Molecular phylogeny and revised classification of *Eucosma* Hübner and related genera (Lepidoptera: Tortricidae: Eucosmini)

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Abstract. *Eucosma* Hübner is the largest genus in Tortricidae, currently comprising 298 described species. Its circumscription and those of the closely related genera *Pelochrista* Lederer, *Phaneta* Stephens and *Epiblema* Hübner have long been matters of confusion. Prior to the mid-1920s, assignment to any of these genera was largely arbitrary due to a lack of clearly defined morphological limits. Here we present the first study to examine the monophyly of *Eucosma* and related genera using a molecular phylogenetic framework. We find that the *Eucosma*/*Pelochrista* group splits into three lineages: (i) a new genus of Pinaceae-feeding species formerly assigned to *Eucosma*; (ii) a refined notion of *Eucosma* that is consistent with Palearctic usage and includes current North American *Phaneta*; and (iii) a refined concept of *Pelochrista* that is distinguishable from *Eucosma* based on female genital morphology. The new genus, described here as *Eucopina* Gilligan & Wright **gen.n.**, contains the following species: *Eucopina bobana* (Kearfott) **comb.n.**; *E. cocana* (Kearfott) **comb.n.**; *E. crymalana* (Powell) **comb.n.**; *E. franclemonti* (Powell) **comb.n.**; *E. gloriola* (Heinrich) **comb.n.**; *E. monitorana* (Heinrich) **comb.n.**; *E. monoensis* (Powell) **comb.n.**; *E. ponderosa* (Powell) **comb.n.**; *E. rescissoriana* (Heinrich) **comb.n.**; *E. siskiyouana* (Kearfott) **comb.n.**; *E. sonomana* (Kearfott) **comb.n.**; *E. tocullionana* (Heinrich) **comb.n**. In addition, *Ioplocama* Clemens **syn.n.** is synonymized with *Eucosma* and *Pygolopha* Lederer **syn.n.** is synonymized with *Pelochrista*. This work is the basis for a revised world catalogue of *Eucosma*, *Pelochrista* and *Phaneta* in preparation.

Introduction

Eucosma Hübner is the largest genus in Tortricidae, currently comprising 298 described species (Gilligan *et al.*, 2012). It is morphologically similar to three other genera: *Pelochrista* Lederer, with 87 described species, *Phaneta* Stephens, with 119 described species, and *Epiblema* Hübner, with 89 described species (Gilligan *et al.*, 2012). These genera are Holarctic in distribution. With few exceptions, their larvae are stem- or root-borers in Asteraceae.

Historically there has been confusion over the circumscription of *Eucosma* and related genera. Hübner (1823) described

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Eucosma, with the type species *E. circulana* Hübner, from a specimen collected in Pennsylvania, and the application of *Eucosma* was restricted to the North American type until the end of the 19th century. *Pelochrista* was described by Lederer (1859) as a subgenus of *Grapholitha* (a misspelling of *Grapholita* Treitschke), with the type species *Paedisca mancipiana* Mann, and shortly thereafter was elevated to generic status by Walker (1863). In the late 1800s and early 1900s, various authors (e.g. Fernald, 1882; Walsingham, 1897) treated *Eucosma* as a synonym of *Paedisca*. Fernald (1908) synonymized *Pelochrista* and 25 other generic names with *Eucosma*, and Walsingham (1914) expanded that list to a total of 38 generic synonyms.

Early 20th century advances in tortricid taxonomy resulted from the use of genitalic characters, pioneered by Dampf

(1908). Pierce & Metcalfe (1922) published the first comprehensive taxonomic work to include genitalia descriptions and illustrations for European Tortricidae. They treated *Eucosma* as the modern-day *Pelochrista*, likely because of a misinterpretation of the *Eucosma* type (Gilligan & Wright, 2013), and referred the remainder of the species that would today be considered *Eucosma* to *Catoptria* Guenée. Heinrich (1923) relied heavily on male genitalic characters in his revision of the Nearctic Eucosminae. He resurrected many of the generic names previously synonymized by Fernald (1908) and Walsingham (1914) but retained the synonymy of *Eucosma* and *Pelochrista*. He also proposed an interpretation of *E. circulana*, the *Eucosma* type species, that has since met with general acceptance (Gilligan & Wright, 2013). Much of his classification system is still in use today.

In the middle of the 20th century, Nicholas Obraztsov began a revision of the Palearctic Tortricidae. His initial classification system for the Eucosmini (1946) attempted to reconcile the differences between the North American and European interpretations of *Eucosma* and closely related genera. He treated the subfamily Eucosminae as the tribe Eucosmini, synonymizing *Thiodia*, *Semasia*, *Phaneta* and part of Heinrich's (1923) *Eucosma* under *Catoptria* and transferring Pierce & Metcalfe's (1922) *Eucosma* (= *Pelochrista*) species to *Pseudeucosma* Obraztsov. In the next decade he refined this arrangement, influenced in part by continued communication with other Old World tortricid experts such as Bradley, Hannemann and Kuznetsov. His new Eucosmini classification first appeared in Agenjo's (1955) list of the Spanish fauna, where several Palearctic species were assigned to *Eucosma*. Hannemann (1961) followed suit, recognizing many species in *Eucosma* and dividing the genus into three subgenera, *Eucosma*, *Phaneta* and *Pygolopha* Lederer. In two posthumous publications (1967, 1968), Obraztsov proposed his most influential changes to Heinrich's system, separating *Pelochrista* from *Eucosma* based on differences in the male and female genitalia. Following Hannemann (1961), he included subgeneric divisions in *Pelochrista* (*Pelochrista* and *Pseudeucosma*) and *Eucosma* (*Eucosma*, *Palpocrinia* Kennel, *Phaneta* and *Pygolopha*), but the subgenera were not retained by subsequent authors (e.g. Powell, 1983; Razowski, 1989).

In the 19th Century, many Eucosmini were assigned to the genus *Semasia* Stephens (now considered a synonym of *Cydia* Hübner). Walsingham (1897) treated *Semasia* as a synonym of *Thiodia* Hübner, and Fernald (1903) concurred, transferring to *Thiodia* the North American species listed as *Semasia* in his 1882 and 1891 publications. *Thiodia* was synonymized under *Eucosma* by Walsingham (1914) but subsequently resurrected by Heinrich (1923) for the purpose of dividing Nearctic *Eucosma* into two genera of more manageable size. He used the male costal fold as the diagnostic character, stating that '. . . the [costal] fold enables division and easier handling of what would otherwise be a most unwieldy group'. In this arrangement, species placed under *Eucosma* possessed a costal fold, and those placed under *Thiodia* lacked a costal fold. He realized that this division was simply 'a convenience', and that the type of *Thiodia* – *Tortrix*

citrana Hübner – differed from these North American species in male genitalia. Obraztsov (1952) determined that the Nearctic and Palearctic species of *Thiodia* were not congeneric, stating that 'The American species [of *Thiodia*] are closely related to *Eucosma* Hb. whereas the Palearctic *Thiodia* have more resemblance to *Rhyacionia* Hb. in their genitalia'. He transferred the Nearctic *Thiodia* (*sensu* Heinrich, 1923) to *Phaneta*, thus introducing a discrepancy in the North American and European concepts of *Phaneta* and *Eucosma*: Palearctic *Phaneta* remained monotypic, with the type species *Cochylis pauperana* Duponchel; the Nearctic fauna expanded to include close to 100 species which would have been placed in *Eucosma* (or *Pelochrista*) if described from Europe. Subsequent North American authors (e.g. Miller, 1987; Gilligan *et al.*, 2008) retained Obraztsov's expanded concept of *Phaneta*, whereas European authors (e.g. Razowski, 2003) continued to restrict *Phaneta* to one or two species.

Two primary issues have led to the confusion in assigning species to the genera discussed here: a lack of morphological synapomorphies defining *Eucosma* and *Pelochrista*, and the unfounded importance placed on the presence or absence of the male costal fold in *Eucosma* and *Phaneta*. With regard to the first, there is no extant specimen upon which Hübner based his description of *E. circulana* (the *Eucosma* type) and therefore no definitive basis for characterizing the genus. This situation has been addressed by Gilligan & Wright (2013), who reviewed the history of the problem and designated a neotype for *E. circulana*. Male genitalic characters previously used to separate *Eucosma* and *Pelochrista* include the presence or absence of a lobe, or 'pulvinus', on the distal margin of the basal excavation of the valva (Obraztsov, 1967, 1968; Razowski, 1989) and the presence or absence of a single large spiniform seta on the margin of the cucullus (Heinrich, 1923; Wright, 2007, 2008), but reduction or loss of these structures has produced many exceptions. Similarly, loss of the 'clasper' on the male valva in some species of *Epiblema* has caused some uncertainty as to the distinction between that genus and *Eucosma* (Razowski, 1989). As for the second issue, the male costal fold has been used in tortricid classification since Heinemann (1863) but was considered unreliable by Barrett (1885) and by Heinrich himself (1923). There are many tortricid genera in which a male costal fold is both present or absent (e.g. *Clepsis*, *Choristoneura*, *Dichrorampha*, *Epinotia*, to name a few).

Another inconsistency in the current circumscription of *Eucosma* is the inclusion of several Pinaceae-feeding species. The vast majority of *Eucosma* with recorded hosts are stem- or root-borers in Asteraceae, but Kearfott (1907) described three species in the genus that are known to bore in shoots or cones of *Pinus* or other coniferous hosts (Powell, 1968; Gilligan *et al.*, 2008). Additional such species have been described by Heinrich (1920, 1931) and Powell (1968) for a current total of 12, all restricted to North America.

The goals of this study are to test the monophyly of *Eucosma*, *Pelochrista*, *Phaneta* and *Epiblema* as currently defined, identify morphological character states that define each genus, and examine the relationship of the Pinaceae-feeding *Eucosma* to the rest of the genus. Because previously

studied morphological characters proved unreliable for separating these taxa, we generated a molecular dataset consisting of 2692 bp using the mitochondrial gene cytochrome c oxidase 1 (*COI*; 658 bp) and the nuclear genes carbamoylphosphate synthetase-aspartate transcarbamylase-dihydroorotase (*CAD*; 638 bp), elongation factor-1a (*EF-1α*; 568 bp), and 28S ribosomal DNA (*28S* rDNA; 828 bp). These data were analysed together with a morphological character set. The results presented here will be used to provide an updated classification and world catalogue for *Eucosma* and related genera in an upcoming contribution.

Methods

Taxon sampling

A total of 71 taxa were sampled (Appendix 1), comprising 60 ingroup and 11 outgroup taxa. From the ingroup, two specimens were sampled for seven taxa and three for two taxa, for a total of 82 terminals included in the simultaneous analysis (Kluge, 1989; Nixon & Carpenter, 1996). All specimens are stored in 95–100% ethanol and will be deposited in the ATOLep alcohol collection at the University of Maryland (Regier *et al.*, 2012; details at http://www.leptree.net/collection).

The ingroup taxa consisted of 13 species of North American *Phaneta*, 6 species of *Epiblema*, and a broad sample of primarily North American *Eucosma* and *Pelochrista*, including four Pinaceae-feeding *Eucosma*. We were unable to obtain a specimen of the type species of *Phaneta* for molecular analysis, but several morphological synapomorphies clearly demonstrate that European and North American *Phaneta* are not the same genus (Razowski, 1989). Outgroup taxa consisted of three Microcorsini, two Olethreutini and six additional Eucosmini.

