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A molecular phylogeny for the oldest (nonditrysian) lineages of extant Lepidoptera, with implications for classification, comparative morphology and life-history evolution

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Abstract. Within the insect order Lepidoptera (moths and butterflies), the so-called nonditrysian superfamilies are mostly species-poor but highly divergent, offering numerous synapomorphies and strong morphological evidence for deep divergences. Uncertainties remain, however, and tests of the widely accepted morphological framework using other evidence are desirable. The goal of this paper is to test previous hypotheses of nonditrysian phylogeny against a data set consisting of 61 nonditrysian species plus 20 representative Ditrysia and eight outgroups (Trichoptera), nearly all sequenced for 19 nuclear genes (up to 14 700 bp total). We compare our results in detail with those from previous studies of nonditrysians, and review the morphological evidence for and against each grouping The major conclusions are as follows. (i) There is very strong support for Lepidoptera minus Micropterigidae and Agathiphagidae, here termed Angiospermivora, but no definitive resolution of the position of Agathiphagidae, although support is strongest for alliance with Micropterigidae, consistent with another recent molecular study. (ii) There is very strong support for Glossata, which excludes Heterobathmiidae, but weak support for relationships among major homoneurous clades. Eriocraniidae diverge first, corroborating the morphological clade Coelolepida, but the morphological clades Myoglossata and Neolepidoptera are never monophyletic in the molecular trees; both are contradicted by strong support for Lophocoronoidea + Hepialoidea, the latter here including

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Mnesarchaeoidea **syn.n.** (iii) The surprising grouping of Acanthopteroctetidae + Neopseustidae, although weakly supported here, is consistent with another recent molecular study. (iv) Heteroneura is very strongly supported, as is a basal split of this clade into Nepticuloidea + Eulepidoptera. Relationships within Nepticuloidea accord closely with recent studies based on fewer genes but many more taxa. (v) Eulepidoptera are split into a very strongly supported clade consisting of Tischeriidae + Palaephatidae + Ditrysia, here termed Euheteroneura, and a moderately supported clade uniting Andesianidae with Adeloidea. (vi) Relationships within Adeloidea are strongly resolved and Tridentaformidae **fam.n.** is described for the heretofore problematic genus *Tridentaforma* Davis, which is strongly supported in an isolated position within the clade. (vii) Within Euheteroneura, the molecular evidence is conflicting with respect to the sister group to Ditrysia, but strongly supports paraphyly of Palaephatidae. We decline to change the classification, however, because of strong morphological evidence supporting palaephatid monophyly. (viii) We review the life histories and larval feeding habits of all nonditrysian families and assess the implications of our results for hypotheses about early lepidopteran phytophagy. The first host record for Neopseustidae, which needs confirmation, suggests that larvae of this family may be parasitoids.

This published work has been registered in ZooBank: http://zoobank.org/urn:lsid:zoobank.org:pub:C17BB79B-EF8F-4925-AFA0-2FEF8AC32876.

Introduction

Studies of the oldest divergences within the insect order Lepidoptera, based on comprehensive examination of internal as well as external anatomy, represent prominent early applications of Hennigian phylogenetics (Hennig, 1953; Kristensen & Nielsen, 1983; Kristensen, 1984; Davis, 1986; Kobayashi & Ando, 1988; Nielsen & Kristensen, 1996; reviews in Kristensen & Skalski, 1998; Kristensen *et al.*, 2007). In contrast to those of the mega-diverse derived clade Ditrysia, which contains 98% of lepidopteran species (van Nieukerken *et al.*, 2011a), the so-called nonditrysian superfamilies are mostly species-poor but highly divergent in morphology, offering numerous synapomorphies and hence some of the strongest evidence for higher-level relationships in any insect order. Although some points of uncertainty and controversy remain, the well-resolved morphology-based hypothesis of nonditrysian phylogeny by Kristensen (2003b) (Fig. 1A) has been widely accepted. Among the major clades recognized are: Glossata, defined by the haustellate mouthparts typical for the order; Coelolepida, defined principally by hollow wing scales; Myoglossata, defined chiefly by possession of a proboscis with intrinsic musculature; Neolepidoptera, defined by, among other synapomorphies, musculate, crochet-bearing larval abdominal prolegs; Heteroneura, defined broadly speaking by differing venation in the forewings versus hindwings, frenular wing coupling and associated increase in size difference between the pterothoracic segments; and Eulepidoptera, defined by multiple synapomorphies including origin of the pilifers and of an advanced mechanism locking together the two halves of the proboscis.

DNA sequence data have gradually been providing an independent test and additional clarification of the morphological hypothesis. An early two-gene molecular phylogeny for nonditrysians (Wiegmann *et al.*, 2000) (Fig. 1B) strongly supported a majority of the morphology-based deep-level divergences while contradicting none, but taxon sampling was limited. The same is true of a combined analysis of morphology and the 18S rDNA gene (Wiegmann *et al.*, 2002) (Fig. 1C). The first multi-gene estimate of nonditrysian phylogeny was provided by Mutanen *et al.* (2010), who sequenced eight genes (6303 bp total) in 350 lepidopterans, including 24 nonditrysians. They found agreement with the morphological hypothesis (Fig. 1D), as well as several points of discord, but few nodes above the superfamily level were well supported.

In this paper we present a molecular phylogeny for the nonditrysian lineages based on 61 nonditrysian species plus 20 representative Ditrysia and eight outgroups (Trichoptera), nearly all sequenced for 19 nuclear genes (up to 14 700 bp total). The taxon and gene sampling overlap extensively with the 483-taxon estimate of phylogeny across Lepidoptera by Regier *et al.* (2013), but the latter study included five fewer nonditrysians and did not specifically discuss the findings within non-Ditrysia. Here we compare our results in detail with those from previous studies of nonditrysians and review their implications for classification, comparative morphology and the interpretation of early ecological evolution in Lepidoptera. Intense interest in the last was generated by the early phylogenetic analyses of basal lepidopterans. The central question posed is how, when and why this order, arising from a probable soil-dwelling ancestor shared with Trichoptera, has developed into one of the most species-rich animal clades that feed primarily

