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A molecular phylogeny and revised classification for the oldest ditrysian moth lineages (Lepidoptera: Tineoidea), with implications for ancestral feeding habits of the mega-diverse Ditrysia

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Abstract. The Tineoidea are the earliest-originating extant superfamily of the enormous clade Ditrysia, whose 152 000+ species make up 98% of the insect order Lepidoptera. Though more diverse than all non-ditrysian superfamilies put together (3719 vs 2604 species), the tineoids are not especially species-rich among ditrysian superfamilies. Their phylogenetic position, however, makes tineoids potentially important for understanding the causes of ditrysian hyperdiversity, through their effect on inferences about the traits of ancestral ditrysians. To reconstruct early ditrysian evolution, we need a firmly established ground plan for tineoids themselves, which in turn requires a robust knowledge of their biodiversity and phylogeny. Tineoid systematics is under-studied. The description of the world fauna remains very patchy, especially in the largest family, Tineidae, and phylogenetic studies within and among families have been few. Recently, molecular analyses have shown strong promise for advancing tineoid systematics. Here we present the largest tineoid molecular study to date, sampling five to 19 nuclear gene regions (6.6–14.7 kb) in 62 species, representing all tineoid groups ever assigned family rank, 25 of the 31 subfamilies recognized in recent classifications, and 40 genera spanning the morphological diversity of Tineidae, for which monophyly has not been established. Phylogenetic analysis used maximum likelihood, with synonymous substitutions alternatively included and excluded. The main findings confirm and extend those of other recent studies, as follows: (i) monophyly is strongly supported for Psychidae subsuming Arrhenophanidae, for Eriocottidae, and for Tineidae subsuming Acrolophidae but excluding Dryadaulinae and two genera previously assigned to Meessiinae; (ii) two new families are described, Dryadaulidae **stat. rev.** and Meessiidae **stat. rev.**, based on subfamilies previously included in Tineidae but strongly excluded from this and all other families by our molecular results; (iii) *Doleromorpha*, formerly placed in Meessiinae sensu lato, is likewise here excluded from Tineidae, but left incertae sedis pending better characterization of what is potentially another new family; (iv) basal division of Tineidae

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sensu novo into 'tineine' and 'acrolophine' lineages is moderately to strongly supported, but most subfamily relationships within these lineages are very weakly supported, and polyphyly is confirmed for Meessiinae and Myrmecozelinae as previously defined; (v) basal division of Psychidae sensu novo into 'arrhenophanine' and 'psychine' lineages is moderately to strongly supported, as are most subfamily relationships within these lineages; (vi) Tineoidea are paraphyletic with respect to all other Ditrysia when synonymous substitutions are eliminated, with branching order (Meessiidae **stat. rev.** (Psychidae sensu novo ((Eriocottidae (Dryadaulidae **stat. rev.** + *Doleromorpha*)) (Tineidae sensu novo + all other Ditrysia)))). Support for tineoid non-monophyly varies, among the relevant nodes and among analyses, from weak to moderate to strong; and (vii) paraphyly of Tineoidea, coupled with parsimony mapping of feeding habits on the molecular phylogeny, suggests that the earliest ditrysians may typically have been detritivores and/or fungivores as larvae, like most extant tineoids, rather than host-specific feeders on higher plants, as in most non-ditrysians and most non-tineoid Ditrysia, i.e., the great majority of Lepidoptera. Thus, radiation of Ditrysia, a leading example of insect diversification linked to that of higher plants, may have started with reversion to feeding habits more like those of ancestral amphiesmenopterans.

Introduction

The Tineoidea sensu lato have long been considered (Robinson, 1988) to include the earliest-originating extant families of the enormous clade Ditrysia, whose 152 284 species (van Nieukerken *et al.*, 2011) make up 98% of the insect order Lepidoptera. Until recently, however, the prevailing concept of Tineoidea was broad and ill-defined. In the first cladistic study of tineoid families, Robinson (1988) argued for a basal split within Tineoidea as then defined between a 'tineoid lineage', consisting of Tineidae, Psychidae, Acrolophidae and Eriocottidae, and a 'gracillarioid lineage', consisting of Gracillarioidea, Roeslerstammiidae and Bucculatricidae (see Fig. 1A). He further concluded that the 'tineoid lineage' sensu stricto is the sister group to the remaining Ditrysia. A very similar conclusion was advanced independently by Davis (1988). Davis (1990) also considered the Eriocottidae to be the most plesiomorphic among the Tineoidea because they were the only ditrysian moths known to possess microtrichia randomly scattered over all wing surfaces. Most of these proposals were widely accepted (e.g. Kristensen, 2003), and molecular evidence now strongly supports the basal position of Tineoidea sensu stricto (= the 'tineoid sensu strictu lineage' of Robinson, 1988) within Ditrysia. In addition, the 'gracillarioid lineage' is now strongly established by molecular data to comprise, together with the Yponomeutoidea, the oldest non-tineoid lineage to branch off from the rest of the Ditrysia (Fig. 2; Regier *et al.*, 2009, 2013; Mutanen *et al.*, 2010).

The Tineoidea sensu stricto (hereafter referred to as simply Tineoidea or tineoids), at 3719 species (van Nieukerken *et al.*, 2011), are not especially species-rich among superfamilies of Ditrysia, though they are more diverse than all non-ditrysian superfamilies put together (2604 species). Tineoids are nevertheless of potential importance for understanding the species richness of the entire ditrysian clade, because as the earliest-diverging extant lineages of Ditrysia, they are likely to strongly affect our inferences about the ancestral ditrysians that gave rise to this diversity (Robinson, 1988). To learn what tineoids imply about ancestral Ditrysia, we need a firmly established ground plan for tineoids themselves, which in turn requires a robust knowledge of their biodiversity and phylogeny. Tineoid systematics is still very incomplete. Knowledge of the world fauna remains patchy, especially in Tineidae, and phylogenetic studies, beyond the pioneering effort of Robinson (1988), have been few. Robinson and colleagues provide morphology-based hypotheses of relationships within several subfamilies of Tineidae (e.g. Robinson & Tuck, 1997; Davis & Robinson, 1998), but deeper relationships within this large family (about 2400 species) remain obscure, and many genera are unplaced (Davis & Robinson, 1998).

Recently, molecular analyses have shown strong promise for clarifying relationships in Tineoidea. Yen *et al.* (2004) assessed phylogenetic relationships within Psychidae using two genes sequenced for 17 exemplars, obtaining strong bootstrap support for relationships among tribes within the three subfamilies sampled (see Fig. 1B). The first molecular overview of relationships across Tineoidea, based on 30 exemplars sequenced for eight genes (6303 bp) and summarized in Fig. 1C, was provided by Mutanen *et al.* (2010) as part of a comprehensive phylogeny estimate for Lepidoptera. They found strong bootstrap support for three family-level groupings: (i) Eriocottidae, consisting of Eriocottinae plus Compsocteninae, originally proposed by Nielsen (1978); (ii) Psychidae, incorporating Arrhenophanidae as argued by Robinson (1988), with strong support for a deeply subordinate position for arrhenophanids [by contrast, Arrhenophanidae had been treated as a separate family by Davis & Robinson (1998) and Davis (2003)]; and (iii) Tineidae incorporating Acrolophidae, although support for a subordinate position for acrolophids was not strong. The phylogenetic positions of

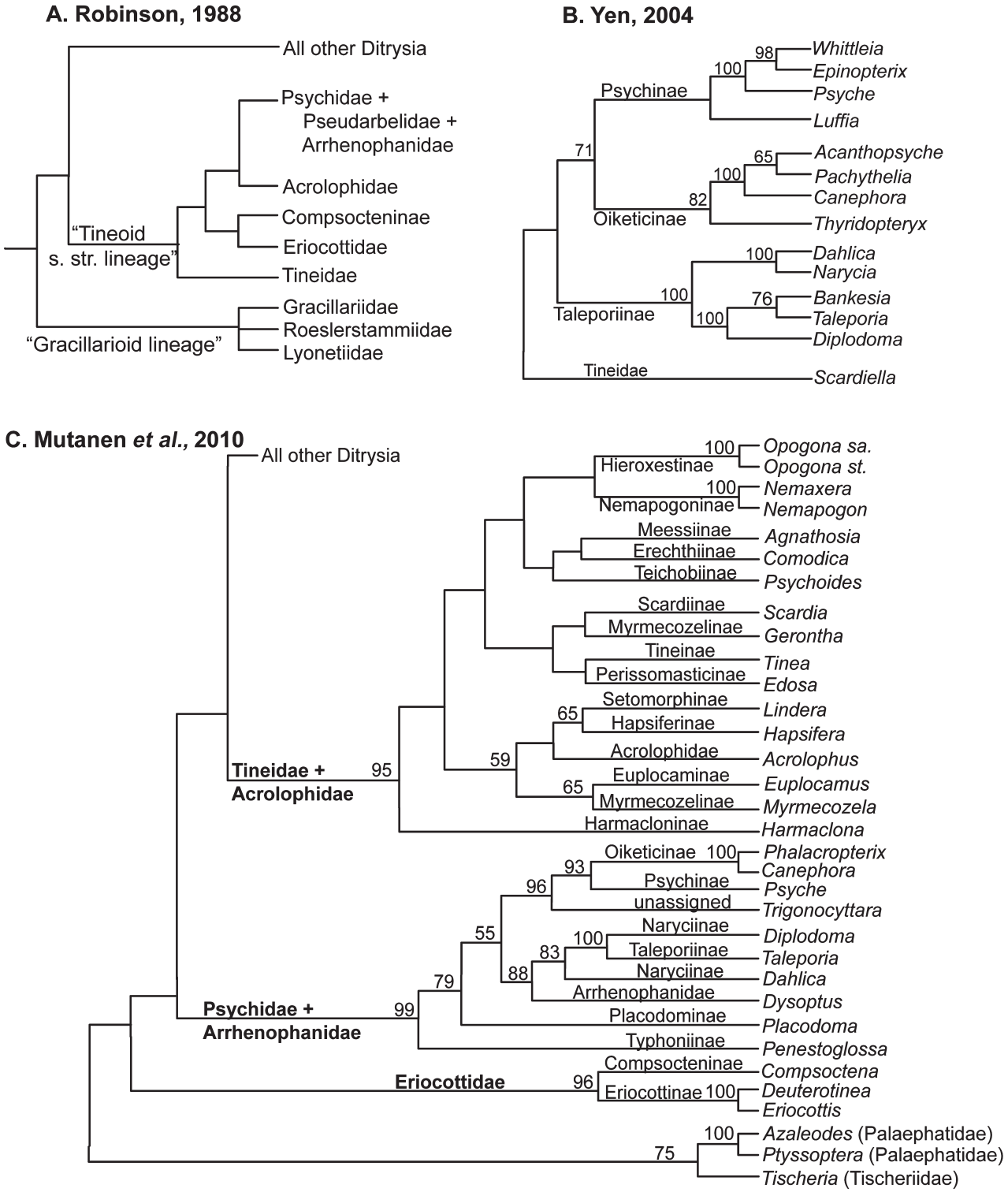

Fig. 1. Previous hypotheses on tineoid phylogeny. (A) Relationships among families inferred from morphology for Tineoidea sensu lato by Robinson (1988). (B) Most parsimonious tree and bootstraps for representative genera of three subfamilies in Psychidae, based on combined analysis of 28S rDNA and mitochondrial cytochrome b (Yen *et al.*, 2004). (C) Relationships among tineoids in the 350-taxon, eight-gene maximum likelihood (ML) tree of Mutanen *et al.* (2010), with bootstrap values above branches; third-codon positions, which are enriched in synonymous change, were eliminated except in EF-1α.

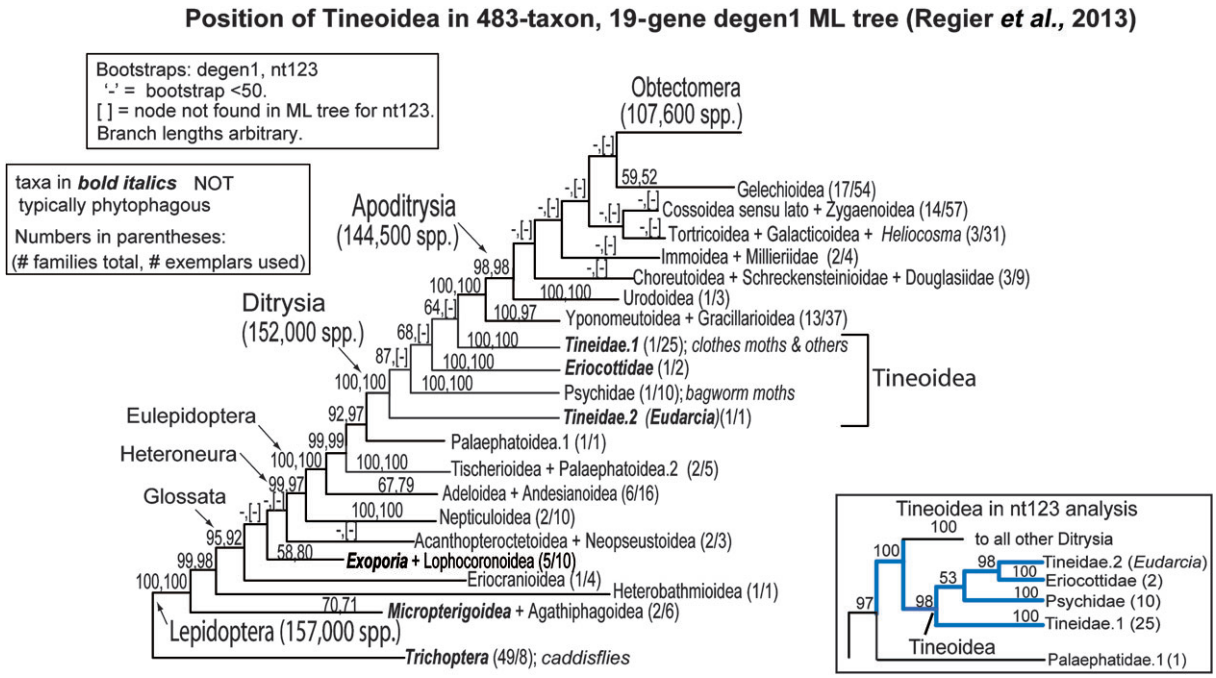

Fig. 2. Position of tineoids in the 483- taxon, 19-gene degen1 maximum likelihood (ML) tree of Lepidoptera by Regier *et al.* (2013), simplified from fig. 3 of that paper.

these families to each other were weakly supported, but the maximum likelihood (ML) tree shows Tineoidea as paraphyletic, with Tineidae as sister group to all non-tineoid Ditrysia.