Morphological characters

Twenty-seven morphological characters were coded for all species, including structures of the male and female genitalia traditionally used to define species in Eucosmini, the male forewing costal fold, and two wing venation characters (Appendix 2). When applicable, character state coding follows Horak (2006). Other structures on the head, thorax, leg, and wings (Horak, 2006; Gilligan *et al.*, 2008) were examined and determined to be invariant or otherwise parsimony uninformative for the ingroup.

Molecular methods

Total genomic DNA was extracted using a Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, U.S.A.). One to three legs from an adult moth were crushed, incubated overnight at 56°C and eluted in 100 μL of AE buffer after following the manufacturer's recommended protocol. All four gene regions were amplified using conventional PCR on an Eppendorf Mastercycler gradient 5331 thermal cycler (Eppendorf AG, Hamburg, Germany). Reactions were performed with TaKaRa Ex Taq HS polymerase (Takara Bio, Shiga, Japan) in total volumes of 50 μL using the manufacturer's recommended volumes of 10× Ex Taq buffer, dNTP mixture, and water.

Amplifications of *COI* were performed using the primers LCO-1490 and HCO-2198 (Folmer *et al.*, 1994). PCR conditions included an initial denaturation step of 94°C (3 min), 32 cycles of 94°C (20 s)/50°C (20 s)/72°C (30 s), and an extension step of 72°C (5 min). Amplifications of *28S* rDNA were performed using the primers WF&LD2F and A335R (A. Zwick, personal communication) and following the same PCR conditions. To minimize the effects of rDNA secondary structure, 3 μl of water was replaced with dimethylsulfoxide (DMSO) in all *28S* rDNA reactions. Amplifications of *EF-1α* were performed using the primers M51.9tort (A. Zwick, personal communication) and rcM4 (Cho *et al.*, 1995). PCR conditions included an initial denaturation step of 94°C (4 min), 5 cycles of 94°C (30 s)/52°C (30 s)/72°C (1 min), 7 cycles of 94°C (30 s)/51°C (1 min)/72°C (1 min), 36 cycles of 94°C (30 s)/45°C (20 s)/72°C (1 min, 30 s), and a final extension step of 72°C (3 min). Amplicons of *COI*, *28S* rDNA and *EF-1α* were purified using a Qiaquick PCR Purification Kit (Qiagen) and eluted into 35 μL of EB buffer. Amplifications of *CAD* were performed using the primers 791F (Regier *et al.*, 2008) and 1028R (Wahlberg & Wheat, 2008). The PCR conditions were identical to those used in amplifying *EF-1α*. Because *CAD* amplification resulted in multiple PCR products for many taxa, all PCR products were gel extracted using a QIAquick Gel Extraction Kit (Qiagen). The PCR product and 6 μL of loading dye were loaded into a single well on a 2.0% low-melt agarose gel. After performing electrophoresis for approximately 3 h at 75 V, individual bands were excised using gel-cutting pipette tips (BioExpress, Kaysville, UT, U.S.A.), dissolved in 500 μL of buffer QC, and eluted into 35 μL of EB buffer after following the manufacturer's recommended gel extraction protocol.

All purified PCR products were sequenced by the University of Chicago Cancer Research Center DNA Sequencing Facility using an Applied Biosystems 3730XL DNA sequencer (Applied Biosystems, Foster City, CA, U.S.A.). The same primers used for PCR were also used for sequencing. Individual contigs were assembled and trimmed using Geneious Pro v5.4.6 (Drummond *et al.*, 2012). All DNA sequences generated by this study were submitted to GenBank under accession numbers KC430336–KC430616 (Appendix 1).

Data analysis

Individual gene regions were aligned using MAFFT v6 (Katoh *et al.*, 2002). The Q-INS-i algorithm was used for *28S* rDNA sequences as it considers secondary structure of rRNA (Katoh & Toh, 2008), whereas the G-INS-i algorithm was used for all other gene regions. Parameters for all gene regions used the '1PAM/k = 2' scoring matrix, a gap opening penalty of 1.53, and gap offset value of 0.1. Single-read CAD sequences

for six specimens that failed to assemble were aligned to the 5′-end or 3′-end of the initial *CAD* alignment and manually assembled into a single sequence.

With the exception of the six manually assembled *CAD* sequences, no gaps were present in the *COI*, *EF-1α* or *CAD* alignments. Manual adjustments to the *28S* rDNA alignment were performed in MacClade v4.08 (Maddison & Maddison, 2005) using the similarity method described in Simmons (2004) following Zurawski & Clegg (1987). A total of 26 ambiguously aligned positions in three regions were excluded from the *28S* rDNA alignment. Five gap characters were scored using modified complex indel coding (Simmons & Ochoterena, 2000) from unambiguously aligned regions and included in the parsimony analyses.

Several separate process partitions (Bull *et al.*, 1993) were analysed as a method of data exploration. The four gene regions were analysed as separate coalescent genes (Doyle, 1995), and their gene trees compared for well-supported topological incongruencies that may be a sign of introgression, lineage sorting or unrecognized paralogy (Doyle, 1992). All genes were analysed in a combined molecular matrix and a simultaneous parsimony analysis was performed using all molecular and morphological data. Individual and simultaneous analysis data matrices are posted as supplemental online data (Appendix S1).

Equally weighted parsimony tree searches were conducted for each data matrix using TNT v1.1 (Goloboff *et al.*, 2008). Five thousand random addition tree-bisection-reconnection (TBR) searches were performed with a maximum of 50 trees held per replicate, and the ratchet (Nixon, 1999) set for 100 iterations with a 10% probability of upweighting a character and a 5% probability of downweighting a character. Parsimony jackknife (JK; Farris *et al.*, 1996) analyses were conducted using TNT with the removal probability set to 0.37. One thousand JK replicates were performed with 100 random addition TBR searches and a maximum of 50 trees held per replicate. PartitionFinder v1.0.1 (Lanfear *et al.*, 2012) was used to estimate the best-fit partitioning scheme and nucleotide substitution model for likelihood analyses (Felsenstein, 1973). A total of 28 substitution models were considered; invariant-site models were excluded because models containing the gamma distribution were evaluated (Yang, 1993, 2006). The Akaike information criterion (AIC; Akaike, 1974) was used to select the best model with linked branch lengths between subsets. Data blocks were partitioned into genes and codon position for each coding gene, and all search schemes were considered (exhaustive search). A total of ten subsets (each codon position in each gene for the coding genes + *28S* rDNA) were chosen for the combined molecular matrix, with Q-matrices alternately consisting of GTR, TVM, TIM, TrN, HKY and F81. All models except F81 incorporated the gamma distribution. Three subsets (each codon position) were chosen for each individual gene, with the same set of models as in the combined matrix.

Likelihood analyses of nucleotide characters were performed as tests for long-branch attraction (Felsenstein, 1978; but see Siddall, 1998) using GARLI v2.0 (Zwickl, 2006). Optimal likelihood trees were searched for using 1000 independent searches. The partitioning schemes and models suggested by PartitionFinder were specified along with different models and different subset rates in the GARLI configuration file. Likelihood bootstrap (BS; Felsenstein, 1985) values were obtained using at least 1000 replicates and 10 searches per replicate for each matrix.

Results

The simultaneous analysis parsimony strict consensus tree is presented in Fig. 1 with parsimony JK values ≥ 50% above each branch and likelihood BS values ≥ 50% below each branch from the combined molecular likelihood analysis. Equivalent trees for each individual gene and the combined molecular likelihood tree are presented in Figs S1–S5.

All trees were created using TreeGraph v2 (Stöver & Müller, 2010), and SumTrees from the DendroPy v3.11 package (Sukumaran & Holder, 2010) was used to map support values. Support values were mapped onto the parsimony strict consensus tree instead of being presented on the majority-rule-consensus tree to avoid frequency-within-replicates and undersampling-within-replicates JK and BS artifacts (Davis *et al.*, 1998; Simmons & Freudenstein, 2011). Unambiguously supported clades refer to those with JK/BS values = 100%, highly supported clades refer to those with JK/BS values ≥ 90%, well-supported clades refer to those with JK/BS values 89 to 70%, and weakly supported clades refer to those with ≤ 69% JK/BS values. Statistics for data matricies and corresponding trees are presented in Table 1.

Process partitions

No mutually well-supported incongruencies were resolved between the parsimony and likelihood trees for the individual gene data matrices or between the simultaneous analysis parsimony strict consensus tree (Fig. 1) and the combined molecular likelihood tree (Fig. S5). Minor incongruencies were resolved between the *COI* and nuclear gene trees, likely as a result of introgression, lineage sorting or unrecognized parology (Doyle, 1992; Maddison, 1997) in closely related taxa. The *COI* gene tree conflicts with the three other genes in the arrangement of taxa in the *Eucosma agricolana* clade. All gene trees resolve the clade with high support (≥ 88% JK/≥ 85% BS), but *E. agricolana* (635) and *E. smithiana* (653) are resolved as sisters (85% JK/85% BS) in the *COI* tree, whereas *E. smithiana* + *E. morrisoni* are weakly supported as sister to the *E. agricolana* individuals in the three other gene trees (< 69% JK/BS). Similarly, *E. ridingsana* (TOR-DNA-468) and *E. fernaldana* are resolved as sister taxa in the *COI* gene tree (66% JK/85% JK), whereas the other *E. ridingsana* specimen (TOR-DNA-0676) is resolved as sister to *E. fernaldana* in the the *EF-1α* gene tree (83% JK/ < 50% BS).