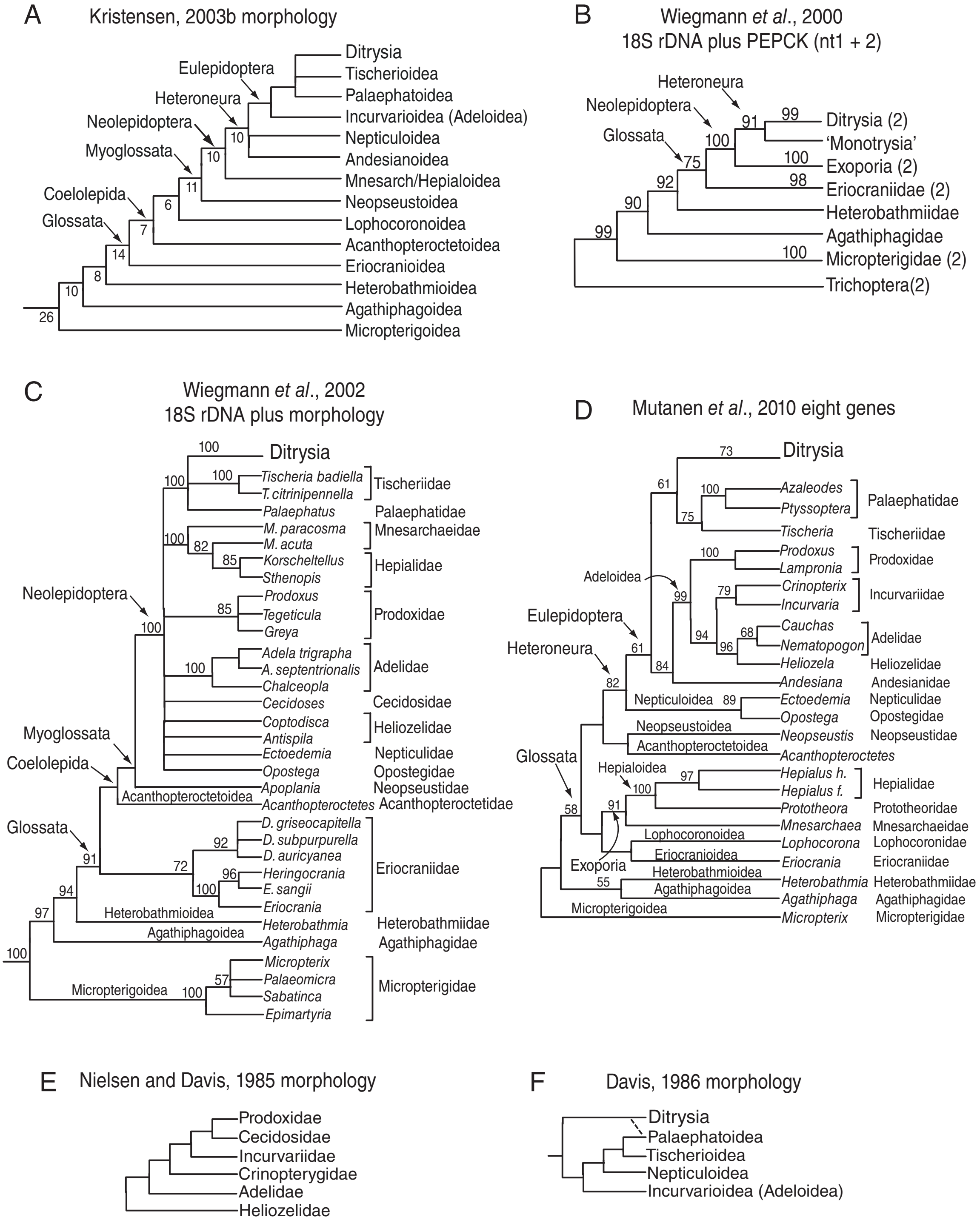


Fig. 1. Previous hypotheses on relationships among nonditrysian lepidopteran lineages. (A) Synopsis of relationships inferred from morphology, redrawn from Kristensen (2003b). Numbers below branches are numbers of synapomorphies hypothesized by Kristensen (1984). (B) Most parsimonious tree for combined 18S rDNA and nt1 + nt2 of PEPCK, from Wiegmann *et al.* (2000). Bootstrap values, when > 50%, above branches; number of exemplar species in parentheses after taxon name if > 1. (C) Most parsimonious tree for combined 18S rDNA and ground-plan morphological traits scored for major clades by Nielsen & Kristensen (1996) and Krenn & Kristensen (2000), from Wiegmann *et al.* (2002). Bootstrap values, when > 50%, above branches. (D) Nonditrysian portion of 350-taxon, eight-gene maximum likelihood tree showing bootstraps (RAXML), when > 50%, from Mutanen *et al.* (2010; their figure ESM 1). (E) Relationships among families of Incurvarioidea (= Adeloidea) inferred from morphology by Nielsen & Davis (1985). (F) Relationships among superfamilies of monotrysian Heteroneura inferred from morphology by Davis (1986).

on higher plants (Kristensen, 1997; Powell *et al.*, 1998; Menken *et al.*, 2010).

Recently, the new monobasic homoneurous family, Aenigmatineidae (included species *Aenigmatinea glatzella* Kristensen & Edwards), was discovered and described from South Australia (Kristensen *et al.*, 2015). Analyses for the present paper did not include the new taxon, but we include discussion of it where relevant. Both studies make use of data from Regier *et al.* (2013), but Kristensen *et al.* (2015) focus almost exclusively on the description and placement of *Aenigmatinea*, whereas we aim for a broad review of the nonditrysian families.

Materials and methods

Taxon and gene sampling

The goal of our molecular study was to estimate relationships among the families and superfamilies of nonditrysian Lepidoptera, as well as the position of Ditrysia among these. The 61 species of nonditrysians included here represent all 14 superfamilies of non-Ditrysia and 21 of the 23 nonditrysian families recognized by van Nieukerken *et al.* (2011a). The two missing families are both monotypic, rarely collected members of Hepialoidea. Three of the taxa, namely two species of *Palaephatus* Davis and one of *Metaphatus* Davis, were obtained and partially sequenced only after the main analyses had been completed, as a further check on the surprising finding of strongly supported nonmonophyly for Palaephatidae. Ditrysia were represented by 20 species spread across lineages suggested by recent studies (Regier *et al.*, 2009, 2013; Mutanen *et al.*, 2010) to have diverged relatively early in lepidopteran evolution. Eight species of Trichoptera, representing eight families and six superfamilies, served as outgroups. The nonditrysian species sampled and their distribution across the new family classification proposed in this paper are shown in Table 1. The complete list of specimens included and their distribution across the previous classification of van Nieukerken *et al.* (2011a) are given in Table S1.