A subsequent Lepidoptera 'backbone' study (Regier *et al.*, 2013), based on 483 exemplars sequenced for up to 19 genes (14.7 kb), included 38 tineoids, whose disposition in the resulting phylogeny estimate is summarized in Fig. 2. The results reinforce and extend those of Mutanen *et al.* (2010). There is strong support for Eriocottidae, for subordination of Arrhenophanine within a monophyletic Psychidae, and for subordination of Acrolophidae within a clade containing most Tineidae (*Tineidae.1* in Fig. 2). Tineoidea are paraphyletic. The evidence for this last conclusion is strong but complex, due to convergence in base composition at sites undergoing synonymous change (see Discussion below and figs. 5, 6 in Regier *et al.*, 2013). *Eudarcia* Clemens, 1860, a tineid genus not previously studied, is placed, with strong support, as sister group to the remaining Ditrysia.

In this study we seek to further clarify relationships within and among the tineoid families, by extending the molecular analyses of Regier *et al.* (2013) to a new total of 62 species. We use the results to propose two additional tineoid families as well as new groupings within the larger families. We also explore the implications of the new phylogeny for early ecological evolution of the Ditrysia. Unlike their closest relatives among the non-ditrysians, as well as subsequently diverging lineages of Ditrysia, all of which exhibit the specialized feeding on higher plants typical for Lepidoptera, most tineoid families and species are ground-dwelling detritivores or fungivores. These habits resemble those inferred for the common ancestor of Lepidoptera + Trichoptera (Kristensen, 1997; Menken *et al.*, 2010). Especially given the apparent paraphyly of tineoids with respect to the remaining ditrysians, the possibility must be considered that the radiation of Ditrysia, one of the foremost examples of insect diversification linked to that of higher plants, began with a reversion to ancestral amphiesmenopteran feeding habits.

Materials and methods

Taxon sampling

The goal of this study was to estimate relationships among the subfamilies and families of tineoid Lepidoptera, as well as their position with respect to the other Ditrysia. The 61 genera and 62 species for which we were able to obtain material represent all tineoid groups that have ever been assigned family rank, 25 of the 31 subfamilies recognized in recent reviews (Davis & Robinson, 1998; Kristensen, 2003; van Nieukerken *et al.*, 2011), and six genera unplaced to subfamily. The missing subfamilies include three small groups of Tineidae and three of Psychidae. Because the monophyly of Tineidae is doubtful, and the internal structure of this family is especially obscure, we made a particular effort to span the range of morphological diversity in tineids, of which we sampled 40 genera (10–15% of the world total). The non-tineoid Ditrysia were represented by 26 species spread across lineages suggested by recent studies (Regier *et al.*, 2009, 2013; Mutanen *et al.*, 2010) to be relatively early-diverging. As outgroups we used five species from the clade consisting of Tischeriidae and Australian Palaephatidae,

previously shown to be among the closest relatives to Ditrysia (Regier *et al.*, 2013). The species sampled, and their distribution across the classifications of van Nieukerken *et al.* (2011) and Kristensen (2003), are detailed in Table 1, which also shows the subfamilies that are missing.

Specimens for this study, obtained with the kind help of collectors around the world (see the Acknowledgements section), are stored in 100% ethanol at −80 °C as part of the ATOLep collection at the University of Maryland, USA. DNA extraction used only the head and thorax for larger species, leaving the rest of the body, including the genitalia, as a voucher. The entire specimen was used for smaller species. Wing vouchers were retained for nearly all exemplars. DNA 'barcodes' were generated for all taxa, either by us using standard primer sequences with M13 tails (Regier & Shi, 2005) or, more typically, by the All-Leps Barcode of Life project (http://www.lepbarcoding.org). Cytochrome oxidase I DNA 'barcodes' were checked against the Barcode of Life Data system reference library (Ratnasingham & Hebert, 2007) to confirm specimen identifications and also to facilitate future identification of specimens whose identity is still pending, i.e., species listed as 'sp.' or 'unidentified' in this report.

Gene sampling

Nearly all species were sequenced for five protein-coding nuclear gene regions (6.6 kb) shown previously to provide generally strong resolution within superfamilies (Regier *et al.*, 2009). To increase resolving power for deeper relationships, in 32 species we sequenced an additional 14 genes, for a total of 14.7 kb. The 14 additional gene regions are a subset of the 21 new gene regions first tested across ditrysian Lepidoptera by Zwick *et al.* (2011) and Cho *et al.* (2011). Gene names/functions and full lengths of the individual gene regions are given in table S1 of Cho *et al.* (2011). Ten species were sequenced instead for a subset of eight of the 19 genes, chosen for relatively high amplification success rates and phylogenetic utility in samples that were too small or too degraded to be reliably sequenced for 19 genes. A list of the eight genes is given by Regier *et al.* (2013). The number of gene regions attempted for each exemplar, the total amount of sequence obtained, and the GenBank accession numbers for these sequences, can all be found in Table S1. All outgroups and non-tineoid Ditrysia were sequenced for 19 genes.

Generation of DNA sequence data

A detailed protocol of all laboratory procedures is provided by Regier *et al.* (2008c). Further descriptions, including gene amplification strategies, polymerase chain reaction (PCR) primer sequences, and sequence assembly and alignment methods, can be found in Regier *et al.* (2008a,b,c, 2009).

To summarize, species-specific templates for mRNA amplification were prepared by first extracting total nucleic acids. Extracted nucleic acids were stored at −80°C in RNAse-free deionized water (diethyl-pyrocarbonate-treated). Specific regions of the cognate mRNAs were amplified by reverse transcription followed by PCR. Specific bands were gel-isolated and reamplified by PCR using hemi-nested primers, when available. Visible bands that were too faint to sequence were reamplified using as primers the M13 sequences at the 5′ ends of all gene-specific primers. PCR amplicons were sequenced directly on a 3730 DNA Analyzer (Applied Biosystems, Foster City, CA). Sequences were edited and assembled using the TREV, PREGAP4, and GAP4 programs in the STADEN package (Staden, 1999). Individual sequences were concatenated, and alignments were made automatically using the 'TRANSLATION ALIGN' software in the GENEIOUS PRO v. 5.3.4 package [60]. In the alignment process, splitting of individual codons was not allowed. A data-exclusion mask of 1440 unalignable characters out of 20 373 total aligned characters (= 7.1% of total) for all 89 species was applied.

Character partitions, taxon × gene dataset design and phylogenetic analyses

Three distinct data sets that include all sequences were constructed. The first consists of unaltered nucleotides from all three nucleotide positions (nt123). The second (nt123_partition) contains the same nucleotides, but with these partitioned into two non-overlapping character sets that separate non-synonymous-only from mostly synonymous change. These two complementary character sets are called noLRall1nt2 and LRall1nt3 [see table 1 in Regier & Zwick (2011) for complete definitions; see also http://www.phylotools.com]. We chose this bipartition procedure over the more common tripartition by codon position because the approach is simpler, having only two character sets, and yet generates a larger non-synonymous-only set. Scripts to generate the two character sets are freely available (appendix 4 of Regier *et al.*, 2008c; http://www.phylotools.com). The third data set (nt123_degen1) is based on the degen1 approach [23], in which in-frame codons of the same amino acid are fully degenerated with respect to synonymous change, e.g. CAT → CAY. Leu codons (TTR + CTN) are degenerated to Leu + Phe (YTN), and Arg codons (AGR + CGN) are degenerated to Arg + Ser2 (MGN). Phe and Ser2 are degenerated to TTY and AGY, respectively. The basic idea of the degen1 approach is to capture the non-synonymous signal while excluding the synonymous signal and any compositional heterogeneity it produces. The degen1 script is freely available (Regier *et al.*, 2010; Zwick *et al.*, 2012; http://www.phylotools.com). The substitution model used in all analyses was a general time-reversible nucleotide model with a term for invariant sites and among-site rate heterogeneity accounted for by a discrete Γ distribution (GTR + G + I). This model was applied separately to each character subset in the partitioned analysis. To test whether the missing data from taxa sequenced for only five or eight genes had a marked effect on the results from the all-data matrix (five to 19 genes), we carried out parallel analyses on a reduced gene sample, including only the five gene regions that were sequenced in nearly all taxa.

Table 1. Distribution of species sequenced across the (earlier) classification of van Nieukerken *et al.* (2011). See Table S1 for accession number, collecting locality and life stage used.

Tineoidea Latreille, 1810
- **Eriocottidae** Spuler, 1898 (six genera, 80 species):
  - Eriocottinae Spuler, 1898 (five genera, 26 species): *Eriocottis* Zeller, 1847, **sp.n.**
  - Compsocteninae Dierl, 1968 (one genus, 54 species): *Compsoctena* Zeller, 1852, **sp.n.**
- **Psychidae** Boisduval, 1829 (211 genera, 1246 species)
  - Naryciinae Tutt, 1900 (14 genera, 146 species): *Dahlica triquetrella* (Hübner, 1813), *Kearfottia albifasciella* Fernald, 1904, *Narycia duplicella* (Goeze, 1783)
  - Pseudarbelinae Clench, 1959 (three genera, six species): *Pseudarbela* Sauber, 1902, **sp.n.**
  - Typhoniinae Lederer, 1853 (22 genera, 165 species): *Typhonia ciliaris* (Ochsenheimer, 1810)
  - Scoriodytinae Hättenschwiler, 1989 (three genera, four species): *Scoriodyta suttonensis* Hättenschwiler, 1989
  - Psychinae Boisduval, 1829 (12 genera, 76 species): *Psyche crassiorella* (Bruand, 1851)
  - Epichnopteriginae Tutt, 1900 (15 genera, 93 species): *Peloponnesia haettenschwileri* Hauser, 1996, *Rebelia thomanni* Rebel, 1937
  - Oiketicinae Herrich-Schäffer, 1855 (95 genera, 488 species): *Acanthopsyche zelleri* Mann, 1855, *Oreopsyche tenella* (Speyer, 1862), *Eumeta* Walker, 1855 sp., *Thyridopteryx ephemeraeformis* (Haworth, 1803)
  - Arrhenophaninae Walsingham, 1913 (five genera, 10 species): *Arrhenophanes perspicilla* (Stoll, 1790), *Dysoptus bilobus* Davis, 2003
  - Psychidae, Incertae sedis (23 genera, 116 species): *Perisceptis carnivora*, Davis, 2008
  - Metisinae Sauter & Hättenschwiler, 1999 (six genera, 36 species): not sampled
  - Taleporiinae Herrich-Schäffer, 1857 (10 genera, 63 species): not sampled
  - Placodominae Sauter & Hättenschwiler, 1999 (three genera, seven species): not sampled
- **Tineidae** Latreille, 1810 (357 genera, 2393 species)
  - Myrmecozelinae Capuše, 1968 (62 genera, 321 species): *Cephimallota chasanica* Zagulajev, 1965, *Myrmecozela ochracella* (Tengström, 1848), *Moerarchis inconcisella* (Walker, 1863), *Xystrologa* Meyrick, 1919 sp.
  - Harmacloninae Davis, 1998 (two genera, 22 species): *Harmaclona* Busck, 1914, **sp.n.**
  - Meessiinae Capuše, 1966 (35 genera, 248 species): *Bathroxena heteropalpella* Meyrick, 1919, *Doleromorpha porphyria* Braun, 1930, *Diachorisia velatella* Clemens, 1860, *Eudarcia simulatricella* Clemens, 1860, *Homosetia* Clemens, 1863 *sp.*, *Hybroma servulella* Clemens, 1862, *Leucomele miriamella* Dietz, 1905, *Mea bipunctella* (Dietz, 1905)
  - Dryadaulinae Bradley, 1966 (one genus, 35 species): *Dryadaula* Meyrick, 1893 **sp.n.**
  - Scardiinae Eyer, 1924 (24 genera, 112 species): *Moraphaga bucephala* (Snellen, 1884), *Scardiella approximatella* (Dietz, 1905)
  - Nemapogoninae Hinton, 1955 (10 genera, 97 species): *Nemapogon cloacella* (Haworth, 1828)
  - Tineinae Latreille, 1810 (41 genera, 355 species): *Monopis pavlovskii* Zagulajev, 1955, *Praeacedes atomosella* (Walker, 1863), *Phereoeca uterella* (Walsingham, 1897), *Tineola bisselliella* (Hummel, 1823), *Tinea columbariella* Wocke, 1877, *Trichophaga tapetzella* (Linnaeus, 1758)
  - Setomorphinae Walsingham, 1891 (three genera, eight species): *Setomorpha rutella* Zeller, 1852
  - Perissomasticinae Gozmány, 1965 (five genera, 254 species): *Edosa*, Walker, 1866 sp., *Perissomastix* Warren & Rothschild, 1905, sp.
  - Hapsiferinae Gozmány, 1968 (20 genera, 122 species): *Hapsifera* Zeller, 1847 sp., *Paraptica concinerata* Meyrick, 1917
  - Hieroxestinae Meyrick, 1893 (11 genera, 289 species): *Opogona thiadelpha* Meyrick, 1934
  - Erechthiinae Meyrick, 1880 (two genera, 140 species): *Erechthias zebrina* (Butler, 1881), *Pyloetis mimosae* (Stainton, 1859)
  - Acrolophinae Fracker, 1915 (five genera, 271 species): *Acrolophus arcanellus* Clemens, 1859, *Acrolophus panamae* Busck, 1914, *Amydria brevipennella* Dietz, 1905, *Exoncotis umbraticella* (Busck, 1914)
  - Tineidae, Incertae sedis (119 genera, 290 species): *Euprora* Busck, 1906 *sp.*, *Dyotopasta yumaella* (Kearfott, 1907), *Xylesthia pruniramiella* Clemens, 1859, *Corythophora sp.* (previously placed in Lyonetiidae) Braun, 1915, *Pelecystola nearctica* Davis & Davis, 2009, *CRunidentified (an unidentified species from Costa Rica) Tineovertex melanochrysa* (Meyrick, 1911)
  - Euplocaminae Walsingham, 1891 (one genus, six species; Palearctic): *Psecadioides asperses*, Butler 1881
  - Siloscinae Gozmány, 1968 (three genera, 20 species; Afrotropical): not sampled
  - Stathmopolitinae Sauter, 1982 (one genus, one species; Canary Islands): not sampled
  - Teichobiinae Heinemann, 1870 (three genera, 22 species; Palearctic): Not sampled