Systematic implications

In agreement with other studies (Regier *et al.*, 2009, 2012), Eucosmini are resolved as monophyletic, although weakly
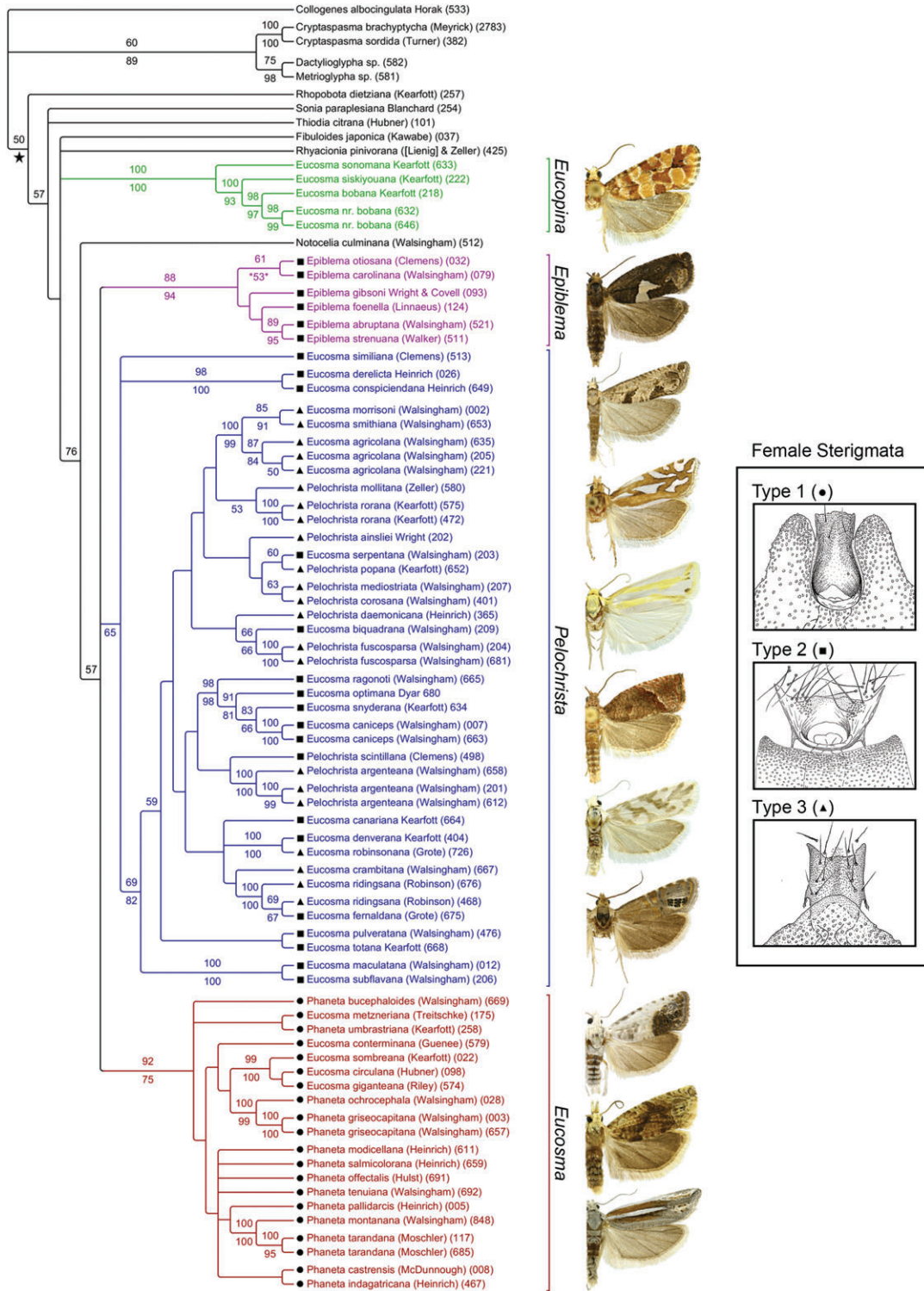
Fig. 1. Simultaneous analysis parsimony strict consensus tree. Parsimony JK values are above each branch and likelihood BS are below each branch. The single clade that was contradicted by ≥ 50% BS support is indicated by *XX* with BS support for the contradictory clade. The base of the Eucosmini is indicated with a star. Ingroup taxa are labelled with generic names proposed in this revision and colour-coded as follows: *Eucopina* green; *Epiblema* purple; *Pelochrista* blue; *Eucosma* red. Female sterigmata types are mapped onto the tree for the *Epiblema-Eucosma-Pelochrista* clade and indicated with the following symbols: type 1, circle; type 2, square; type 3, triangle. Moth photos represent typical wing patterns found in each ingroup clade.

Table 1. Data matrix and tree statistics.

Matrix	# terminals	# characters analysed	# of parsimony informative characters	% missing/ inapplicable	Most parsimonious tree length	# of most parsimonious trees	# of jacknife/ bootstrap clades ≥ 50%	Average jacknife/ bootstrap support (%)	CI	RI
28S rRNA	73	828	105	5.5	383	532	16/16	76/75	0.54	0.79
COI	82	658	236	0.2	1928	9	28/23	85/86	0.22	0.50
EF-1α	71	566	117	1.3	461	62 300	17/18	77/77	0.43	0.66
CAD	60	638	207	3.1	812	480	26/28	82/81	0.49	0.72
Simultaneous[a]	82	2719	691	14.8	4095	14	41/45	86/85	0.31	0.57

[a] Bootstrap statistics calculated from the combined molecular likelihood tree.
RI, ensemble retention index (Farris, 1989); CI, ensemble consistency index (Kluge & Farris, 1969) on the most parsimonious trees for the parsimony-informative characters.

supported (50% JK/ < 50% BS). The single synapomorphy for the tribe is the stalked M_3-CuA_1 vein in the hindwing. Because Eucosmini are a large tribe consisting of 227 genera (Gilligan *et al.*, 2012), taxon sampling was not sufficient to adequately test sister relationships between the several outgroup Eucosmini taxa and the ingroup clades. Thus, the remainder of the results and discussion pertains to the ingroup clades as resolved in the simultaneous analysis parsimony strict consensus tree (Fig. 1), which is preferred because it includes additional data (morphological and gap characters) not sampled in the likelihood analysis. The parsimony strict consensus was preferred over a possible Bayesian MCMC analysis of all data because parsimony is more resilient to missing-data artifacts wherein highly supported clades may be resolved despite lack of comparable information (Simmons, 2012a,b) and the reliance of Bayesian MCMC analyses on 'uninformative priors' that can actually be determinate to the results (Pickett & Randle, 2005; Randle & Pickett, 2010; Efron, 2013).

Eucosma, as currently defined, consists of at least three separate lineages. The first is an unambiguously supported (100% JK/100% BS) clade of Pinaceae-feeding *Eucosma*: *E. sonomana*, *E. siskiyouana*, *E. bobana* and a likely unde-scribed species '*E*. nr. *bobana*'. This group is well separated from all other *Eucosma*-containing clades and is distinguished by a ridge at the base of the neck of the male valva. The rest of the ingroup is contained in a single clade (57% JK/ < 50% BS) consisting of *Epiblema*, *Eucosma* + *Pelochrista* and *Eucosma* + *Phaneta*, although the relationships between these three groups are unresolved. *Epiblema* is well supported as a single lineage (88% JK/94% BS) and is distinguished by the presence of a clasper on the male valva.

The second *Eucosma* lineage consists of a weakly supported (< 50% JK/65% BS) clade of *Eucosma* + *Pelochrista*. Possible morphological synapomorphies include the presence of hook-tipped setae on the papillae anales and one or more spiniform setae at the distal end of the neck or on the apex of the anal angle in the male valva. *Eucosma similiana* and the clade of *E. derelicta* + *E. conspiciendana* are in a polytomy with a clade consisting of all other members of this lineage (69% JK/82% BS). Higher level relationships within this larger subclade are weakly supported, with *Pelochrista* sorting into four separate

subclades. Unambiguously or highly supported clades containing more than one species include: *E. morrisoni*, *E. smithiana* and *E. agricolana* (100% JK/99% BS); *E. ragonoti*, *E. optimana*, *E. snyderana* and *E. caniceps* (98% JK/98% BS); *E. denverana* and *E. robinsonana* (100% JK/100% BS); *E. ridingsana* and *E. fernaldana* (100% JK/100% BS); and *E. maculatana* and *E. subflavana* (100% JK/100% BS).

The third *Eucosma* lineage is a well-supported (92% JK/75% BS) clade of *Eucosma* + North American *Phaneta*. The morphological synapomorphy for this clade is the relationship between the sterigma and the posterior margin of sternum 7, the latter being U-shaped and approximate to or fused with the lateral margins of the former. Relationships within the clade are largely unresolved, with the exception of high support (100% JK/≥ 99% BS) for three subclades consisting of: *E. sombreana*, *E. circulana* and *E. giganteana*; *P. ochrocephala* and *P. griseocapitana*; and *P. montanana* and *P. tarandana*.

Discussion

This is the first study to test the monophyly and infer inter-specific relationships in the largest of the olethreutine genera using a molecular phylogentic framework. *Eucosma* is divided into three separate lineages, including a monophyletic group of Pinaceae-feeders. *Epiblema* is inferred as monophyletic, and *Pelochrista* and North American *Phaneta* are divided among the other two *Eucosma* lineages. Changes in classification are required to redefine these genera as natural groups.

The Pinaceae-feeding species of *Eucosma* form a well-defined group of 12 Nearctic species that feed on *Pinus*, *Picea*, *Abies* and *Pseudotsuga* (Pinaceae) (Powell, 1968). Morphological synapomorphies for this group include a strong overlap of the ventral projection of the cucullus with the ventral margin of the valval neck, and a raised transverse ridge on the medial surface of the valval neck (reduced to nearly absent in *E. gloriola* and *E. sonomana*). Other distinguishing characters include several short spiniform setae along the distal margin of the cucullus, a long ovipositor and semitriangular, ventrally facing papillae anales. The forewing in most species has fasciate red-orange maculation, as in many other genera of Pinaceae-feeding Olethreutinae. The

Fig. 2. Representative adults. (a) *Eucosma circulana*; (b) *E. giganteana*; (c) *E. castrensis*, (d) *E. argenticostana*; (e) *Pelochrista mancipiana*; (f) *P. corosana*; (g) *P. ridingsana*; (h) *P. canariana*; (i) *Eucopina bobana*; (j) *E. cocana*; (k) *E. monitorana*; (l) *E. siskiyouana*; (m) *Phaneta pauperana*; (n), *Epiblema carolinana*; (o) *E. otiosana*; (p) *E. strenuana*.

Pinaceae-feeding *Eucosma* clade is resolved well outside of the main *Epiblema–Eucosma–Pelochrista–Phaneta* clade, contradicting the hypothesis that these species are derived from an Asteraceae-feeding lineage within *Eucosma* (Powell, 1968; Powell & Opler, 2009). For these reasons, we describe this group as a new genus, *Eucopina* (description below).

Other genera of Pinaceae-feeding Eucosmini include *Barbara*, *Retinia* and *Rhyacionia*. Although genus-level characters are poorly defined for these groups (Razowski, 1989),

