A molecular phylogeny of Cochyliina, with confirmation of its relationship to Euliina
(Lepidoptera: Tortricidae)

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**This is the peer reviewed version of the following article: Brown, J.W., Aarvik, L., Heikkilä, M.,
Brown, R. and Mutanen, M. (2020), A molecular phylogeny of Cochyliina, with confirmation of its
relationship to Euliina (Lepidoptera: Tortricidae). Syst Entomol, 45: 160-174., which has been
published in final form at <https://doi.org/10.1111/syen.12385>.**

Abstract. We conducted a multiple-gene phylogenetic analysis of 70 species representing 24 genera of Cochyliina and eight species representing eight genera of Euliina, and a maximum likelihood analysis based on 293 barcodes representing over 220 species of Cochyliina. The results confirm the hypothesis that Cochyliina is a monophyletic group embedded within a paraphyletic Euliina. We recognize and define six major monophyletic lineages within Cochyliina: a *Phtheochroa* Group, a *Henricus* Group, an *Aethes* Group, a *Saphenista* Group, a *Phalonidia* Group, and a *Cochylis* Group. We summarize the groups (including related genera not included in our analysis), provide morphological characters that support the molecular data, and compare our results to previous phylogenies of Cochyliina. We propose the following nomenclatural changes: *Brevicornutia*, revised status; *Neocochylis*, revised status; *Paracochylis*, revised status; *Pontoturania*, revised status; and *Platphalonidia*, revised status.

Key Words: *Phtheochroa*, *Saphenista*, *Henricus*, *Aethes*, *Cochylis*, *Phalonidia*, monophyly, Euliina, Cochyliina

Introduction

As presently defined, the tortricid tribe Cochylini comprises two large subtribes - Cochyliina (with about 2,234 described species) and Euliina (with about 1,084 described species) (Gilligan *et al.*, 2018) - each of which historically was considered its own tribe (*i.e.*, Cochylini and Euliini) (Horak & Brown, 1991; Brown & Powell, 1991; Horak, 1999). As recent as 1983 (Powell, 1983), Cochyliina was considered a distinct family (*i.e.*, Cochylidae), even though Kuznetsov & Stekolnikov (1977) had earlier proposed that Cochylini was a tribe within Tortricinae. A molecular phylogeny of Tortricidae by Regier *et al.* (2012) recognized a monophyletic

Cochylina embedded within a paraphyletic Euliina. Unfortunately, that study included exceedingly few taxa, *i.e.*, four species/genera of Euliina and three species (two in genera that are now considered synonyms) of Cochylina, so the results are not particularly robust.

There is no comprehensive phylogeny or classification of the genera of Cochylina worldwide. Razowski (1970) presented an “intuitive” phylogeny for the Palearctic genera (n = 21) (Fig. 1), and Pogue & Mickevitch (1990) presented a parsimony analysis of North American genera (n = 20) (Fig. 2). Hence, it is impossible to place many previously described and/or new genera into a meaningful system or classification.

In this contribution we focus primarily on two issues: 1) we test the hypothesis that Cochylina is a monophyletic group within a paraphyletic Euliina; and 2) we define generic groups within Cochylina and propose a classification. We also propose taxonomic changes (*i.e.*, the elevation of previously described subgenera to generic status) that result in more natural or monophyletic genera.

Historical Background

Cochylina (as Cochylidi) was recognized by Guenée (1845) as one of 10 higher groups in Tortricidae. Stephens (1852) considered Cochylina a subfamily of Tortricidae (*i.e.*, Cochylinae), and Morris (1898) elevated it to family rank (*i.e.*, Phaloniidae). This concept was followed by Stainton (1859), Meyrick (1882, 1895), Clarke (1963), Diakonoff (1961), and others for over 100 years. Razowski (1960) proposed the name Cochylidae for the group based on the oldest higher taxon name used for it – Cochylidi (Guenée, 1845) – but in the years that followed, the group was referred to inconsistently as either Cochylidae (*e.g.*, Diakonoff, 1961; Falkovitsh, 1963; Razowski, 1967a, 1967b, 1968a, b, c; Bradley et al., 1973) or Phaloniidae (*e.g.*, Obraztsov, 1967;

Clarke, 1963, 1968). Based on larvae, Swatschek (1958) and MacKay (1959, 1962) continued the exclusion of Cochyliina from Tortricidae, although larval characters provided little evidence for this.

In the 1970s, Kuznetsov & Stekolnikov (1973, 1977) and Razowski (1976) proposed phylogenies of Tortricidae relying primarily on musculature of the male genitalia. Kuznetsov and Stekolnikov (1973, 1977) were the first to return Cochyliina to Tortricidae, treating it as the supertribe Cochyliidii (Tortricinae). They also proposed Euliae as a subtribe of Cochyliidii. Razowski (1976) likewise included Cochyliina within the subfamily Tortricinae. However, these results were not immediately accepted by all. For example, in the *Check list of the Lepidoptera of America north of Mexico* (Powell, 1983), the group was retained as a distinct family (*i.e.*, Cochyliidae). However, by the late 1980s momentum was growing for recognition of the group as a tribe (*e.g.*, Gibeaux, 1985; Pogue & Friedlander, 1987; Pogue, 1988; Razowski, 1989), and by the early 1990s there was general consensus that the group was best considered a tribe within the subfamily Tortricinae (Horak & Brown, 1991). With few exceptions, it has been treated as such in virtually all taxonomic revisions and systematic treatments since then (*e.g.*, Razowski, 1990, 1992, 1993, 1995, 1997; Horak, 1999; Metzler, 2000; Pogue, 2001; Metzler & Sabourin, 2002; Sabourin *et al.*, 2002).

Relationship Between Euliina and Cochyliina

Kuznetsov and Stekolnikov (1977) were the first to recognize Euliina (comprised of the two genera *Eulia* Hübner and *Pseudargyrotoza* Obraztsov) as a higher category, placing it as a subtribe of Cochylini. Prior to their work, Nearctic genera currently assigned to Euliina had been placed in Cnephysiini by Powell (1964), and the Neotropical genera had been considered part of

Archipini by Razowski (*e.g.*, 1987a, b, 1988). Powell (1986) elevated the concept of Euliini to tribal level, into which he placed all the Neotropical genera from his previous concept of Cnephasiini and Razowski's group of Archipini. Brown & Powell (1991) reviewed the *Chrysoxena* group of Euliini and proposed a preliminary, morphology-based phylogeny for the tribe (including 23 genera), but the number of genera now associated with the group has quadrupled. Brown (2005) retained Powell's concept of Euliini in the world catalogue of the family to include a single Palearctic genus (*i.e.*, *Eulia*) and over 100 Neotropical genera.

Most recently, a molecular phylogenetic analysis of Tortricidae by Regier *et al.* (2012) concluded that Cochyliina is best treated as a subtribe within a broader, paraphyletic Euliina. They recommended the retention of the two taxa as subtribes (Euliina and Cochyliina) for purposes of stability, even though Euliina were shown to be paraphyletic. Because Regier *et al.* (2012) included only four species/genera of Euliina and three species/genera of Cochyliina, their results indicated that further investigation was necessary, stimulating the research presented herein.

Materials and Methods

Taxon sampling and specimen acquisition

A primary objective was to maximize sampling at the genus level in the subtribes Cochyliina and Euliina, and multiple representatives of each genus were included when available. Because dry specimens more than 10 years old are unlikely to provide data for nuclear genes, we limited the sampling for full genetic analyses to taxa that we considered likely to be functional. We sampled six species representing six genera of Euliina and 71 species representing 27 genera of

Cochylina for full genetic analyses. As outgroups, we included one species of Chlidanotinae (*Olindia schumacherana* (Fabricius)), two species of Olethreutinae (*Apotomis betuletana* (Haworth), *Bactra lancealana* Hübner), and seven species of tribes of Tortricinae (Archipini: *Zelotherses paleana* (Hübner), *Pandemis cinnamomeana* (Treitschke), *Thrinophora lignigerana* (Walker); Cnephasiini: *Exapate congelatella* (Clerck), *Arotrophora arcuatalis* (Walker); Sparganothini: *Sparganothis rubicundana* (Herrich-Schäffer); Tortricini: *Tortrix viridana* Linnaeus). The multi-gene dataset was supplemented by sequences of the euliine genera *Netechma* (CAD, COI), *Pseudomeritastis* (CAD, COI), and *Bonagota* (CAD) published in Regier *et al.* (2012). For *Lorita scarificata* (Meyrick), we used COI data concatenated from BIOUG01827-G12 (COI barcode region) and MH_USNM_18 (COI-end); and for *Neocochylis molliculana* (Zeller) we used data concatenated from IT_3 (CAD, EF1a-begin and EF1a-end) and TLMF_Lep_23781 (COI barcode region).

Because we were unable to obtain suitable material of many genera, we also conducted a phylogenetic analysis of all species of Cochylina based on the mitochondrial COI gene data (DNA barcode region) available to us in the BOLD database, which slightly increased generic-level sampling and greatly increased species-level sampling. Additionally, if barcodes of a species fell into more than one BIN (Barcode Index Number operational taxonomic unit, see Ratnasingham & Hebert 2013), a representative of each BIN was included. In this analysis, 294 specimens plus *Eulia ministrana* as an outgroup were included, altogether representing 199 species and 279 BINs.

