteria volcanica
Heppnerographa tricesimana
Auratonota dispersa
Phricanthes asperana
Acleris semipurpurana
Acleris affinatana
Decodes asapheus
Cnephasia alfacarana
Eulia ministrana
Aethes promptana
Eugnosta busckana
Carolella sartana
Anacrusis nephrodes
Amorbia humerosana
Sparganothis reticulatana
Platynota ideausalis
Dichelia cosmopis
Clepsis melaleucanus
Choristoneura rosaceana
Pandemis limitata
Argyrotaenia alliselana
Cryptaspasma querula
Ancylis sparulana
Episimus tyrius
Lobesia aeolopa
Hedya dimidiana
Olethreutes fasciatana
Afroploce karsholti
Endothenia hebesana
Bactra maiorina
Bactra furfurana
Pelochrista zomonana
Epiblema abruptana
Spilonota eremitana
Gypsonoma picrodelta
Dichrorampha cancellatana
Cryptophlebia illepida
Grapholita delineana
Cydia pomonella
Grapholita packardi
Multiquaestia purana

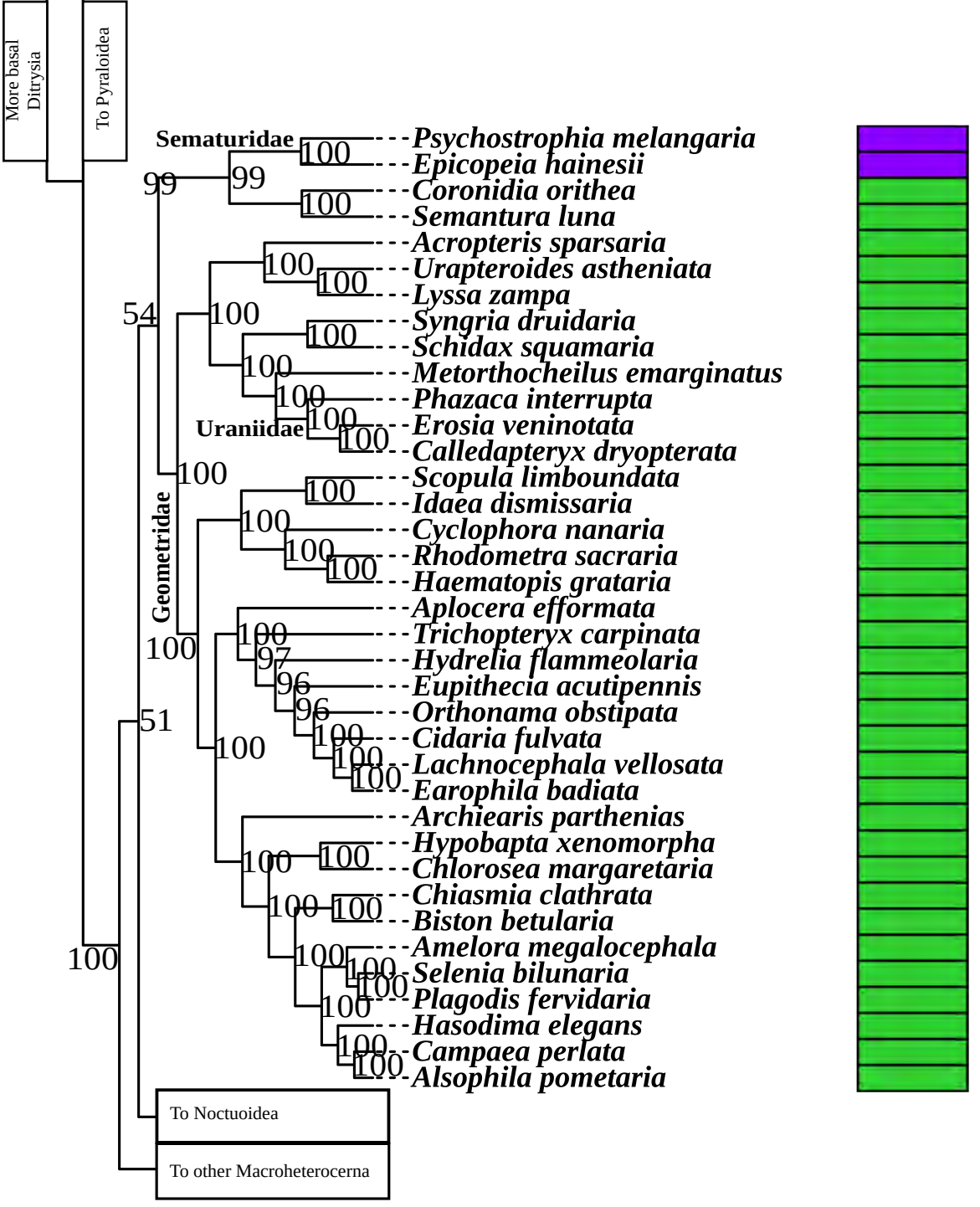

To other species
Epermenioidea
Blastobasidae + Scythrididae + Stathmopodidae
Batrachedridae
Momphidae
Elachistidae
Gelechiidae
Elachistidae + Oecophoridae
Elachistidae
Cosmopterigidae
Peleopodidae
Lecithoceridae
Elachistidae
Autostichidae + Lecithoceridae + Oecophoridae + Chimabachidae
Cycloplasis panicifoliella
Epermenia stolidota
Epermenia sinjovi
Epermenia chaerophyllella
Coleophora artemisicolella
Coleophora cratipennella
Scythris immaculatella
Neoblastobasis spiniharpella
Stathmopoda melanochra
Hieromantis kurokoi
Batrachedra pinicolella
Mompha cephalonthiella
Cosmiotes illectella
Elachista tengstromi
Cnaphostola biformis
Pectinophora gossypiella
Hypatima mediofasciana
Faristenia furtumella
Encolapta tegulifera
Dichomeris punctidiscella
Lyonetia ledi
Lyonetia prunifoliella
Monochroa cleodorides
Aristotelia mesotenebrella
Friseria cockerelli
Teleiodes pekunensis
Exoteleia pinifoliella
Caryocolum pullatella
Aroga trialbamaculella
Ethmia eupostica
Idioglossa miraculosa
Stenoma patens
Antaeotricha renselariana
Filinota brunniceps
Pancalia schwarzella
Euclemensia bassettella
Hyposmocoma turdella
Anatrachyntis japonica
Acria ceramitis
Rhyzosthene falciformis
Odites leucostola
Psilocorsis reflexella
Bibarrambla allenella
Agonopterix alstromeriana
Aeolanthes semiostrina
Thudaca haplonota
Eupselia carpocapsella
Hypertropha tortriciformis
Diurnea fagella
Lypusa maurella
Promalactis jezonica
Deuterogonia pudorina
Leistarcha scitissimella
Mimobrachyoma hilaropa
Wingia aurata
Tymbophora peltastis
Galagete protozona
Deoclona yuccasella
Autosticha modicella
Tisis mesozosta
Lecithocera cheristis
Torodora babeana
Homaloxestis croceata
To other species