Eucopina differs from each in the structure of the male genitalia. In *Barbara* and *Retinia*, the socii are long and pendulous, and the valval neck is narrow with a scooped-out emargination of the ventrolateral margin. In *Rhyacionia* the basoventral margin of the cucullus does not strongly overlap the valval neck, and the anal angle is often developed into a prominent projection. In an unpublished analysis of Palearctic Eucosmini using molecular data, many of the Eucosmini Pinaceae-feeding genera were recovered in the same clade, suggesting a single
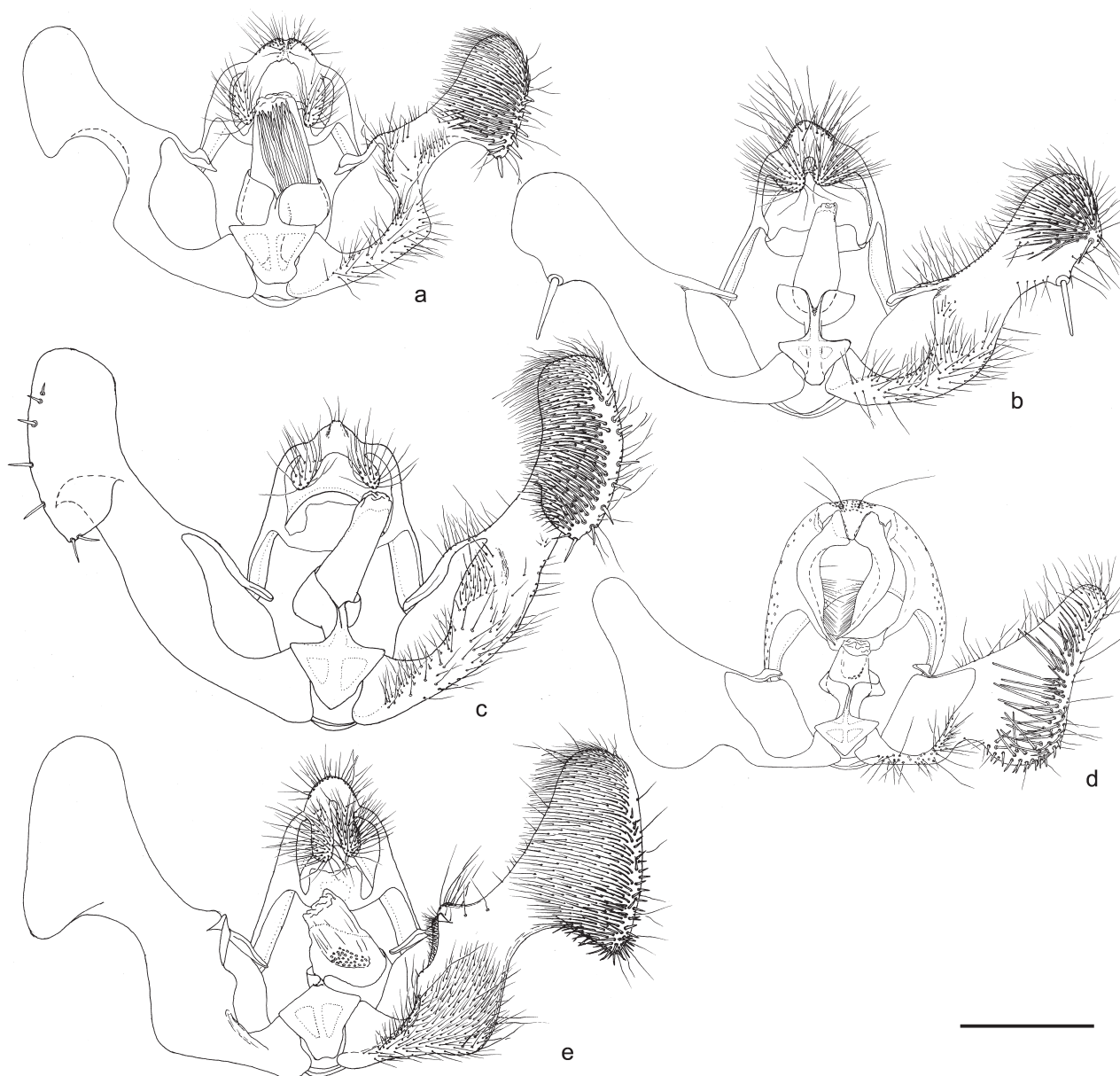
Fig. 3. Male genitalia. (a) *Eucosma circulana*; (b) *Pelochrista mancipiana*; (c) *Eucopina bobana*; (d) *Phaneta pauperana*; (e) *Epiblema foenella*. Scale bar: 0.5mm.

origin of Pinaceae-feeding within the family (J. Baixeras, personal communication). Evidence in favour of this hypothesis is found here in that *Rhyacionia pinivorana* is well supported as sister to *Eucopina* in the combined likelihood analysis.

The term 'clasper' has been applied in Lepidoptera to various projections of the male valva, but the use of the name across different groups can lead to confusion due to uncertainty as to the homology of the various structures (Klots, 1970; Horak, 1984). According to Kristensen (2003), 'clasper' refers to a topographically inner valve process that is movable by a muscle originating from the basal wall of the valva, and it is considered taxonomically informative in the Noctuidae

(e.g. Lafontaine & Poole, 2010). Gilligan *et al.* (2008) define 'clasper' in Olethreutinae as a 'prominent tetrahedron-shaped structure on the distal margin of the basal excavation'. It is present in *Epiblema* and *Notocelia* and has been used to distinguish *Epiblema* from *Eucosma* (Heinrich, 1923; Gilligan *et al.*, 2008). Here we employ the latter meaning for the term, without implying homology with similar structures in other families.

Razowski (1989) hypothesized that the absence of a clasper in *Eucosma* could be the result of a reduction, suggesting that *Eucosma* and *Epiblema* might be congeneric. In the present study, we find *Epiblema* to be a well-supported
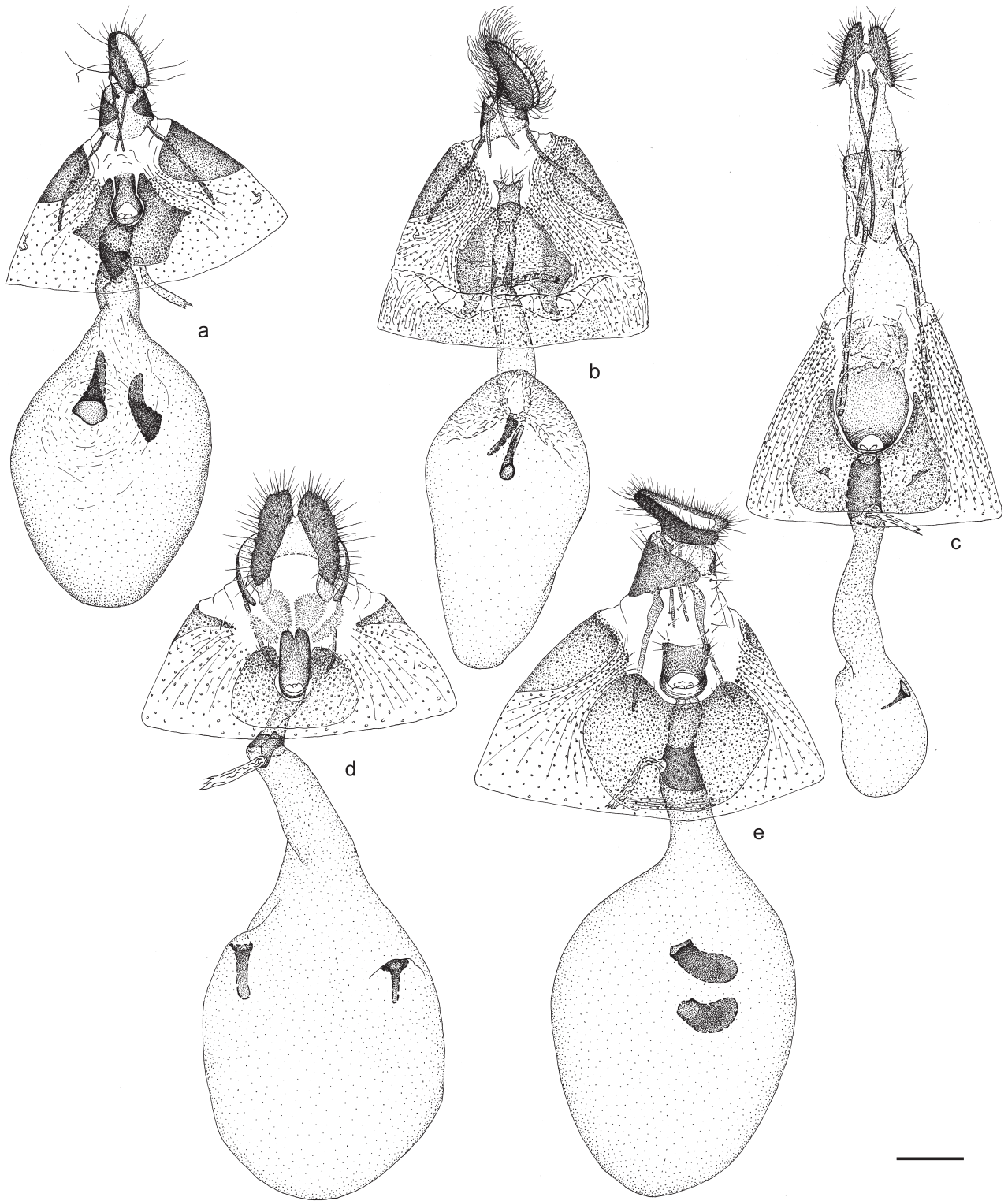
Fig. 4. Female genitalia. (a) *Eucosma circulana*; (b) *Pelochrista rorana*; (c) *Eucopina bobana*; (d) *Phaneta pauperana*; (e) *Epiblema foenella*. Scale bar: 0.5mm.
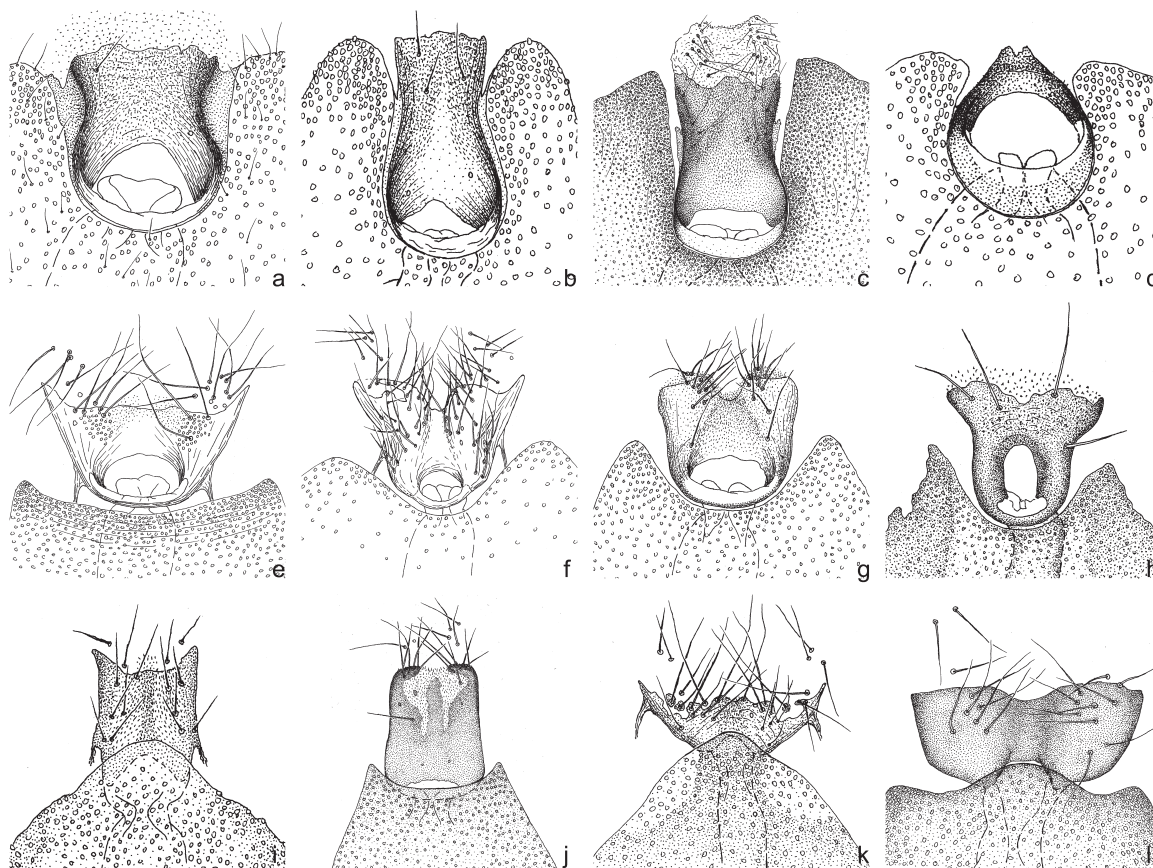
Fig. 5. Female sterigmata. Type 1: (a) *Eucosma umbrastriana*; (b) *E. raracana*; (c) *E. bipunctella*; (d) *E. castrensis*. Type 2: (e) *Pelochrista caniceps*; (f) *P. agassizii*; (g) *P. optimana*; (h) *P. pulveratana*. Type 3: (i) *P. rorana*; (j) *P. mancipiana*; (k) *P. robinsonana*; (l) *P. lafontainei*.

monophyletic group, resolved in the same polytomy as the two *Eucosma* + *Phaneta*/*Eucosma* + *Pelochrista* clades, and hence see no reason to modify the circumscription of *Epiblema* based on these results. In the few *Epiblema* where the clasper is reduced or absent, females can be separated by sterigma type (as described below): type 2 in *Epiblema*, type 1 in *Eucosma*.