Outgroups
- Superfamily **Choreutoidea** Stainton, 1858
  - Family **Choreutidae** Stainton, 1858 (18 genera, 406 species): *Brenthia* Clemens, 1860 sp.; *Anthophila fabriciania* Linnaeus 1867
- Superfamily **Cossoidea** Leach, 1815 (134 genera, 857 species)
  - Family **Cossidae** Leach, 1815**:** Cossinae Leach, 1830: *Prionoxystus robiniae* Peck, 1818
- Superfamily **Gelechioidea** Stainton, 1854
  - Family **Gelechiidae** Stainton, 1854 (507 genera, 4700 species): Gelechiinae: *Aroga trialbomaculella* Chambers, 1875
  - Family **Elachistidae** Bruand, 1850 (161 genera, 3201 species): Hypertrophinae (11/50): *Eupselia carpocapsella* Walker, 1864
- Superfamily **Gracillarioidea** Stainton, 1854
  - Family **Roeslerstammiidae** Bruand, 1850 (13 genera, 53 species): *Roeslerstammia pronubella* (Denis & Schiffermüller, 1775), *Agriothera elaeocarpophaga* Moriuti, 1978
  - Family **Gracillariidae** Stainton, 1854 (100 genera, 1855 species): Oecophyllembiinae: *Eumetriochroa hederae* Kumata 1998; Gracillariinae: *Epicephala relictella* Kuznetzov 1979; Phyllocnistinae: *Phyllocnistis longipalpus* Chambers, 1878
  - Family **Bucculatricidae** Fracker, 1915 (four genera, 297 species) *Bucculatrix* Zeller, 1839 sp.
- Superfamily Unassigned
  - Family **Douglasiidae** Heinemann & Wocke, 1876 (two genera, 29 species): *Klimeschia transversella* (Zeller, 1839)
  - Family **Millieriidae** (three genera, four species) Heppner, 1982: *Millieria dolosalis* (Herrich-Schäffer, 1854)

Table 1. Continued.

Superfamily **Immoidea** Common, 1979
Family **Immidae** Common, 1979 (two genera, 245 species): *Imma tetrascia*, Meyrick 1912
Superfamily **Hyblaeoidea** Hampson, 1903
Family **Hyblaeidae** Hampson, 1903 (two genera, 18 species): *Hyblaea ibidias* Turner, 1902
Superfamily **Palaephatoidea** Davis, 1986
Family **Palaephatidae** Davis, 1986 (seven genera, 57 species): *Azaleodes micronipha* Turner, 1923, *Ptyssoptera* Turner, 1933 sp.
Superfamily **Schreckensteinioidea** Fletcher, 1929
Family **Schreckensteiniidae** Fletcher, 1929 (two genera, eight species): *Schreckensteinia* Hübner (1825) sp.
Superfamily **Tischerioidea** Spuler, 1898
Family **Tischeriidae** Spuler, 1898 (three genera, 110 species): *Tischeria ekebladella* Bjerkander 1795, *Coptotriche malifoliella* (Clemens 1860), *Astrotischeria* Puplesis & Diškus, 2003 **sp.n.**
Superfamily **Tortricoidea** Latreille, 1802
Family **Tortricidae** Latreille, 1802 (1043 genera, 9757 species): Chlidanotinae: *Histura perseavora* J.W. Brown, 2010; Tortricinae: *Cnephasia alfacarana*, Razowski 1958
Superfamily **Urodoidea** Kyrki, 1988
Family **Urodidae** Kyrki, 1988 (three genera, 65 species): *Urodus decens* Meyrick, 1925
Superfamily **Yponomeutoidea** Stephens, 1829 (10 families)
Family **Glyphipterigidae** Stainton, 1854 (29 genera, 535 species): Acrolepiinae Heinemann, 1870: *Digitivalva hemiglypha* Diakonoff & Arita, 1976
Family **Bedelliidae** Meyrick, 1880 (one genus, 16 species): *Bedellia somnulentella* (Zeller, 1847)
Family **Heliodinidae** Heinemann & Wocke, 1876 (13 genera, 69 species): *Aetole tripunctella* (Walsingham, 1892)
Family **Plutellidae** Guenée, 1845 (48 genera, 150 species): *Plutella xylostella* Linnaeus, 1867
Family **Praydidae** Moriuti, 1977 (three genera, 45 species): *Prays fraxinella* Bjerkander, 1784
Family **Yponomeutidae** Stephens, 1829 (95 genera, 363 species): Yponomeutinae: *Yponomeuta multipunctella* Clemens, 1860
Family **Ypsolophidae** Guenée, 1845 (seven genera, 163 species): Ypsolophinae: *Ypsolopha nigrimaculata* Byun & Park, 2001
Superfamily **Zygaenoidea** Latreille, 1809
Family **Limacodidae** Duponchel, 1845 (298 genera, 1660 species): *Prolimacodes badia* Hübner, 1835

All phylogenetic analyses were based on the ML criterion as implemented in GARLI (Genetic Algorithm for Rapid Likelihood Inference; v2.0; Zwickl, 2006). We used the program default settings, including random stepwise addition starting trees, except that we halved the number of successive generations yielding no improvement in likelihood score that prompts termination (genthreshfortopoterm = 10 000), as suggested for bootstrapping in the GARLI manual. Each search for the single best ML tree consisted of 970–1000 separate GARLI ML search replicates run to completion on each of the full data sets (nt123, nt123_partition, nt123_degen1). Bootstrap analyses consisted of 708–750 pseudo-replicates, each based on 15 heuristic search replicates run to completion. Optimal-tree searches and bootstrap analyses were parallelized using Grid computing (Cummings & Huskamp, 2005) through The Lattice Project (Bazinet & Cummings, 2008). For consistency in the characterization of results, we will refer to bootstrap support of 70–79% as 'moderate,' 80–89% as 'strong' and ≥90% as 'very strong'.

Rogue taxon analyses

Despite the addition of 14 genes for more than half the taxa in our initial five- or eight-gene data set, many nodes in our best-supported trees have low bootstrap values. One possible cause of low support is the sensitivity of bootstrap values to taxa of unstable placement (Sanderson & Shaffer, 2002), termed 'rogues' by Wilkinson (1994). Multiple approaches have been suggested for detecting and removing the effects of rogue taxa (review in Aberer, 2011). We investigated the potential contribution of rogue taxa to low bootstrap values in our data set using the RogueNaRok (RNR) approach of Aberer *et al.* (2011). The key feature of RogueNaRok is a new optimality criterion for rogue taxon removal, the 'Relative Bipartition Information Criterion' (RBIC; Aberer & Stamatakis, 2011). The RBIC strikes a balance between improving per-node support in the reduced bootstrap consensus tree (with rogues deleted) and retaining total information by minimizing the loss of bipartitions in the bootstrap consensus tree that results from such deletions. Maximizing the Relative Bipartition Information Criterion is probably a non-deterministic polynomial-time hard (NP-hard) problem (Aberer *et al.*, 2011). Aberer & Stamatakis (2011) compared multiple heuristic approaches to maximizing the RBIC. The best results came from their single-taxon algorithm, which begins by removing taxa one at a time to find the taxon (if any) whose deletion most improves the RBIC. After that taxon is removed, one removes each remaining taxon again, to find the next most 'roguish' taxon. The process is repeated until the optimality score stops improving. The RogueNaRok algorithm is a fast generalization of the single-taxon algorithm, which allows for 'deletion sets' – groups of taxa deleted simultaneously – of varying sizes.

To identify rogue taxa, we used the online version of RogueNaRok at http://193.197.73.70:8080/rnr/roguenarok, which is built on RAXML (Stamatakis *et al.*, 2008). Bootstrap files were first generated and submitted to RogueNaRok, which identified possible rogue taxa (i.e. ones whose removal increases the RBIC). The reduced data set was then analyzed with RAXML,

and the bootstrap outputs again submitted to RogueNaRok. This procedure was repeated until RogueNaRok no longer identified any additional rogues. Finally, the putatively rogue-free data sets were subjected to bootstrap analyses using GARLI, to make them directly comparable to the original analyses. This procedure was carried out only on the full five- to 19-gene degen1 data set.

Results

In what follows, the term '19-gene data set' will be used to refer to the matrix containing all available data, ranging from five to 19 genes per taxon. The results of the phylogenetic analyses are summarized in Fig. 3, which presents the ML topology for the 19-gene degen1 data set together with bootstrap percentages (BP) for the other analyses. Figure S1 shows the same topology in phylogram form, while Figure S2 shows the ML topology and bootstrap values for the 19-gene, nt123 analysis. Our presentation follows Fig. 3. Although there are significant differences between the degen1 and nt123 topologies, as discussed in the following, the two analyses agree that all tineoids can be assigned to one of five strongly supported, mutually exclusive lineages, three of which correspond nearly or entirely to previously recognized families. These are: (i) a clade consisting of the genera *Eudarcia* and *Bathroxena* Meyrick (Fig. 3, node 2; BP = 100, all analyses), previously placed in the subfamily Meessiinae of Tineidae; (ii) the family Psychidae, incorporating Arrhenophanidae (node 4; BP = 100, all 19-gene analyses); (iii) Eriocottidae (BP ≥ 99, all analyses); (iv) a clade consisting of *Dryadaula* Meyrick, previously placed in its own subfamily of Tineidae, plus *Doleromorpha* Braun, previously in Tineidae: Meessiinae (node 17; BP = 100, all 19-gene analyses); and, (v) Tineidae sensu novo, excluding the genera just named and incorporating Acrolophidae (node 19; BP ≥ 99, all 19-gene analyses).

The evidence on relationships among the five major lineages is more complicated. Under degen1 (Fig. 3), Tineoidea are paraphyletic, with three tineoid lineages – *Eudarcia* + *Bathroxena*, Psychidae, and Eriocottidae + (*Dryadaula* + *Doleromorpha*) – diverging successively before the remaining Ditrysia diverge from their sister group, Tineidae.

The bootstrap values for the nodes rendering Tineoidea paraphyletic, in order from oldest to youngest, are 73, 62, and 66, rising to 74, 70 and 80 after rogue taxon removal (see later). By contrast, under nt123 (Figure S2), the Tineoidea are monophyletic, with bootstrap support of 83. [In the Discussion section and in Regier *et al.* (2013), we argue that tineoid monophyly is probably an artifact of base compositional heterogeneity.] Under nt123, Eriocottidae are strongly grouped with *Eudarcia* + *Bathroxena* (BP = 91), but all other relationships among the five tineoid lineages have very weak support.

Within the largest family, Tineidae, both degen1 and nt123 support a basal divergence into two large clades, one containing Acrolophinae and relatives (labelled 'acrolophine lineage' in Fig. 3; node 20, BP = 100, all 19 gene analyses), the other containing Tineinae and relatives (labelled 'tineine lineage' in Fig. 3; node 30, BP = 76/58, degen1/nt123). Although several individual subfamilies within these two clades have strong bootstrap support, as do two groupings of genera (nodes 34, 37) that might be the nuclei of previously unrecognized subfamilies, there is almost no strong support within either clade, in any analysis, for any relationships among subfamilies. The one exception is that under nt123, Setomorphinae are strongly placed as the earliest divergence lineage member of the lineage containing Acrolophinae (Figure S2, BP = 98), but this grouping is contradicted, albeit with very weak support, by degen1 (Fig. 3, node 23). There is, however, strong support for relationships within the subfamily Tineinae, for which our sample of genera is largest.

Relationships among subfamilies within Psychidae are somewhat more strongly supported. Both degen1 and nt123 strongly support two major lineages, one containing Arrhenophaninae and relatives (Fig. 3, node 12, BP = 81/70, degen1/nt123), the other containing Psychinae and relatives (node 5, BP = 100, all 19-gene analyses). The only uncertainly placed subfamily is Naryciinae, which groups with the lineage containing Arrhenophaninae under degen1 (Fig. 3, node 10, BP = 73) but with the lineage containing Psychinae under nt123 (Figure S2; BP = 78). Inter-subfamily relationships are strongly supported within the Psychinae-containing major lineage (all BP ≥ 90), and only somewhat less so in the Arrhenophaninae-containing lineage.

The rogue taxon analysis using RogueNaRok identified 21 taxa as 'rogues', defined as taxa for which the information lost by deleting them is more than compensated for by the gain in support values for the remaining nodes (Aberer & Stamatakis, 2011). The distribution of these rogues across our tree estimate is shown in Fig. 3 by # signs after their taxon names. Fifteen of the rogue taxa are tineoids, while the remainder are other Ditrysia. Eleven of the 15 (73%) had been sequenced for only five or eight genes, while four (27%) had been sequenced for 19 genes. Given that 32 of the 62 tineoids (52%) had been sequenced for 19 genes, it appears that the probability of being judged a rogue was higher for taxa sequenced for fewer than 19 genes. Rogue taxon removal did not dramatically affect topology or node supports overall, but it did raise support notably for several nodes in the tree for all taxa. These increased values are shown in square brackets in Fig. 3.