Molecular techniques

Legs of dry and pinned, but sometimes alcohol preserved, adult specimens were used for extraction of genomic DNA with DNeasy Blood & Tissue Kit (Qiagen) at the University of Oulu, Finland. One mitochondrial (cytochrome c oxidase subunit I, COI) and the following seven nuclear regions were PCR amplified: carbamoylphosphate synthase domain protein (CAD), elongation factor 1 alpha (EF1 α), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), isocitrate dehydrogenase (IDH), cytosolic malate dehydrogenase (MDH), ribosomal protein S5 (RpS5), wingless (see Table S2). Altogether, the sequenced regions comprise 6211 base pairs. This set of markers has become the standard in Lepidoptera phylogenetics and has been used in numerous studies (*e.g.*, Mutanen *et al.*, 2010; Heikkilä *et al.*, 2015). Sequencing pipeline largely followed that of Wahlberg & Wheat (2008), except PCR clean-up was carried out with ExoSAP-IT (Affymetrix) and Sephadex columns (Sigma-Aldrich), and sequencing that was done using an ABI 3730 DNA Analyzer (Applied Biosystems). Sequences were manually aligned and edited using BioEdit (Hall 1999). Sequencing of the COI barcode region was conducted primarily at the Canadian Centre for DNA Barcoding (CCDB) following protocols explained in detail in DeWaard *et al.* (2008). GenBank accession numbers for the sequences of full-gene analysis are provided in Table S1 and sequence lengths in Table S2. Full collection and taxonomic data as well as sequences and GenBank accession numbers for the specimens used in the COI analysis can be retrieved from the public BOLD dataset DS-COCHY at DOI.XXXXX.

Phylogenetic analyses

Maximum Likelihood (ML) analyses of the multiple-gene dataset were conducted using RAxML (Stamatakis, 2014) in CIPRES (Miller *et al.*, 2010) with GTR for nucleotide substitution and gamma model for among-site rate heterogeneity. Support for nodes was

evaluated with 100–1000 bootstrap replicates. Separate analyses with the dataset partitioned by gene, by codon position, and without the third codon position were performed. Resulting trees were examined in FigTree 1.4.3. and rooted at *Olindia schumacherana*. Gene trees were also generated following the same method with the exception of using the unpartitioned model and rooting the RpS5 gene tree at *Sparganothis rubicundana* because we did not have the RpS5 sequence for *Olindia schumacherana*.

A phylogenetic analysis based on Bayesian inference was also performed with the program MrBayes v3.2.6 (Ronquist & Huelsenbeck, 2003) in CIPRES (Miller *et al.*, 2010). Molecular data were partitioned by genes, and the number of substitution types set to nst = mixed with among-site rate variation modelled by a gamma distribution (rates = gamma). The analyses were run for 10 million generations and sampled every 1000 generations. Convergence was assessed in Tracer v1.6 (Rambaut & Drummond, 2007). The first 25% of generations were discarded as burn-in. FigTree 1.4.2 was used to view the tree.

A Maximum Likelihood analysis for COI barcode sequence data was performed using RAxML-NG Black Box service available at <https://raxml-ng.vital-it.ch/#/> (Kozlov *et al.*, 2018) under the following settings: GTR for nucleotide substitution with gamma model for among-site rate heterogeneity, unpartitioned model, and automatic bootstrapping (bootstopping) with a value of 0.03 for cutoff. The resulting tree was rooted with *Eulia ministrana*, and FigTree 1.4.2 was used for the depiction of the tree.

Results and Discussion

The different partition strategies used in our phylogenetic analyses based on maximum likelihood did not result in different topologies, and we choose to present the tree based on the data partitioned by gene as our primary result (Fig. 3). The topology obtained in the Bayesian inference analysis (see supplementary material: Fig. S1) is identical to that of the ML analysis (apart from small differences in the placement of taxa within the outgroup and the placement of species within a couple genera in the ingroup) and therefore is not discussed separately.

Our multi-gene analysis provides support for the conclusions of Regier *et al.* (2012). With one notable exception (*i.e.*, *Hyptiharpa* Razowski), all Euliina and Cochyliina form a strongly supported (*i.e.*, 93) monophyletic lineage. Within this lineage, *Bonagota*+*Apotomops* are sister to *Eulia*. The close relationship between *Bonagota* Razowski and *Apotomops* Powell & Obraztsov has been recognized previously based on morphology (Brown & Powell, 1991; Brown & Razowski, 2003). *Cuproxena*+*Dorithia* are sister to *Pseudomeritastis* Obraztsov, a relationship supported by a similarly shaped signum in the female genitalia. Together with *Anopina* Obraztsov and *Netechma* Razowski, all these euliine genera form a paraphyletic assemblage surrounding a monophyletic Cochyliina. Hence, our results corroborate and significantly expand the findings of Regier *et al.* (2012), with the addition of four euliine genera and 22 cochyline genera.

Hyptiharpa, an enigmatic monotypic genus (*i.e.*, *H. baboquavariana* (Kearfott), with its synonym *H. hypostas* (Razowski)) considered to belong to either Euliini or Cochylini by Razowski (1992) and Brown (2016), did not cluster with other euliine genera. Instead, it found a position closest to Eucosmini, and this result cannot be explained. To rule out the possibility of contamination in the laboratory, we examined the gene trees of the taxa included in our study. In each gene tree *Hyptiharpa* was grouped with the outgroup taxa. We also ran the barcode region

of our *Hyptiharpa* specimen through the specimen identification engine in BOLD and the closest matches obtained were species of Eucosmini and another specimen of *Hyptiharpa baboquavariana* (JWB-08-0210). GenBank's BLAST tool also gave olethreutine species as closest matches. These tests speak against the possibility of contamination as does the fact that specimens belonging in the outgroup were not handled in the laboratory.

Generic Classification of Cochylinea

The British genera of Cochylinea were classified by Meyrick (1895) based primarily on wing venation. Meyrick's phylogenetic tree portrayed *Hysterosia* Stephens (currently treated as a synonym of *Phtheochroa* Stephens) as the most primitive genus. Razowski (1970) presented a classification of the Palearctic Cochylini, placing the 21 genera into three large groups (Fig. 1), and his treatment remains the most comprehensive study on the taxon to date. In an unpublished thesis on North American Cochylini, Pogue (1986) recognized 23 genera, 10 of which were new, and Pogue & Mickevitch (1990) proposed a phylogeny for the North American members of the tribe (Fig. 2) (20 genera) based on a parsimony (transformation series) analysis of morphological characters.

Based on our multi-gene analysis, six monophyletic generic groups can be recognized and defined (Fig. 3, Table 1): a *Phtheochroa* Group, a *Henricus* Group, an *Aethes* Group, a *Saphenista* Group, a *Phalonidia* Group, and a *Cochylis* Group. Each group is detailed below.

As would be expected, the ML barcode analysis resulted in a tree with less compelling structure than that of the multi-gene analysis (Figs. 4–7). It successfully recovered the monophyly of only three of the six groups recognized in the multi-gene tree, *i.e.*, the *Henricus* Group, the *Saphenista* Group (although embedded with the *Aethes* Group), and the *Cochylis*

Group. Nonetheless, the ML barcode tree provides evidence, although limited, of the approximate position of some genera either not included, or represented by a single species, in the multi-gene analysis. It also provides additional insight into genera that appear to be para- or polyphyletic in the multi-gene analysis based on more thorough sampling; *i.e.*, it provides evidence of relationships among congeneric species, which is particularly helpful for untangling the large, polyphyletic genus *Cochylis*. The ML barcode tree is divided by generic group and is presented in Figs. 4–7 as support for the narrative of each generic group below.

Phtheochroa Group

The *Phtheochroa* Group is our best sampled taxon, with 23 species representing nine genera. Its monophyly is well supported (*i.e.*, 94) (Fig. 3), and it is sister to the remaining generic groups of Cochylina. Most of the genera included by Razowski (1970) in his three large lineages [*i.e.*, *Hysterosia*, *Phtheochroa* (variously treated as *Hysterosia*, *Phtheochroa*, and *Prohysterophora* Razowski), *Hysterophora* Obraztsov, *Cochylimorpha* Razowski (as *Stenodes* Guenée, 1845), *Ceratoxanthia* Razowski, *Fulvoclysia* Obraztsov, *Agapeta* Hübner, and *Phtheochroides* Obraztsov] are also present in our circumscription of the group. Differences between our tree and that of Razowski (1970) include our placement of *Phalonidia* Le Marchand in the *Phalonidia* Group (rather than in the *Phtheochroa* Group), and Razowski's assignment of *Eugnosta* Hübner and *Eupoecilia* Stephens to the *Aethes* Group, both of which we include in the *Phtheochroa* Group.

Among the plesiomorphic features found in this group are the female frenulum with three acanthi rather than two (present in *Agapeta hamana* (Linnaeus), *Hysterophora*, a few species of *Eugnosta*, many species of *Cochylimorpha*, and most *Phtheochroa*, *Phtheochroides*,

Prochlidonia Razowski, and *Commophila* Hübner) (Monsalve *et al.*, 2011); the presence of a male forewing costal fold (found in many *Phtheochroa*); the presence of an uncus in the male genitalia (in most *Phtheochroa*); and the distally united or fused arms of the vinculum (present in *Phtheochroa* and *Hysterophora*). Also, the rigid, erect socii of many genera of the *Phtheochroa* Group are found nowhere else in the Cochyliina. Although these character states are not uniform or consistent throughout the *Phtheochroa* Group, they are encountered rarely in other generic groups of Cochyliina.