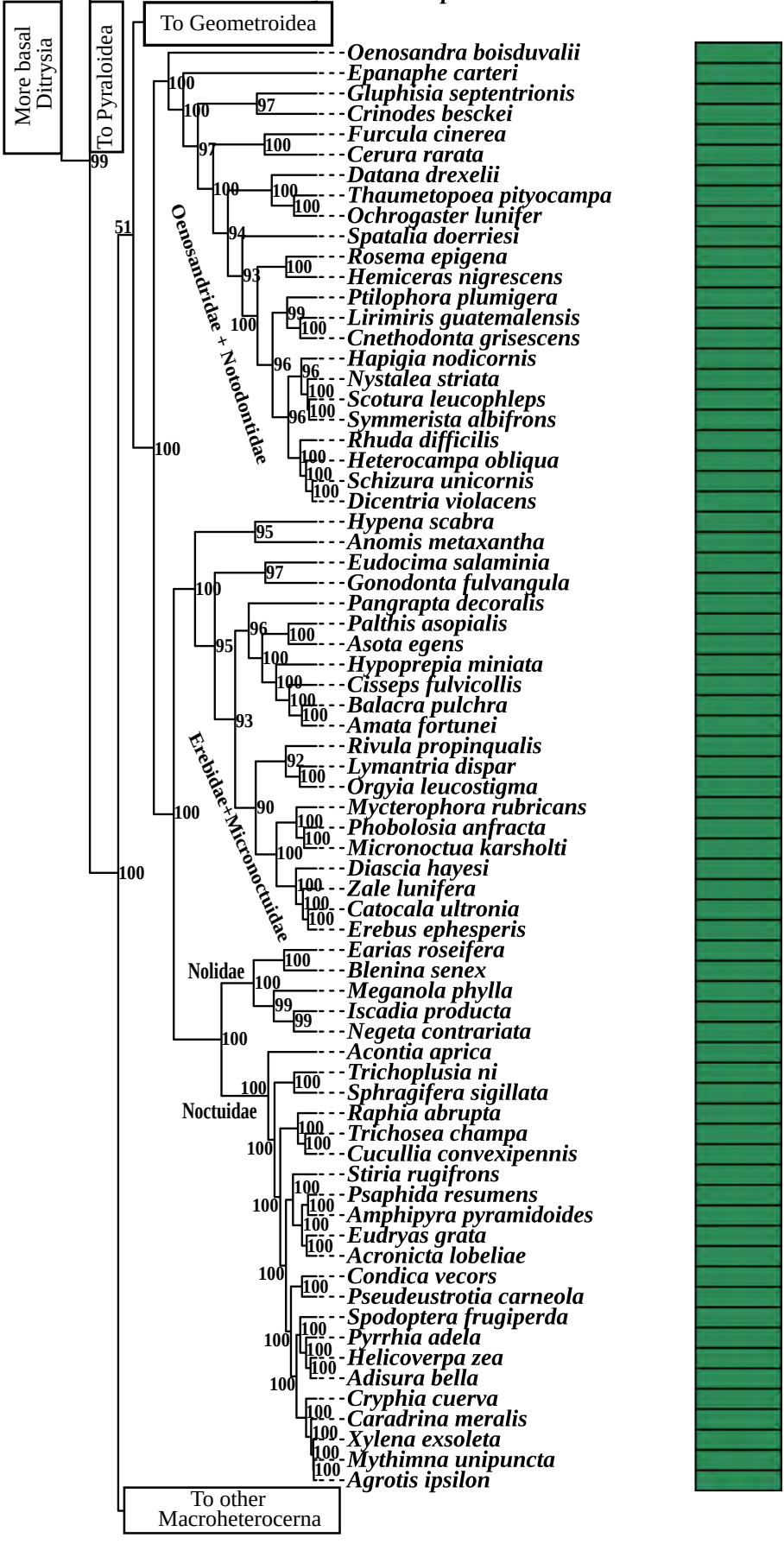

Key:
Sesioidea
Cossioidea
To other species
Nigilgia toulgoetella
Heliocosma melanotypa
Heliocosma argyroleuca
Pennisetia hylaeiformis
Lophocnema eusphyra
Melittia cucurbitae
Vitacea polistiformis
Ichneumenoptera chrysophanes
Synanthedon exitiosa
Podosesia syringae
Metarbela naumanni
Lebedodes cossula
Langsdorfia lunifera
Philiodoron frater
Givira mucidus
Pseudocossus boisduvalii
Synechodes coniophora
Psychogena personalis
Endoxyla encalypti
Zeuzera coffeae
Xyleutes mineus
Prionoxystus robiniae
Culama crepera
Chilecomadia valdiviana
Archaeoses pentasema
Spinulata maruga
Cossula coerulescens
Synemon plana
Zegara polymorpha
Paysandisia archon
Amauta cacica
Xanthocastnia evalthe
Telchin licus
To Zygaenoidea
To Papilionoidea
To Macroheterocerna