Discussion

Major lineages within Tineoidea and their classification: overview

Family composition

Our results strongly confirm the monophyly and composition of the three tineoid families recognized by van Nieukerken *et al.* (2011), which in turn were based on the findings of Mutanen *et al.* (2010) (see Fig. 1C). We find 100% bootstrap support (Fig. 2) for: (i) Eriocottidae, consisting of Eriocottinae plus Compsocteninae; (ii) Psychidae, with Arrhenophaninae, sometimes treated as a separate family, deeply and strongly

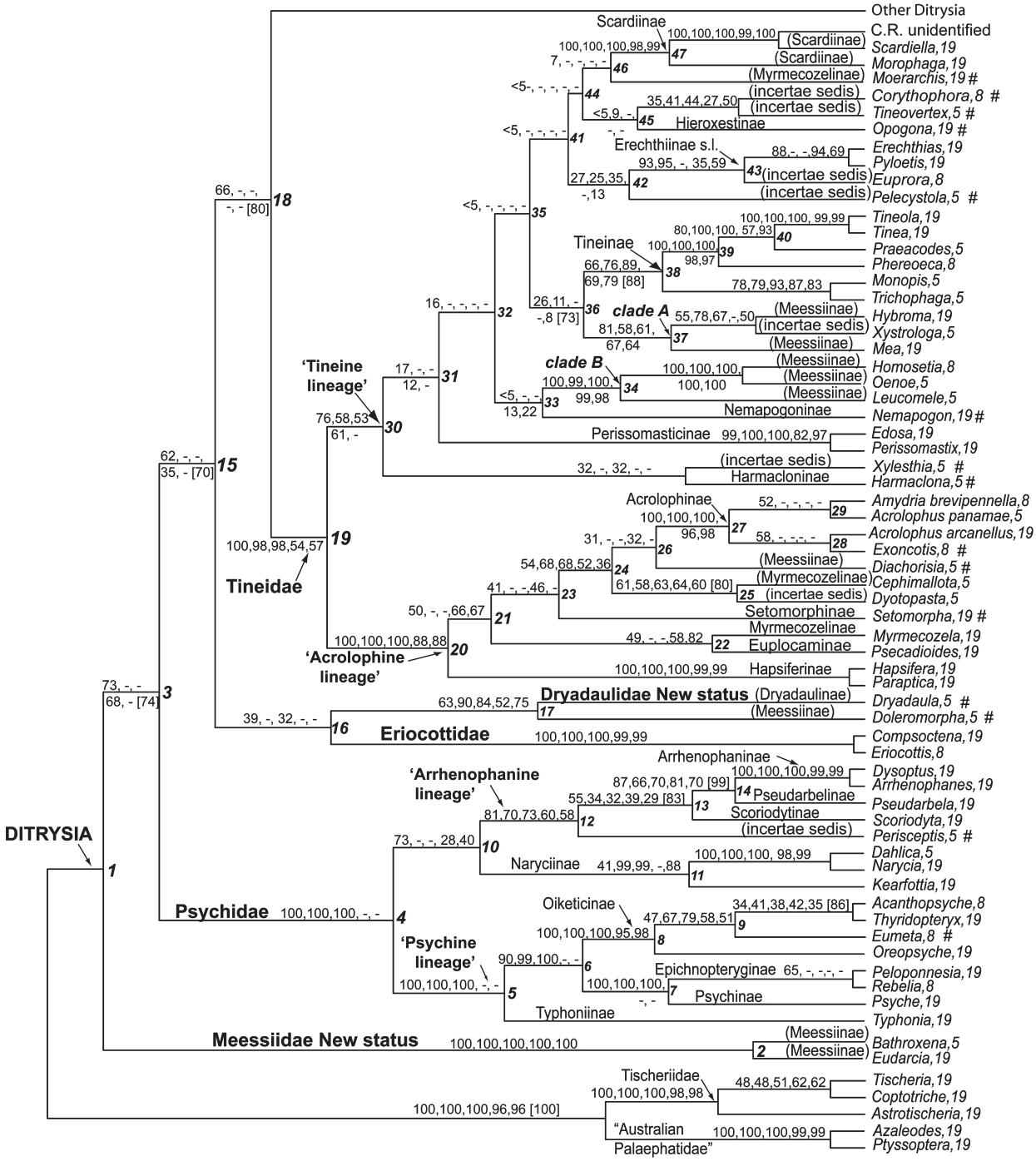

Fig. 3. Maximum likelihood (ML) cladogram for the present 19-gene degen1 analysis, with summary of bootstrap values for all analyses, in the following order: degen1 (19 genes), nt123 (19 genes), partition (19 genes), degen1 (five genes), nt123 (five genes); degen1NoRog in [ ]. '–', node not found in ML tree for that analysis; #, taxon removed as 'rogue' by RogueNaRok analysis. 'CRunidentified' is an unidentified specimen from Costa Rica.

nested therein; and, (iii) Tineidae, with Acrolophinae, previously treated as a separate family, strongly nested therein.

Because of our more extensive taxon sampling, we have also identified two additional tineoid lineages that we believe merit family status. One of these consists, as thus far known, of *Eudarcia* plus *Bathroxena*, both previously assigned to the tineid subfamily Meessiinae. This clade, which has 100% bootstrap support, merits recognition as a separate family because: (i)

it is strongly excluded from all previously recognized tineoid families; and (ii) it has a clear phylogenetic position. In the current study and that of Regier *et al.* (2013), it is moderately to strongly supported as the sister group to all other Ditrysia (see later). Because *Eudarcia* is the type genus of Meessiinae, we apply the name Meessiidae (Căpuşe, 1966) **stat. nov.** to the new family, for which a formal description is provided in a later section. Our results firmly corroborate the long-suspected polyphyly of Meessiinae as previously recognized: all of the other five exemplars sampled from this subfamily are strongly placed elsewhere (see later). The Meessiidae as here defined include about 90 species, primarily Holarctic in distribution. Recognition of this family is a hypothesis that is currently based on sequences from only two genera (one specimen each), albeit securely identified ones using both morphology and DNA barcodes, in combination with the morphological evidence for monophyly of *Eudarcia*. (*Bathroxena* is monobasic.) Given the pivotal phylogenetic position of Meessiidae, sequencing of additional *Eudarcia* species, and of additional genera of the former Meessiinae sensu lato, is desirable, to test and potentially expand the definition of the new family.

The other lineage that we consider to merit the status of a new family consists, in our sample, of *Dryadaula*. *Dryadaula* is strongly excluded from all previously recognized tineoid families in our molecular analyses, and makes up most of the former tineid subfamily Dryadaulinae, which is characterized by many morphological apomorphies (Davis & Robinson, 1998). Raising this subfamily to family status is a hypothesis that is currently based on sequences from a single specimen, albeit one securely identified by both morphology and DNA barcodes, in combination with the morphological evidence for monophyly of *Dryadaula*. Sequencing of additional species of *Dryadaula* and related genera is desirable, to confirm the definition of the new family, for which a formal description is given in a later section. The Dryadaulidae as here defined include 46 species and have a cosmopolitan distribution.

It would be defensible to also include within Dryadaulidae the monobasic genus *Doleromorpha*, previously assigned to Meessiinae. This taxon is invariably placed as sister group to *Dryadaula*, with bootstrap support up to 90% for nt123, 19 genes. We decided against including it because: (i) it shares no apparent morphological apomorphies with *Dryadaula*, whereas without it, Dryadaulidae are well defined by such synapomorphies; and (ii) little would be gained by erecting a new family for a single species. For the time being, we treat *Doleromorpha* as incertae sedis, while noting its close relationship to Dryadaulidae. Although *Doleromorpha* shares no known synapomorphy with any other tineid genus, it is possible that further sampling of currently unplaced Tineidae could turn up a larger nucleus of genera on which to base a new family that includes *Doleromorpha*.

The five-family system (plus *Doleromorpha*) proposed here, although provisional, provides a reasonable summary of the diversity of Tineoidea as presently understood. However, sequencing of additional insecurely placed genera of Tineidae sensu lato, including members of subfamilies of doubtful monophyly (in particular, Meessiinae and Myrmecozelinae, as previously delimited), might well reveal additional family-level lineages.

Phylogeny and classification within Tineidae

Molecular data now strongly support the monophyly of Tineidae modified to include Acrolophinae and to exclude the genera newly assigned to Meessiidae and Dryadaulidae + *Doleromorpha.* However, no morphological synapomorphies for the family in this sense, which includes about 2200 species, have yet been identified. Seventeen subfamilies of Tineidae, included in Table 1, are recognized in the review of Davis & Robinson (1998), who identify synapomorphies supporting monophyly for 15 of these. Synapomorphies are lacking for Meessiinae and Myrmecozelinae as then delimited. Relationships among the tineid subfamilies have long been recognized as problematic. Robinson & Nielsen (1993) concluded that no synapomorphies had yet been found to link any tineid subfamilies together. Our results present a partial, though far from complete, solution to this problem. Within the newly defined, monophyletic Tineidae, our data support a basal split between an 'acrolophine lineage' and a 'tineine lineage' (Fig. 3). A similar division can be seen in the tree of Mutanen *et al.* (2010) (Fig. 1C). The acrolophine lineage in our sample (node 20, BP = 100) includes four of the tineid subfamilies thought to be monophyletic (Davis & Robinson, 1998), namely, Acrolophinae, Setomorphinae, Euplocaminae and Hapsiferinae. These total about 400 species. Monophyly is strongly confirmed for two of these subfamilies, Acrolophinae and Hapsiferinae, for which we sampled multiple genera. All genera comprising the Acrolophinae are characterized largely by their greatly reduced adult maxillae and the general reduction of the female oviscapt. The acrolophine lineage also includes the nominate genus of Myrmecozelinae, a subfamily which our results forcefully confirm to be polyphyletic: none of the three other myrmecozelines sampled group with *Myrmecozela*, and two are placed in the tineine lineage. We suspect that a monophyletic subfamily bearing that name will contain little besides *Myrmecozela*; other genera previously included in Myrmecozelinae should probably be regarded as unplaced. Remarkably, there is almost no strong support for any relationships among acrolophine lineage subfamilies, the sole exception being 98% bootstrap support for Setomorphinae as sister group to all the others under nt123 (Figure S2). Even this grouping is contradicted, albeit weakly, by degen1 (Fig. 3, node 23).

The tineine lineage, less strongly supported (node 30, BP = 76/58, degen1/nt123), is also much larger and more heterogeneous than its postulated sister group. Among the subfamilies thought to be monophyletic, it includes Erechthiinae, Harmacloninae, Hieroxestinae, Nemapogoninae, Perissomasticinae, Scardiinae, and Tineinae, which together total about 1300 species. Monophyly is confirmed for the four of these subfamilies that have multiple representatives in our sample, and relationships among the six genera of Tineinae sequenced are strongly supported. Our results robustly confirm the reassignment of *Pyloetis* Meyrick from Myrmecozelinae to Erechthiinae (Miyamoto *et al.*, 2007), and strongly imply

that *Euprora* (Busck), previously unplaced, also belongs to Erechthiinae (node 43; BP = 93/95, degen1/nt123).

Our sample of the 'tineine lineage' also includes multiple genera representing the subfamilies Meessiinae and Myrmecozelinae. Although these genera are scattered across the tree, there are two unrelated clusters of three genera each that have strong support and might represent the nuclei of yet-to-be-described subfamilies. One, labelled 'clade A' in Fig. 3 (node 37; BP = 81, degen1), consists of *Xystrologa* Meyrick (incertae sedis; seven species, Neotropical) plus the meessiines *Hybroma* Clemens (eight species; North and South America) and *Mea* (five species, North America). When rogue taxa elsewhere in Tineidae are removed, there is 73% bootstrap support for a sister-group relationship between the subfamily Tineinae and 'clade A.' The second un-named cluster of genera, labelled 'clade B' in Fig. 3 (node 34; BP ≥ 98), consists of the meessiines *Oenoe* Chambers (nine species; Australia, Fiji, North America, Neotropics), *Homosetia* Clemens (17 species; North and South America), and *Leucomele* Deitz (one species; North America).

While our results thus provide modest additional clarification of subfamily composition, the lack of support for relationships among subfamilies is even more dramatic in the tineine lineage than in the acrolophine lineage: bootstrap values for nodes subtending two or more genera that are not in the same subfamily are always less than 50%, and most are vanishingly small (<5%). Apart from the division into two major lineages, relationships among the subfamilies of Tineidae, and of these to the hundreds of unplaced species (to which most members of Meessiinae and Myrmecozelinae as previously recognized should now be added), appear to constitute one of the most difficult problems in Lepidoptera systematics.

Phylogeny and classification within Psychidae

The Psychidae, including Arrhenophaninae, total 1246 species (van Nieukerken *et al.*, 2011). Within-family phylogeny and classification appears to be an easier problem in psychids than in Tineidae. All of the psychids we sampled, except for Naryciinae, fall into one of two strongly supported major lineages. The smaller of these, the 'Arrhenophanine lineage' (Fig. 3, node 12; BP = 81/70, degen1/nt123), consists of Arrhenophaninae, Pseudarbelinae and Scoriodytinae, plus the newly described, previously unplaced predatory genus *Perisceptis* (Davis *et al.*, 2008), totaling about 35 species. Within this lineage, *Pseudarbela* Sauber appears to be the sister group to Arrhenophaninae (node 14; BP = 87/66, degen1/nt123). Our data consistently but weakly support Scoriodytinae as sister group to this pair.

The other main psychid clade in our sample, the 'psychine lineage' (node 5; BP =100, all 19-gene analyses), includes Psychinae, Epichnopteriginae, Oiketicinae, and Typhoniinae, which together total about 820 species. Within this lineage, the strongly supported basal divergence is between Typhoniinae and all others (node 6; BP = 90–100, all 19-gene analyses). The subsequent split is between Oiketicinae and Psychinae + Epichnopteriginae (node 7; BP = 100, all 19-gene analyses).

The position of the final subfamily studied, Naryciinae, is only partially determined because synonymous and non-synonymous changes yield conflicting signal (Fig. 3, Figure S2). Under degen1, it is sister group to the 'Arrhenophanine lineage', with BP = 73, while under nt123 it is sister group to the 'Psychine lineage,' with BP = 78.