Pelochrista has been characterized by the presence of a basally projecting lobe on the distal margin of the basal excavation of the male valva, often referred to as a 'pulvinus' (Obraztsov, 1967; Razowski, 1989, 2003). The term 'pulvinus' for this structure in Eucosmini is incorrect; Horak (1984) defines pulvinus as a 'bristled pad at the base of the valva' found in Tortricinae but absent in Olethreutinae outside of Microcorsini. To avoid confusion and implied homology with the pulvinus *sensu* Horak (1984), we suggest referring to this structure in Eucosmini as the 'basal process' of the valva. In the genera included in this study, this process is variable, ranging from absent to strongly developed. It serves better as a species-level character, as it is strongly developed in many of the *Eucosma* + *Pelochrista* species.

On at least one occasion (Wright, 2011), the basal process of the valva has been interpreted as a 'clasper' in *Eucosma* and *Pelochrista*, but the two structures are present simultaneously in some *Epiblema*, inferring that they are not homologous

(e.g. Gilligan *et al.*, 2008, species 185). In these species, the process is located on the margin of the basal excavation ventrad to the clasper. A similar arrangement occurs in some *Notocelia* (Gilligan *et al.*, 2008, species 198), and the single representative this genus included here is resolved as sister to the polytomy containing *Eucosma*, *Phaneta*, *Pelochrista* and *Epiblema*. It is possible that the clasper is a symplesiomorphy for this group and has been lost in the two *Eucosma* + *Phaneta*/*Eucosma* + *Pelochrista* clades, although the *Notocelia* sister-group relationship to these other genera is weakly supported (57% JK/ < 50% BS). A pair of nondeciduous cornuti in the male vesica distinguishes *Notocelia* from *Epiblema* (Gilligan *et al.*, 2008).

In North America, *Pelochrista* has at times been separated from *Eucosma* by the presence of a large spiniform seta ('spike') on the ventral margin of either the valval neck or the anal angle of the cucullus (Wright, 2007, 2008). This character is also variable, but such 'spikes' are present in the *Eucosma* + *Pelochrista* clade and absent from the *Eucosma* + *Phaneta* clade. Some species in the *Eucosma* + *Phaneta* clade do have one or more spiniform setae at the apex of the anal angle, but the seta or setae are always accompanied by a cluster of setae of nearly the same size on the medial surface of the cucullus. We suggest that a large

isolated spiniform seta or a small group of such setae on the margin of the male valva may be a synapomorphy for the *Eucosma + Pelochrista* clade and that the absence of this character in many of those species may be the result of a secondary loss. A forewing costal fold is present in all of the *Eucosma* and *Pelochrista* and absent (by definition) in all of the *Phaneta* included in this study. Thus, presence of this character state supports the *Eucosma + Pelochrista* clade and conflicts with the *Eucosma + Phaneta* grouping.

Female characters, specifically the structure of the sterigma and its relationship to sternum VII, are more congruent than male characters among the ingroup taxa in the simultaneous analysis tree. Razowski (2003) hinted at the importance of the sterigma, stating that North American *Phaneta* could be 'characterized chiefly by a short sterigma terminating at the level of the posterior parts of subgenital sternite'. The sterigmata in *Eucosma*, *Pelochrista* and *Phaneta* can be divided into three types: (1) lamella postvaginalis rectangular, lamella antevaginalis ring-like, posterior margin of sternum VII deeply emarginated (usually to full length of sterigma) and approximate to or fused with lateral margins of lamella postvaginalis; (2) lamella postvaginalis well developed and variable in shape, posterior margin of sternum VII diverging laterally from sterigma and separated from ostium by ring-like lamella antevaginalis; and (3) lamella postvaginalis well developed and variable in shape, lamella antevaginalis absent, anterior margin of ostium fused with sternum VII. The three types are illustrated and mapped onto the simultaneous analysis tree in Fig. 1. Type 1 is a synapomorphy for members of the *Eucosma + Phaneta* clade, whereas type 2 or 3 occurs in each member of the *Eucosma + Pelochrista* clade (and in other genera). Additional illustrations are provided in Figs 4 and 5. A possible synapomorphy for species in the *Eucosma + Pelochrista* clade is the presence of hook-tipped setae arising from the female papillae anales. These setae are presumed to be used to prepare the substrate for oviposition and are not present in any species in the *Eucosma + Phaneta* clade.

Although not included in this study, we are confident, based on the long tapering laterally sclerotized socii in the male and the microspinulate pads on the postsegmental membrane in the female, that the type species of *Phaneta* (*P. pauperana*) is not congeneric with North American *Phaneta*. Because the type of *E. circulana* (the type species of *Eucosma*) shares the same female morphology (e.g. sterigma type (1) as North American *Phaneta*, and these taxa are resolved in the same well-supported (92% JK/75% BS) clade, we transfer all of these species into *Eucosma* and redefine the genus using these characters (redescription below).

The clade of *Eucosma + Pelochrista* includes many species that would be considered *Pelochrista* in both North America and Europe. All taxa in this clade are characterized by the female having sterigma type 2 or 3. Sterigma type 2 is likely plesiomorphic within the Eucosmini, and the two sterigma types do not segregate into separate lineages within *Pelochrista*. Other distinguishing characters include the presence of hook-tipped setae on the female papillae anales and spiniform setae on the margin of the male valva. Additional

taxon sampling is needed to adequately resolve intrageneric relationships, as is evident by the varying levels of support for groups within the genus, and by the low support values (< 50% JK/65% BS) for the *Pelochrista* clade itself. Higher support (69% JK/82% BS) is found for the clade that contains all *Eucosma + Pelochrista* species except *Eucosma similiana*, *E. derelicta* and *E. conspiciendana*, but the latter three species do not differ morphologically from the rest of the genus. Future studies may allow for division of *Pelochrista* into two or more genera, but in the interim we transfer all *Eucosma* with sterigma type 2 or 3 to *Pelochrista* and redescribe the genus using this character (redescription below).

Generic descriptions and redescriptions

Eucosma Hübner

(Figs 2a–d, 3a, 4a, 5a–d)
Eucosma Hübner, 1823, Zutr. Samml. exot. Schmett. 2: 28. Type species: *Tortrix circulana* Hübner, 1823.
Affa Walker, 1863, List Specimens lepid. Insects Colln. Br. Mus. 27: 202. Type species: *Affa bipunctella* Walker, 1863.
Ascelodes Fletcher, 1929, Mem. Dep. Agric. India (Ent.) 11: 25; nomen nudum.
Calosetia Stainton, 1859, Man. Br. Butterflies Moths 2: 271. Type species: *Tortrix nigromaculana* Haworth, [1811].
Catoptria Guenée, 1845, Annls Soc. ent. Fr (2) 3: 187. Type species: *Tortrix cana* Haworth, [1811]; preoccupied by *Catoptria* Hübner [1825], Pyralidae. [corrected from Gilligan *et al.*, 2012]
Exentera Grote, 1877, Can. Ent. 9: 227. Type species: *Exentera apriliana* Grote, 1877.
Exenterella Grote, 1883, Can. Ent. 15: 23; unnecessary replacement name for *Exentera*.
Ioplocama Clemens, 1860, Proc. Acad. Nat. Sci.Philad. 12: 360. Type species: *Ioplocama formosana* Clemens, 1860; **syn.n.**
Palpocrinia Kennel, 1919, Mitt. mnch. ent. Ges. 8: 66. Type species: *Palpocrinia ottoniana* Kennel, 1919.

Diagnosis. Eucosma is separated from *Epiblema*, *Eucopina*, *Pelochrista* and *Phaneta* by the following combination of female character states: lamella postvaginalis rectangular, lamella antevaginalis ring-like, posterior margin of sternum VII deeply emarginated and approximate to or fused with lateral margins of lamella postvaginalis. *Eucosma* females have laterally facing papillae anales that lack hook-tipped setae, and most species have two signa of nearly equal size in the corpus bursae. Male character states do not reliably diagnose *Eucosma* species, but most males lack the large spiniform seta on the anal angle of the cucullus (present in many *Pelochrista* species) as well as the clasper on the distal margin of the basal excavation (present in most *Epiblema* species).

Wings. Forewing with R_4 and R_5 separate, M_2 and M_3 separate, chorda weak; male costal fold present (occasionally) or absent (usually), maculation variable but usually including a

well-developed ocellus. Hindwing with R_s and M_1 approximate, M_2 and M_3 approximate, M_3 and Cu_1 stalked or united.

Male genitalia. Uncus weakly to moderately developed, usually well differentiated from dorsolateral shoulders of tegumen, with apical margin rounded or medially indented; socii finger-like and setose; phallus stout, often tapering distally; caulis short; vesica with cluster of long deciduous cornuti; valva with costal margin moderately concave to nearly straight, neck well-defined, ventral margin broadly to deeply emarginate, distal margin of basal excavation sometimes with weakly developed basal process, saccular corner usually angulate and obtuse to slightly acute; cucullus with medial surface densely setose, apex rounded and weakly to moderately produced, distal margin convex, anal angle weakly to strongly developed and occasionally with cluster of spiniform setae extending onto medial surface.

Female genitalia. Papillae anales usually flat, laterally facing, sparsely to densely setose, without ventral extensions; lamella postvaginalis usually rectangular; lamella antevaginalis ring-like; posterior margin of sternum VII deeply emarginated (usually to full length of sterigma) and approximate to or fused with lateral margins of lamella postvaginalis; ductus bursae with sclerotized ring approximate to juncture with ductus seminalis; corpus bursae with two well-developed signa, usually of nearly equal size.

Biology. Larvae feed almost exclusively on Asteraceae. Feeding behaviours include webbing of terminal leaves (particularly in early instars) and boring into seeds, flower heads, stems and roots. Many species appear to be univoltine, with adults present between mid-April and mid-October.

Distribution. Approximately 230 species are currently included, all from the Holarctic.