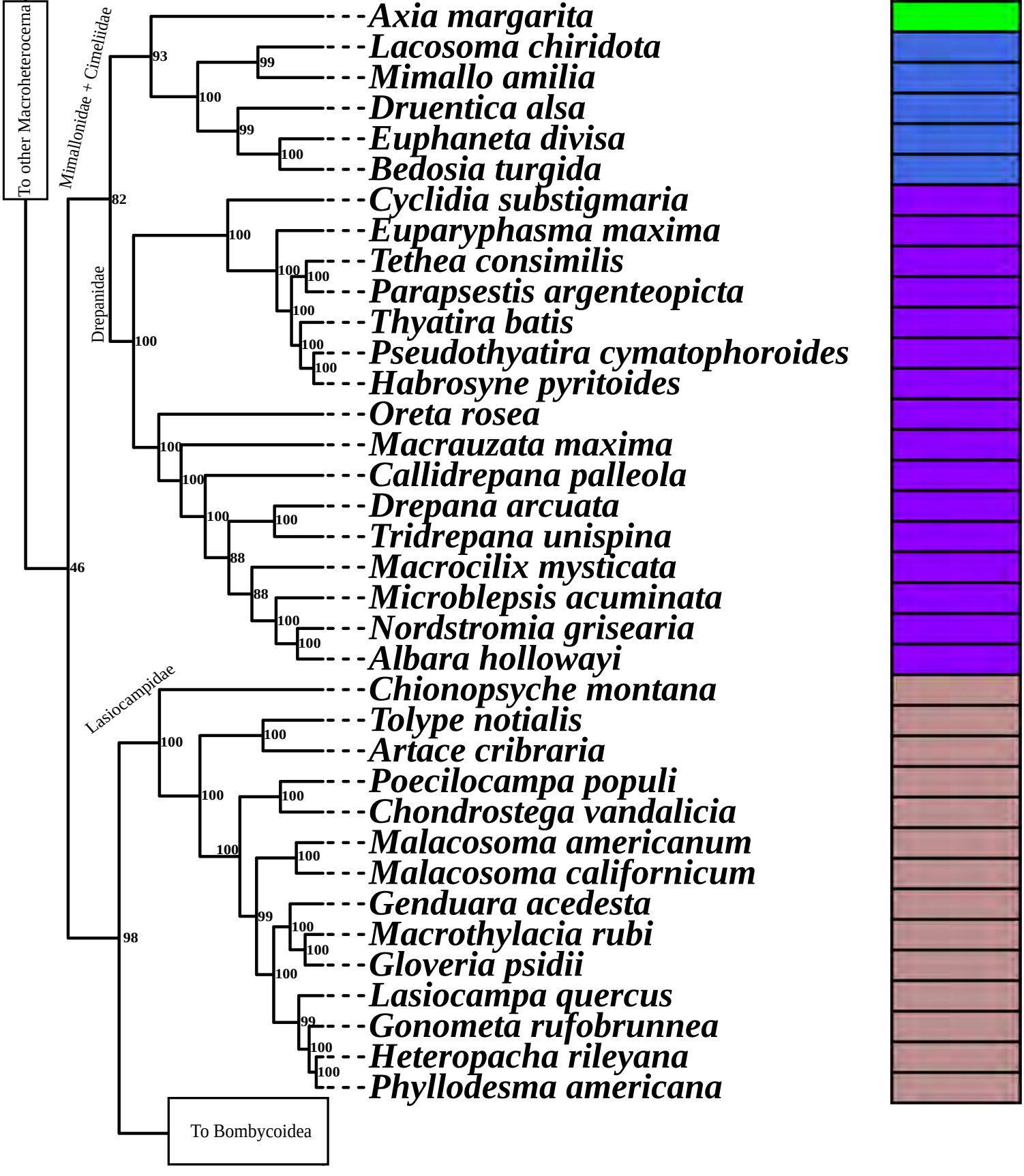

To other species
To Cossioidea & Sesioidea
Lacturidae
Zygaenidae
Aididae
Megalopygidae
Limacodidae +Dalceridae
Lactura subfervens
Anticrates phaedima
Pryeria sinica
Zygaena fausta
Pyromorpha dimidiata
Acoloithus falsarius
Eterusia aedea
Pidorus glaucopis
Brachycodilla osorius
Mesoscia dyari
Norape tener
Podalia contigua
Megalopyge lapena
Lagoa crispata
Pantoctenia prasina
Strigivenifera venata
Minacraga plata
Dalcerides ingenita
Acraga philetera
Acraga coa
Perola murina
Darna pallivitta
Hadraphe aprica
Euclea delphinii
Doratifera quadriguttata
Belippa horrida
Apoda biguttata
Prolimacodes badia
Isochaetes beutenmuelleri
Phobetron hipparchia
To Papilionoidea
To Macroheterocerna
76
78
100
54
74