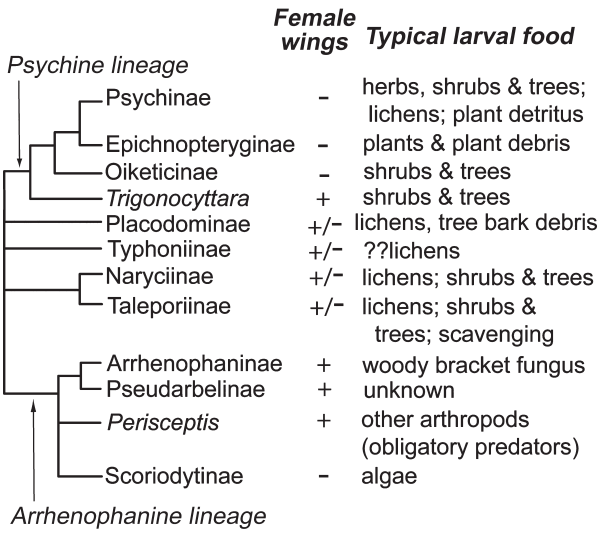

Fig. 4. Semi-strict consensus tree of Psychidae subfamilies, combining groupings from the present analysis (Fig. 3), Yen *et al.* (2004) and the maximum likelihood (ML) tree of Mutanen *et al.* (2010).

The three molecular studies of psychid subfamily phylogeny to date (Yen *et al.*, 2004; Mutanen *et al.*, 2010; present study) overlap only partially in taxon sampling, and are mostly compatible in topology. Together they encompass all of the 11 currently recognized subfamilies (including Arrhenophaninae) except Metisinae. It is therefore possible to get a somewhat more complete estimate of subfamily phylogeny by combining their results than can be had from any single study. Figure 4 shows a form of semi-strict consensus tree (Goloboff & Pol, 2002) for the subfamily-level psychid phylogenies from Figs 1B, 1C and 3. It includes all groupings supported by bootstrap of 70% or more in one tree, and not contradicted by the others. The consensus tree includes the arrhenophanine and psychine lineages identified in our results, except that Typhoniinae are removed from the psychine lineage because this position, with its 100% bootstrap support, conflicts strongly with their placement in the Mutanen *et al.* (2010) study (Fig. 1C). (As a reviewer noted, however, this conflict could be the result of the two studies using different exemplar genera.) The unplaced Australian genus *Trigonocyttara* (Turner) included only in the tree of Fig. 1C is grouped in the consensus tree with the psychine lineage.

In the foregoing discussion, we have adopted the subfamily classification of Sauter & Hättenschwiler (1999) as modified by van Nieukerken *et al.* (2011). That system, although widely accepted and clearly based on extensive morphological observation (Rhainds *et al.*, 2009), is not the result of explicit phylogenetic analysis, and no formal defence has been advanced for the monophyly of its individual subfamilies. Partial evidence on monophyly for a few subfamilies is provided by the three molecular studies to date. The trees in Figs 1B, 1C and 3 each contain

two or four genera, and collectively sample six genera, of the largest subfamily, Oiketicinae. In each tree, the monophyly of Oiketicinae is strongly supported. Monophyly for Arrhenophaninae, for which morphological synapomorphies are known, is strongly supported in the two trees (Figs 1C, 3) that include two genera thereof. In the one tree (Fig. 1B) that includes multiple representatives of Psychinae, this subfamily is monophyletic, but with low support. However, there is strong support for the subclade of psychines that excludes *Luffia* (Tutt).

By contrast, it appears that Naryciinae may be paraphyletic. In each tree there is strong support for a group consisting of Naryciinae alone or Naryciinae plus Taleporiinae, if the latter are sampled. The total sample of genera comprised two for Taleporiinae and four for Naryciinae, including *Kearfottia* Fernald, previously placed in several other families, whose tentative assignment to Naryciinae (Davis & Robinson, 1998) is confirmed here (Fig. 3). In both trees, which include both subfamilies (Fig. 1B, C), Naryciinae are strongly supported as paraphyletic with respect to Taleporiinae: *Diplodoma* Zeller groups with the Taleporiinae instead of with the other Naryciinae. In the one tree that includes two representatives of Epichnopteriginae (Fig. 3), the evidence is ambiguous, possibly because relatively little total sequence was obtained from them (621–2792 bp): under degen1, Epichnopteriginae are monophyletic, albeit with weak support (BP = 68), but under nt123 (Figure S2), the epichnopterigine *Rebelia* Heylaerts is grouped with the representative of Psychinae, also with weak support (BP = 68).

Several unusual aspects of life history in Psychidae have attracted attention from ecologists (Rhainds *et al.*, 2009). All larval psychids live and feed from within a portable case; in a substantial fraction of species, the adult female is wingless (sometimes never leaving the case), dispersal is achieved by larval ballooning, and the larvae are broadly polyphagous. This kind of life history is, in turn, associated with elevated frequency of irruptive population dynamics and with evolution of parthenogenesis (Schneider, 1980; Barbosa *et al.*, 1989; Hunter, 1995; Rhainds *et al.*, 2009). A detailed phylogeny for Psychidae would help in understanding how these syndromes evolve. A step in that direction is suggested by the distribution of female winglessness on the consensus phylogeny for psychid subfamilies (Fig. 4). From this figure, we can infer that female wing condition is to some degree phylogenetically conserved: the arrhenophanine lineage is typically winged, while the psychine lineage is typically wingless. At the same time, we can confidently confirm the conjecture (Yen *et al.*, 2004; Rhainds *et al.*, 2009) that winglessness has evolved repeatedly: multiple subfamilies that may lie phylogenetically intermediate between the two larger lineages contain both female-winged and female-wingless species.

Among-family relationships and monophyly versus paraphyly of Tineoidea.

In the 483-taxon Lepidoptera study of Regier *et al.* (2013), which included 38 tineoids, the Tineoidea were found to be monophyletic with 98% bootstrap support under nt123 (Fig. 2, inset). By contrast, under degen1 (non-synonymous change only), Tineoidea are maximally paraphyletic, the families forming a phylogenetic 'comb' leading up to the remaining Ditrysia. Regier *et al.* (2013) conclude that the monophyly of Tineoidea under nt123 is an artifact of convergent acquisition of similar base composition at sites undergoing synonymous substitution, and that the degen1 tree is more likely to be correct. The evidence for this assertion is as follows. (i) Monophyly under nt123 is critically dependent on inclusion of two taxa, *Eudarcia* and *Compsoctena*. If these are removed, Tineoidea are paraphyletic under both nt123 and degen1. (ii) The base compositions of *Eudarcia* and *Compsoctena* are unusual specifically at sites that undergo synonymous change. When synonymous differences are included (nt123), *Eudarcia* and *Compsoctena* share a base composition that is very divergent from those of most other tineoids, non-ditrysians and basal non-tineoid Ditrysia. In contrast, if synonymous differences are excluded, compositional heterogeneity largely disappears. (iii) Nt123 and degen1 results are in agreement when analyses are restricted to compositionally homogeneous taxa. If phylogenetic analysis is restricted to a subset of taxa among which there are no marked discontinuities or extremes of base composition, tineoid paraphyly is strongly supported by both nt123 and degen1 (figs 5 and 6 of Regier *et al.*, 2013). Paraphyly of Tineoidea is also seen, although with less bootstrap support, in the analysis of Mutanen *et al.* (2010) (Fig. 1C), from which nt3, and hence the great majority of synonymous change, is excluded for all but one gene.

The present results for degen1, based on 62% more exemplars, are closely similar to those of Regier *et al.* (2013) with respect to deeper tineoid relationships, differing only in having: (i) an additional family (Dryadaulidae), weakly supported as sister group to *Doleromorpha* and these two then weakly joined with Eriocottidae; and (ii) somewhat lower bootstrap values for the earliest two 'backbone' nodes but slightly higher support for the node uniting Tineidae with non-tineoid Ditrysia (73/62/66, nodes 3/15/18 in Fig. 3, vs 87/66/64 for the analogous nodes in Fig. 2). The present nt123 results are likewise closely similar to those of the earlier study, with: (i) somewhat lesser but still strong support for tineoid monophyly (BP = 83, Fig. 3, Figure S2, vs BP = 98, Fig. 2); (ii) the same relationships among families, including very strong support for Meessiidae + Eriocottidae; (iii) addition of the new family Dryadaulidae plus the monobasic *Doleromorpha*, placed by nt123 as sister group to Tineidae, with very weak support. There is thus strong reason to believe that monophyly of Tineoidea under nt123 in the present study, as in Regier *et al.* (2013), is an artifact of extensive change and convergence of composition at sites undergoing synonymous substitutions.

The preponderance of molecular evidence, then, favours paraphyly for Tineoidea, and suggests that the comb-like topology characterizing early divergences in Lepidoptera extends up through the initial divergences in Ditrysia. Within Ditrysia, the molecular evidence is strongest for a basal split between Meessiidae and all other ditrysians. Bootstrap support for Ditrysia minus Meessiidae is moderate to strong, i.e. 87% in the 483-taxon study (Fig. 2) and 73% in the current study (Fig. 3, node 3). Support for the next oldest group, Ditrysia minus Meessidae and Psychidae (node 15), is somewhat lower, namely

66% in the 483-taxon study, and 62% in the present study (but rising to 70% following rogue taxon removal). Support for Tineidae plus non-tineoid Ditrysia is 73% in the 483-taxon study and 66% in the present study, rising to 80% following rogue taxon removal.

The molecular evidence as a whole strongly contradicts the morphology-based conclusions of Robinson (1988) and Robinson & Nielsen (1993) concerning both the monophyly of Tineoidea and the composition of and relationships among the tineoid families. The molecular trees therefore require homoplasy in the synapomorphies identified by those authors. For example, Robinson & Nielsen (1993) argue that a group consisting of Eriocottidae, Acrolophidae and Psychidae is 'strongly supported' by seven synapomorphies: bipectinate antennae; reduced or absent maxillary palpi; vein R5 terminating on forewing termen; male retinaculum arising between Sc and costa; female frenulum with supernumerary bristles; thorn-like sensilla at apex of male sacculus; and, male valve with basal pulvillus. By contrast, two independent molecular studies, using both all changes and only or mainly non-synonymous change, find 95–100% bootstrap support for including Acrolophidae in Tineidae sensu novo. Similarly, the molecular trees require homoplasy in the five synapomorphies advanced by Robinson & Nielsen (1993) for Tineoidea, which are frons with erect scales; labial palpus with lateral bristles; proboscis short, uncoiled; telescopic ovipositor; and, ovipositor with ventral rods. The conflict between these two sources of evidence, however, may be more apparent than real. There has, as yet, been no explicit, quantitative phylogenetic analysis with extensive sampling of both morphological characters and exemplars of tineoid subclades as well as other Ditrysia. In the absence of such a study, we regard the molecular tree as the most credible working hypothesis to date.

The finding of probable paraphyly for Tineoidea has implications for their classification. If the precedent established for non-ditrysians were to be followed (Kristensen, 2003; van Nieukerken *et al.*, 2011), each of the five tineoid families identified in this study would merit its own superfamily, because there is no strong support for any grouping consisting of just two or more of these families and no other Ditrysia (Fig. 3). For the moment, however, we decline to propose changes in the superfamily classification, until the number, circumscriptions and relationships among the constituent families are much better clarified. The number of superfamilies of early-arising ditrysians is likely to increase substantially in the future.

Early ecological evolution in Ditrysia

The finding of probable paraphyly for Tineoidea raises the strong possibility that character states pervasive in tineoids reflect the ground plan of Ditrysia. The implications are especially striking for the evolution of larval feeding habits. As illustrated in Fig. 2, most lineages of non-ditrysians, including those most closely related to Ditrysia, live and feed on or within living plants, most often trees or shrubs; many are leaf miners, at least in the early instars. Most are host-specific, feeding on a single plant order, family or subgroup thereof (Menken *et al.*, 2010). The same habits characterize the ditrysian lineages

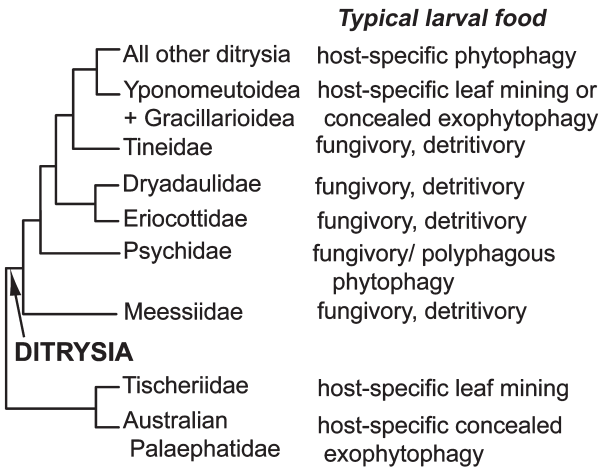

Fig. 5. Phylogenetic synopsis of predominant larval feeding habits in the tineoid lineages, taken mainly from Davis & Robinson, 1998. Topology simplified from Fig. 3.

that branch off immediately after Tineoidea, such as Gracillariidae + Yponomeutoidea. The tineoids depart dramatically from this typical lepidopteran phytophagy, as summarized in Fig. 5. In four of the five families recognized here, containing a majority of tineoid species, the larvae typically live on the ground and feed mostly on detritus and/or fungi including lichens, though some also feed on living higher plants. (It should be noted that some forms of detritivory such as eating keratin could be considered highly specialized, and mycophagous species can be quite host-specific.) Similar non-phytophagous habits are found in at least some species of most subfamilies of Psychidae, and appear predominant in some. The remaining psychids otherwise mostly feed on living higher plants, most often trees and shrubs, but are unusual in being invariably case-bearing external feeders, and are nearly always broadly polyphagous (Rhainds *et al.*, 2009). In an attempt to determine which habit, fungivory or phytophagy, was likely ancestral for this family, we plotted the available information on larval habits onto the consensus phylogeny of psychid subfamilies (Fig. 4). It appears that the arrhenophanine lineage is mostly or entirely non-phytophagous. Species in the psychine lineage are typically polyphagous vascular plant feeders, although some are known to eat lichens or detritus. Lichen feeding and polyphagous vascular plant feeding are both common in Naryciinae + Taleporiinae. The phylogeny resolution and feeding habit detail are not yet sufficient to allow a strong statement about the ancestral condition, but it is clear that fungivory and generalized phytophagy are both plausible candidates. Both are found throughout much of psychid evolution, and it seems likely that there have been multiple transitions between them.