Within the *Phtheochroa* Group (Fig. 3) the genus *Phtheochroa* is represented by a monophyletic clade with *Hysterophora* embedded within, and this clade is sister to the remainder of the genera. While this topology suggests that *Hysterophora* should be synonymized with *Phtheochroa*, the combined morphological and molecular evidence is not altogether convincing. Hence, for the interim, *Hysterophora* is retained as a valid genus, and it is considered the sister to *Phtheochroa*. In the barcode tree (Fig. 4) there is a large, uniform cluster of *Phtheochroa* species (32 OTUs) that is sister to *Actihema* Razowski plus two potentially misplaced species: *Eugnosta percnoptila* (Meyrick) and *Phtheochroa aarviki* Razowski & Brown.

Eugnosta percnoptila is sister to *Actihema* in the multi-gene tree and sister to *Actihema*+*Phtheochroa aarviki* in the barcode tree. Its genitalia retain many plesiomorphic features, with the valvae, phallus, and transtilla similar to that of many species in the *Phtheochroa* Group, and the rigid socii characteristic of *Eugnosta*, *Actihema*, and several other genera. In *Actihema* the socii arise from a broad sclerotized plate, whereas in *Eugnosta* they arise much closer together; however, there is considerable transition between the two states. In the putative sister relationship between *E. percnoptila* and *Actihema* (Fig. 3) the broad base of the socii in the former can be interpreted as homologous with that of *Actihema*. Also, the ring-like

sclerite in the corpus bursae of the female genitalia of *E. percnoptila* resembles that of *Actihema*. Hence, *E. percnoptila* may represent an undescribed genus sister to *Actihema*.

There is also morphological support for the sister relationship between *Actihema*+*E. percnoptila* and *Phtheochroa aarviki* (and its sister *P. kenyana* Aarvik) - the presence of a long, rod-like, dorso-median process of the juxta. Otherwise, the genitalia of *P. kenyana* and *P. aarviki* are characterized by plesiomorphies. The African genus *Afropoecilia* Aarvik also has a dorso-median extension of the juxta, but it is broad and band-like. If the positions of *E. percnoptila* and *P. aarviki* (plus *P. kenyana*) are correct, these species should be removed from *Eugnosta* and *Phtheochroa*, respectively, and two new genera should be proposed. Alternatively, their potential assignment to *Actihema*, which is very compact and distinct, is not a particularly compelling resolution. In *E. percnoptila* the forewing has numerous tufts of raised scales. There is a tendency for this in *Actihema*, but the tufts are not as pronounced as in *E. percnoptila*. This feature may help distinguished *E. percnoptila* from other (“true”) *Eugnosta*, which lack raise scales or tufts.

Our multi-gene phylogeny (Fig. 3) also shows a clade of *Eugnosta* (four species) as sister to *Cochylimorpha* (two species), but again, with weak branch support. It also captures a monophyletic *Agapeta* as sister to *Ceratoxanthia*+*Fulvoclysia*, similar to the hypothesis of Razowski (1970) (Fig. 1). The adults of the last three genera all share a large forewing length and bright yellow forewing maculation.

In our multi-gene tree (Fig. 3) *Cochylimorpha* occurs in two widely separated branches, with one represented by the single species *C. alternana* (Curtis). The COI tree (Fig. 4) also shows two clusters of *Cochylimorpha* species: one a monophyletic group (13 OTUs; support of 49) sister to a large clade of genera (*i.e.*, *Eugnosta*+*Cryptocochylis*+*Fulvoclysia*+*Agapeta*), and the second a

monophyletic group (5 OTUs; support of 22) embedded within the last-mentioned clade. Hence, evidence from both the multi-gene and barcode trees suggests that *Cochylimorpha* may represent two different genera. Within the smaller *Cochylimorpha* cluster, *C. alternana* is sister to *C. straminea* (Haworth). Razowski (1960) treated these two species, along with *C. chamomillana* (Herrich-Schäffer) (= *decolorella* (Zeller)) and *C. santolinana* (Staudinger), as a separate genus, *Euxanthoides* Razowski, with *C. straminea* as the type species. Within *Euxanthoides*, he further placed *C. alternana* in a separate subgenus (*Bleszynskiella* Razowski). Although these “species groups” are fairly distinct morphologically, their circumscription into subgenera leaves a large number of outliers and species clusters unaffiliated or unassigned to a genus or subgenus. Consequently, Razowski (1970) subsequently gave up on the subgeneric division of *Cochylimorpha* (as *Stenodes*), concluding that *Cochylimorpha* is a large and complicated genus. Our analysis does not include enough representatives to provide compelling conclusions; nonetheless, it suggests that *Euxanthoides* [to include *C. straminea* and *C. alternana*, and perhaps *C. perfusca* (Guenée), as well] may be a valid genus, possibly sister to *Cryptocochylis* Razowski.

The most incongruent aspect of the COI tree (Fig. 4) is the presence of three separate lineages of *Eugnosta*: one that represents a group of species formerly placed in *Carolella* Busck (which is considered a synonym of *Eugnosta*); one that includes the single Palearctic species *E. magnificana* (Rebel); and one that includes the remainder of the *Eugnosta* species (Nearctic and Afrotropical representatives). The synonymy of *Carolella* and *Eugnosta* is supported by morphological features, and this relationship is reflected in our multi-gene tree (Fig. 3). However, the position of *E. magnificana* is inexplicable. The two African species of *Eugnosta* in our sample cluster convincingly with North American species. These two (*i.e.*, *E. misella*

319 Razowski and *E. trimeni* (Felder & Rogenhofer)) represent extremes in male genitalia: *E. trimeni*
320 has a massive process of the transtilla (similar to that of *E. percnoptila*) and weak, broad socii; *E.*
321 *misella* has a slender process of the transtilla and slender, rigid socii. These observations
322 exemplify one of the major difficulties in reconstructing the phylogeny of Cochylini, *i.e.*, the
323 genitalia of species within a clade are sometimes more similar to those of species outside the
324 clade than they are to species within the same clade. Palearctic species of *Eugnosta* are mostly
325 characterized by a silvery forewing ground color, whereas virtually all New World and
326 Afrotropical species have a whitish or brownish ground color.

327 Genera not included in our multi-gene analysis (Fig. 3) that likely belong in the *Phtheochroa*
328 Group include the following: *Acarolella* Razowski & Becker, *Afropoecilia*, *Anielia* Razowski &
329 Becker, *Combosclera* Razowski, *Commophila*, *Cryptocochylis* (associated by barcodes),
330 *Mimeugnosta* Razowski, *Oligobalia* Diakonoff, *Prochlidonia*, *Phtheochroides*, and
331 *Rigidsociaria* Razowski. Among these, *Commophila* was placed by Razowski (1970) (Fig. 1) in
332 an unresolved trichotomy with *Eugnosta* and *Eupoecilia*, supporting its putative assignment to
333 the *Phtheochroa* Group. According to Razowski (2011), *Eugnosta*, *Commophila*, and
334 *Prochlidonia* form a distinct group characterized by long, erect socii, but the long rigid socii
335 occur in many *Phtheochroa* Group genera. Razowski (2011) also mentioned that the Neotropical
336 genera *Anielia* and *Acarolella* are closely related to genera that we include in the *Phtheochroa*
337 Group.

338 *Afropoecilia* likewise can be assigned to the *Phtheochroa* Group based on morphology.
339 According to Aarvik (2010), the structure of the socii of its male genitalia is the same as
340 that of *Eupoecilia* and *Actihema*, and the ring-shaped sclerite in corpus bursae in the female
341 genitalia is shared with *Actihema*.

Although the biology of the majority of the members of the *Phtheochroa* Group is unknown, the existing records indicate a strong tendency for an internal/concealed feeding mode, primarily in Asteraceae. For example, Razowski (2002) stated that the larvae of *Phtheochroa* feed in seeds, fruit, stems, and roots of dicotyledonous plants in eight different families, but primarily Asteraceae. Likewise, nearly all rearings of *Cochylimorpha* are from seeds, stems, roots, or galls of Asteraceae; and nearly all known larvae of *Eugnosta* are gall-inducers in the stems of Asteraceae (*e.g.*, Razowski, 1970; Goeden & Riker, 1981; Vargas *et al.*, 2015). *Actihema* was recorded from the seeds/fruit of Asteraceae in Kenya (Brown *et al.*, 2014). *Eupoecilia* and *Agapeta* appear to have slightly broader host ranges, but both have been recorded from Asteraceae, as well, and internal feeding is common in these two genera.

Henricus Group

In our multi-gene analysis (Fig. 3), the monophyly of the *Henricus* Group is strongly supported (*i.e.*, 100), but it is represented by only two genera that are almost certainly sisters (Brown 2013): *Henricus* Busck, with 43 described species, and *Eupinivora* Brown, with eight described species. The two genera share a number of features with many members of the *Phtheochroa* group, including large forewing length, the presence of three acanthi in the female frenulum (Monsalve *et al.*, 2011), and the presence of an uncus (although small in the *Henricus* group), all of which are almost certainly plesiomorphies. The similarities are so remarkable that Razowski (1986) described two species of *Eupinivora* in *Phtheochroa* and one in *Henricus*. None of the genera included in the *Henricus* Group was included in Razowski's (1970) phylogeny because they are found only in the New World, so there is no clue of where he might have placed them. However, his original assignment of two species of *Eupinivora* to

Phtheochroa suggests he would have placed the *Henricus* Group within his *Phtheochroa* Group. Similarly, Pogue & Mickevitch (1990) placed *Henricus* as sister to *Eugnosta* among North American Cochylinea.