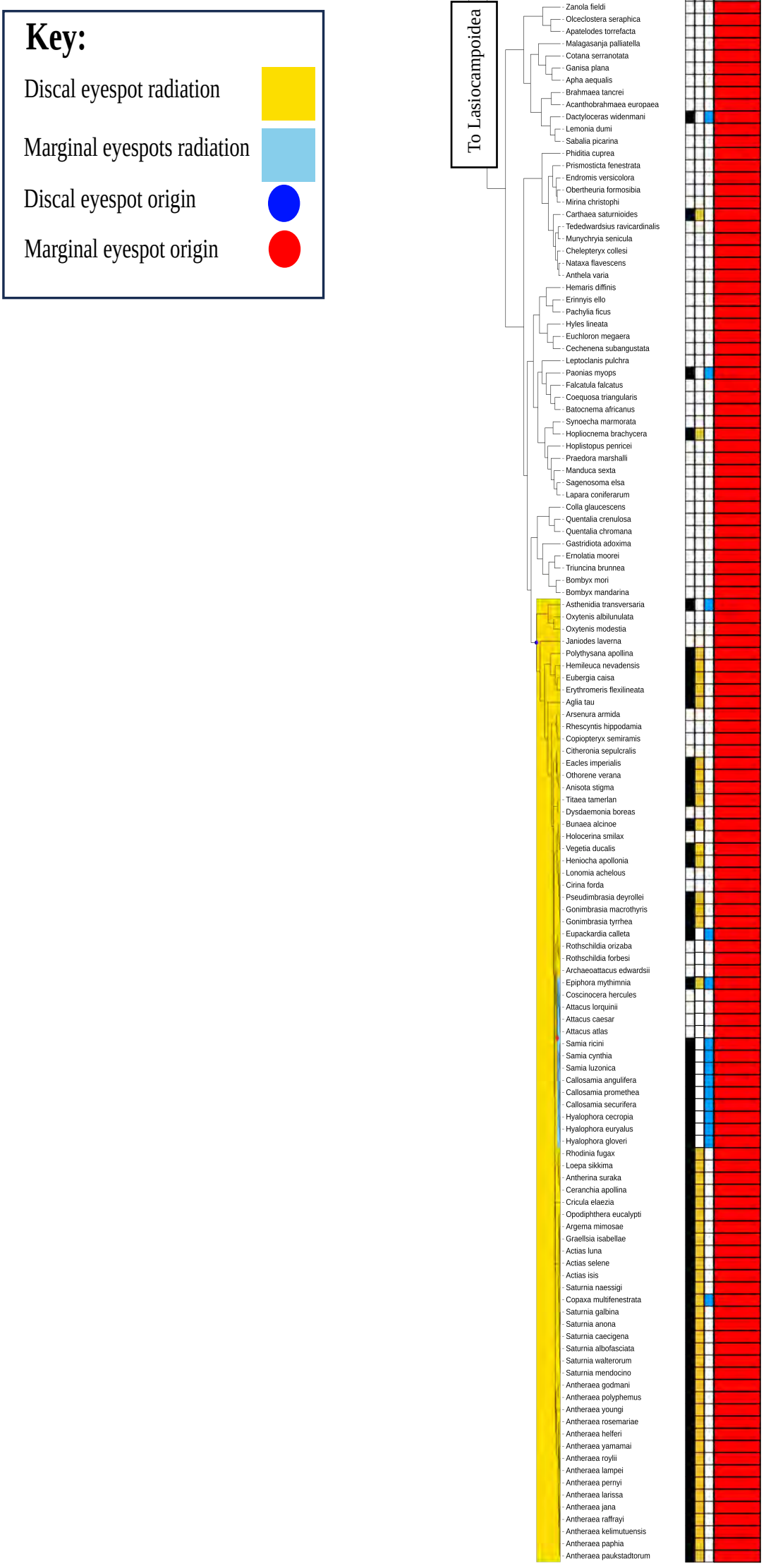

Key:
Discal eyespot radiation
Marginal eyespots radiation
Discal eyespot origin
Marginal eyespot origin
To Macroheterocerna
To other species
Nymphalidae
Lycaenidae
Riodinidae
Pieridae
Hesperiidae
Hedylidae
Thyrididae
Carposinidae + Copromorphidae
Callidulidae
Hyblaeidae
Vanessa carye
Hypanartia godmani
Phyciodes phaon
Marpesia petreus
Dynamine sosthenes
Hamadryas arinome
Asterocampa celtis
Heliconius sara
Eueides isabella
Limenitis arthemis
Lethe sicelis
Neope goschkevitschii
Mycalesis gotama
Taygetis andromeda
Manataria hercyna
Pierella luna
Caligo telamonius
Archaeoprepona demophon
Mechanitis polymnia
Danaus plexippus
Libytheana carinenta
Eumaeus godarti
Strymon eurytulus
Pseudozizeeria maha
Liphyra brassolis
Poritia erycinoides
Curetis bulis
Mesosemia carissima
Napaea eucharila
Emesis lucinda
Symmachia tricolor
Euselasia mystica
Pieris rapae
Pereute charops
Pseudopontia paradoxa
Eurema boisduvaliana
Kricogonia lyside
Colias eurytheme
Dismorphia amphiona
Astraptes enotrus
Urbanus doryssus
Venada nevada
Dyscophellus phraxanor
Morvina fissimacula
Cyclosemia subcaerulea
Mysoria ambigua
Orses cynisca
Calpodes ethlius
Hasora chromus
Coeliades ramanatek
Macrosoma satellitiata
Macrosoma conifera
Eurytides branchus
Parnassius apollo
Papilio glaucus
Parides iphidamas
Zeuzerodes caenosa
Rhodoneura terminalis
Loxiorhiza unitula
Microsca paullula
Microsca nullula
Glanycus insolitus
Pyrinioides sinuosis
Aglaopus pyrrhata
Striglina suzukii
Pentina flammans
Meridarchis excisa
Sosineura mimica
Carposina fernaldana
Phycomorpha prasinochroa
Agdistopis sinhala
Helicomitra pulchra
Pterothysana laticilia
Griveaudia vieui
Pterodecta felderi
Hyblaea ibidias
Hyblaea firmamentum

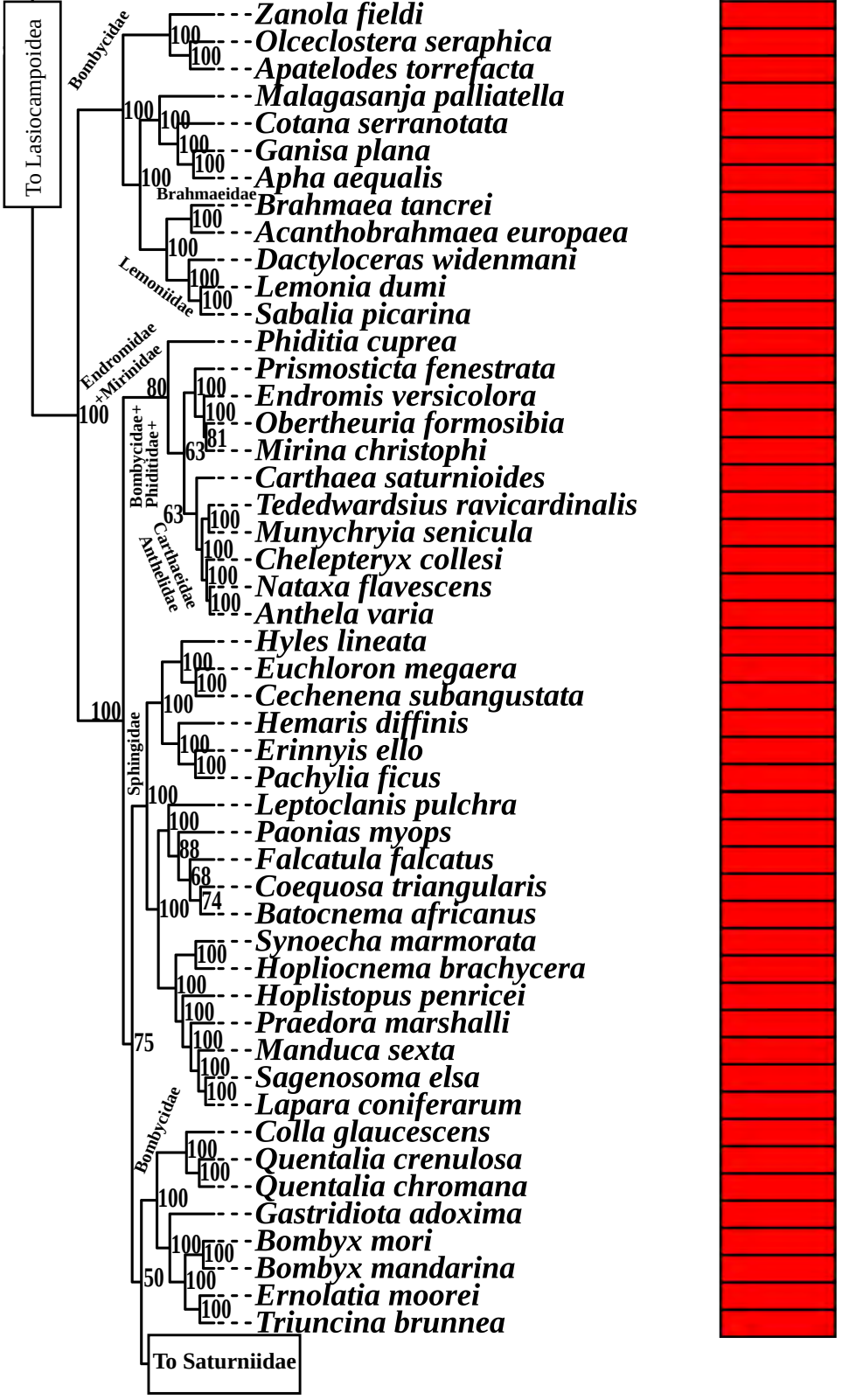

More basal Ditrysia
Pyralidae
Crambidae
Macroheterocerna
To Geometroidea, Noctuoidea etc...
Polyterpnes polyrrhoda
Monoloxis flavicinctalis
Galleria melonella
Plodia interpunctella
Dioryctria auranticella
Ambesa laetella
Salma pyrastis
Accinctapubes albifasciata
Gauna aegusalis
Pyralis farinalis
Orthopygia glaucinalis
Dolichomia olinalis
Pyrausta nexalis
Ostrinia furnacalis
Mesocondyla dardusalis
Diaphania indica
Niphopyralis chionesis
Phaedropsis alitemeralis
Syntonarcha iriastis
Cliniodes opalalis
Dichogama colotha
Dicymolomia metalliferalis
Chalcoela iphitalis
Noorda blitealis
Cosmopterosis spatha
Evergestis subterminalis
Crocidolomia luteolalis
Neurophyseta conantia
Scoparia isochroalis
Eudonia spenceri
Chilo suppressalis
Catoptria oregonicus
Crambus agitatellus
Rupela albina
Petrophila confusalis
Scirpophaga incertulas
Dismidila atoca
Cacographis osteolalis
Midila daphne