Specimens for this study, obtained with the kind help of collectors around the world (see the Acknowledgements section), are stored in 100% ethanol at −85°C as part of the ATOLep collection at the University of Maryland. 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 (see Table S1). 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 *c* oxidase subunit 1 (COI) 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.

Most species were sequenced for five protein-coding nuclear gene regions (6.6 kb) shown previously to provide generally strong resolution within superfamilies. To increase resolving power for relationships among superfamilies, in nearly all species (about 90%) we sequenced an additional 14 genes, for a total of 14.7 kb. Gene names/functions and full lengths of the individual gene regions are given in Table S1 of Cho *et al.* (2011). Four species were sequenced instead for a subset of eight of the 19 genes, chosen for its relatively high amplification success rates and phylogenetic utility in specimens that were too small or too degraded to be reliably sequenced for all 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 accession and GenBank numbers for these sequences can be found in Table S1.

Generation and analysis of DNA sequence data

A detailed protocol of all laboratory procedures is provided by Regier *et al.* (2008c). Further descriptions, including gene amplification strategies, PCR primer sequences and sequence assembly and alignment methods can be found in Regier *et al.* (2008a,b,c, 2009). Three distinct data sets that include all sequences were constructed. The first consists of nucleotides from all three nucleotide positions (nt123). The second (nt123_partition) contains the same nucleotides, but with these partitioned into two nonoverlapping character sets that separate nonsynonymous-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]. 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 (degen1) is based on the degen1 approach of Regier *et al.* (2010; see also Zwick *et al.*, 2012; http://www.phylotools.com), which eliminates nonsynonymous change. The substitution model used in all analyses was GTR + gamma + 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.

All phylogenetic analyses were based on the maximum likelihood (ML) criterion as implemented in Genetic Algorithm for Rapid Likelihood Inference (GARLI) v1.0; 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 an optimal tree consisted of 970–1000 GARLI runs, whereas bootstrap analyses consisted of 708–750 pseudo-replicates, each based on 15 heuristic search replicates. Optimal-tree searches and bootstrap analyses were parallelized using Grid computing (Cummings & Huskamp, 2005) through the Lattice Project (Bazinet & Cummings, 2009). For consistency in the

Table 1. Nonditrysian Lepidoptera species sampled, with a revised family classification of extant nonditrysian Lepidoptera.

Order **Lepidoptera** Linnaeus (15 578/157 424)
Superfamily **Micropterigoidea** Herrich-Schäffer
  Family **Micropterigidae** Herrich-Schäffer (23/265+): *Epimartyria pardella* (Walsingham); *Micropterix calthella* (Linnaeus); *Sporaphaga costaricensis* Wagner & Davis; *Sabatinca chalcophanes* (Meyrick); *Zealandopterix zonodoxa* (Meyrick)
Superfamily **Agathiphagoidea** Kristensen
  Family **Agathiphagidae** Kristensen (1/2): *Agathiphaga queenslandensis* Dumbleton
Clade **Angiospermivora** Regier *et al.* **nov** (all following taxa)
 Superfamily **Heterobathmioidea** Kristensen & Nielsen
  Family **Heterobathmiidae** Kristensen & Nielsen (1/10): *Heterobathmia pseuderiocrania* Kristensen & Nielsen
Clade **Glossata** Fabricius (all following taxa)
 Superfamily **Eriocranioidea** Rebel
  Family **Eriocraniidae** Rebel (7/30): *Dyseriocrania griseocapitella* (Walsingham); *Eriocraniella aurosparsella* (Walsingham); *Eriocrania semipurpurella* (Stephens); *unidentified sp.*
Clade **Coelolepida** Nielsen & Kristensen (all following taxa)
 Superfamily **Lophocoronoidea** Common
  Family **Lophocoronidae** Common (1/6): *Lophocorona astiptica* Common, 1973
 Superfamily **Hepialoidea** Stephens
  Family **Mnesarchaeidae** Eyer (1/14): *Mnesarchaea acuta* Philpott
  Family **Hepialidae** Stephens (69/629): *Phymatopus hectoides* (Boisduval); *Callipielus arenosus* Butler; *Elhamma australasiae* (Walker); *Gazoryctra mathewi* (Edwards); *Korscheltellus gracilis* (Grote); *Oxycanus dirempta* (Walker); *Sthenopis argenteomaculatus* (Harris); *Trictena argyrosticha* Turner
  Newly synonymized with Hepialidae:
   Palaeosetidae Turner (4/9): *Ogygioses* Issiki & Stringer sp.
   Prototheoridae Meyrick (1/12): *Prototheora* Meyrick sp.
   Neotheoridae Kristensen (1/1): not sampled
   Anomosetidae Tillyard (1/1): not sampled
 Superfamily **Neopseustoidea** Hering
  Family **Neopseustidae** Hering (4/13): *Apoplania valdiviana* Davis & Nielsen; *Neopseustis meyricki* Hering
  Family **Aenigmatineidae** Kristensen & Edwards (1/1): not sampled
  Family **Acanthopteroctetidae** Davis (2/8): *Acanthopteroctetes unifascia* Davis
Clade **Heteroneura** Tillyard (all following taxa)
 Superfamily **Nepticuloidea** Stainton
  Family **Nepticulidae** Stainton (12/852): Nepticulinae Stainton: *Enteucha acetosae* (Stainton); *Enteucha basidactyla* (Davis); *Pectinivalva* Scoble sp. B; *Stigmella anomalella* (Goeze); Trifurculinae Scoble: *Ectoedemia (Ectoedemia) populella* Busck; *Ectoedemia (Fomoria) hypericella* (Braun); *Trifurcula pallidella* (Duponchel)
  Family **Opostegidae** Meyrick (7/194): *Opostega* Zeller **sp.n.**; *Opostega sp.2*; *Pseudopostega quadristrigella* (Frey & Boll)
Clade **Eulepidoptera** Kiriakoff (all following taxa)
 Superfamily **Andesianoidea** Davis & Gentili
  Family **Andesianidae** Davis & Gentili (1/3): *Andesiana lamellata* Gentili
 Superfamily **Adeloidea** Bruand
  Family **Cecidosidae** Bréthes (6/16): *Cecidoses eremita* Curtis; *Dicranoses capsulifex* Kieffer & Jörgensen
  Family **Prodoxidae** Riley (8/97): *Lampronia aenescens* (Walsingham); *Prodoxus decipiens* Riley; *Tegeticula yuccasella* (Riley)
  Family **Tridentaformidae Davis fam.n.** (1/1)**:** *Tridentaforma fuscoleuca* (Braun)
  Family **Incurvariidae** Spuler (12/51): Crinopteriginae Spuler: *Crinopteryx familiella* Peyerimhoff; Incurvariinae Spuler: *Perthida* Common sp. Canberra, *Vespina quercivora* (Davis)
  Family **Heliozelidae** Heinemann & Wocke (12/124): *Antispila voraginella* Braun; *Heliozela aesella* Chambers
  Family **Adelidae** Bruand (5/294): Nematopogoninae Nielsen: *Nematopogon magna* (Zeller); Adelinae Bruand: *Adela trigrapha* Zeller; *Cauchas simpliciella* (Walsingham); *Nemophora* Illiger & Hoffmannsegg sp.
Clade **Euheteroneura** Regier *et al.* **nov.** (all following taxa)
 Superfamily **Tischerioidea** Spuler
  Family **Tischeriidae** Spuler (3/112): *Astrotischeria* Puplesis & Diškus **sp.n.**; *Coptotriche malifoliella* (Clemens); *Tischeria ekebladella* Bjerkander;
 Superfamily **Palaephatoidea** Davis
  Family **Palaephatidae** Davis (7/57): *Azaleodes micronipha* Turner; *Metaphatus ochraceus* Davis; *Palaephatus dimorphus* Davis; *Palaephatus pallidus* Davis; *Palaephatus luteolus* Davis; *Ptyssoptera* Turner sp.
Clade **Ditrysia** Börner (29 superfamilies)