In our barcode tree (Fig. 5), *Henricus* forms a large monophyletic group sister to the rest of Cochylinea, as in our multi-gene tree (Fig. 3), as in our multi-gene tree (Fig. 3), within which *Eupinivora* is embedded, suggesting it is a synonym of *Henricus*. The *Henricus* Group is exclusively New World and includes at least three other genera not included in our analysis: *Cartagogenia* Razowski, *Imashpania* Razowski & Wojtusiak, and *Parirazona* Razowski. The first encompasses three high-elevation species from Costa Rica; Razowski (2011) suggested that it may be synonymous with *Henricus*. The second is monotypic and likewise was considered closely related to *Henricus* by Razowski & Wojtusiak (2008). The third is a small Neotropical group (nine species) known only from Brazil; the name is derived from *Irazona* Razowski, currently considered a synonym of *Henricus*. The type species of *Irazona* (i.e., *comes* Walsingham) is convincingly embedded within *Henricus* (Fig. 5). Although barcodes place *Parirazona* near *Nycthia* Pogue (Fig. 7), morphology argues for its placement in the *Henricus* Group.

Different clades within the *Henricus* Group appear to have radiated on different host families, but primarily on conifers. For example, all species of *Eupinivora* either have been recorded from, or are suspected to feed within, the cones of Pinaceae (Brown, 2013), as does *Henricus fuscodorsanus* (Kearfott) and *H. melanoleucana* (Clarke). Three species of *Henricus*, *H. infernalis* (Heinrich), *H. macrocarpana* (Walsingham), and *H. inchoatus* Razowski & Becker, are recorded only from Cupressaceae; and *H. umbrabasana* (Kearfott) shows a strong preference for *Quercus* (Fagaceae).

Aethes Group

In the multi-gene tree (Fig. 3), the *Aethes* Group is comprised of a relatively well-supported (*i.e.*, 61), monophyletic group of *Aethes* Billberg, 1820 (11 OTUs) plus *Rudenia* Razowski (a single example) as its sister; the latter is rather weakly associated with the *Aethes* Group. In the barcode tree, *Rudenia* (at the bottom right side of Fig. 6) is sister to *Spinipogon* Razowski, and the two are fairly distant from *Aethes* (the last represented by 54 OTUs). The female genitalia of *Spinipogon* argue convincingly for its placement near *Gynnidomorpha* Turner and *Phalonidia* in the *Phalonidia* Group. Hence, it is possible as well that *Rudenia* belongs in the *Phalonidia* Group.

Razowski (1985a) originally hypothesized that *Rudenia* was closely related to *Eugnosta* (in our *Phtheochroa* Group); he subsequently (Razowski 1994) placed the genus near *Lorita* Busck (in our *Phalonidia* Group) based on the similarity of the female genitalia. Pogue & Mickevitch (1990) likewise placed *Rudenia* near *Lorita*. In our barcode tree *Rudenia* (8 OTUs) forms a monophyletic group near *Gynnidomorpha* (in our *Phalonidia* Group). Hence, the position of *Rudenia* in the *Aethes* Group is likely incorrect. *Rudenia* is a small group (5 described species) ranging across the southern portion of North America (from the Atlantic to the Pacific), south to Venezuela as a complex of closely related species that are not easily separated by genital morphology, but can be separated by barcodes; they feed exclusively on Fabaceae.

In the *Aethes* Group the most significant conflict between our multi-gene (Fig. 3) and barcode trees (Fig. 6) is the presence of a branch that supports and a monophyletic *Saphenista* Walsingham (5 OTUs) sister to *Aphalonina* Razowski+*Aethes turialba* (Busck) that is deeply embedded within *Aethes* in the barcode tree (Fig. 6). This placement of *Saphenista* is

inexplicable and is almost certainly incorrect. Also, five species of *Aethes* fall outside the large monophyletic group of this genus, somewhat scattered throughout the *Phlaonidia* group.

The monophyly of *Aethes* is strongly supported by a pair of unusual, sickle-shaped socii from the dorsum of the tegumen in the male genitalia that are present in nearly all species. The genus is widely distributed throughout Europe, Asia, North America, and South America (absent from Australia and Africa), from boreal forests to rain forests, encompassing about 150 described species that feed mostly on Asteraceae and Apiaceae, but with many exceptions. Among the Neotropical species of *Aethes* is a small group of closely related species that are large and superficially similar to *Phtheochroa* species (e.g., *A. turialba*, *A. macasiana* Razowski & Pelz, *A. chilesi* Razowski & Wojtusiak), represented in our dataset by *A. turialba*. Species of *Aphalonia* Razowski are also large and superficially similar to these large *Aethes*, and in his description of *Aphalonia*, Razowski (1984) indicated that the type species (*Aphalonia monstrata* Razowski) is similar to species of the *Aethes agelasta* Razowski species group, with similar wing venation. Hence, the placement of *Aphalonia* within the *Aethes* Group is not surprising. The only other genera that are assigned convincingly in the *Aethes* Group are *Aethesoides* Razowski, a small Neotropical group that is almost certainly sister to *Aethes*, and *Lincicochylis* Razowski, which may be a synonym of *Aethesoides*. According to Razowski (1994), *Aethes* and *Aethesoides* share the presence of slender, curved socii (the processes mentioned above) from a broad, hairy base and a rod-like sclerite coupling the tegumen with the valva. *Aethesoides* and *Lincicochylis* share a pair of stout, sclerotized processes from the dorso-posterior end of the tegumen, reminiscent of similar processes in *Eugnosta*; a valva that has a well-developed, rod-like sacculus and a short, mostly atrophied remainder; and an unusual, semicircular, sometimes spiny flap, located immediately anterior to the socii.

Saphenista Group

In our multi-gene tree (Fig. 3), the *Saphenista* Group is represented by a single Nearctic species. However, in our barcode tree (Fig. 6), three Neotropical and two Nearctic species of *Saphenista* form a monophyletic group sister to *Aphalonia*+*Aethes turialba*, and this cluster is embedded within the main lineage of *Aethes*. *Aphalonia* and *Aethes turialba* are large, superficially similar species that are quite distinct from *Saphenista* in facies and genital morphology. Hence, the relationships of *Saphenista* to these groups in the barcode tree does not seem particularly reliable. The monophyly of *Saphenista* is convincingly supported by the broadly “Y”- or “T”-shaped distal expansion of the median process of the transtilla. The monotypic *Amallectis* Meyrick, 1917, for which we have no molecular data, has a median process of the transtilla that is very similar to that of *Saphenista*, and Razowski (2011) suggested that based on wing venation and male genitalia, the two may be synonymous. Hence, its inclusion in the group is supported by morphology.

Saphenista includes 97 described species that are restricted to the New World, occurring in the Nearctic and Neotropical regions. Recorded hosts include Asteraceae, Garryaceae, Rhamnaceae, and Rutaceae (Brown *et al.*, 2018).

Phalonidia Group

The *Phalonidia* Group is a well-supported (*i.e.*, 87) monophyletic unit comprised of *Gynnidomorpha* Turner and *Phalonidia* Le Marchand (Fig. 3). The three species of *Gynnidomorpha* included in our analysis form a monophyletic group, and *Phalonidia* is shown as paraphyletic, with *Gynnidomorpha* embedded within. However, support for this arrangement

is not particularly strong, so the paraphyly of *Phalonidia* is not altogether convincing. The close relationship of *Gynnidomorpha* to *Phalonidia* is strongly supported by a unique circle of spines in the corpus bursae of the female genitalia (Razowski 1985b), somewhat reminiscent of that of *Actihema* (in our *Phtheochroa* Group). An extremely similar and probably homologous structure in the corpus bursae of most *Spinipogon* Razowski (barcodes only) and *Pogospinia* Brown (not included in the analysis) appears to link these genera, as well, although *Spinipogon* is sister to *Rudenia* in our barcode tree (Fig. 6).

Gynnidomorpha includes 13 described species and has a broad geographic distribution (*i.e.*, Europe, Asia, Australia, and North America); recorded larval hosts include numerous families of dicotyledonous plants. *Phalonidia*, likewise, is nearly worldwide (Europe, Asia, North America, and South America) and encompasses about 88 described species; larval hosts encompass several plant families, but the majority of records are from Asteraceae.

Our circumscription of the *Phalonidia* Group closely parallels that of the *Saphenista* Group of Razowski (1985b). Additional taxa assigned to the *Saphenista* Group by Razowski (1985b) but not included in our analysis are the following Neotropical genera: *Amallectis*, *Banhadoa* Razowski & Becker, *Dinophalia* Razowski & Becker, *Juxtolena* Razowski & Becker, *Lasiothyris* Meyrick (barcode data), *Macasinia* Razowski & Pelz, *Marylinka* Razowski & Becker, *Mielkeana* Razowski & Becker, *Mourecochylis* Razowski & Becker, *Phaniola* Razowski & Becker, *Spinipogon*, and *Thysanphalonia* Razowski & Becker. Most of these genera have very few species; seven are monotypic. As mentioned above, *Amallectis* is probably best assigned to the *Saphenista* Group based on the shape of the distal expansion of the median process of the transtilla. Although no synapomorphy has been identified to link the remaining genera, they show many similarities in the male and female genitalia. Barcodes (Fig. 6) place *Cirrothaumatia*

Razowski & Becker and *Honca* Pogue in this group; the former likely belongs, but morphological features of the latter argue for its placement elsewhere.