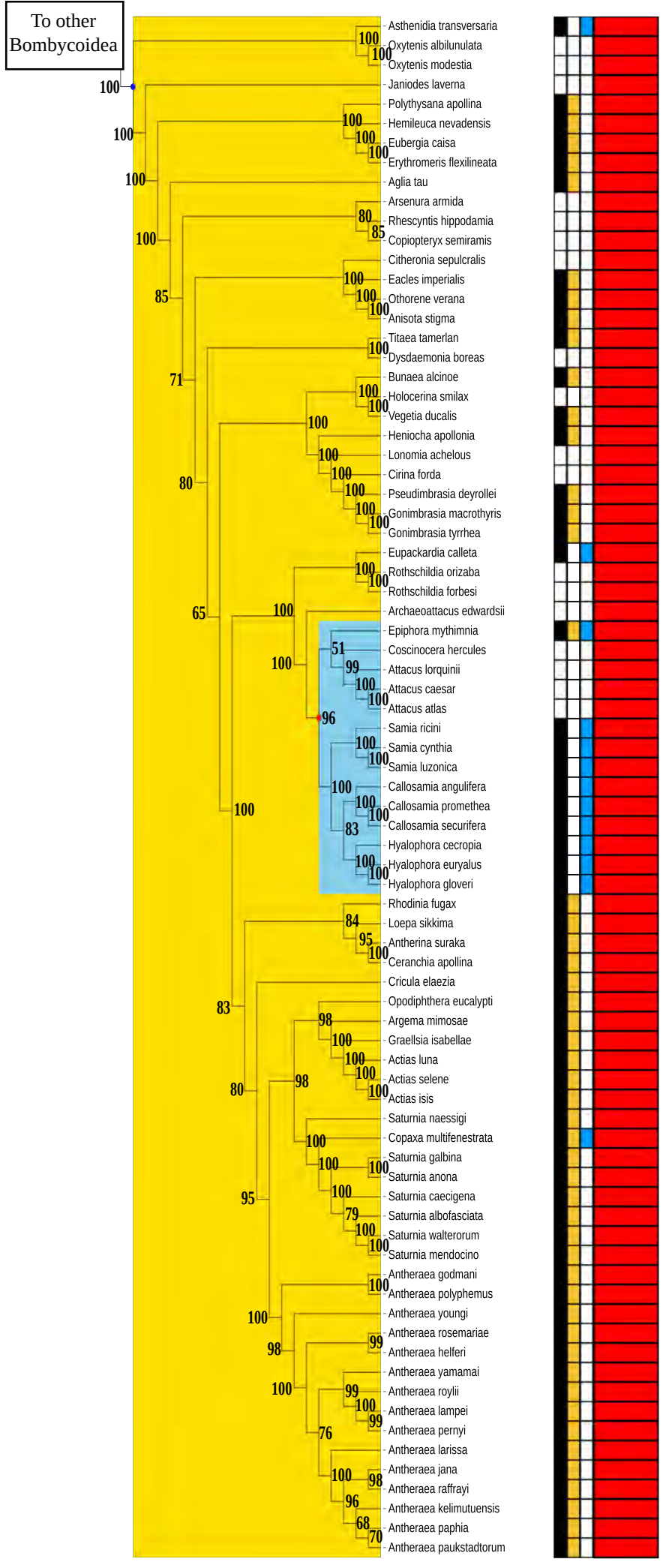

More basal Ditrysia
To Pyraloidea
Sematuridae
Psychostrophia melangaria
Epicopeia hainesii
Coronidia orithea
Semantura luna
Acropteris sparsaria
Urapteroides astheniata
Lyssa zampa
Syngria druidaria
Schidax squamaria
Metorthocheilus emarginatus
Phazaca interrupta
Uraniidae
Erosia veninotata
Calledapteryx dryopterata
Scopula limboundata
Idaea dismissaria
Cyclophora nanaria
Rhodometra sacraria
Haematopis grataria
Geometridae
Aplocera efformata
Trichopteryx carpinata
Hydrelia flammeolaria
Eupithecia acutipennis
Orthonama obstipata
Cidaria fulvata
Lachnocephala vellosata
Earophila badiata
Archiearis parthenias
Hypobapta xenomorpha
Chlorosea margaretaria
Chiasmia clathrata
Biston betularia
Amelora megalocephala
Selenia bilunaria
Plagodis fervidaria
Hasodima elegans
Campaea perlata
Alsophila pometaria
To Noctuoidea
To other Macroheterocerna