Numbers in parentheses are number of genera/number of species.

characterization of results, we will refer to bootstrap support of 70–79% as ‘moderate’, 80–89% as ‘strong’ and ≥ 90% as ‘very strong’.

Post hoc addition of taxa and genes for South American Palaephatidae

The foregoing description applies to the 86 taxa originally included in the study. A striking finding from those initial analyses (Fig. 2) and from Regier *et al.* (2013) was nonmonophyly of Palaephatidae. The two Australian palaephatid genera were grouped very strongly with Tischeriidae, to the exclusion of *Palaephatus luteolus* Davis, whereas the latter was strongly supported as sister group to Ditrysia. This surprising result raised the question of where the remaining palaephatid genera would fall. Moreover, because of the outcome’s potential importance for a key node in lepidopteran phylogeny, it seemed desirable to expand the sampling of *Palaephatus* beyond a single specimen (albeit securely identified) amplified for only five genes, of which one (DDC) yielded no sequence. We searched for additional palaephatids in an accession of 20-year-old unsorted material from Chile in the ATOLep collection and found one specimen each of *Palaephatus dimorphus* Davis, *Palaephatus pallidus* Davis, and *Metaphatus ochraceus* Davis. We attempted reverse transcription polymerase chain reaction amplification of our standard five genes for these, but were able to obtain sequence for only two, CAD (about 900 bp) and wingless (about 300 bp). We then sought additional sequence from the specimen of *P. luteolus* by including it in a pilot study applying transcriptome RNA-Seq to lepidopteran phylogeny (Bazinet *et al.*, 2013). An Illumina Hi-Seq 1000 was used to generate 100-bp paired-end reads of mRNA. After assembly of transcript fragments using Trinity (Grabherr *et al.*, 2011), we were able to retrieve homologues to 13 of the 14 additional Sanger sequences obtained in the initial study, plus a partial sequence of DDC, using GENEIOUS PRO v5.6.6. The alignments of these additional taxa and genes were checked using MUSCLE (http://www.ebi.ac.uk/Tools/msa/muscle/) and were added to the existing matrix of sequences using SEAVIEW (downloaded from http://pbil.univ-lyon1.fr/software/seaview.html). We assessed the phylogenetic effects of adding the new taxa and gene sequences to both the five-gene and 19-gene analyses of the 86-taxon data set, and of adding the 14 new genes for *P. luteolus* to the 19-gene analyses of the 483-taxon data set of Regier *et al.* (2013). The additional sequences from derived from Illumina sequencing are given in File S1.

Results

The results of the phylogenetic analyses of the original 86-taxon data set are summarized in Fig. 2, which presents the 19-gene degen1 ML topology along with bootstrap values for the other analyses of that data set. The ML topologies and bootstraps for the other 86-taxon analyses are shown in Figures S1–S3. The topologies in the present 19-gene, 86-taxon analyses are identical to those in the corresponding 19-gene, 483-taxon analyses of Regier *et al.* (2013). The bootstrap values are nearly identical as well. The only notable exceptions are that bootstrap support for grouping Lophocoronidae with Exoporia is somewhat higher for 86 taxa than for 483 taxa (69/96/96 vs 58/80/81, degen1/nt123/nt123_partition), whereas support for *Palaephatus* + Ditrysia is somewhat lower for 86 taxa than for 483 taxa (75/90/87 vs 92/97/94).

A majority of the major clades in the morphological hypothesis, though not all, are corroborated by the molecular data. In the morphological tree of Fig.1A, there are 13 nodes that subtend two or more superfamilies. Of these, seven received very strong bootstrap support from one or more of our 19-gene analyses: Lepidoptera, Heterobathmioidea + Glossata, Glossata, Exoporia (Mnesarchaeoidea/Hepialoidea), Heteroneura, Eulepidoptera, Tischerioidea + Palaephatoidea + Ditrysia and Ditrysia. One morphological clade, Coelolepida, received only very weak molecular support. Two morphological clades, Lepidoptera minus Micropterigidae and Coelolepida minus Acanthopteroctetidae, were weakly contradicted by the molecular data. Finally, two morphological clades, Myoglossata and Neolepidoptera, were strongly contradicted by the molecular data, specifically by the strong grouping of Lophocoronidae with Exoporia by nt123 (bootstrap percentage [BP = 69]), corroborated, albeit with less support, by degen1 (BP = 69; Fig. 2). Early divergences within Glossata represent the most weakly supported region of the molecular phylogeny.