In a large number of genera in Cochylina, there is a unique, although variable, fascicle of male secondary scales in a roll along the costa of the hindwing (Baixeras *et al.*, personal communication). Males of nearly all species in the *Saphenista*, *Phalonidia*, and *Cochylis* groups possess this feature. Because it is absent (or different in its development) in the *Phtheochroa* and *Henricus* groups, it may represent a synapomorphy for these three generic groups.

Cochylis Group

The *Cochylis* Group is our second most sampled generic group, with 13 genera and 22 species. The monophyly of the group is strongly supported (*i.e.*, 84). Our *Cochylis* Group includes many of the genera included by Razowski (1970, 1985b) in his *Cochylis* Group. Genera in common between the two include *Cochylis* Treitschke, *Diceratura* Djakonov, *Cochylidia* Obraztsov, and *Falseuncaria* Obraztsov & Swatschek. *Platphalonidia* Razowski, *Atroposia* Pogue, and *Nycthia* Pogue are New World genera not included in Razowski's (1970) study of the Palearctic fauna.

Within the *Cochylis* Group, *Platphalonidia*, with its type species *P. felix* (Walsingham), is a well-defined group with *Lorita* Busck embedded within it. This branch (*e.g.*, *Platphalonidia* plus *Lorita*) is sister to the remainder of the group (Fig. 3). Razowski (2011) synonymized *Platphalonidia* with *Phalonidia* because he believed that the type species of the former (*i.e.*, *P. felix*) belonged in *Phalonidia*. Then he described *Platphalonidia* Razowski to accommodate the remaining species. However, our results strongly support *Platphalonidia* as distinct from *Phalonidia*, and we return it to generic status (see Appendix S1). Although *Lorita* falls within

Platphalonidia, this placement is based only on COI data and is incorrect based on morphology. *Lorita* includes four described species occurring in the Nearctic and Neotropical regions. Its monophyly is convincingly supported by the unique ventral “scoop” of the male abdomen (Pogue, 1988).

Within the *Cochylis* Group, females of nearly all species of *Platphalonidia* have three acanthi in the frenulum, whereas females all of the remaining genera have two (Monsalve *et al.*, 2011). It is remarkable that while this character is highly variable within many species of *Cochylina*, it is remarkably consistent within the *Cochylis* Group. Although our multi-gene tree (Fig. 3) places *Lorita* within *Platphalonidia*, our barcode tree (Fig. 7) shows it as sister to *Platphalonidia*, the latter of which is much more compelling based on morphology.

The monophyly of the lineage that is sister to *Platphalonidia*+*Lorita* is also well supported (*i.e.*, 91). Within this group, the three sampled species of *Cochylidia* form a monophyletic group (support of 55) with *Falseuncaria* as its sister (support of 89). According to Razowski (2002, 2011), synapomorphies for *Falseuncaria*, *Cochylidia*, *Diceratura*, and *Cochylis* include the presence of a cluster of minute spines in the vesica of the phallus in the male genitalia, and a membranous sack anterior to the sterigma in the female genitalia. Furthermore, according to Razowski (1987c), “*Cochylidia* is extremely similar to *Diceratura* and differs from it only by a single supposed autapomorphy, viz. the presence of minute setae or spines at the end of the costal arm of the valva.” The unique costal arm of the valva represents a convincing morphological synapomorphy for the two genera, and the male genitalia of *Falseuncaria* are quite different from those of *Cochylidia* and *Diceratura*. Hence, the sister relationship between *Cochylidia* and *Falseuncaria* in our tree (Fig. 3) is not particularly compelling even though the molecular support is strong (*i.e.*, 89).

Two other species, *Cochylidia rupicola* (Curtis) and the Japanese *C. contumescens* (Meyrick), are closely related other based on morphology of the male genitalia, and differ considerably from other *Cochylidia*. Barcodes of *C. rupicola* indicate that there is considerable genetic distance between this pair and “true” *Cochylidia*, and a new genus may be necessary to accommodate these two species.

In our multi-gene analysis (Fig. 3) we recovered monophyly for *Nycthia*, *Cochylidia*, and *Diceratura*. However, monophyly was enhanced considerably by the recognition of several subgenera of *Cochylis* as detailed below.

Cochylis Treitschke has long been considered a polyphyletic assemblage of similar appearing species, and our initial results confirm this. *Cochylis* was subdivided into several subgenera by Razowski (1960), but less than a decade later, all were synonymized by Razowski (1970). More recently, in a review of the *Cochylis* Group of genera, Razowski (1985b) stated “Almost all subgenera [of *Cochylis*] require re-examination and probably some of them shall be treated as valid genera.” By elevating some of the subgenera, several species groups are circumscribed that result in more convincing monophyly within our multi-gene tree. Hence, we propose the following modified concepts for the subgenera of *Cochylis* (see Appendix S2) that have been incorporated in the multi-gene and barcode trees.

Cochylis (type species: *C. roseana* (Haworth)) includes *C. roseana* and *C. flaviciliana* (Westwood), which cluster together in our COI tree (Fig. 7). The two species share a slender, deeply notched valva; a slender phallus that lacks cornuti; and a telescopic ovipositor. Although Razowski (1960) indicated that “Several species belong here,” we know of no other species that can be convincingly associated with *C. roseana* and *C. flaviciliana* based on morphology. Hence, we propose a significantly narrowed concept of *Cochylis* (sensu stricto).

Neocochylis Razowski (type species: *C. molliculana* (Zeller)), **revised status**, includes *N. molliculana*, *N. dubitana* (Hübner), *N. hybridella* (Hübner), *N. millierana* Peyerimhoff (syn. *sannitica* Trematerra), and *N. salebrana* (Mann), which share a broad process of the transtilla and a phallus that lacks cornuti but has spinules. In the multi-gene tree (Fig. 3), *C. hybridella* and *C. dubitana* are sisters, and this pair is sister to *C. molliculana*. Likewise, in our COI tree (Fig. 7), *C. molliculana*, *C. hybridella*, *C. dubitana*, and *C. millierana* form a monophyletic group.

Paracochylis Razowski (type species: *C. amoenana* Kennel), **revised status**, is considered monotypic, with the single species *P. amoenana* (syn. *apricana* Kennel) from Asia Minor. The valva is simple, broad basally and gradually tapering distally, and the phallus has two groups of cornuti plus a patch of spinules. We know of no other species that belong here.

Cochylichroa Swatschek (type species: *C. atricapitana* (Stephens)) was recently returned to generic status by Brown (2019) and includes the following: *C. hoffmanana* (Kearfott), *C. viscana* (Kearfott), *C. avita* (Razowski), *C. hospes* (Walsingham), and *C. foxcana* (Kearfott), all from North America, and *C. atricapitana* from Europe. The species share extremely similar male genitalia with a large rounded sacculus with a large field of spines, and a slender phallus with a group of short spines. A second group of species with quite different genitalia are associated with this species group by barcodes (Fig. 7), i.e., *C. arthuri* (Dang), *C. aurorana* (Kearfott), and *C. temerana* (Busck), and these were also transferred to *Cochylichroa* by Brown (2019). Given their different genital morphology, their assignment to *Cochylichroa* may be only an interim solution.

Brevicornutia Razowski (type species: *C. pallidana* Zeller), **revised status**, is considered to include two species: *B. pallidana* and *B. dolosana* (Kennel) (the latter considered a subspecies of *pallidana* by Brown (2005)). In these two species the cucullus is small and narrow, the sacculus is stout with a heavily sclerotized ridge and teeth, and the phallus has a group of small cornuti.

572 *Pontoturania* Obraztsov (type species: *C. defessana* Mann), **revised status**, includes *P.*
573 *defessana*, *P. maestana* Kennel, *P. piana* (Kennel), *P. faustana* (Kennel), *P. lutosa* Razowski, *P.*
574 *indica* Razowski, *P. aestiva* (Walsingham), and *P. posterana* Zeller. Razowski (1970) included
575 only *P. defessana* in this subgenus, but in reference to *P. posterana* he commented that the “male
576 genital armature resembles *C. refessana* [sic.]” The male genitalia of these species share the
577 following features: 1) phallus with a long, free, terminal process; 2) vesica bearing a dense patch
578 of extremely long, slender, spinelike cornuti; and 3) apex of median process of transtilla with a
579 small patch of teeth.

580 *Thyraylia* Walsingham (type species: *T. bunteana* (Robinson)) [with its synonym *Acornutia*
581 Obraztsov (type species *C. nana* (Haworth))] was treated as a valid genus (as its junior synonym
582 *Acornutia*) in the *Phtheochroa* Group by Razowski (1960). He (Razowski, 1970, 1997, 2011)
583 later considered *Acornutia* a synonym of *Cochylis*. However, *Thyraylia* has long been considered
584 a valid genus in North America (*e.g.*, Powell, 1983; Metzler & Brown, 2014) with the following
585 species: *bana* (Kearfott), *bunteana* (Robinson), *discana* (Kearfott), *gunniana* (Busck),
586 *hollandana* (Kearfott), *nana*, and *voxcana* (Kearfott). The included species have an elongate,
587 somewhat upcurved, distally attenuate valva; a sacculus with a long, free distal tip; and a slender
588 phallus that lacks cornuti.