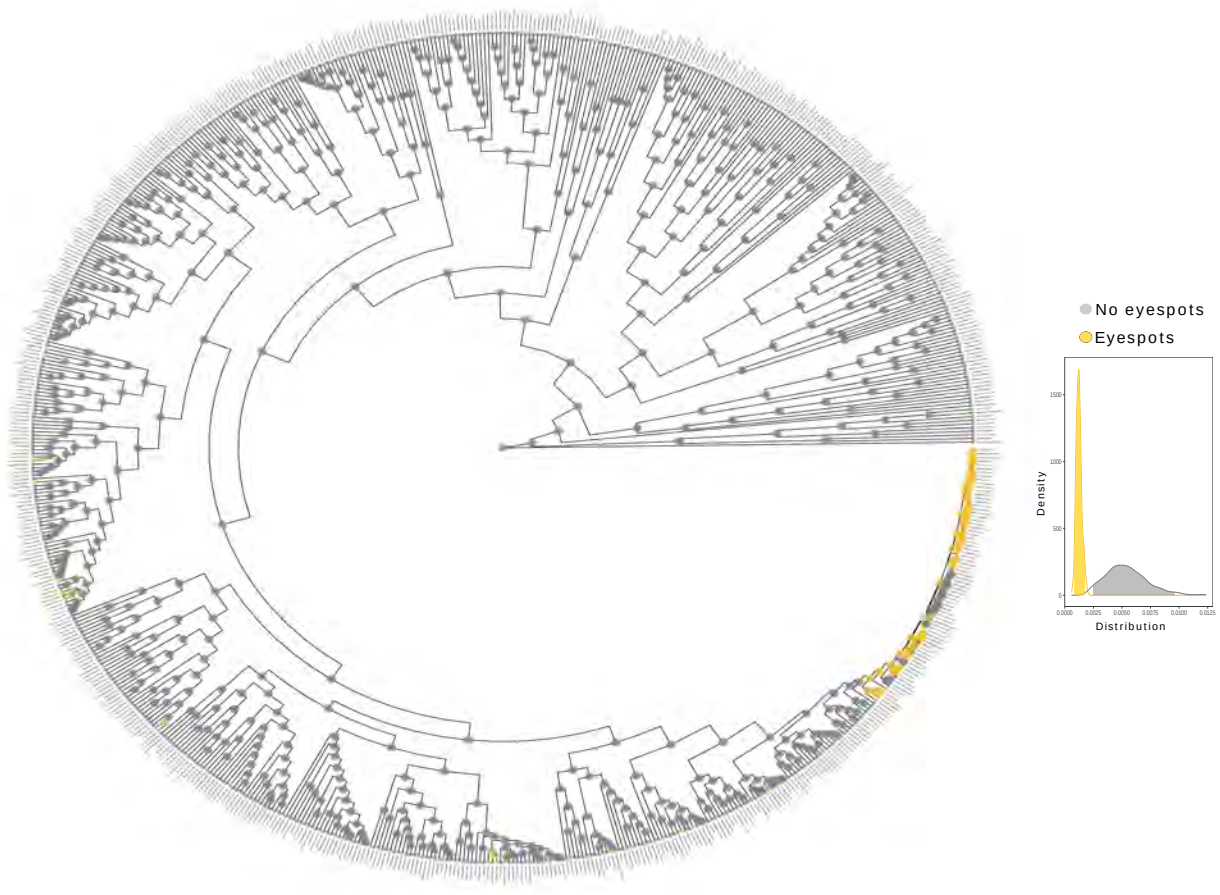

More basal Ditrysia
To Pyraloidea
To Geometroidea
Oenosandridae + Notodontidae
Erebidae+Micronoctuidae
Nolidae
Noctuidae
To other Macroheterocerna
Oenosandra boisduvalii
Epanaphe carteri
Gluphisia septentrionis
Crinodes besckei
Furcula cinerea
Cerura rarata
Datana drexelii
Thaumetopoea pityocampa
Ochrogaster lunifer
Spatalia doerriesi
Rosema epigena
Hemiceras nigrescens
Ptilophora plumigera
Lirimiris guatemalensis
Cnethodonta grisescens
Hapigia nodicornis
Nystalea striata
Scotura leucophleps
Symmerista albifrons
Rhuda difficilis
Heterocampa obliqua
Schizura unicornis
Dicentria violacens
Hypena scabra
Anomis metaxantha
Eudocima salaminia
Gonodonta fulvanqula
Pangrapta decoralis
Palthis asopialis
Asota egens
Hypoprepia miniata
Cisseps fulvicollis
Balacra pulchra
Amata fortunei
Rivula propinqualis
Lymantria dispar
Orgyia leucostigma
Mycterophora rubricans
Phobolosia anfracta
Micronoctua karsholti
Diascia hayesi
Zale lunifera
Catocala ultronia
Erebus ephesperis
Earias roseifera
Blenina senex
Meganola phylla
Iscadia producta
Negeta contrariata
Acontia aprica
Trichoplusia ni
Sphragifera sigillata
Raphia abrupta
Trichosea champa
Cucullia convexipennis
Stiria rugifrons
Psaphida resumens
Amphipyra pyramidoides
Eudryas grata
Acronicta lobeliae
Condica vecors
Pseudeustrotia carneola
Spodoptera frugiperda
Pyrrhia adela
Helicoverpa zea
Adisura bella
Cryphia cuerva
Caradrina meralis
Xylena exsoleta
Mythimna unipuncta
Agrotis ipsilon

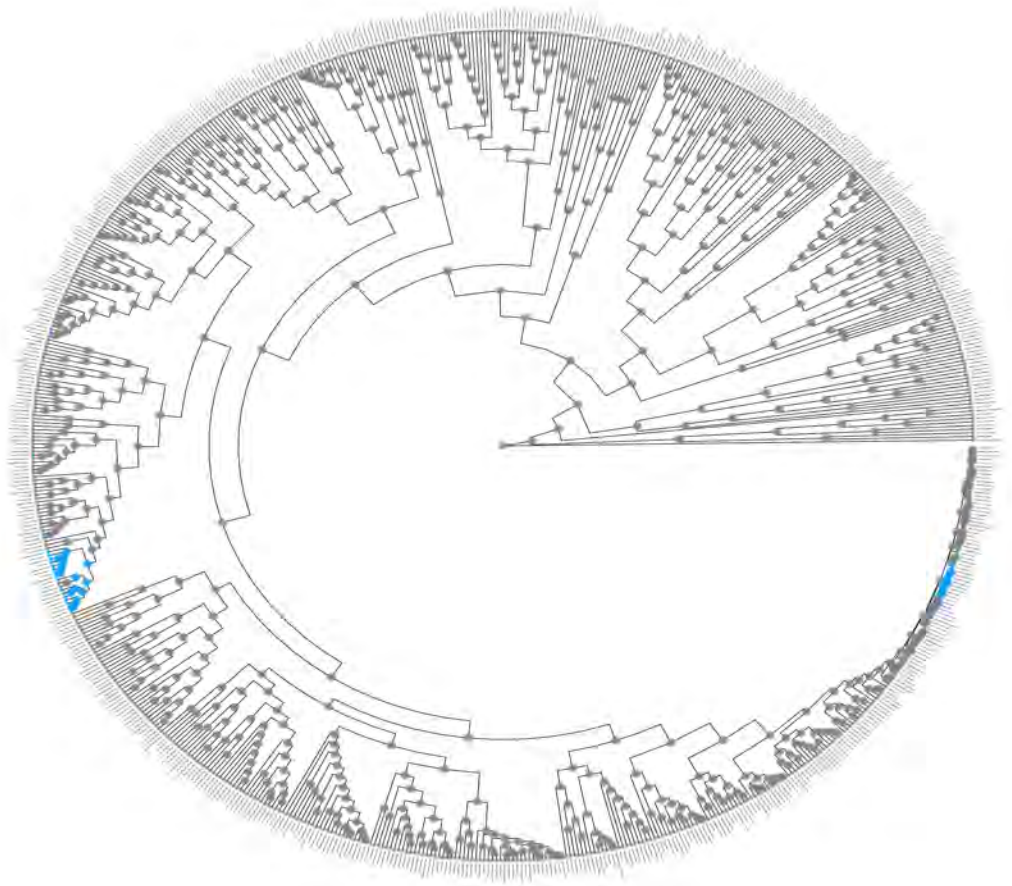

To other Macroheterocerna
Mimallonidae + Cimeliidae
Drepanidae
Lasiocampidae
To Bombycoidea
Axia margarita
Lacosoma chiridota
Mimallo amilia
Druentica alsa
Euphaneta divisa
Bedosia turgida
Cyclidia substigmaria
Euparyphasma maxima
Tethea consimilis
Parapsestis argenteopicta
Thyatira batis
Pseudothyatira cymatophoroides
Habrosyne pyritoides
Oreta rosea
Macrauzata maxima
Callidrepana palleola
Drepana arcuata
Tridrepana unispina
Macrocilix mysticata
Microblepsis acuminata
Nordstromia grisearia
Albara hollowayi
Chionopsyche montana
Tolype notialis
Artace cribraria
Poecilocampa populi
Chondrostega vandalicia
Malacosoma americanum
Malacosoma californicum
Genduara acedesta
Macrothylacia rubi
Gloveria psidii
Lasiocampa quercus
Gonometa rufobrunnea
Heteropacha rileyana
Phyllodesma americana
93
99
100
99
100
82
100
100
100
100
100
100
100
100
100
100
100
88
88
100
100
46
100
100
100
100
100
100
100
100
99
100
100
100
99
100
100
98