PELOCHRISTA Lederer

(Figs 2e–h, 3b, 4b, 5e–l)
Pelochrista Lederer, 1859, Wien. ent. Monatschr. 3: 331. Type species: *Paedisca mancipiana* Mann, 1855.
Callimosema Clemens, 1865, Proc. ent. Soc. Philad.5 141. Type species: *Callimosema scintillana* Clemens, 1865.
Eucosmoides Obraztsov, 1946, Z. Wien. ent. Ges. 30: 38. Type species: *Paedisca decolorana* Freyer, 1842.
Pseudeucosma Obraztsov, 1946, Z. Wien. ent. Ges. 30: 37. Type species: *Tortrix caecimaculana* Hübner, [1776–1799].
Pygolopha Lederer, 1859, Wien. ent. Monatschr. 3: 123. Type species: *Pygolopha trinacriana* Lederer, 1859; **syn.n.**

Diagnosis. *Pelochrista* differs from *Eucosma* in female sterigma structure. In *Pelochrista* the sterigma is present in two forms: posterior margin of sternum VII diverging laterally from sterigma and separated from ostium by ring-like lamella antevaginalis (type 2), or lamella antevaginalis absent and anterior margin of ostium fused with sternum VII (type 3). Some *Pelochrista* females have hook-tipped setae arising from the papillae anales, usually on the anterior lobes and along the margins of the anal opening. Frequently the papillae anales

have ventrally facing posterior lobes and ventrally developed anterior lobes that face laterally and flank the anal opening, the latter referred to as ventral extensions. No characters have been identified that consistently separate males of the two genera, but many *Pelochrista* have a large isolated spiniform seta on the anal angle of the cucullus or on the ventral margin of the valval neck, a feature that is lacking in *Eucosma*. Details for separating *Pelochrista* from *Epiblema*, *Eucopina* and *Phaneta* are found under those generic descriptions.

Wings. Forewing with costal fold in males, venation as in *Eucosma*, maculation variable. Hindwing venation as in *Eucosma*, with M_3 and Cu_1 usually stalked.

Male genitalia. Uncus as in *Eucosma*; socii finger-like, moderately elongate and setose; phallus stout to elongate, tapering distally, caulis often elongate; vesica with or without cornuti; valva with costal margin concave to nearly straight, neck usually well defined, ventral margin straight to deeply emarginated; distal margin of basal excavation often with weakly to strongly developed basal process; saccular corner angulate and nearly straight to strongly acute; cucullus with medial surface densely setose, apex variably produced and usually rounded, distal margin convex, anal angle variably developed; distal margin of cucullus and/or ventral margin of neck often with spiniform setae; margin of anal angle often with one or more large spiniform setae near vertex.

Female genitalia. Papillae anales moderately to densely setose, laterally facing and flat to ventrally facing with ventral extensions, often with hook-tipped setae on distal extremities of anterior lobes and/or margins of anal opening; lamella postvaginalis well developed, variable in shape; posterior margin of sternum VII diverging laterally from sterigma and separated from this by ring-like lamella antevaginalis or fused with anterior margin of ostium, with lamella antevaginalis absent; ductus bursae usually with sclerotized ring or patch approximate to juncture with ductus seminalis; corpus bursae usually with two signa of unequal size, infrequently with one or none, sometimes with sclerotization of the membrane adjacent to the smaller signum.

Biology. Larval biology as in *Eucosma*.

Distribution. Approximately 200 named species, all from the Holarctic Region.

EUCOPINA Gilligan & Wright, *gen.n.*

(Figs 2i–l, 3c, 4c)
Type species: *Eucosma bobana* Kearfott, 1907

Diagnosis. *Eucopina* is distinguished from other genera treated here by the following genitalic characters: ovipositor long and telescoping, with papillae anales flat and ventrally facing; valva with ridge on medial surface at base of neck; cucullus with strongly developed ventral lobe overlapping ventral margin of neck and with several short spiniform setae along distal margin. Presence of a forewing costal fold separates *Eucopina* males from those of similar looking Pinaceae-feeding olethreutines in the genera *Rhyacionia* and

Retinia, as does genitalic structure (illustrations in Gilligan *et al.*, 2008).

Wings. Venation as in *Pelochrista*; males with a forewing costal fold. Forewing pattern uniform, with orange to red fasciate markings and silver, grey, white, orange or tan interfascial areas.

Male genitalia. Uncus weakly to moderately developed, well differentiated from dorsolateral shoulders of tegumen, semitriangular, often with medial indentation at apex; socii finger-like, moderately setose; phallus moderately long and narrow, tapering distally; vesica lacking cornuti; valva with costal margin weakly concave, neck well defined, transverse ridge on medial surface at base of neck (barely discernible in *E. gloriola* and *E. sonomana*), saccular corner obtusely angulate; cucullus with medial surface densely setose, apex rounded and strongly produced, distal margin convex, anal angle well developed and strongly overlapping distal end of neck; distal margin of cucullus with series of uniformly spaced spiniform setae extending from anal angle nearly to apex.

Female genitalia. Papillae anales small, flat, semitriangular, ventrally facing; apophyses anteriores and posteriores long; tergum VIII long, relatively narrow, and semirectangular; sterigma largely plate-like, semirectangular to ovate; lamella antevaginalis ring-like; sternum VII with posterior margin roundly invaginated to 1/2 to 3/4 length of sterigma, lateral and anterior margins strongly sclerotized, median area weakly sclerotized; ductus bursae elongate, often with posterior extremity sclerotized; corpus bursae with one thorn-like signum.

Biology. Larvae feed on *Abies*, *Picea*, *Pinus* and *Pseudotsuga* (Pinaceae). Those of *E. gloriola* and *E. sonomana* bore into shoots and stems; in the other species they bore into cones and feed on seeds (Powell, 1968).

Distribution. Twelve species are described, all from the Nearctic Region.

Etymology. The generic name is derived from 'Euco + pina', referring to *Eucosma* as the former genus and Pinaceae as the larval host.

Species included. *Eucopina bobana* (Kearfott) **comb.n.**; *E. cocana* (Kearfott) **comb.n.**; *E. crymalana* (Powell) **comb.n.**; *E. franclemonti* (Powell) **comb.n.**; *E. gloriola* (Heinrich) **comb.n.**; *E. monitorana* (Heinrich) **comb.n.**; *E. monoensis* (Powell) **comb.n.**; *E. ponderosa* (Powell) **comb.n.**; *E. rescissoriana* (Heinrich) **comb.n.**; *E. siskiyouana* (Kearfott) **comb.n.**; *E. sonomana* (Kearfott) **comb.n.**; *E. tocullionana* (Heinrich) **comb.n**.

Remarks. Included in the analysis are two specimens of an *Eucopina* species 'near *bobana*' from southeastern Wyoming. They were not collected near pinyon pine, the larval host of *E. bobana*, and they are larger than most *E. bobana* in collections. They could represent a new species or simply a population of *E. bobana* that has expanded its host range onto other species of pine.

PHANETA Stephens

(Figs 2m, 3d, 4d)

Phaneta Stephens, 1852, List Specimens Br. Animals Colln. Br. Mus. 10: 32. Type species: *Cochylis pauperana* Duponchel, 1842.

Astenodes Kuznetzov, 1966, Trudy Zool. Inst. Leningrad 37: 196. Type species: *Astenodes bimaculata* Kuznetzov, 1966.

Diagnosis. *Phaneta* is distinguished from the other genera treated here by the long, tapering, laterally sclerotized socii in males and the microspinulate pads on the postsegmental membrane in females.

Wings. Venation as in *Eucosma*; forewing greyish brown with dark brown fasciate markings, lacking a costal fold in males.

Male genitalia. Uncus undeveloped; socius long, tapering to sharply pointed apex, laterally sclerotized, with medial surface setose; phallus short, tapering distally; vesica with deciduous cornuti; valva with costal margin weakly concave, neck short, broad and weakly defined, saccular corner obtusely angulate; cucullus with dorsal projection strongly developed and tapering toward rounded apex, distal margin weakly concave, anal angle broadly rounded; medial surface of cucullus with small stout setae along margin of anal angle and a submarginal band of long stout setae extending from anal angle nearly to apex.

Female genitalia. Papillae anales flat, ventrally facing, moderately setose, without ventral extensions; apophyses posteriores fused basally; postsegmental membrane with two pairs of blister-like microspinulate pads; lamella postvaginalis semirectangular, microspinulate, with posterior margin divided into two semicircular lobes; lamella antevaginalis ring-like; posterior margin of sternum VII emarginated to about three fourths length of sterigma, closely approximate to lateral margins of lamella postvaginalis, but separated from lamella antevaginalis by membranous band; ductus bursae with sclerotized ring at juncture with ductus seminalis; corpus bursae with two signa of unequal size.

Biology. Larvae feed in buds, fruit and flowers of *Rosa* (Rosaceae). Pupation occurs in webbed leaves on the ground. There is one generation per year, with adults in April and May (Razowski, 2003).

Distribution. As revised, *Phaneta* consists of two species, both from the Palearctic. *Phaneta pauperana* is found from western Europe to Asia Minor (Razowski, 2003), and *P. bimaculata* is recorded from Europe, Russia, China and Japan (Zhang & Li, 2005).

EPIBLEMA Hübner

(Figs 2n–p, 3e, 4e)

Epiblema Hübner, [1825] 1816, Verz. bekannter Schmett. 375. Type species: *Phalaena* (*Tinea*) *foenella* Linnaeus, 1758.

Cacochroea Lederer, 1859, Wien. ent. Monatschr. 3: 331. Type species: *Paedisca grandaevana* Lienig & Zeller, 1846.

Epiblemma Hübner, [1825] 1816, Verz. bekannter Schmett. 63; misspelling of *Epiblema*.

Euryptychia Clemens, 1865, Proc. ent. Soc. Philad. 5: 140. Type species: *Euryptychia saligneana* Clemens, 1865.

Eurytychia Heinrich, 1923, Bull. U.S. natn. Mus. 123: 137; misspelling of *Euryptychia*.

Monosphragis Clemens, 1860, Proc. Acad. Nat. Sci. Philad. 12: 354. Type species: *Monosphragis otiosana* Clemens, 1860.

Diagnosis. Most *Epiblema* species are distinguished by the presence of a prominent clasper on the distal margin of the basal excavation of the male valva. In the few species in which this structure is reduced or absent, the male genitalia resemble those of *Eucosma*, but the females differ from *Eucosma* in sterigma type (type 2 rather than type 1).

Wings. Venation as in *Eucosma*; males with a forewing costal fold. Many species have a conspicuous interfascial spot on the dorsal margin of the forewing between the subbasal and median fasciae.

Male genitalia. Uncus weakly to moderately developed, often rounded apically, sometimes with shallow medial indentation, usually well differentiated from dorsolateral shoulders of tegumen; socii finger-like and setose; phallus stout, tapering distally; caulis short; vesica with cluster of long deciduous cornuti; valva with costal margin concave, neck well defined, ventral margin moderately emarginated to nearly straight, distal margin of basal excavation usually with prominent tetrahedron-shaped clasper and often with weakly developed basal process; saccular corner angulate to absent, obtuse when present; cucullus with apex rounded and strongly produced, distal margin weakly to moderately convex and frequently with series of short stout setae extending from anal angle to about 3/4 distance to apex, anal angle well developed and lacking large spiniform setae at vertex.

Female genitalia. Papillae anales moderately to densely setose, ventrally facing along margins of anal opening, laterally facing otherwise, lacking ventral extensions; sterigma semirectangular to ovate; posterior margin of sternum VII diverging laterally from sterigma and separated from ostium by ring-like lamella antevaginalis; ductus bursae often with sclerotized ring approximate to juncture with ductus seminalis; corpus bursae sometimes with one signum, usually with two of unequal size.