The ground-dwelling, non-phytophagous or mixed habits prevalent in tineoids resemble, to some degree, Hepialoidea (including Mnesarchaeoidea) as well as Micropterigidae, and may approximate those of the ancestral panorpid (Kristensen, 1997). The repeated occurrence of such habits has prompted the hypothesis that they represent the ancestral condition

through the early history of Lepidoptera, up to and including the tineoids, and have given rise multiple times independently to the lepidopteran-typical condition of specialized feeding on higher plants (e.g., Grehan, 1989). The widely accepted counter-argument (Kristensen, 1997; Powell *et al.*, 1998; Menken *et al.*, 2010) has been that assuming an early origin of strict phytophagy, with a few reversions to scavenging, is more parsimonious, because the alternative requires a substantially larger number of evolutionary changes (up to seven), of an arguably less likely kind (origins of phytophagy).

While this argument still holds for non-ditrysians, it now appears that the ancestral ditrysians may not have been primarily phytophagous, but rather may have gone through an extended phase in which larval life history resembled that of the earliest lepidopterans. Figure 5 presents a simplified, provisional synopsis of the predominant, potentially ancestral larval feeding habits of the main early-diverging lineages of Ditrysia, based primarily on Davis & Robinson (1998). On this phylogeny we can distinguish two broad feeding habit categories or character states: typical lepidopteran phytophagy, i.e. at least somewhat host-specific feeding on higher plants, characterizing all non-tineoids; and, fungivory/detritivory, here assumed to characterize four of the five tineoid families, with the ancestral state for Psychidae uncertain. Parsimony mapping (not shown) favours fungivory/detritivory as the ancestral state for Ditrysia if this condition is assigned to the psychid ground plan, or if the latter is viewed as undetermined. If the psychid ground plan is assigned 'typical lepidopteran phytophagy' (a doubtful proposition, given the unusual nature of psychid phytophagy), the two hypotheses for the ancestral feeding habits of Ditrysia become equally parsimonious. Much additional gene and taxon sampling is needed to test this hypothesis conclusively, but it seems likely that the specialized phytophagy now dominant among lepidopteran species re-evolved later in ditrysian history. Alternatively, it could be that evolutionary shifts between fungivory/detritivory and typical phytophagy occurred so often during early ditrysian evolution that the ancestral condition can no longer be determined. In either case, the nature of feeding habit evolution during the early existence of Ditrysia would have been markedly different from that in the intervals immediately before and afterwards. Why the ditrysian lineage would have passed through a phase of prevailing fungivory/detritivory, before undergoing such spectacular secondary radiation on higher plants, is not obvious.

Descriptions of new families

Illustrations of the adults and larvae of *Eudarcia*, *Bathroxena*, *Dryadaula* and *Doleromorpha*, discussed earlier as definitely or possibly belonging to new families, are provided in Figs 6–11.

Meessiidae new status

Meessiinae Zagulyaev, 1958, Ent Obozr 37: 920. Nomen nudum. Type genus: *Meessia* Hofmann, 1898.

Meessiinae Căpuşe, 1966. Tijdschr. Ent. 109: 106. Type genus *Meessia* Hoffmann, 1898.

Meneessiini Zagulyaev, 1977, Ent. Obozr. 56: 663. Type genus: *Meneessia* Zagulyaev, 1974.

The subfamily name Meessiinae first appeared in print as a footnote in a paper by Zagulyaev (1958) but without a formal description or designation. The name was first formally proposed and described by Căpuşe (1966).

Adult (Fig. 6A). Small moths with wingspans ~5–12 mm. Forewings relatively slender, with tapering, subacute apices. Venation of hindwing reduced, M3 absent. Male genitalia symmetrical. Female oviscapt long and extensible with posterior apophyses nearly 3× the length of anterior apophyses.

Head (Fig. 7A, B). Vestiture rough; frons and vertex densely covered with long, piliform scales with acute apices. Antenna simple, approximately 0.85–1.0× the length of forewing; antennal pecten present, with up to 20 bristles; each flagellomere covered with two annuli of appressed scales. Eyes relatively small, interocular index (Davis, 1975) ~0.6. Mouthparts well developed; pilifers and mandible greatly reduced; haustellum more than half the length of labial palpus; maxillary palpus elongate, five-segmented and folded, occasionally with one to two additional segments in *Eudarcia*, with ratios from base ~1.0:0.8:1.6:4.8:3.3; labial palpus slightly shorter in length than haustellum; second segment of labial palpus with lateral and apical bristles.

Thorax. Forewing relatively slender (Fig. 7C); forewing length/width (L/W) ratio ~3.9–4.3; with seven separate and two forked veins usually arising from discal cell, excluding Sc, which is located at extreme base of cell; R arising near basal third to half of cell; Rs1 and Rs2 stalked; Rs 3 and Rs4 either separate or stalked; Rs4 terminating slightly above wing apex; chorda absent; discal cell narrow, with discocellular cross-vein very weak in *Bathroxena*; base of M poorly developed within cell; M unbranched within cell; M with M1 and M2 fused; CuP weak; A1 + A2 either with basal loop; retinaculum of male apically curled and arising from base of Sc. Metafurcasternum with furcal apophyses free, slender and directed slightly caudad. Hindwing more slender than forewing in width; L/W index ~4.1–5.1; four veins typically arising separate from distal region of discal cell; discal cell narrow and poorly defined; discocellular cross-vein incomplete; base of M usually distinct; M two-branched with M3 lost, possibly by fusion with M2; CuP absent; 1A + 2A weak or absent; 3A either present or absent; frenulum a single long bristle in male; female with two frenula. Foreleg with epiphysis present.

Abdomen. Sternum VIII of male unmodified; coremata from segment VIII of male absent. Female without corethrogyne.

Male genitalia (Fig. 7D–G). Uncus varying from simple and subacute in *Eudarcia* to deeply bilobed in *Bathroxena*; gnathos either bell-shaped in *Bathroxena* or U-shaped in *Eudarcia* with lateral arms sometimes spinose; vinculum broadly V-shaped

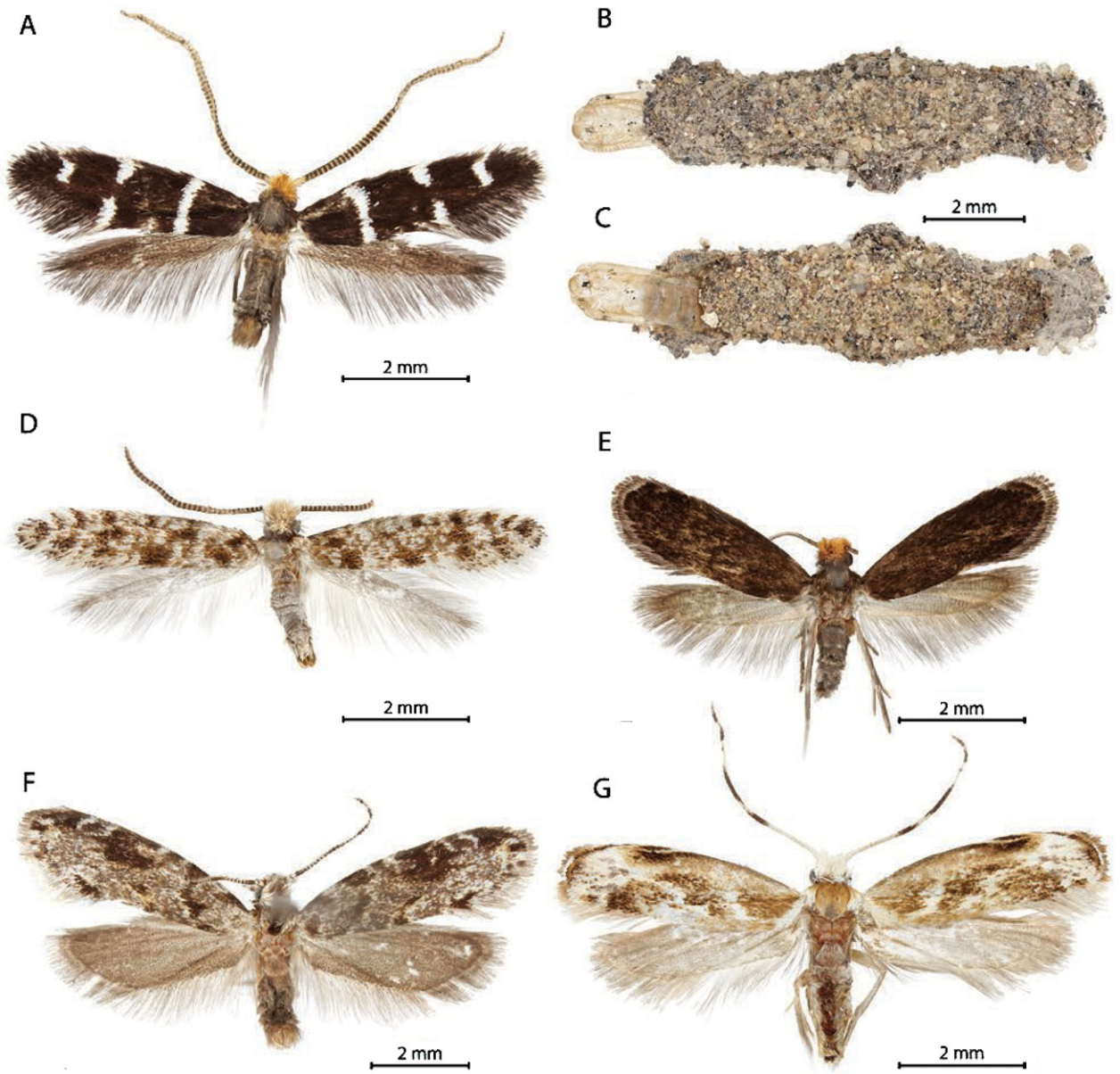

Fig. 6. Adult moths and larval cases. (A) *Eudarcia simulatricella* Clemens; (B) *Eudarcia simulatricella* larval case, dorsal view; (C) larval case, ventral view; (D) *Bathroxena heteropalpella* (Dietz); (E) *Doleromorpha porphyria* Braun, 1930; (F) *Dryadaula visaliella* (Chambers); (G) *Dryadaula terpsichorella* (Busck).

in *Eudarcia*, with a slender, elongate saccus in *Bathroxena*; valva symmetrical, highly variable from simple to with prominent saccular lobes; aedeagus usually simple and cylindrical, elongate and sinuate in *Bathroxena*, with cornuti sometimes present.

Female genitalia (Fig. 7H). Oviscapt long and extensible with posterior apophyses up to 2.0–2.5× length of anterior apophyses; ostium bursae located near anterior margin of sternum VIII; antrum usually short and triangular or more elongated; ductus bursae lined with microspicules; corpus bursae slender to elliptical; a single signum present in *Bathroxena* or absent in *Eudarcia*.

Discussion. The most recent review of the former Meessiinae (Robinson, 2009) listed 35 genera and 248 species for the world. As Gozmány & Vári (1973), Robinson (2009) and others have noted, no morphological synapomorphies are known to define this probably polyphyletic group. Most genera formerly included in Meessiinae shared typical tineid family features

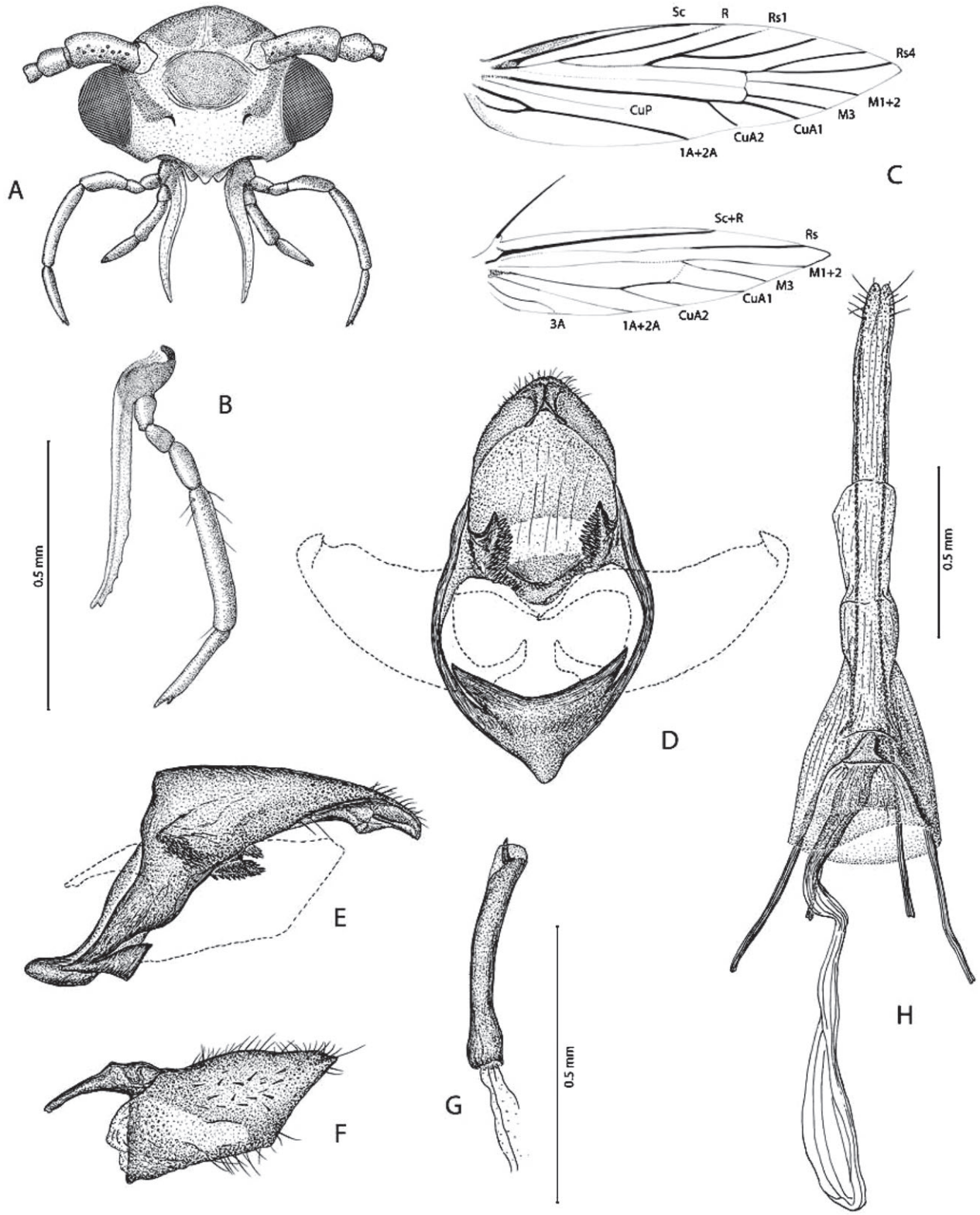

Fig. 7. Adult morphology, *Eudarcia simulatricella* Clemens: (A) head, anterior view; (B) left maxilla, anterior view; (C) wing venation; (D) male genitalia, ventral view; (E) male genitalia, lateral view; (F) male valva, mesal view; (G) Aedeagus; (H) female genitalia, ventral view.