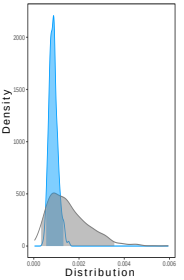

Key:
Discal eyespot radiation
Marginal eyespots radiation
Discal eyespot origin
Marginal eyespot origin
To Lasiocampoidea
Zanola fieldi
Olceclostera seraphica
Apatelodes torrefacta
Malagasanja palliatella
Cotana serranotata
Ganisa plana
Apha aequalis
Brahmaea tancrei
Acanthobrahmaea europaea
Dactyloceras widenmani
Lemonia dumi
Sabalia picarina
Phiditia cuprea
Prismosticta fenestrata
Endromis versicolora
Obertheuria formosibia
Mirina christophi
Carthaea saturnioides
Tededwardsius ravicardinalis
Munychryia senicula
Chelepteryx collesi
Nataxa flavescens
Anthela varia
Hemaris diffinis
Erinnyis ello
Pachylia ficus
Hyles lineata
Euchloron megaera
Cechenena subangustata
Leptoclanis pulchra
Paonias myops
Falcatula falcatus
Coequosa triangularis
Batocnema africanus
Synoecha marmorata
Hopliocnema brachycera
Hoplistopus penricei
Praedora marshalli
Manduca sexta
Sagenosoma elsa
Lapara coniferarum
Colla glaucescens
Quentalia crenulosa
Quentalia chromana
Gastridiota adoxima
Ernolatia moorei
Triuncina brunnea
Bombyx mori
Bombyx mandarina
Asthenidia transversaria
Oxytenis albilunulata
Oxytenis modestia
Janiodes laverna
Polythysana apollina
Hemileuca nevadensis
Eubergia caisa
Erythromeris flexilineata
Aglia tau
Arsenura armida
Rhescyntis hippodamia
Copiopteryx semiramis
Citheronia sepulcralis
Eacles imperialis
Othorene verana
Anisota stigma
Titaea tamerlan
Dysdaemonia boreas
Bunaea alcinoe
Holocerina smilax
Vegetia ducalis
Heniocha apollonia
Lonomia achelous
Cirina forda
Pseudimbrasia deyrollei
Gonimbrasia macrothyris
Gonimbrasia tyrrhea
Eupackardia calleta
Rothschildia orizaba
Rothschildia forbesi
Archaeoattacus edwardsii
Epiphora mythimnia
Coscinocera hercules
Attacus lorquinii
Attacus caesar
Attacus atlas
Samia ricini
Samia cynthia
Samia luzonica
Callosamia angulifera
Callosamia promethea
Callosamia securifera
Hyalophora cecropia
Hyalophora euryalus
Hyalophora gloveri
Rhodinia fugax
Loepa sikkima
Antherina suraka
Ceranchia apollina
Cricula elaezia
Opodiphthera eucalypti
Argema mimosae
Graellsia isabellae
Actias luna
Actias selene
Actias isis
Saturnia naessigi
Copaxa multifenestrata
Saturnia galbina
Saturnia anona
Saturnia caecigena
Saturnia albofasciata
Saturnia walterorum
Saturnia mendocino
Antheraea godmani
Antheraea polyphemus
Antheraea youngi
Antheraea rosemariae
Antheraea helferi
Antheraea yamamai
Antheraea roylii
Antheraea lampei
Antheraea pernyi
Antheraea larissa
Antheraea jana
Antheraea raffrayi
Antheraea kelimutuensis
Antheraea paphia
Antheraea paukstadtorum

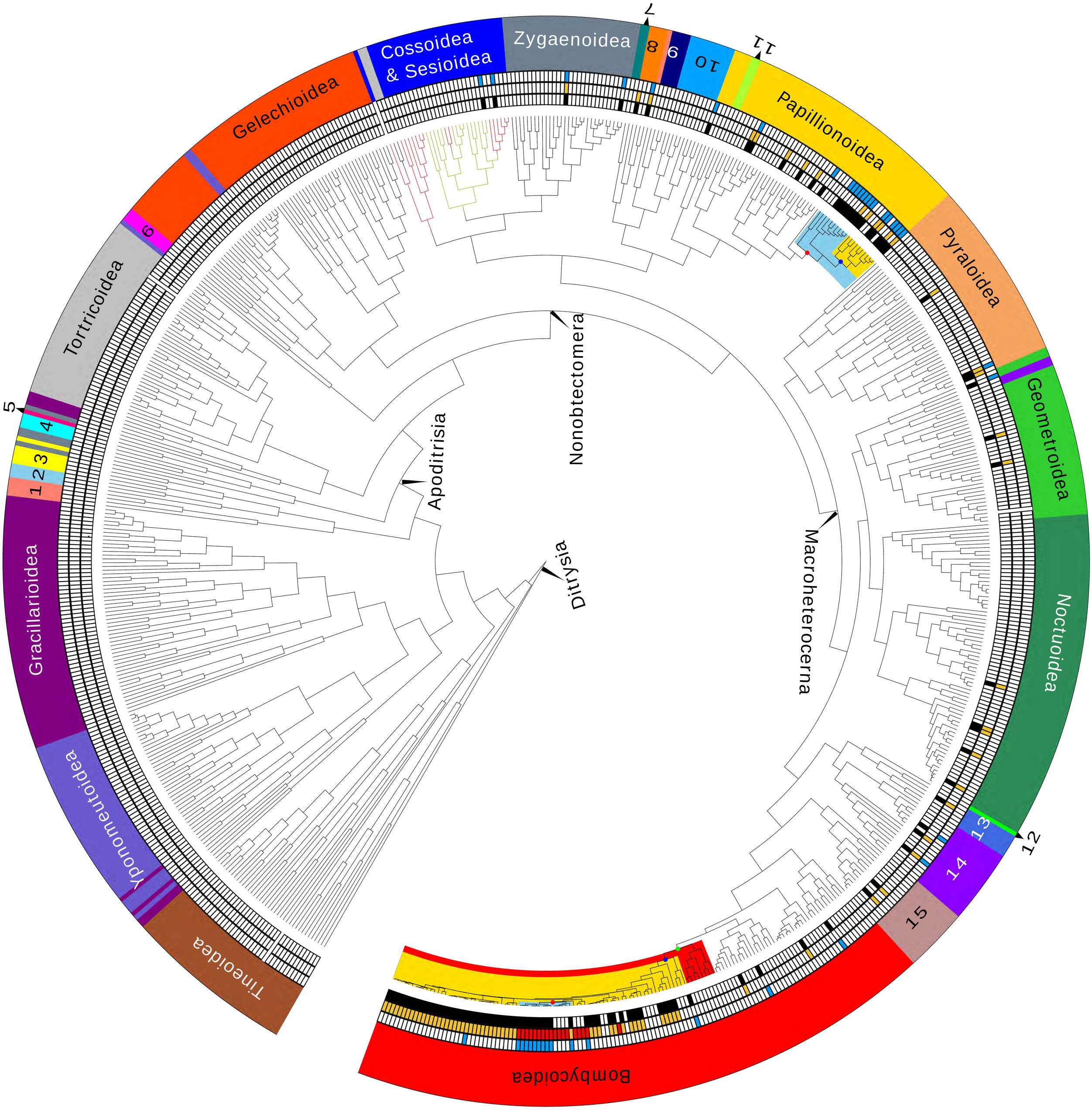

To Lasiocampoidea
Bombycidae
Zanola fieldi
Olceclostera seraphica
Apatelodes torrefacta
Malagasanja palliatella
Cotana serranotata
Ganisa plana
Apha aequalis
Brahmaeidae
Brahmaea tancrei
Acanthobrahmaea europaea
Dactyloceras widenmani
Lemoniidae
Lemonia dumi
Sabalia picarina
Endromidae +Mirinidae
Phiditia cuprea
Prismosticta fenestrata
Endromis versicolora
Obertheuria formosibia
Mirina christophi
Bombycidae+ Phiditidae+
Carthaea saturnioides
Tededwardsius ravicardinalis
Carthaeidae
Munychryia senicula
Anthelidae
Chelepteryx collesi
Nataxa flavescens
Anthela varia
Hyles lineata
Euchloron megaera
Cechenena subangustata
Hemaris diffinis
Erinnyis ello
Pachylia ficus
Sphingidae
Leptoclanis pulchra
Paonias myops
Falcatula falcatus
Coequosa triangularis
Batocnema africanus
Synoecha marmorata
Hopliocnema brachycera
Hoplistopus penricei
Praedora marshalli
Manduca sexta
Sagenosoma elsa
Lapara coniferarum
Bombycidae
Colla glaucescens
Quentalia crenulosa
Quentalia chromana
Gastridiota adoxima
Bombyx mori
Bombyx mandarina
Ernolatia moorei
Triuncina brunnea
To Saturniidae