Biology. Larvae are stem- or root-borers in Asteraceae. Pupation occurs in the spring, often in an elongate gall. Adults fly from late April to September.

Distribution. Holarctic, with approximately 90 species described.

Remarks. The only identified synapomorphy for *Epiblema* is the clasper on the male valva.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12036

Appendix S1. The complete data matrix used for the phylogenetic analysis (in Nexus format).

Figure S1. Parsimony strict consensus gene tree for *28S* rDNA. Parsimony JK values are above each branch and likelihood BS values are below each branch.

Figure S2. Parsimony strict consensus gene tree for *COI*. Parsimony JK values are above each branch and likelihood BS values are below each branch.

Figure S3. Parsimony strict consensus gene tree for *EF-1a*. Parsimony JK values are above each branch and likelihood BS values are below each branch.

Figure S4. Parsimony strict consensus gene tree for *CAD*. Parsimony JK values are above each branch and likelihood BS values are below each branch.

Figure S5. Combined molecular maximum likelihood tree showing relative branch lengths.

Acknowledgements

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Appendix 1: List of taxa sampled with taxonomic authorities, voucher information and GenBank accession numbers for DNA sequences.

Collogenes albocingulata: TORTAG-TMG-533, Australia, 2009, T. M. Gilligan, det. T. M. Gilligan & M. Horak; CAD KC430409, COI KC430464; *Cryptaspasma brachyptycha*: ANIC DNA 002783, Australia, M. Horak, det. M. Horak;

CAD KC430410, COI KC430465, EF-1α KC430546; *Cryptaspasma sordida*: TOR-DNA-382, Australia, 2009, T. M. Gilligan, det. T. M. Gilligan & M. Horak; 28S rDNA KC430336, COI KC430466, EF-1α KC430547; *Dactylioglypha* **sp.**: TOR-DNA-582, Australia, 2009, T. M. Gilligan, det. T. M. Gilligan & M. Horak; 28S rDNA KC430337, CAD KC430411, COI KC430467, EF-1α KC430548; *Metrioglypha* **sp.**: TOR-DNA-581, Australia, 2009, T. M. Gilligan, det. T. M. Gilligan & M. Horak; 28S rDNA KC430338, CAD KC430412, COI KC430468, EF-1α KC430549; *Fibuloides japonica*: SWC-07-2037, Korea, det. C. Soowon & J. Sohn; 28S rDNA KC430339, COI KC430469, EF-1α KC430550; *Sonia paraplesiana*: TOR-DNA-0254, AL: Baldwin Co., Weeks Bay, 21 June 2008, Gilligan, Wright, Gibson, det. T. M. Gilligan; 28S rDNA KC430340, CAD KC430413, COI KC430470, EF-1α KC430551; *Rhopobota dietziana*: TOR-DNA-0257, MS: Oktibbeha Co., 27 June 2008, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430341, CAD KC430414, COI KC430471, EF-1α KC430552; *Rhyacionia pinivorana*: TOR-DNA-0425, Spain, Castello, Parc Natural de Penyagolosa, 22 June 2009, Gilligan, Baixeras, det. T. M. Gilligan & J. Baixeras; 28S rDNA KC430342, CAD KC430415, COI KC430472, EF-1α KC430553; *Notocelia culminana*: TOR-DNA-0512, OH: Hancock Co., 31 August 2009, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430343, CAD KC430416, COI KC430473, EF-1α KC430554; *Thiodia citrana*: TORTAG-TMG-101, Spain: Parc Natural de Penyagolosa, 22 June 2009, T. M. Gilligan, J. Baixeras, det. T. M. Gilligan; COI KC430474, EF-1α KC430555; *Epiblema foenella*: KTP-06-0124-6, Korea, det. Park & Kyu Tek; 28S rDNA KC430344, CAD KC430417, COI KC430475, EF-1α KC430556; *Epiblema abruptana*, KTP-94-0521, USA, det. Park & Kyu Tek; 28S rDNA KC430345, COI KC430476; *Epiblema otiosana*: TOR-06-0032, OH: Wyandot Co., Killdeer WLA, 16 August 2006, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430346, CAD KC430418, COI KC430477, EF-1α KC430557; *Epiblema carolinana*: TOR-06-0079, KY: Gallatin Co., Markland Dam, 13 August 2006, L. D. Gibson, det. L. D. Gibson; 28S rDNA KC430347, CAD KC430419, COI KC430478, EF-1α KC430558; *Epiblema gibsoni*: TOR-06-0093, KY: Larue Co., Cecil Ridge, 4 mi. W of New Haven, 31 July 2006, L. D. Gibson, det. L. D. Gibson; 28S rDNA KC430348, COI KC430479, EF-1α KC430559; *Epiblema strenuana*: TOR-DNA-511, OH: Hancock Co., 16 August 2009, T. M. Gilligan, det. T. M. Gilligan; COI KC430480, EF-1α KC430560; *Eucosma bobana*: TOR-DNA-218, WA: Chelan Co., 10 mi. NE Leavenworth, 8 July 2010, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430349, CAD KC430420, COI KC430481, EF-1α KC430561; *Eucosma siskiyouana*, TOR-DNA-222, WA: Chelan Co., 10 mi. NE Leavenworth, 9 July 2010, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430350, CAD KC430421, COI KC430482, EF-1α KC430562; *Eucosma* **nr.** *bobana*: TOR-DNA-0632, Albany Co., WY, south of Happy Jack Rd, NE of Pole Mt, 12 June 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430351, CAD KC430422, COI KC430483, EF-1α KC430563; *Eucosma* **nr.** *bobana*: TOR-DNA-0646, Albany Co, just north of Rd 726, 1 July 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430352, COI KC430484, EF-1α KC430564; *Eucosma sonomana*: TOR-DNA-0633, Albany Co., WY, just SW of road 712H off Happy Jack Rd, 13 June 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430353, CAD KC430423, COI KC430485, EF-1α KC430565; *Eucosma morrisoni*: DJW-06-0002 WY: Albany Co., 6 July 2006, D. J. Wright, det. D. J. Wright; 28S rDNA KC430354, CAD KC430424, COI KC430486, EF-1α KC430566; *Eucosma caniceps*: TOR-06-0007, UT: Sanpete Co., Ephraim Canyon, 20 July 2006, T. M. Gilligan, det. T. M. Gilligan & D. J. Wright; 28S rDNA KC430355, CAD KC430425, COI KC430487, EF-1α KC430567; *Eucosma caniceps*: TOR-DNA-0663, Albany Co. west of Woods Landing, Hyw 130, 30 July 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430356, CAD KC430426, COI KC430488, EF-1α KC430568; *Eucosma maculatana*: DJW-06-0012, ID: Oneida Co., 15 July 2006, D. J. Wright, det. D. J. Wright; 28S rDNA KC430357, COI KC430489; *Eucosma sombreana*: TOR-06-0022, OH: Wyandot Co., Killdeer WLA, 16 August 2006, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430358, CAD KC430427, COI KC430490, EF-1α KC430569; *Eucosma derelicta*: DJW-06-0026, OH: Wyandot Co., Killdeer WLA, 16 August 2006, D. J. Wright, det. D. J. Wright; 28S rDNA KC430359, CAD KC430428, COI KC430491, EF-1α KC430570; *Eucosma circulana*: TOR-06-0098, KY: McCracken Co., Paducah, Littleville zip track, 27 June 2008, L. D. Gibson, det. L. D. Gibson; 28S rDNA KC430360, CAD KC430429, COI KC430492, EF-1α KC430571; *Eucosma metzneriana*: TORTAG-TMG-175, Romania: Cluj, 26 May 2009, T. M. Gilligan & J. Powell, det. T. M. Gilligan; COI KC430493; *Eucosma serpentana*: TOR-DNA-0203, MT: Custer Co., 2.5 mi. S. Miles City, 12 July 2010, D. J. Wright, det. D. J. Wright; 28S rDNA KC430361, CAD KC430430, COI KC430494, EF-1α KC430572; *Eucosma agricolana*: TOR-DNA-0205, WA: Chelan Co., FR 7520, N of Eagle Cr. Rd., 9 July 2010, D. J. Wright, det. D. J. Wright; 28S rDNA KC430362, CAD KC430431, COI KC430495, EF-1α KC430573; *Eucosma agricolana*: TOR-DNA-221, WA: Chelan Co., 10 mi. NE Leavenworth, 8 July 2010, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430363, CAD KC430432, COI KC430496, EF-1α KC430574; *Eucosma agricolana*: TOR-DNA-0635, Albany Co., WY, 2217 Sky View Lane, 22 June 2011, J. Nordin det. J. Nordin & D. J. Wright; 28S rDNA KC430364, CAD KC430433, COI KC430497, EF-1α KC430575; *Eucosma subflavana*: TOR-DNA-0206, WA: Chelan Co., FR 7520, N of Eagle Cr. Rd., 9 July 2010, D. J. Wright, det. D. J. Wright; 28S rDNA KC430365, COI KC430498, EF-1α KC430576; *Eucosma biquadrana*: TOR-DNA-0209, WA: Chelan Co., FR 7520, N of Eagle Cr. Rd., 9 July 2010, D. J. Wright, det. D. J. Wright; 28S rDNA KC430366, CAD KC430434, COI KC430499, EF-1α KC430577; *Eucosma denverana*: TOR-DNA-404, CO: Cheyenne Co., Wild Horse, post office, 11 August 2009, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430367, COI KC430500, EF-1α KC430578; *Eucosma*