such as heads with erect piliform setae and labial palpi with lateral bristles. Those with slender wings, associated with reduced venation, were usually assigned to this subfamily. Of the 35 genera listed by Robinson, seven were included and sequenced in the current study. Of the seven, four (*Homosetia*, *Hybroma*, *Leucomele*, and *Oenoe*) were found to associate with other generic groupings within Tineidae sensu stricto; one (*Doleromorpha*) was grouped strongly with the new family Dryadaulidae; and two (*Eudarcia* and *Bathroxena*) were found to be even further removed from Tineidae than Dryadaulidae. We regard *Eudarcia* and *Bathroxena* as the only confirmed members of Meessiidae as defined here, while membership in the new family is explicitly rejected for the other five former Meessiinae examined here. The remaining 28 genera formerly assigned to Meessinae should be regarded as incertae sedis until they can be tested for membership in Meessiidae **stat. rev.**

Robinson & Nielsen (1993) listed 14 generic synonyms under *Eudarcia*, including *Meessia*, which had been synonymized earlier by Davis (1983). The closely related genera *Eudarcia* and *Bathroxena* share significant larval synapomorphies which unfortunately cannot be compared with any of the other 28 genera previously assigned to Meessiinae because the larval morphology of these remains either unknown or poorly studied. Sakai & Saigusa (1999) published the only detailed report on the immature stages of a species of *Eudarcia*, using the name *Obesoceras orbiculidomus*. The illustrations of the pupae of *Eudarcia orbiculidomus* show the absence of dorsal abdominal spines, whereas most Tineidae have such spines. Larvae of *Eudarcia simulatricella* Clemens and *Bathroxena heteropalpella* (Dietz) have been collected near Washington, D.C., USA, and studied by D. R. Davis. Larvae of both genera feed from within portable cases (Fig. 6B, C) on small, crustose lichens that are usually found on sandstone rocks. The cases are typically covered with granules of sand and lichen fragments. The opening of the case is relatively broad and laterally oblique, creating a cover over the larval head. As a special adaptation for life largely concealed within the larval case, the larvae of both *Eudarcia* and *Bathroxena* have evolved greatly elongated tactile setae (Fig. 8G, H), projecting anteriorly from the pronotum (seta L1) and posteriorly from the anal plate (seta SD1). The prothorax is also unusual in both genera in having the lateral plate and spiracle fused to the pronotum, a specialization also developed in Psychidae. The larval head (Fig. 8A–F) is unspecialized with five to six stemmata and six well-developed labral setae. Larvae of both genera have also evolved a stout comb of specialized frass-flicking setae (Figs 8G, H, 9A, B) located immediately dorsal to the anal opening (Dominguez-Romero, 1996). The development and utilization of these setae constitutes the earliest known appearance of this behavioural specialization in the Lepidoptera. As discussed by Weiss (2003), at least 17 families of Lepidoptera with larvae living within restricted spaces have evolved such setae, to ballistically eject their faecal pellets great distances away from their feeding site, thereby eliminating chemical cues for natural enemies. In addition to the relatively prominent, primary comb of setae located dorsad of the anal opening, the larvae of both *Eudarcia* and *Bathroxena* possess a pair of smaller, secondary anal combs (Figs 8G, H, 9A–D) located ventrad to the anal opening and dorsad to each anal proleg. The function of these secondary combs has not been observed, but possibly they assist the primary comb in frass ejection.

As research on the immature stages and relationships of the other genera formerly assigned to Meessiinae proceeds, it will be interesting to discover whether the unusual larval morphology and behaviour of *Eudarcia* and *Bathroxena* are typical of the new family Meessiidae, or whether they are instead synapomorphies supporting the monophyly of a subgroup therein.

Dryadaulidae new status

Dryadaulinae Bradley, 1966, Entomologist's Gaz. 17: 218. Type genus: *Dryadaula* Meyrick, 1893.

Archimeessiini Zagulajev, 1977, Ent. Obozr. 56: 663. Type genus: *Archimeessia* Zagulajev, 1970.

Adult (Figs 6F, G, 10). Small moths with wingspans ~7–13 mm. Forewings slender, with moderately broad, subacute apices. Venation of hindwing reduced, M3 absent. Male genitalia typically with asymmetrical valvae. Female oviscapt greatly reduced in length; anterior apophyses usually absent, or greatly reduced.

Head (Fig. 10A, B). Vestiture rough; frons and vertex densely covered with long, piliform scales with acute apices. Antennae ~0.7× length of forewing; scape without pecten; flagellomeres with one to two annuli of slender scales. Eyes relatively small, interocular index (Davis, 1975) 0.7–0.8. Pilifers short, rounded, each bearing around four elongate stiff bristles. Mandible reduced, relatively slender, ~equal to third palpal segment in length. Maxillary palpus well developed, five-segmented, with ratios from base ~1.0:0.8:1.2:6.0:1.7; segment 5 (terminal) with subapical vom Rath organ; segment 4 (subterminal) with as many as eight lateral bristles; segment 2 with one to two apical bristles. Haustellum short, ~0.75–1.0× length of labial palpus and 0.6–0.75× the length of maxillary palpus. Labial palpus nearly 2× the vertical diameter of eye, usually divergent; apical segment typically spatulate.

Thorax. Forewing (Fig. 10C) slender, L/W ratio ~3.2–3.4; with 10 veins typically arising separately from discal cell, excluding Sc, which is located at extreme base of cell; R arising near basal third of cell; Rs3 and 4 usually separate, sometimes stalked nearly one-third of their lengths; Rs4 terminating slightly anterior to wing apex; chorda and base of M poorly developed within cell; M either divided or unbranched within cell; CuP very weak; A2 very weak or absent; retinaculum a long, narrow, subcostal fold. Hindwing approximately equal to forewing in width; L/W index ~2.7–3.0; five veins typically arising separately from distal region of discal cell; Rs and M1 sometimes shortly stalked; M two-branched with M3 lost, possibly by fusion with M2; CuP and 1A + 2A weak; 3A either weak or absent; frenulum a single long bristle in

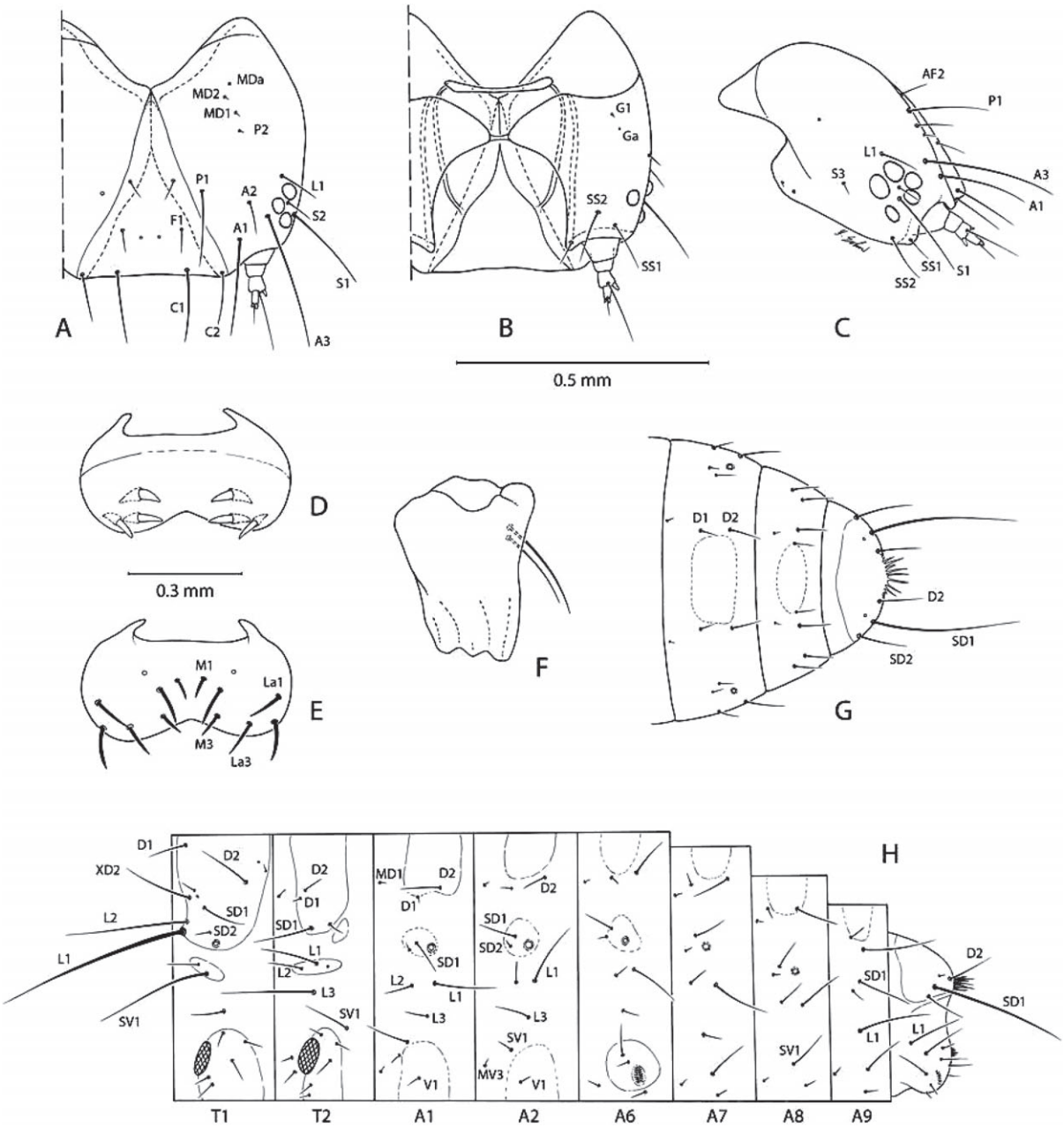

Fig. 8. Larva, *Eudarcia simulatricella* Clemens: (A) head, anterior view; (B) head posterior view; (C) head lateral view; (D) labrum, ventral view; (E) labrum, dorsal view; (F) mandible, mesal view; (G) abdomen, dorsal view of *A8–10*; (H) thorax (segments *T1–2*) and abdomen (segments A1, 2, 6–10), lateral view.

male; two frenula in female arising from two closely set follicles, with the distal portions of the frenula sometimes contiguous and thus appearing as one. Metafurcasternum with furcal apophyses free, slightly curved forwards. Foreleg with epiphysis present.

Abdomen. Tergum III with a median pocket of androconial scales in males of some *Dryadaula*. Male segment VIII without coremata. Sternum VIII of male (Fig. 10E) partially sclerotized, slightly to greatly asymmetrical and highly modified with various processes, which are often incorporated into the male genitalia; tergum VIII lost or greatly reduced, possibly consisting of a few free sclerites in some species.

Male genitalia (Fig. 10D). Extremely asymmetrical, especially in *Dryadaula.* Uncus bilobed to moderately bifid.

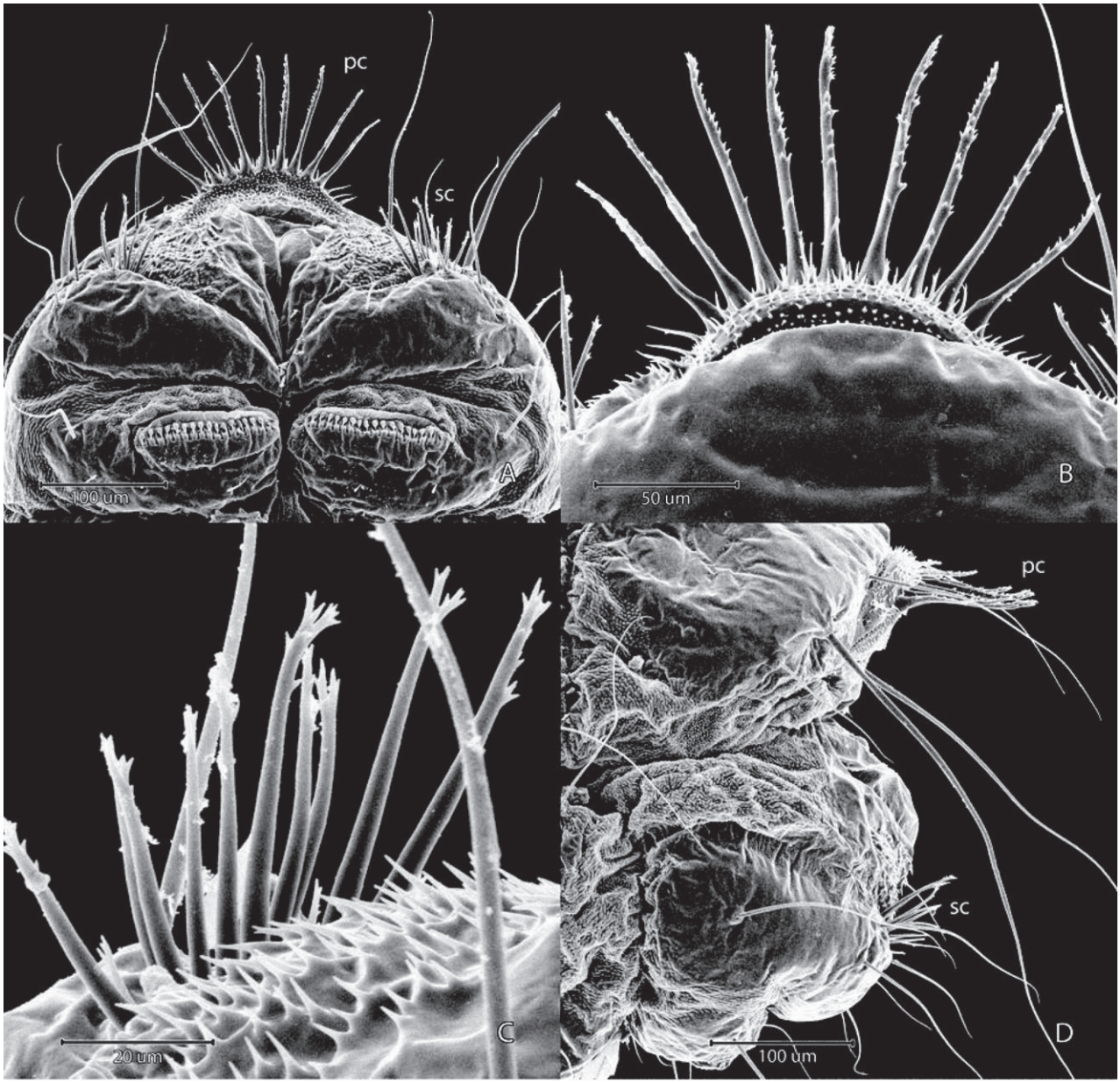

Fig. 9. Larva, *Bathroxena heteropalpella* (Dietz): (A) caudal-ventral view of abdominal segment 10, (pc, primary anal comb; sc, secondary anal comb); (B) primary anal comb of A10, dorsal view; (C) secondary anal comb of A10, caudal-ventral view; (D) lateral view of A10.