For one or more nodes within several superfamilies, especially Hepialoidea and Adeloidea, the molecular data were internally inconsistent (Figs 2, 3). In some instances, groupings inferred from nonsynonymous change only (degen1) strongly contradicted those inferred from mostly synonymous change (nt123); there are also examples of strong conflict among genes. The results of adding more taxa and genes for South American Palaephatidae are particularly complex (Fig. 4). The two additional *Palaephatus* species group strongly and consistently with *P. luteolus* in both five-gene and 19-gene analyses, despite having only 1190 bp of sequence. However, with the addition of 14 more genes for *P. luteolus*, the phylogenetic position of *Palaephatus* becomes ambiguous. With all changes (nt123), it remains weakly supported as the sister group to Ditrysia. With synonymous change excluded (degen1), however, Tischeriidae plus the two Australian palaephatids become the sister group to Ditrysia, also with weak support. The position of the remaining added palaephatid, *M. ochraceus*, for which only 1180 bp of sequence were obtained, is also contradictory and ambiguous. In both the five-gene and 19-gene, 89-taxon analyses, *Metaphatus* groups strongly with the Australian palaephatids for nt123 and strongly with *Palaephatus* instead under degen1.

Discussion

In this section, we review the agreement and disagreement of our molecular results with previous hypotheses and previous morphological and molecular evidence. Our account proceeds sequentially through the tree in Fig. 2, following node numbers.

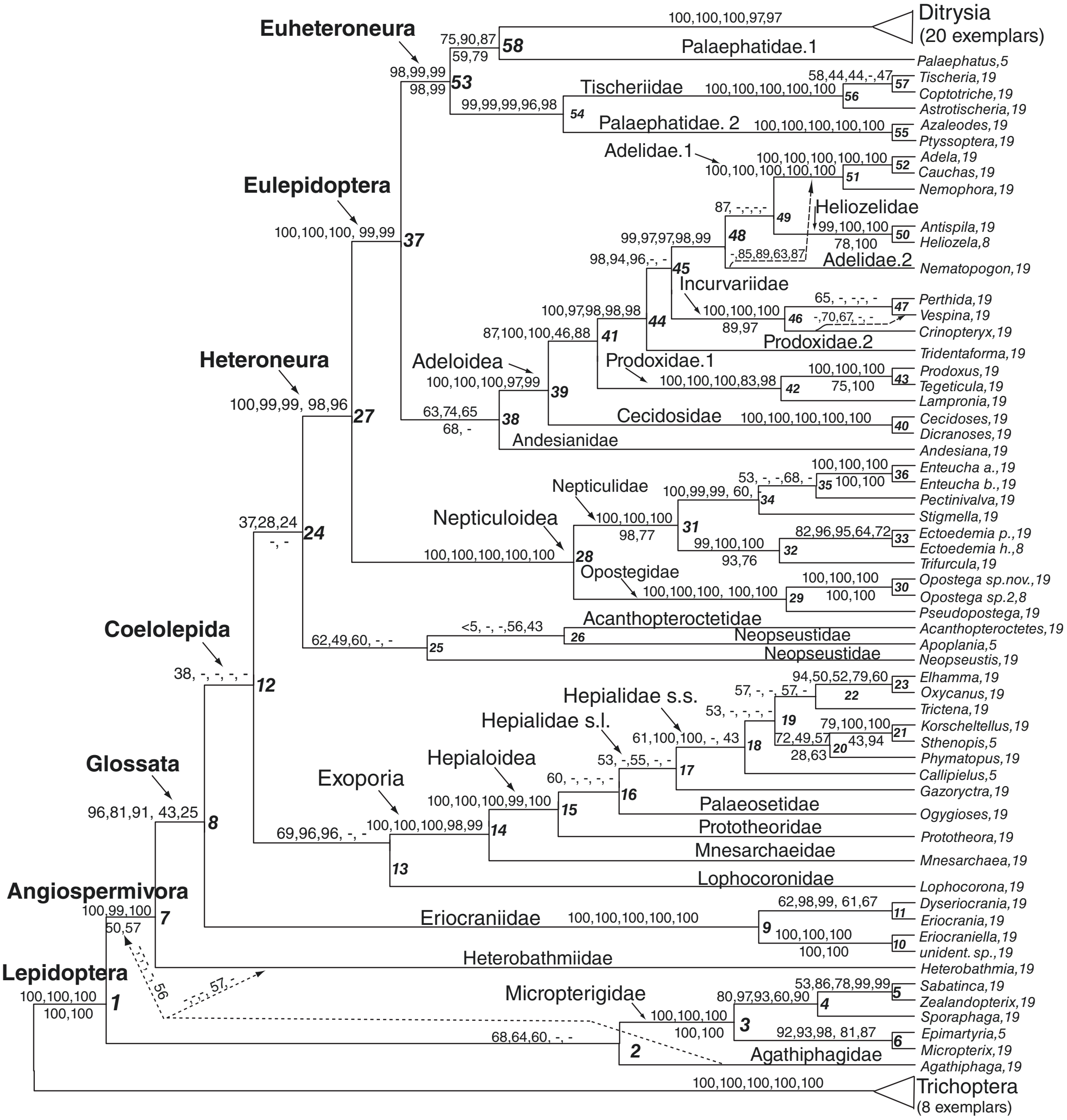


Fig. 2. Maximum likelihood (ML) estimate of phylogenetic relationships among nonditrysian Lepidoptera. Best tree obtained from 1000 GARLI searches under a GTR + gamma + I model for degen1 (nonsynonymous change only). Bootstrap (742–901 replicates) above and/or below branches for: degen1 (19 genes), nt123 (19 genes), nt123_partitioned (19 genes), degen1 (five genes), nt123 (five genes). '–', node not present in ML tree for that analysis. Nodes within Lepidoptera are numbered (to the right of node) for the purposes of discussion. Number of genes sequenced (or attempted) given to right of exemplar name. Family and superfamily names follow van Nieukerken *et al.* (2011a); some have changed as a result of this study (see Table 1).