589 *Rolandylis* was described as monotypic by Gibeaux (1985) based on a single North American
590 species apparently introduced into Europe. Although it was considered a synonym of *Cochylis* by
591 Razowski (2011), Pogue (1986) recognized it as a distinct North American genus (under the
592 manuscript name “*Clothoa*”) in his unpublished Ph.D. dissertation, and he (Pogue, 2001) later
593 revised the genus, adding two more species. Metzler & Brown (2014) likewise considered the
594 genus as valid.

Cochylis epilina Duponchel is an isolated species that cannot be assigned convincingly to any of these genera, and may require a new genus. In the barcode tree (Fig. 7) it occupies a position sister to *Cochylis* (*sensu stricto*). In addition, there are many species currently included in *Cochylis* for which we have no convincing generic assignments, and hence for the time being must remain in a large polyphyletic *Cochylis* (*sensu lato*).

The three most basal genera in the *Cochylis* Group (*i.e.*, *Platphalonidia*, *Atroposia*, and *Nycthia*) are restricted to the New World. *Platphalonidia* includes 21 species, with Asteraceae as the most common foodplants. *Atroposia* is monotypic, feeding on Onagraceae. And *Nycthia* includes two described species, both of which specialize on Agavaceae. Hence, the three genera have little in common biologically.

Cochylidia is recorded from Europe and Asia, with one species (*C. subroseana* (Haworth)) either Holarctic or introduced to North America inadvertently. With very few exceptions, the larvae of *Cochylidia* feed on Asteraceae. *Falseuncaria* includes seven species that occur in Europe, Asia, and Africa; foodplants have been reported for only two species (*i.e.*, *F. ruficiliana* (Haworth) and *F. degreyana* (McLachlan)), encompassing Scrophulariaceae, Plantaginaceae, Primulaceae, and Asteraceae.

Genera not included in our molecular analyses that likely belong in the *Cochylis* Group include the following: *Cochylidichnium* Razowski, *Coristaca* Razowski, *Geitocochylis* Razowski, *Gryposcleroma* Razowski, *Mimcochylis* Razowski, *Monoceratuncus* Razowski, *Revertuncaria* Razowski, and *Rolandylis*.

Summary and Conclusions

Based on our multi-gene analysis, we recognize six major monophyletic lineages within Cochyliina: a *Phtheochroa* Group, a *Henricus* Group, an *Aethes* Group, a *Saphenista* Group, a *Phalonidia* Group, and a *Cochylis* Group. Our ML analysis of DNA barcodes resulted in a tree that is much less resolved, but provides insight into relationships among species and genera within the major lineages identified in the multi-gene analysis, especially those in the *Cochylis* Group.

The *Phtheochroa* Group is sister to the remaining Cochyliina. Its members retain the most plesiomorphic morphological characters of the subtribe, and most appear to be internal feeders (crown borers, gall-inducers, fruit-feeders) as larvae, primarily in Asteraceae. The monotypic *Hysterophora* is embedded within *Phtheochroa*, but this position is only weakly supported. The relationship among *Agapeta*, *Ceratoxanthia*, and *Fulvoclysia* is well resolved, but *Eugnosta* and *Cochylimorpha* are both represented by two widely separated branches, suggesting that neither is monophyletic as currently defined. In the case of *Eugnosta*, the disjunct position of *E. magnificana* is puzzling. In the case of *Cochylimorpha*, the clade represented by *C. alternana* may be a distinct genus for which the name *Euxanthoides* is available.

The *Henricus* Group, with only two genera included in our analysis, is well supported and is sister to the remaining generic groups (after the *Phtheochroa* Group). Most of the species for which hosts are known feed in the seeds and cones of conifers, primarily Pinaceae and Cupressaceae. The *Aethes* Group is comprised of a relatively well-supported, monophyletic *Aethes* with *Rudenia* as its sister. However, the position of *Rudenia* is weakly supported and is not particularly consistent with morphological evidence. Hence, it is possible that *Rudenia* is incorrectly placed in the *Aethes* Group. The *Saphenista* Group is a small, monophyletic lineage comprised of *Saphenista* and *Amallectis*, the latter included in the group based on morphology.

There are many inconsistencies between the multi-gene tree and the barcode tree, and the position of the genus *Saphenista* embedded within the genus *Aethes* in the barcode tree is almost certainly incorrect. In the barcode tree, *Aethes turialba*, which is a member of a small group of exceptionally large and superficially similar species of *Aethes*, clusters with *Aphalonia*, and this relationship is convincing based on facies and morphology of the male genitalia.

The *Phalonidia* Group is well supported, comprised of *Gynnidomorpha* and *Phalonidia*. However, the three species of *Gynnidomorpha* included in our analysis form a monophyletic group embedded within a paraphyletic *Phalonidia*. The association of *Gynnidomorpha* and *Phalonidia* is strongly supported by morphological characters, especially features of the female genitalia.

The *Cochylis* Group includes several genera that are convincingly supported as monophyletic (e.g., *Nycthia*, *Diceratura*, *Cochylidia*), however, a few compelling relationships based on morphology are not captured in our multi-gene tree. For example, *Diceratura* and *Cochylidia* are assumed to be sisters based on synapomorphies of the male genitalia, but they are widely separated in our tree. *Platphalonidia* is shown to be distinct from its putative senior synonym *Phalonidia*, but *Lorita* falls between the two species groups of *Platphalonidia* (Appendix S1). To no surprise, species assigned to the polyphyletic genus *Cochylis* were scattered nearly throughout the *Cochylis* Group. However, by elevating many of the previously proposed subgenera of *Cochylis* (e.g., *Pontoturania*, *Neocochylis*, *Brevicornutia*), we are able to define several monophyletic groups, thus providing better resolution to relationships within the *Cochylis* Group. Unfortunately, many species of *Cochylis* cannot be convincingly associated with one of the subgenera, and additional phylogenetic studies are required to place these “leftover” species.

Author contributions

MM and MH designed the study and conducted the analyses, and JB and LA interpreted the results and prepared the initial draft of the paper. MM and MH provided text on methods, and all authors commented on various drafts of the manuscript. JB, LA, and RB provided specimens. MH prepared the illustrations. The authors declare that there are no conflicting financial interests.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Explanation of revised status for *Platphalonidia*

Appendix S2. Proposed taxonomic changes and arrangement of genera related to *Cochylis*.

Table S1. Taxa and genes used in phylogenetic analysis.

Table S2. Sequence lengths for genes used in phylogenetic analysis.

Figure S1. Bayesian analysis of Cochylini and out-groups.

Acknowledgements

We thank David Agassiz for specimens of Cochylini from Africa; Pasquale Trematerra and Kai Berggren for filling gaps in our sample of European species; and John Phillips, who provided the type species of *Phtheochroa*, *P. rugosana*. We also thank all of those who contributed specimens of Cochylini to BOLD and generously shared barcode data with us, especially Yves Bassett, Sophia Gripenberg, Jean-François Landry, Daniel Janzen, Winnie Hallwachs, and Scott Miller. We also express our gratitude to Paul Hebert, Jeremy DeWaard, Allison Brown, and other staff of the Biodiversity Institute of Ontario, University of Guelph, who provided considerable assistance accessing barcode data. Laura Törmälä is thanked for supervising the lab work, and Vlad Dinca for kindly lending a hand in the lab. Funding for this study was provided by the Academy of Finland (MM). The following provided helpful reviews that enhanced the clarity and quality of the paper: Joaquin Baixeras (University of Valencia), Jason Dombroskie (Cornell University), and Józef Razowski (Polish Academy of Sciences).

Literature Cited

- Aarvik, L. (2010) Review of East African Cochylini (Lepidoptera, Tortricidae) with description of new species. *Norwegian Journal of Entomology*, **57**, 81–108.
- Bradley, J.D., Tremewan, W.G. and Smith, A. (1973) British tortricoid moths. Cochylidae and Tortricidae: Tortricinae. The Ray Society, London. 251 pp.
- Brown, J.W. (2005) World catalogue of insects. Volume 5: Tortricidae (Lepidoptera). Apollo Books, Stenstrup. 741 pp.

709

710 Brown, J.W. (2013) A new genus of pine-feeding Cochyliina from the western United States and
 711 northern Mexico (Lepidoptera: Tortricidae: Euliini). *Zootaxa*, **3640**, 270–283.

712

713 Brown, J.W. (2016) A new generic assignment for *Tortrix baboquavariana* Kearfott, 1907
 714 (Lepidoptera: Tortricidae) with comments on its tribal assignment. *Journal of the Lepidopterists’*
 715 *Society*, **70**, 173–175.

716

717 Brown, J. W., Robinson, G. & Powell, J. A. (2018) Food plant database of the leafrollers of the
 718 world (Lepidoptera: Tortricidae) (Version 1.0). <http://www.tortricid.net/foodplants.asp>.

719

720 Brown, J.W. (2019) New genera, new species, and new combinations in New World Cochyliina
 721 (Lepidoptera: Tortricidae: Tortricinae). *Zootaxa*, in press.