ridingsana: TOR-DNA-468, CO: Lincoln Co., Hugo, hospital, 11 August 2009, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430368, CAD KC430435, COI KC430501, EF-1α KC430579; *Eucosma ridingsana*: TOR-DNA-0676, Albany Co., WY, 2217 Sky View Lane, 18 August 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430369, COI KC430502, EF-1α KC430580; *Eucosma pulveratana*: TOR-DNA-476, CO: Cheyenne Co., Wild Horse, post office, 11 August 2009, T. M. Gilligan, det. T. M. Gilligan & D. J. Wright; COI KC430503, EF-1α KC430581; *Eucosma similiana*: TOR-DNA-0513, OH: Hancock Co., 31 August 2009, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430370, CAD KC430436, COI KC430504, EF-1α KC430582; *Eucosma giganteana*: TOR-DNA-0574, MS: Oktibbeha Co., 24 June 2008, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430371, CAD KC430437, COI KC430505; *Eucosma conterminana*: TOR-DNA-0579, France: Mormoiron, 17 June 2009, T. M. Gilligan, det. J. Baixeras & T. M. Gilligan; 28S rDNA KC430372, CAD KC430438, COI KC430506, EF-1α KC430583; *Eucosma snyderana*: TOR-DNA-0634, Albany Co., WY, 2217 Sky View Lane, 22 June 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430373, CAD KC430439, COI KC430507, EF-1α KC430584; *Eucosma conspiciendana*: TOR-DNA-0649, Albany Co., WY, just west of Gelatt Lake, 3 July 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430374, CAD KC430440, COI KC430508, EF-1α KC430585; *Eucosma smithiana*: TOR-DNA-0653, Albany Co., WY, 2217 Sky View Lane, 6 July 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430375, CAD KC430441, COI KC430509, EF-1α KC430586; *Eucosma canariana*: TOR-DNA-0664, Albany Co. west of Woods Landing, Hyw 130, 30 July 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430376, CAD KC430442, COI KC430510, EF-1α KC430587; *Eucosma ragonoti*: TOR-DNA-0665, Albany Co., WY, 2217 Sky View Lane, 30 July 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430377, CAD KC430443, COI KC430511, EF-1α KC430588; *Eucosma crambitana*: TOR-DNA-0667, Albany Co., WY, 2217 Sky View Lane, 4 August 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430378, CAD KC430444, COI KC430512, EF-1α KC430589; *Eucosma totana*: TOR-DNA-0668, Albany Co. 1.1 miles west of Woods Landing, 5 August 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430379, CAD KC430445, COI KC430513, EF-1α KC430590; *Eucosma fernaldana*: TOR-DNA-0675, Albany Co., WY, 2217 Sky View Lane, 18 August 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430380, CAD KC430446, COI KC430514, EF-1α KC430591; *Eucosma optimana*: TOR-DNA-0680, Albany Co just north of Rd 726, 22 August 2011 J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430381, COI KC430515, EF-1α KC430592; *Eucosma robinsonana*: JD0726, FLA: Marion Co.: Ocala National Forest, 21 June 2006, J. J. Dombroskie, et al., det. J. J. Dombroskie; 28S rDNA KC430382, CAD KC430447, COI KC430516, EF-1α KC430593; *Phaneta griseocapitana*: DJW-06-0003, WY: Albany Co., 6 July 2006, D. J. Wright, det. D. J. Wright; 28S rDNA KC430383, COI KC430517, EF-1α KC430594; *Phaneta griseocapitana*: TOR-DNA-0657, Albany Co., WY, 2217 Sky View Lane, 18 July 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430384, COI KC430518, EF-1α KC430595; *Phaneta pallidarcis*: DJW-06-0005, ID: Oneida Co., 9 July 2006, D. J. Wright, det. D. J. Wright; 28S rDNA KC430385, CAD KC430448, COI KC430519, EF-1α KC430596; *Phaneta castrensis*: DJW-06-0008, ID: Oneida Co., 15 July 2006, D. J. Wright, det. D. J. Wright; 28S rDNA KC430386, COI KC430520; *Phaneta ochrocephala*: TOR-06-0028, OH: Wyandot Co., Killdeer WLA, 16 August 2006, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430387, CAD KC430449, COI KC430521, EF-1α KC430597; *Phaneta tarandana* (group): JD2117, Canada: AB: Kootenay Plains, near Whirlpool Point, 30 May 2007, J. J. Dombroskie, det. J. J. Dombroskie; 28S rDNA KC430388, CAD KC430450, COI KC430522, EF-1α KC430598; *Phaneta tarandana*, TOR-DNA-0685, Albany Co., WY, 2217 Sky View Lane, 24 August 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430389, CAD KC430451, COI KC430523, EF-1α KC430599; *Phaneta umbrastriana*: TOR-DNA-0258, MS: Oktibbeha Co., 27 June 2008, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430390, COI KC430524, EF-1α KC430600; *Phaneta indagatricana*: TOR-DNA-467, CO: Lincoln Co., Hugo, hospital, 11 August 2009, T. M. Gilligan, det. T. M. Gilligan & D. J. Wright; 28S rDNA KC430391, COI KC430525, EF-1α KC430601; *Phaneta modicellana*: TOR-DNA-611, CO: Weld Co., Pawnee Nat'l Grassland, 28 June 2010, T. M. Gilligan & D. J. Wright, det. T. M. Gilligan & D. J. Wright; CAD KC430452, COI KC430526, EF-1α KC430602; *Phaneta salmicolorana*: TOR-DNA-0659, Albany Co., WY, 2217 Sky View Lane, 20 July 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430392, CAD KC430453, COI KC430527, EF-1α KC430603; *Phaneta bucephaloides*: TOR-DNA-0669, Albany Co., WY, 2217 Sky View Lane, 6 August 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430393, CAD KC430454, COI KC430528; *Phaneta offectalis*: TOR-DNA-0691, Albany Co., WY, 2217 Sky View Lane, 4 September 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430394, COI KC430529, EF-1α KC430604; *Phaneta tenuiana*: TOR-DNA-0692, Albany Co. 1.1 miles west of Woods Landing, 10 September 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430395, CAD KC430455, COI KC430530; *Phaneta montanana*: JD0848, Canada: AB: Jasper N. P., Opal Mountain, 2263 m, 5 July 2006, J. J. Dombroskie & A. Rose, det. J. J. Dombroskie; 28S rDNA KC430396, COI KC430531, EF-1α KC430605; *Pelochrista ainsliei*: TOR-DNA-0202, MT: Custer Co., 2.5 mi. S. Miles City, 12 July 2010, D. J. Wright, det. D. J. Wright; 28S rDNA KC430397, CAD KC430456, COI KC430532, EF-1α KC430606; *Pelochrista mediostriata*: TOR-DNA-0207, MT: Custer Co., 2.5 mi. S. Miles City, 12 July 2010, D. J. Wright, det. D. J. Wright; 28S rDNA KC430398, CAD KC430457, COI KC430533, EF-1α KC430607; *Pelochrista daemonicana*: TOR-DNA-0365, NM: Colfax Co., 5 August 2008, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430399, CAD KC430458, COI KC430534; *Pelochrista corosana*:

TOR-DNA-401, CO: Cheyenne Co., Wild Horse, post office, 11 August 2009, T. M. Gilligan, det. T. M. Gilligan & D. J. Wright; 28S rDNA KC430400, COI KC430535, EF-1α KC430608; *Pelochrista scintillana*: TOR-DNA-498, IA: Adair Co., Rest Area, I-80 MM 80, 15 August 2009, T. M. Gilligan, det. T. M. Gilligan; COI KC430536, EF-1α KC430609; *Pelochrista rorana*: TOR-DNA-0575, CO: Cheyenne Co., 15 September 2007, T. M. Gilligan & C. E. Harp, det. D. J. Wright; 28S rDNA KC430401, CAD KC430459, COI KC430537, EF-1α KC430610; *Pelochrista rorana*: TOR-DNA-472 CO: Cheyenne Co., Kit Carson, church 11 August 2009 T. M. Gilligan det. T. M. Gilligan, D. J. Wright; 28S rDNA KC430407, COI KC430544, EF-1α KC430615; *Pelocrista popana*: TOR-DNA-0652, Albany Co., WY, 2217 Sky View Lane, 6 July 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430402, COI KC430538; *Pelochrista argenteana*: TOR-DNA-0201 MT: Custer Co., 2.5 mi. S. Miles City 12 July 2010 D. J. Wright det. D. J. Wright; 28S rDNA KC430403, CAD KC430460, COI KC430539, EF-1α KC4306011; *Pelochrista argenteana*: TOR-DNA-612, CO: Larimer Co., 12 mi. NNW Ft. Collins, Owl Canyon, 29 June 2010, T. M. Gilligan & D. J. Wright, det. T. M. Gilligan & D. J. Wright; COI KC430540, EF-1α KC430612; *Pelocrista argenteana*: TOR-DNA-0658, Albany Co., WY, 2217 Sky View Lane, 19 July 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430404, CAD KC430461, COI KC430541, EF-1α KC430613; *Pelochrista fuscosparsa*: TOR-DNA-0204, MT: Custer Co., 2.5 mi. S. Miles City, 12 July 2010, D. J. Wright, det. D. J. Wright; 28S rDNA KC430405, COI KC430542; *Pelocrista fuscosparsa*: TOR-DNA-0681, Albany Co., WY, 2217 Sky View Lane, 3 July 2011, J. Nordin, det. J. Nordin & D. J. Wright; 28S rDNA KC430406, CAD KC430462, COI KC430543, EF-1α KC430614; *Pelochrista mollitana*: TOR-DNA-0580, France: Sisteron, 14 June 2009, T. M. Gilligan, det. T. M. Gilligan; 28S rDNA KC430408, CAD KC430463, COI KC430545, EF-1α KC430616.

Appendix 2: Morphological characters and character states

FOREWING: 1. Male forewing costal fold presence: (0) absent; (1) present. **2**. Venation R$_4$ and R$_5$ divergence: (0) separate; (1) connate; (2) stalked; (3) fused. **HINDWING: 3**. Venation M$_3$-CuA$_1$ divergence: (0) connate; (1) stalked. **MALE GENITALIA: 4**. Uncus presence: (0) absent; (1) present. **5**. Uncus shape: (0) finger-like; (1) spatulate; (2) hump-shaped, often with distal margin medially indented; (3) distally bifid process; (4) with antenna-like processes. **6**. Uncus setation: (0) sparse; (1) moderate; (2) dense; (3) long apical tuft. **7**. Socii shape: (0) short, stubby; (1) finger-like; (2) lobe-like. **8**. Valva clasper presence: (0) absent; (1) present. **9**. Valva process other than costal process from above basal excavation presence: (0) absent; (1) present. **10**. Valva saccular angle: (0) acute; (1) ≈ 90°; (2) obtuse. **11**. Valva overlap of basoventral margin of cucullus on ventral margin of neck: (0) none to weak; (1) moderate to extensive. **12**. Valval setae on margin of cucullus/ventral margin of neck type: (0) filiform/standard; (1) 1 or few stout setae near distal end of neck; (2) 1 stout seta at apex of anal angle, sometimes with lesser setae on distal margin of cucullus; (3) series of stout setae on distal margin of cucullus, sometimes with two or three clustered at ventral apex. **13**. Valval neck with medial ridge presence: (0) absent; (1) present. **14**. Cornuti presence: (0) absent; (1) present. **FEMALE GENITALIA: 15**. Papillae anales size relative to length of sternum 7 + 8: (0) small; (1) medium; (2) large. **16**. Papillae anales orientation: (0) facing laterally; (1) facing ventrally; (2) posterior lobes facing ventrally, anterior lobes facing laterally (inc. ventral extensions). **17**. Papillae anales hook-tipped setae presence: (0) absent; (1) present. **18**. Length of apophyses anteriores versus length of apophyses posteriores: (0) longer; (1) approximately equal; (2) shorter. **19**. Tergum 8 shape: (0) narrow (medial width distinctly smaller than distance between bases of apophyses anteriores); (1) of moderate width (medial width ≈ distance between bases of apophyses anteriores); (2) broad (medial width distinctly larger than distance between bases of apophyses anteriores). **20**. Sterigma connected to apophyses anteriores: (0) no; (1) yes. **21**. Sterigma shape: (0) not differentiated; (1) tube or funnel; (2) plate-like; (3) raised rim; (4) projecting ventral lip. **22**. Sterigma, anterior margin of ostium structure: (0) separated from sternum 7 by lamella antevaginalis and/or band of membrane; (1) fused with sternum 7. **23**. Sterigma, posterior margin sternum 7 shape: (0) with U-shaped emargination, approximate to/fused laterally with sterigma; (1) concave, laterally diverging from sterigma; (2) straight to medially convex; (3) undifferentiated, sterigma entirely fused with sternum 7. **24**. Signa number: (0) one; (1) two. **25**. Signa size: (0) equal-sized; (1) of different sizes. **26**. Signa shape: (0) scobinate; (1) horn-shaped; (2) thorn- or blade-shaped. **27**. Juncture of ductus bursae and ductus seminalis location: (0) approximately midway between ostium and corpus bursae; (1) closer to ostium; (2) closer to corpus bursae.