According to Kristensen *et al.* (2015), the new family Aenigmatineidae is strongly grouped with Acanthopteroctetidae and Neopseustidae (node 26 in our Fig. 2), specifically as sister group to a monophyletic Neopseustidae.

Angiospermivora

Our molecular data strongly support monophyly of Lepidoptera (node 1; BP = 100). They also very strongly support a clade (node 7; BP = 100, degen1) consisting of all lepidopteran families except Micropterigidae and Agathiphagidae. We propose the new name Angiospermivora for this clade, in reference to the fact that it is the most inclusive subset of Lepidoptera in which the larvae feed predominantly on flowering plants. This clade has also appeared strongly corroborated by morphology since first proposed, following the discovery of the heterobathmiid larva (Kristensen & Nielsen, 1983). The latter possesses derived features of the 'typical caterpillar head', such

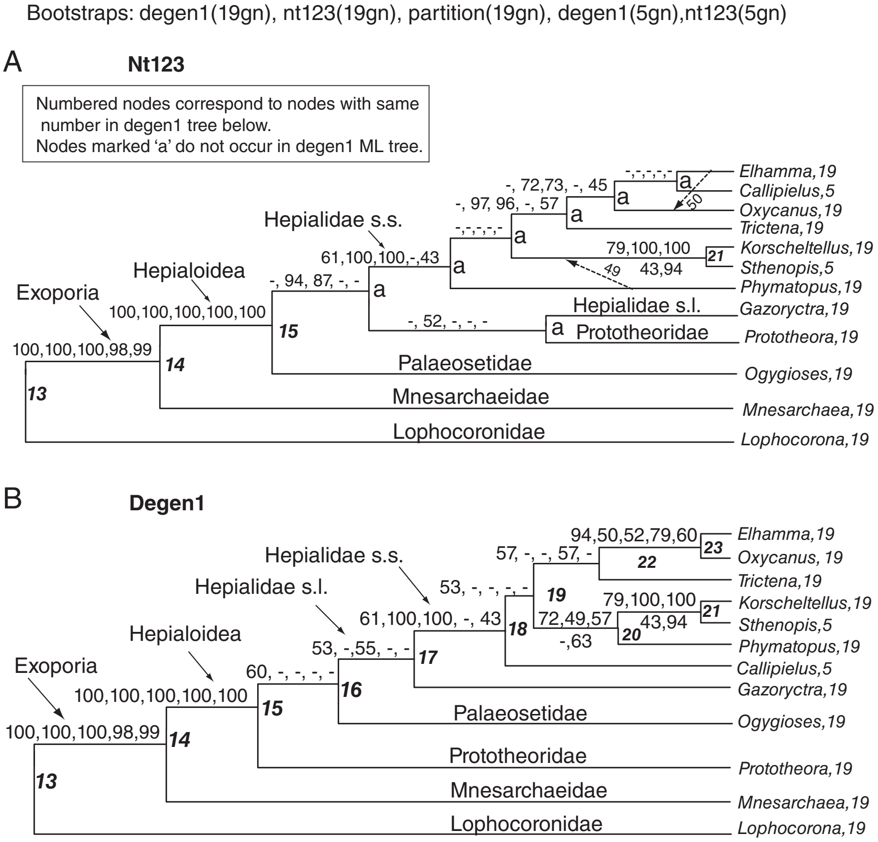


Fig. 3. Conflicting 19-gene topologies for Hepialoidea, extracted from 86-taxon analyses of Fig. 2 and Fig. S1. Bootstrap values are as in Fig. 2. (A) Maximum likelihood (ML) tree for nt123 (all changes); (B) ML tree for degen1 (nonsynonymous changes only).

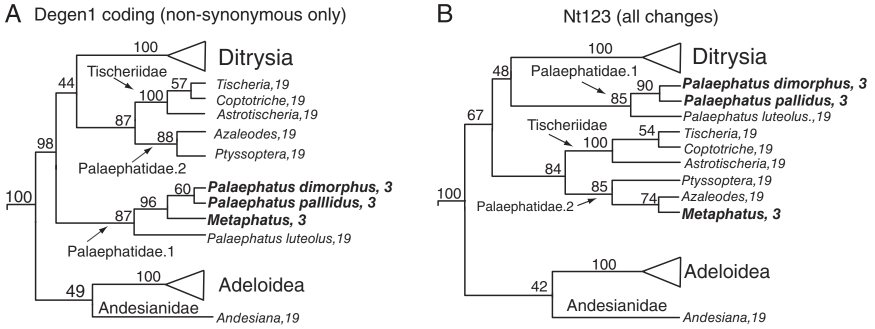


Fig. 4. Effects of additional gene and taxon sampling in Palaephatidae, extracted from 89-taxon, 19-gene maximum likelihood (ML) analyses incorporating three additional species plus 14 additional genes for *Palaephatus luteolus* as compared with Fig. 2. The number of genes sequenced (or attempted) is given to right of the exemplar name. Names of newly added taxa are shown in bold italic. Only relationships within Eulepidoptera are shown; the remainder of trees are nearly identical to Fig. 2 (degen1) or Fig. S1 (nt123). (A) Eulepidoptera portion of 89-taxon ML tree and bootstraps for degen1 (nonsynonymous change only); (B) Eulepidoptera portion of 89-taxon ML tree and bootstraps for nt123 (all changes).

as the presence of adfrontal and hypostomal ridges as well as of a median unsclerotized region in the hypostome. Subsequently the displacement of the antenna to the lateral cranial edge has been suggested to be another potential synapomorphy of the clade (Hasenfuss & Kristensen, 2003), although details of this transformation series remain to be worked out. Adult characters supporting the clade are few, but it is reasonable to uphold the presence of sensilla auricillica on the antennal flagellum as one, even though they have been lost or structurally modified in several subordinate glossatan lineages. That sensilla of this structural type belong to the same 'family' of multiparous chemoreceptors as micropterigid 'ascoids' etc. (Faucheux, 2004) is in itself not an argument against them being a ground plan synapomorphy for Angiospermivora.