722

723 Brown, J.W., Copeland, R.S., Aarvik, L., Luke, Q., Miller, S. & Rosati, M. (2014) New host
 724 records for fruit-feeding Afrotropical Tortricidae (Lepidoptera). *African Entomology*, **22**, 343–
 725 376.

726

727 Brown, J.W. & Powell, J.A. (1991) Systematics of the *Chrysoxena* group of genera
 728 (Lepidoptera: Tortricidae: Euliini). *University of California Publications in Entomology*, **111**, 1–
 729 87.

730

731 Brown, J.W. & Razowski, J. (2003) Description of *Ptychocroca*, a new genus from Chile and
 732 Argentina, with comments on the *Bonagota* Razowski group of genera (Lepidoptera: Tortricidae:
 733 Euliini). *Zootaxa*, **303**, 1–31.

734

735 Brown, J.W., Robinson, G. & Powell, J.A. (2018) Food plant database of the leafrollers of the
 736 world (Lepidoptera: Tortricidae) (Version 1.0). <http://www.tortricid.net/foodplants.asp>.

737

738 Clarke, J.F.G. (1963) Catalogue of the Type Specimens of Microlepidoptera in the British
 739 Museum (Natural History) described by Edward Meyrick, Volume 4. Trustees of the British
 740 Museum, London. 521 pp.

741

742 Clarke, J.F.G. (1968) Neotropical Microlepidoptera, XVII. Notes and new species of
 743 Phaloniidae. *Proceedings of the United States National Museum*, **125** (3600), 1–58.

744

745 DeWaard, J.R., Ivanova, N.V., Hajibabaei, M. & Hebert, P.D.N. (2008) Assembling DNA
 746 barcodes: analytical protocols. *Methods in Molecular Biology: Environmental Genetics* (ed. By
 747 C. Martin), pp. 275–294. Humana Press, Totowaa, New Jersey,.

748

749 Diakonoff, A. (1961) Taxonomy of the higher groups of the Tortricoidea. *XI Internationalen*
 750 *Kongresses fur Entomologie: Wien*, 17, bis 25, August 1960 (Volume 1) (ed. by H. Stouhal).
 751 Verhandlungen, pp. 124–126.

752

753 Drummond A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling
 754 trees. *BMC Evolutionary Biology*, **7**, 214.

755

756 Falkovitsh, M.I. (1963) New species of the family Cochylidae (Lepidoptera) from Kazakhstan
 757 and the Caucasus. *Zoologicheskii Zhurnal Moskva*, **42**, 697–703.

758

759 Gibeaux, C. (1985) Description d'un genre et de trois especes de tordeuses nouveaux pour la
 760 France (Lep. Tortricidae, Cochylini). *Entomologica Gallica*, **1**, 346–351.

761

762 Gilligan, T.M., Baixeras, J. & Brown, J.W. (2018) T@RTS: Online World Catalogue of the
 763 Tortricidae (Ver.4.0). <http://www.tortricid.net/catalogue.asp>.

764

765 Guenée, M.A. (1845) Essai sur une nouvelle classification des Microlepidopteres et catalogue
 766 des especes Europeennes. *Annales de la Société Entomologique de France*, **(2) 3**, 297–344.

767

768 Hall, T. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis
 769 program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, **41**, 95–98.

770

771 Heikkilä, M., Mutanen, M., Wahlberg, N., Sihvonen, P. & Kaila, L. (2015) Elusive ditrysian
 772 phylogeny: An account of combining systematized morphology with molecular data
 773 (Lepidoptera). *BMC Evolutionary Biology*, **15** (260), 1–27. [https://doi.org/10.1186/s12862-015-](https://doi.org/10.1186/s12862-015-0520-0)
 774 [0520-0](https://doi.org/10.1186/s12862-015-0520-0)

775

776 Horak, M. (1999) Tortricoidea. *Lepidoptera, moths and butterflies. Volume 1: Evolution,*
 777 *systematics, and biogeography.* Handbook of Zoology 4 (35), Arthropoda: Insecta (ed. By N.
 778 Kristensen), pp. 199–215. Walter de Gruyter, Berlin & New York,
 779
 780 Horak, M. & Brown, R.L. (1991) 1.2 Taxonomy and phylogeny. *Tortricid Pests, Their Biology,*
 781 *Natural Enemies and Control* (ed. by L.P.S. van der Geest & H. H. Evenhuis), pp. 23–48.
 782 Elsevier Science Publishers, Amsterdam.
 783
 784 Kozlov, A.M., Darriba, D., Flouri, T., Morel, B. & Stamatakis, A. (2018) RAxML-NG: A fast,
 785 scalable, and user-friendly tool for maximum likelihood phylogenetic inference. *bioRxiv*.
 786 doi:10.1101/447110
 787
 788 Kuznetsov, V.I. & Stekolnikov, A.A. (1973) Phylogenetic relationships in the family Tortricidae
 789 (Lepidoptera) treated on the base of study of functional morphology of genital apparatus. *Trudy*
 790 *Russkago Entomologicheskago Obschestva*, 56, 18–43. [In Russian]
 791
 792 Kuznetsov, V I. & Stekolnikov, A.A. (1977) Functional morphology of the male genitalia and
 793 phylogenetic relationships of some tribes in the family Tortricidae (Lepidoptera) fauna of the Far
 794 East. *Trudy Zoologicheskogo Instituta Leningrad*, **70**, 65–97.
 795
 796 MacKay, M.R. (1959) Larvae of the North American Olethreutidae (Lepidoptera). *Canadian*
 797 *Entomologist Supplement*, **10**, 1–338.
 798

799 MacKay, M.R. (1962) Larvae of the North American Tortricinae (Lepidoptera: Tortricinae).
800 *Canadian Entomologist Supplement*, **28**, 1–182.

801

802 Metzler, E. (2000) Two new species of Cochylini (Lepidoptera: Tortricidae: Tortricinae) from
803 the eastern United States. *The Great Lakes Entomologist*, **32** (1999), 185–197.

804

805 Metzler, E.H. & Brown, J.W. (2014) An updated check list the Cochylina (Tortricidae,
806 Tortricinae, Euliini) of North America north of Mexico including Greenland, with comments on
807 classification and identification. *Journal of the Lepidopterists' Society*, **68**, 274–282.

808

809 Metzler, E. & Sabourin, M. (2002) A new species of *Spinipogon* Razowski, 1967 from two
810 remnant prairies in Ohio (Lepidoptera: Tortricidae, Cochylini). *Faberies*, **27**, 69–76.

811

812 Meyrick, E. (1882) Descriptions of New Zealand Micro-lepidoptera. *New Zealand Journal of*
813 *Science*, **1**, 159–162.

814

815 Meyrick, E. (1895) *A handbook of British Lepidoptera*. London: MacMillan, 843 pp.

816

817 Miller, M.A., Pfeiffer, W., & Schwartz, T. (2010) *Creating the CIPRES Science Gateway for*
818 *inference of large phylogenetic trees*, Proceedings of the Gateway Computing Environments
819 Workshop (GCE), 14 November 2010, New Orleans, Louisiana, pp. 1–8.

820

821 Monsalve, S., Dombroskie, J., Lam, W., Rota, J., & Brown, J.W. (2011) Variation in the female
822 frenulum in Tortricidae (Lepidoptera). Part 3. Tortricinae. *Proceedings of the Entomological*
823 *Society of Washington*, **113**, 335–370.

824

825 Morris, F.O. (1898) *A natural history of British moths*, volume 3, 1–223. London.

826

827 Mutanen, M., Wahlberg, N. & Kaila, L. (2010) Comprehensive gene and taxon coverage
828 elucidates radiation patterns in moths and butterflies. *Proceedings of the Royal Society B*, 277
829 (1695), 2839–2848. <https://doi.org/10.1098/rspb.2010.0392>

830

831 Obraztsov, N. S. (1967) Genera Tortricoidarum. Check list of genera and subgenera belonging to
832 the families Tortricidae (Ceracidae, Chlidanotidae, Schoenotenidae and Olethreutidae included)
833 and Phaloniidae. *Journal of the New York Entomological Society*, **75**, 2–11.

834

835 Pogue, M.G. (1986) *A Generic Revision of the Cochylidae (Lepidoptera) of North America*.
836 Ph.D. thesis, University of Minnesota.

837

838 Pogue, M.G. (1988) Revision of the genus *Lorita* Busck (Lepidoptera: Tortricidae: Cochylini),
839 with a description of a new species. *Proceedings of the Entomological Society of Washington*,
840 **90**, 440–457.

841

842 Pogue, M.G. (2001) Revised status of *Rolandylis* Gibeaux (Lepidoptera: Tortricidae: Cochylini),
843 with descriptions of two new species from North America. *Proceedings of the Entomological*
844 *Society of Washington*, **103**, 788–796.

845

846 Pogue, M.G. & Friedlander, T.P. (1987) *Cochylis caulocatax* Razowski (Lepidoptera:
847 Tortricidae: Cochylini): a redescription of the male with descriptions of the female, larva, and
848 pupa. *Proceedings of the Entomological Society of Washington*, **95**, 320–327.

849

850 Pogue, M.G. & Mickevitch, M.F. (1990) Character definitions and character state delineation:
851 the bete noire of phylogenetic inference. *Cladistics*, **6**, 319–361.

852

853 Powell, J.A. 1964. Biological and taxonomic studies on tortricine moths, with reference to the
854 species in California. *University of California Publications in Entomology*, **32**, 1–317.