Gnathos absent. Vinculum and tegumen fused, usually slender but less commonly with vinculum more broad, U-shaped. Transtilla undeveloped. Valvae extremely asymmetrical and of varying forms between species; left valva enlarged and complex and of highly irregular outline, usually with sacculus and cucullus deeply divided; right valva usually greatly reduced, often with deeply divided, irregular lobes. Aedeagus relatively simple but variable in form between species, usually short and tubular to pyriform and sometimes partially fused to base of right valva; rarely elongate and slender.

Female genitalia (Fig. 10F). Oviscapt greatly reduced, less than 0.05× length of abdomen; anal papillae a pair of short, rounded to sometimes partially fused lobes. Posterior apophyses short, ~ equalling the length of shortened sternum VIII. Anterior apophyses usually absent, or extremely reduced and less than half the length of posterior apophyses. Ostium bursae located near caudal margins of either sternum IX or sternum VIII. Ductus bursae slender, elongate; antrum absent. Corpus bursae elliptical to more irregularly elongate, without spicules or signa. Ductus seminalis similar in length and diameter to ductus bursae, usually joining corpus bursae near middle.

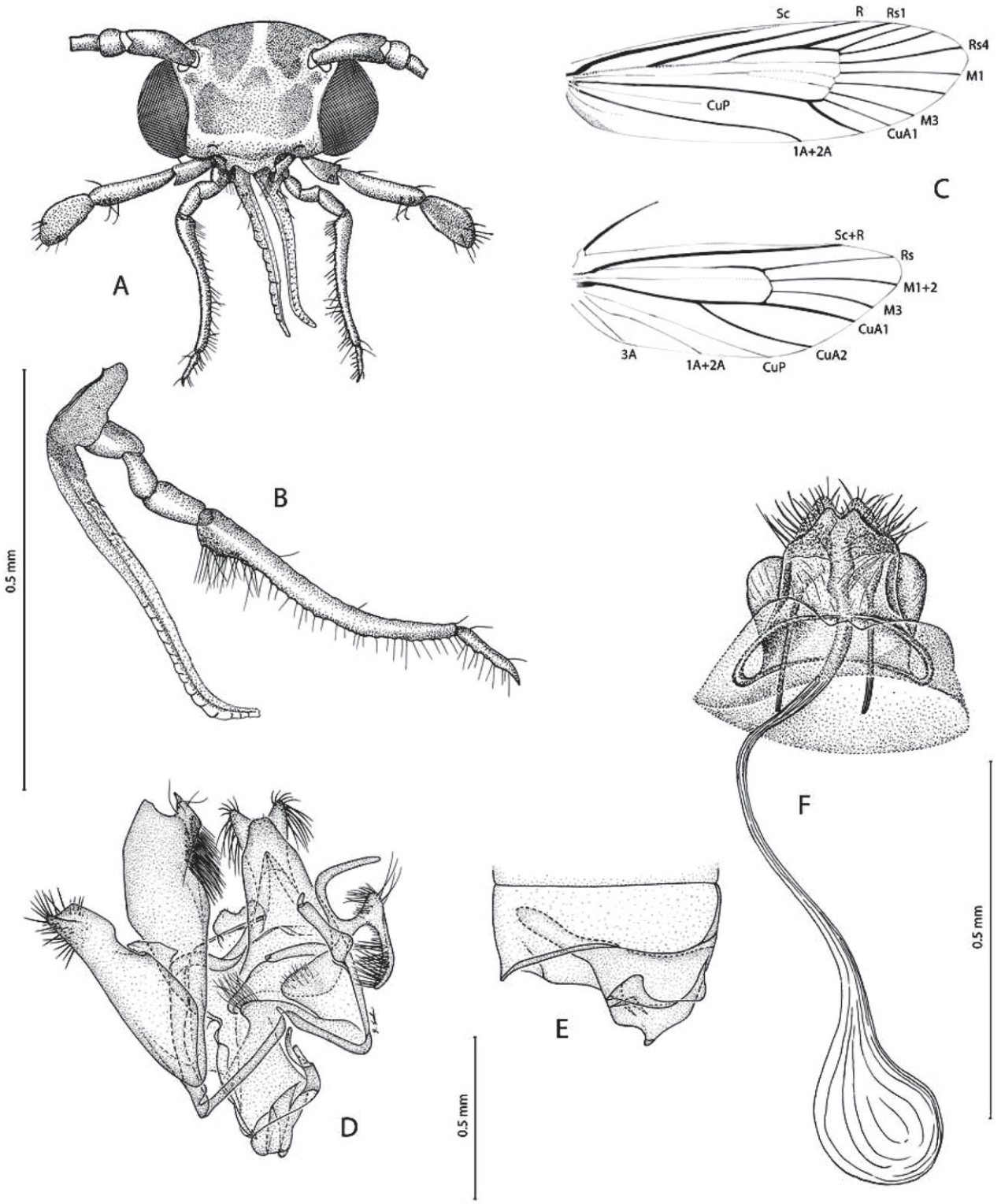

Fig. 10. Adult morphology, *Dryadaula visaliella* (Chambers): (A) head, anterior view; (B) right maxilla, posterior view; (C) wing venation; (D) male genitalia, ventral view; (E) abdominal segment VIII; (F) female genitalia, ventral view.

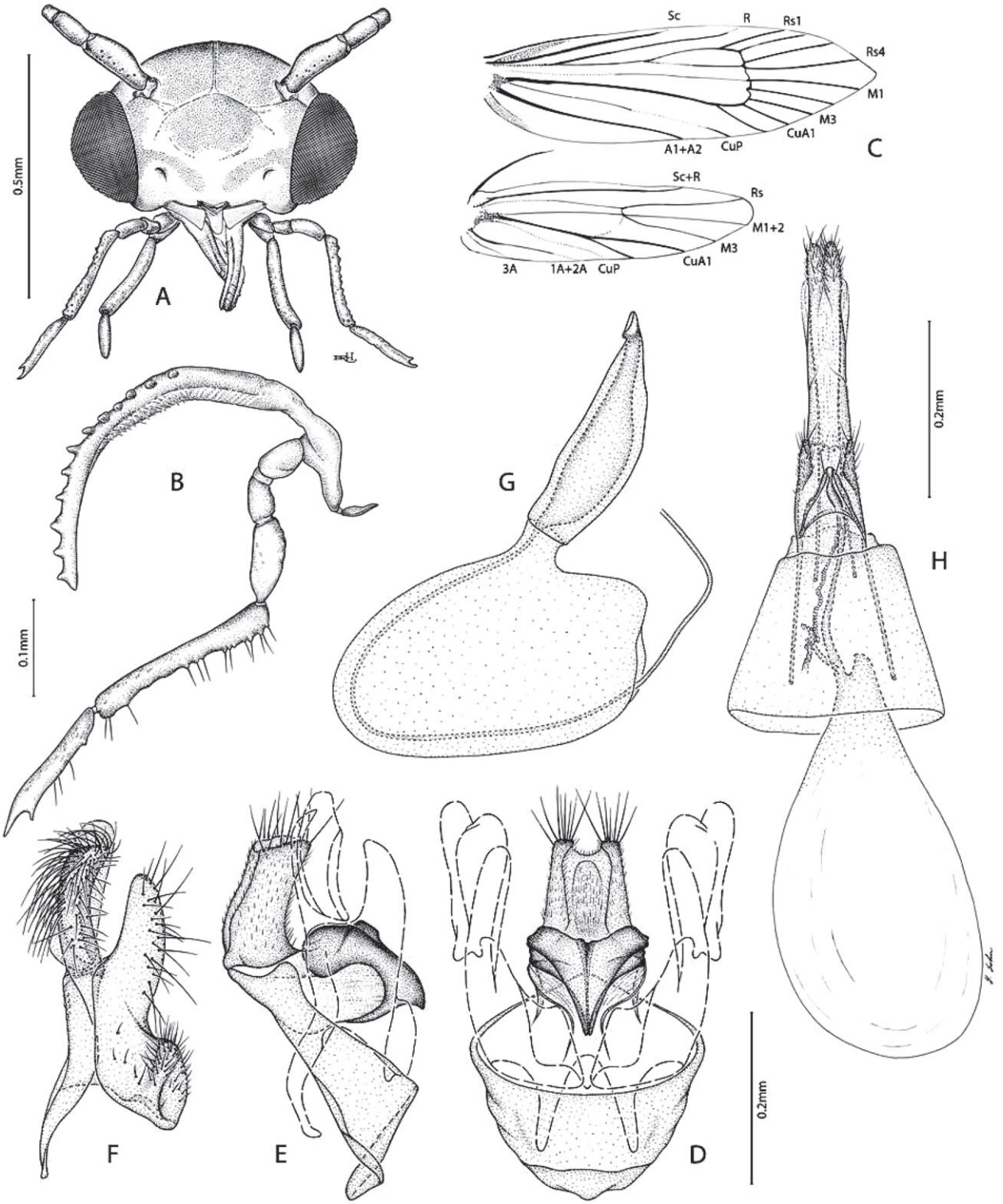

Fig. 11. Adult morphology, *Doleromorpha porphyria* Braun: (A) head, anterior view; (B) left maxilla, anterior view; (C) wing venation; (D) male genitalia, ventral view; (E) male genitalia, lateral view; (F) male valva, mesal view; (G) aedeagus; (H) female genitalia, ventral view.

Discussion. The family Dryadaulidae comprises a small, highly apomorphic group of approximately 50 species, with the great majority of those described within the globally widespread genus *Dryadaula.* Robinson & Nielsen (1993) also considered the Oriental genus *Brachydoxus* to belong to this group and possibly also the New Zealand genera *Eschatotypa*, *Eugennaea*, and *Sagephora.* The distinction of *Dryadaula* from other Tineidae was recognized early by Bradley (1966), who proposed the subfamily Dryadaulinae for this morphologically aberrant genus.

Diagnostic features for the family include the spatulate apical segment of the labial palpi and certain specializations of wing structure, such as the relatively long, narrow male retinaculum and the loss of an M vein (M1 fused with 2) in the hindwing. The eighth abdominal sternum of the male is frequently asymmetrical, often with various processes which can be incorporated into the male genitalia. Some of the most conspicuous specializations are observed in the highly complex, asymmetrical male genitalia, with the right valva typically reduced and the gnathos absent. In some species of *Dryadaula*, the aedeagus is partially fused to portions of the right valva. The female genitalia also differ from most Tineidae, and are similar to Acrolophinae, in being reduced and not extensible; the posterior apophyses are greatly shortened and the anterior apophyses are either vestigial or absent.

Little is known about the biology and immature stages of Dryadaulidae. It is believed that the larvae of most species are general detritivores or feed on lichens and fungi, habits that also are typical of many Tineidae. Larvae of *Dryadaula pactolia* Meyrick have been reported feeding in silk-lined tunnels in mats of a wine cellar fungus, *Rhacodium cellare* Perz. Ex Wall in Britain (Morrison, 1968). Gaedike & Scholz (1998) described the life history and morphology of a new species, *Dryadaula heindeli*, which matches this generic diagnosis closely, and which they interpret as closely related to *D. pactolia*. The larvae develop within the fruiting bodies of the polypore mushroom *Bjerkandera adusta.* An undescribed species of *Dryadaula* has been reared from a rotten log bearing clumps of the polypore mushroom *Trametes versicolor* (L.) Lloyd in the eastern United States by D. R. Davis. Much of what is known about the biology of *Dryadaula* was reviewed by Zimmerman (1978) from previous reports by Swezey (1909) on the life history of the Hawaiian *Dryadaula terpsichorella* (Busck). The larva of this species has been collected from the dead leaves and other parts of various plants, including banana, sugar cane, pineapple, and *Pandanus*. Zimmerman suspected that the larvae fed on arthropod remains. Zimmerman provided illustrations of the larva and pupa of *D. terpsichorella.* The larva appears remarkable in possessing relatively long primary setae, long, slender tarsi, and four stemmata. The abdominal terga of the pupa are smooth and without spines. A cocoon is not constructed, with pupation instead occurring in an irregular network of silk spun on the inner side of a leaf sheath where the larva typically feeds. Adults of *D. terpsichorella* are sometimes referred to as dancing moths (Swezey, 1909; Lee *et al.*, 2014), because of the dance-like gyrations they often display after alighting on a leaf.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12110

Figure S1. Maximum likelihood phylogram with bootstraps for degen1 analysis.

Figure S2. Maximum likelihood cladogram with bootstraps for nt123 analysis (all nucleotide positions).

Table S1. Species sampled, collecting localities, and Genbank numbers.

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