Placement of Agathiphagidae

In contrast to the divergence of Angiospermivora, our molecular data provide no strong evidence on the position of the first split in Lepidoptera. Micropterigidae are always part of the sister lineage diverging from the remaining lepidopterans, but the position of Agathiphagidae is variable. The 19-gene data set consistently favours the grouping of Agathiphagidae + Micropterigidae (node 2), but bootstrap support is not strong in any analysis ($BP \leq 68$), whereas the five-gene analyses, with even weaker support, favour either Agathiphagidae + Angiospermivora or Agathiphagidae + Heterobathmiidae. This last grouping was also reported by Mutanen *et al.* (2010), again with little support. Thus, the data sets of Mutanen *et al.* (2010) and Regier *et al.* (2013) are individually unable to say anything definitive about the position of *Agathiphaga* Dumbleton. In particular, they provide no support for the widely accepted hypothesis that Micropterigidae are the sister group to all other Lepidoptera (Kristensen & Skalski (1998) (cf. Fig. 1). However, the tree of Kristensen *et al.* (2015), based on the combination of these two data sets, showed very strong support for Agathiphagidae + Micropterigidae; this topology is also favoured, albeit weakly, in the current study. In contrast, an earlier molecular analysis based on a much smaller taxon sample and two nuclear genes not used in the later studies (Wiegmann *et al.*, 2000), yielded very strong bootstrap support for Micropterigidae alone as the sister group to the rest of the order, as did a combined analysis of 18S rDNA data and morphology (Wiegmann *et al.*, 2002). Given the conflicting evidence, more study is needed, but we adopt Agathiphagidae + Micropterigidae as a working hypothesis.

Agathiphagidae + Micropterigidae (Node 2) is one of the very few groupings in our tree for which no morphological synapomorphy has so far been identified, but the loss of a prominent, rounded hindwing jugal lobe, ascribed to the trichopteran ground plan by Schmid (1989), might be one. To assume that this loss is a synapomorphy paralleled in the glossatan stem lineage (two steps) is no more parsimonious than the previous implication (viz. loss in lepidopteran stem lineage and reversal in Heterobathmiidae), but it is more parsimonious than assuming independent losses in Micropterigidae, *Agathiphaga* and glossatans. Although *Agathiphaga* was described as a micropterigid genus (Dumbleton, 1952), that was done in a precladistic context and was based on obvious symplesiomorphies exclusively. Agathiphagids are known only from a single genus with two species, which appear structurally and biologically very similar. Long-recognized potential synapomorphies between *Agathiphaga* and all nonmicropterigid Lepidoptera partly comprise regressive larval features (such as loss of a discrete lacinia, median labral retractors, cranial flexors of dististipes and functional metathoracic spiracle, reduction of corpotentorium to a slender strand) but also seemingly noteworthy structural innovations, such as the peculiar muscle that extends laterally between the upper and lower margins of the occipital foramen and, in the adult, the presence of a prominent anterior process on the metafurcal stem, which accommodates the origins of the sternal bundles of the trochanter depressors. The histology of the female spermathecal duct is intermediate between the simple type ascribed to micropterigids and the distinctive two-compartment configuration ascribed to Angiospermivora (node 7; Hünefeld & Kristensen, 2012).

The alternative scenario of *Agathiphaga* being sister group only to heterobathmiids is only weakly supported by morphology (Kristensen, 1984), by the Y- rather than π-configuration of the adult anterior tentorial arms, the posteriorly widened adult postlabium, the mesepisternal sulcus pattern, and a few regressive traits in both larval and adult anatomy. Of the similarities mentioned by Kristensen, the enlarged male phallotheca is now known to be a misinterpretation of the heterobathmiid condition. The strong subapical teeth on the lower surface of the pupal mandible may actually be an amphiesmenopteran ground plan trait, and the loss of postcerebral stomodaeal dilators is now known to have happened multiple times in lepidopteran larvae (including micropterigids). The loss of these muscles is a necessary consequence of the posterior displacement (into the thorax) of the suboesophageal ganglion, which repeatedly occurs in pro- and semiprognathous larvae (N.P. Kristensen, unpublished data). Finally, we note that no molecular analyses support the morphological hypothesis of Shields (1993), that Agathiphagidae are the sister group to all other Lepidoptera.

Micropterigidae

Within Micropterigidae as sampled here (five genera, node 3), the molecular data strongly support a basal split between the Nearctic *Epimartyria* (Walsingham) (representing a sizeable and morphologically well supported, predominantly East-Palaearctic clade) plus the predominantly West-Palaearctic *Micropterix* Hübner (node 6; BP = 92, degen1), and a group (node 4; BP = 97, nt123) consisting of *Sabatinca* Walker + *Zealandopterix* Gibbs (node 5; BP = 86, nt123), both from New Zealand, and a recently discovered genus, *Sporaphaga* Wagner & Davis, from Costa Rica. *Epimartyria*, *Micropterix* and *Zealandopterix* represent three of the five monophyletic groups of micropterigid genera recognized by Gibbs (2010) and Gibbs *et al.* (2004) based on analysis of the mitochondrial 16S rDNA gene. Those authors did not at that time propose any hypotheses about relationships among the groups. An analysis by Gibbs & Lees (2014) based on the COI barcode region, with a larger sampling of micropterigid genera and species but not the Costa Rica taxon, is in agreement with our results, providing further steps toward resolution of intergeneric relationships in micropterigids.

Glossata

Within Angiospermivora (node 7), the molecular data very strongly support the basal split hypothesized by Kristensen & Skalski (1998) between Heterobathmiidae and Glossata (node 8; BP = 96, degen1). The monophyly of the latter, the 'tongue moths', has never been seriously questioned, and it is supported by an impressive syndrome of structural specializations of the adult head. The transformation of the generalized galeae into the coilable proboscis/tongue initially took place with surprisingly little modification of the maxillary musculature (Kristensen, 2003a; Krenn & Kristensen, 2004). In contrast, the physical properties of the proboscis wall (with cuticle elasticity enabling nonmuscle-aided recoil), as well as details of its specialized surface configuration such as the linking mechanism (Krenn & Kristensen, 2000; Kristensen *et al.*, 2013), have in eriocraniids, acanthopteroctetids and lophocoronids a remarkable similarity, which surely reflects the acquisition of these specializations in the stem lineage of Glossata (node 8). Loss of mandibular function in the postpharate adult stage, and associated reduction of mandibular sclerotization and loss of mandibular teeth and cranial articulation are additional glossatan ground plan autapomorphies associated with the reorganization of the feeding apparatus, and so is the loss of a prominent epistomal sulcus; in the maxillary palp, the flexor muscle between segments 2 and 3 is lost. Glossatan autapomorphies not associated with the mouthpart specializations include the strongly developed dorsal tentorial arms, which are present in all homoneurous families but lost in some subordinate hepialoids as well as in basal heteroneurans, reappearing in scattered ditrysians; absence of a free tritocerebral commissure (i.e. it becomes embedded in the suboesophageal ganglion); and the presence of a 'spinneret' process on the apex of the prelabio-hypopharyngeal lobe. Female accessory glands formed by 'type 3' rather than 'type 1' gland cells have been suggested to be another glossatan autapomorphy, because 'type 3' cells occur in Eriocraniidae and those scattered other glossatans for which histological information is available (Hünefeld & Kristensen, 2012), but it is noteworthy, then, that *Aenigmatinea* Kristensen & Edwards has 'type 1' glands (Kristensen *et al.*, 2015).