855

856 Powell, J.A. (1983) Tortricoidea. *Check list of the Lepidoptera of America north of Mexico* (ed.
857 by R. W. Hodges), pp. 31–42. E.W. Classey, Ltd., and Wedge Entomological Research
858 Foundation, London.

859

860 Powell, J.A. (1986) Synopsis of the classification of Neotropical Tortricinae, with descriptions of
861 new genera and species (Lepidoptera: Tortricidae). *Pan-Pacific Entomologist*, **62**, 372–398.

862

863 Ratnasingham, S. & Hebert, P.D.N (2013) A DNA-based registry for all animal species: The
864 Barcode Index Number (BIN) System. *PLoS ONE*, **8**: e66213.

865

866 Razowski, J. (1960) Studies on the Cochylidae (Lepidoptera). Part II. The genera of the

867 Palearctic Cochylidae. *Polskie Pismo Entomologiczne*, **30**, 281–356.

868

869 Razowski, J. (1967a) South American Cochylidae (Lepidoptera) from the collection of the

870 British Museum (Natural History). *Acta Zoologica Cracoviensia*, **12**, 163–210.

871

872 Razowski, J. (1967b) Afghanische Wickler-Arten (Lepidoptera: Tortricidae und Cochylidae).

873 *Beitrage zur Naturkundlichen Forschung in Sudwestdeutschland*, **26**, 91–108.

874

875 Razowski, J. (1968a) Revision of the generic group *Agapeta* Hubner (Lepidoptera, Cochylidae).

876 *Acta Zoologica Cracoviensia*, **13**, 73–100.

877

878 Razowski, J. (1968b) Revision of the genus *Eupoecilia* Stephens (Lepidoptera, Cochylidae). *Acta*

879 *Zoologica Cracoviensia*, **13**, 103–130.

880

881 Razowski, J. (1968c) Revision of the generic group *Cochylis* Treitschke (Lepidoptera,

882 Cochylidae). *Acta Zoologica Cracoviensia*, **13**, 131–147.

883

884 Razowski, J. (1970) Cochylidae. *Microlepidoptera Palaearctica*, volume 3 (ed. by H.G. Amsel,

885 F. Gregor & H. Reiser). Verlag G. Fromme & Co., Wien, 528 pp. + xxx.

886

887 Razowski, J. (1976) Phylogeny and system of Tortricidae (Lepidoptera). *Acta Zoologica*
888 *Cracoviensia*, **21**, 73–120.

889

890 Razowski, J. (1984) Descriptions of the Neotropical Cochylidii (Lepidoptera, Tortricidae).
891 *Annales Zoologici*, **38**, 275–280.

892

893 Razowski, J. (1985a) Descriptions of *Rudenia* gen n. and its two new species (Lepidoptera,
894 Tortricidae). *Polskie Pismo Entomologiczne*, **55**, 519–522.

895

896 Razowski, J. (1985b) On the generic groups *Saphenista* and *Cochylis* (Tortricidae). *Nota*
897 *Lepidopterologica*, **8**, 55–60.

898

899 Razowski, J. (1986) New and little known Neotropical Cochylidii (Lepidoptera, Tortricidae).
900 *Acta Zoologica Cracoviensia*, **29**, 373–396.

901

902 Razowski, J. (1987a) New taxa of Archipini (Lepidoptera: Tortricidae) from South America.
903 *Tinea*, **12** (supplement), 123–138.

904

905 Razowski, J. (1987b) Descriptions of new Neotropical genera of Archipini and rectification of
906 the *Deltinea* problem (Lepidoptera: Tortricidae). *Sciences Nat*, **52** (1986), 21–25.

907

908 Razowski, J. (1987c) The genera of Tortricidae (Lepidoptera). Part 1. Palearctic Chlidanotinae
909 and Tortricinae. *Acta Zoologica Cracoviensia*, **30**, 141–355.

910

911 Razowski, J. (1988) New genera and species of the Neotropical Archipini (Lepidoptera:

912 Tortricidae). *Acta Zoologica Cracoviensia*, **31**, 387–422.

913

914 Razowski, J. (1989) Descriptions of four Neotropical taxa of Cochylini (Lepidoptera:

915 Tortricidae). *SHILAP Revista de Lepidopterologia*, **17** (66), 205–208.

916

917 Razowski, J. (1990) Contribution to Cochylini fauna of Mexico (Lepidoptera: Tortricidae).

918 *SHILAP Revista de Lepidopterologia*, **18**, 337–345.

919

920 Razowski, J. (1992) Descriptions of some Neotropical Euliini and Archipini (Lepidoptera,

921 Tortricidae). *Miscellanea Zoologica*, **14**, 105–114.

922

923 Razowski, J. (1993) Cochylini (Lepidoptera, Tortricidae) from Peru and Bolivia. *Acta Zoologica*

924 *Cracoviensia*, **36**, 161–181.

925

926 Razowski, J. (1994) Synopsis of the Neotropical Cochylini (Lepidoptera: Tortricidae). *Acta*

927 *Zoologica Cracoviensia*, **37**, 121–320.

928

929 Razowski, J. (1995) Catalogue of the species of Tortricidae (Lepidoptera). Part III. Afrotropical

930 Chlidanotinae and Tortricinae: Phricanthini, Cochylini and Tortricini. *Acta Zoologica*

931 *Cracoviensia*, **38**, 183–193.

932

933 Razowski, J. (1997) Cochylini (Lepidoptera: Tortricidae) of Canada. *Acta Zoologica*
 934 *Cracoviensia*, **40**, 107–163.

935

936 Razowski, J. (2002) *Tortricidae of Europe. Part I. Tortricinae and Chlidanotinae*. Frantisek
 937 Slamka, Bratislava, 247 pp.

938

939 Razowski, J. (2011) Diagnoses and remarks on genera of Tortricidae, 2: Cochylini (Lepidoptera:
 940 Tortricidae). *SHILAP Revista de Lepidopterologia*, **39**, 397–414.

941

942 Razowski, J. & Becker, V.O. (1983) Brazilian Cochyliidii (Lepidoptera: Tortricidae). *Acta*
 943 *Zoologica Cracoviensia*, **26**, 421–464.

944

945 Razowski, J. & Wojtusiak, J. (2008) Tortricidae from the mountains of Ecuador. Part III.
 946 Western Cordillera. *Genus*, **19**, 497–575.

947

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

951

952 Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under
 953 mixed models. *Bioinformatics*, **19**, 1572–1574.

954

955 Sabourin, M., Miller, W.E., Metzler, E.H. & Vargo, J.T. (2002) Revised identities and new
 956 species of *Aethes* from, midwestern North America. *Journal of the Lepidopterists' Society*, **56**,
 957 216–233.

958

959 Stainton, H.T. (1859) *A Manual of British Butterflies and Moths*, Volume 2. London. 475 pp.

960

961 Stamatakis, A. (2014). RAxML Version 8: A tool for phylogenetic analysis and post-analysis of
 962 large phylogenies. *Bioinformatics*, **30** (9), 1312–1313.

963

964 Stephens, J.F. (1852) *List of the specimens of British animals in the collection of the British*
 965 *Museum*, **10** (Lepidoptera – continued), 1–120.

966

967 Swatschek, B. (1958) *Die larval systematik der wickler (Tortricidae and Carposinidae) aus dem*
 968 *zoologischen Institut der Universitat Erlangen*. Akademie-Verlag, Berlin. 269 pp.

969 [Abhandlungen zur larvalsystematik Insekten 3.]

970

971 Wahlberg, N. & Wheat, C.W. (2008) Genomic outposts serve the phylogenomic pioneers:
 972 designing novel nuclear markers for genomic DNA extractions of Lepidoptera. *Systematic*
 973 *Biology*, **57**, 231–242.

974

975

976

Explanation of Figures

Figure 1. Phylogenetic tree of Palearctic genera of Cochylini from Razowski (1970).

Figure 2. Phylogenetic tree of North American Cochylini from Pogue & Mickevitch (1990).

Figure 3. Multi-gene phylogenetic tree of Cochylini and out-groups. **Lorita scarifacata* COI

data concatenated from BIOUG01827-G12 (COI barcode region) and MH_USNM_18 (COI-

end). ***Neocochylis molliculana* data concatenated from IT_3 (CAD, EF1a-begin and EF1a-

end), and TLMF_Lep_23781 (COI barcode region).

Figure 4. ML barcode tree of *Phtheochroa* Group species.

Figure 5. ML barcode tree of *Henricus* Group species.

Figure 6. ML barcode tree of *Aethes*, *Saphenista*, and *Phalonidia* Group species.

Figure 7. ML barcode tree of *Cochylis* Group species.

Fig. 1.

Razowski (1970)

Fig. 2.

Pogue & Mickevitch (1990)

Figure 1. Phylogenetic tree of Palearctic genera of Cochylini from Razowski (1970).

Figure 2. Phylogenetic tree of North American Cochylini from Pogue & Mickevitch (1990).

Figure 3. Multi-gene phylogenetic tree based on maximum likelihood.

**Lorita scarificata* COI data concatenated from BIOUG01827-G12 (COI barcode region) and MH_USNM_18 (COI-end).

***Neocochylis molliculana* data concatenated from IT_3 (CAD, EF1a-begin and EF1a-end), and TLMF_Lep_23781 (COI barcode region).