To other Bombycoidea
Asthenidia transversaria
Oxytenis albilunulata
Oxytenis modestia
Janiodes laverna
Polythysana apollina
Hemileuca nevadensis
Eubergia caisa
Erythromeris flexilineata
Aglia tau
Arsenura armida
Rhescyntis hippodamia
Copiopteryx semiramis
Citheronia sepulcralis
Eacles imperialis
Othorene verana
Anisota stigma
Titaea tamerlan
Dysdaemonia boreas
Bunaea alcinoe
Holocerina smilax
Vegetia ducalis
Heniocha apollonia
Lonomia achelous
Cirina forda
Pseudimbrasia deyrollei
Gonimbrasia macrothyris
Gonimbrasia tyrrhea
Eupackardia calleta
Rothschildia orizaba
Rothschildia forbesi
Archaeoattacus edwardsii
Epiphora mythimnia
Coscinocera hercules
Attacus lorquinii
Attacus caesar
Attacus atlas
Samia ricini
Samia cynthia
Samia luzonica
Callosamia angulifera
Callosamia promethea
Callosamia securifera
Hyalophora cecropia
Hyalophora euryalus
Hyalophora gloveri
Rhodinia fugax
Loepa sikkima
Antherina suraka
Ceranchia apollina
Cricula elaezia
Opodiphthera eucalypti
Argema mimosae
Graellsia isabellae
Actias luna
Actias selene
Actias isis
Saturnia naessigi
Copaxa multifenestrata
Saturnia galbina
Saturnia anona
Saturnia caecigena
Saturnia albofasciata
Saturnia walterorum
Saturnia mendocino
Antheraea godmani
Antheraea polyphemus
Antheraea youngi
Antheraea rosemariae
Antheraea helferi
Antheraea yamamai
Antheraea roylii
Antheraea lampei
Antheraea pernyi
Antheraea larissa
Antheraea jana
Antheraea raffrayi
Antheraea kelimutuensis
Antheraea paphia
Antheraea paukstadtorum


No eyespots
Eyespots
Density
1500
1000
500
0
0.0000
0.0025
0.0050
0.0075
0.0100
0.0125
Distribution




Density
2000
1500
1000
500
0
0.000
0.002
0.004
0.006
Distribution


Gelechioidea
Cossoidea
& Sesioidea
Zygaenoidea
Papillionoidea
Pyraloidea
Geometroidea
Noctuoidea
Bombycoidea
Tortricoidea
Gracillarioidea
Yponomeutoidea
Tineoidea
Nonobtectomera
Apoditrisia
Ditrysia
Macroheterocerna
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

Further evidence for possible eyespot radiations

Species in tree	Close relatives with eyespots		
Cossula coerulescens	Cossula magnifica	Simplivalva morgani	Biocellata alfarae
Paysandia archon	Athis clitarcha	Athis delecta	Athis inca
Pantoctenia prasina	Pantoctenia pungtistriga	Pantoctenia gemmans	Taeda connexa
Isochaetes beutenmuelleri	Lepidorytis sulcata	Acrocerides theorini	Hamartia moulini
Parnasius apollo	Parnassius actius	Parnassius behrii	Parnassius davydovi
Cyclosemia subcaerulea	Cyclosemia anastomosis	Cyclosemia ernia	Cyclosemia leppa
Morvina fissmacula	Morvina falsica	Morvina morvus	Tosta platypterus
Colias eurytheme	Colias caucasica	Colias crocea	Colias eriphyle
Mesosemia carissima	Mesosemia ahava	Mesosemia anaterice	Mesosemia coelestis
Porita erycinoides	Mimacraea landbecki	Iridana marina	Poritia philota
Strymon eurytulus	Strymon bubastus	Strymon istapa	Strymon oreala

Species in tree	Close relatives with eyespots		
Neope goschkevitschii	Neope muirheadii	Neope pulaha	Opoptera syme
Phaedropsis alitemeralis	Conchylodes arcifera	Coptobasoides pauliani	Glyphodella flavibrunnea
Cacographis osteolalis*	Cacographis azteca	Eupastranaia fenestra	
Midila daphne*	Midila guianensis	Midila soror	
Semantura luna	Semantura diana	Semantura empedoclaria	Semantura empedocles
Cyclophora nanaria	Cyclophora argentosa	Cyclophora ariadne	Cyclophora frenaria
Orthonoma obstipata	Costaconvexa centrostrigaria	Acolutha pictaria canicosta	Sterrhochaeta constellata
Zale lunifera	Axiocteta turneri	Cyligramma latona	Erebus nyctaculis
Raphia abrupta	Diloba caeruleocephala	Raphia frater	Neomilichia hylea
Trichosea champa	Trichosea androdes	Trichosea diffusa	Trichosea ludifica
Amphiria pyramioides	Amphipyra beber	Amphipyra monolitha	Amphipyra surnia
Xylena exoleta	Xylena brucei	Xylena fragariae	Xylena solidaginis

Species in tree	Close relatives with eyespots		
Mimallo amilia	Mimallo felisi	Mimallo grisea	Mimallo maya
Thyatira batis	Macrothyatira flavida	Thyatira mexicana	Horithyatira takamukui
Habrosyne pyritoides	Habrosyne scripta	Habrosyne gloriosa	Habrosyne petrographa
Tridepana unispina	Tridrepana fulvata	Tridrepana arikana	Tridrepana subtusmaculata
Genduara acedesta	Somadasys brevivenis	Eriogaster catax	Odonestis filigranica
Lasiocampa quercus	Lasiocampa trifolii	Lasiocampa grandis	Lasiocampa eversmani
Dactyloceras widenmani	Dactyloceras barnsei	Dactyloceras bramarbas	Dactyloceras cadioui
Paonias myops	Paonias astylus	Paonias excaecata	Paonias wolfei
Hopilocnema branchycera	Hopilocnema lacunosa	Chelacnema ochra	Dolbina formosana
Asthenidia transversaria	Asthenidia peggyae	Asthenidia stricturaria	Asthenidia terminalis
Copaxa multifenestrata	Copaxa conlani	Copaxa denhezi	Copaxa vanschaycki
Eupackardia calleta	Hyalophora cecropia	Hyalophora euryalus	Hyalophora gloveri

Key

- Cossoidea
- Zygaenoidea
- Calliduloidea$
- Papilionoidea
- Pyraloidea
- Geometroidea
- Noctuoidea
- Mimallonoidea
- Drepanoidea
- Lasiocampoidea
- Bombycoidea