Coelolepida and major divisions therein

The molecular data provide little clear evidence on the basal divergences within Glossata, in striking contrast to the morphological analysis of Nielsen & Kristensen (1996). A basal split between Eriocraniidae (node 9) and all other Glossata (= clade Coelolepida; node 12; BP = 38, degen1) does occur in the best tree for 19 genes/degen1. Support is low, however, and Coelolepida are not monophyletic in any of our other analyses or in those of Mutanen *et al.* (2010). When first proposed, Coelolepida were believed to be characterized by the presence of hollow wing scales. This assumption was subsequently found to be incorrect, as such scales are also present in Agathiphagidae (Simonsen & Kristensen, 2001). However, the presence of scales with perforations in the abwing lamella may be upheld as a coelolepidan autapomorphy, as may, perhaps, the capacity to develop scales with multiple serrations of the apical margin (in spite of the absence of such serrations in scales of Neopseustidae and *Aenigmatinea*). The same applies to the loss of any indication of a frontoclypeal boundary on the adult head and the anteriorly concave shape of the mesobasisternum. A more complex morphological innovation is the structure of the adult first thoracic spiracle, the atrial wall of which is produced into an apodemal arm, whose apex receives occlusor muscle fibres originating on the atrium below, and an elastic opener ligament originating on the pronotum.

According to the morphological hypothesis of Kristensen (2003b) (Fig. 1A), the first split within Coelolepida separates Acanthopteroctetidae from the rest, followed by the divergence of Lophocoronidae from the clade Myoglossata. Myoglossata then are divided basally into Neopseustidae and the clade Neolepidoptera. Our results (Fig. 2) depart extensively from this arrangement. The basal split within Coelolepida in all 19-gene analyses is between a clade consisting of Lophocoronidae plus Exoporia (node 13; BP = 96, nt123) and a very weakly supported clade containing all other families (node 24; BP = 37, degen1). The last is divided basally into Heteroneura (node 27; BP = 100, degen1) and a group consisting of Neopseustidae plus Acanthopteroctetidae (node 25), which, although weakly supported here (BP = 62, degen1), was strongly supported in the analysis including *Aenigmatinea* (Kristensen *et al.*, 2015). The strong pairing of Lophocoronidae and Exoporia is among the greatest surprises emerging from this study, as it contradicts monophyly for both Myoglossata and Neolepidoptera (Fig. 1A). Mutanen *et al.* (2010) report nearly the same arrangement (Fig. 1B), albeit with less support, the only difference being the inclusion of Eriocraniidae as immediate sister group to Lophocoronidae.

The phylogenetic pattern recovered from the molecular data necessitates a less parsimonious hypothesis explaining the evolution of the proboscis with intrinsic musculature, a defining synapomorphy of Myoglossata. The molecular tree appears to require one of two different, equally parsimonious scenarios: (i) the intrinsic musculature evolved, together with the coilable tongue, in the glossatan stem lineage and was subsequently lost in Eriocraniidae, Acanthopteroctetidae and Lophocoronidae; or (ii) it evolved twice independently, once in Exoporia and once in the clade denoted by node 24, to be subsequently lost in Acanthopteroctetidae. With another specialization characterising Myoglossata, namely the upturned acrotergite I (forming a near-vertical phragma analogue which provides a high insertion area for the metathoracic indirect wing depressors), the situation is even more complex, because *Aenigmatinea*, like acanthopteroctetids, has an unmodified acrotergite I. Lophocoronids have the antecosta I deepened to form a sizeable phragma and it is arguably unlikely that the latter should have evolved to compensate for a loss of a functional analogue in the immediate stem lineage. A re-evaluation of the evolution of the wing vestiture in lower Glossata is also required. Simonsen (2001) considered secondarily solid ground scales (often with clear vestiges of perforations) to be an autapomorphy for Neolepidoptera (albeit secondarily lost in some subsequent lineages). Our molecular findings imply that secondarily solid scales must have evolved independently in Exoporia and Eulepidoptera, a scenario also considered by Simonsen, based on the absence of such scales in Nepticuloidea.

The molecular phylogeny also implies increased homoplasy in crochet-bearing larval prolegs, a possible ground plan autapomorphy of Neolepidoptera. Such prolegs must have either evolved twice independently, in Exoporia and in Heteroneura, or evolved in Coelolepida and been subsequently lost in Lophocoronidae (if they are indeed absent in the unknown lophocoronid larva) and in the Acanthopteroctetidae + Neopseustidae clade (or just in acanthopteroctetids, neopseustid larvae also being unknown). A similar postulate of additional homoplasy would be required in the case of the disassociation of the adults' metathoracic aorta from the pulsatile diaphragm, which has been considered another neolepidopteran ground plan autapomorphy (Nielsen & Kristensen, 1996). The same might prove to apply to the configuration of the adult first thoracic spiracle, which, in examined Hepialoidea and Heteroneura (Nielsen & Kristensen, 1989), has the apodeme-bearing atrial sclerotization strongly bent and located in a markedly anterior position; however, a closer examination of more taxa for this character is much needed. In contrast, an assumption of neolepidopteran nonmonophyly would not necessitate greater complexity in the evolution of the adecticous pupal type, inasmuch as only two independent origins are still required, in the Heteroneura and at node 13.

In Eriocraniidae (node 9) we sampled the three most species-rich genera. Among these, the molecular data strongly support the grouping of *Dyseriocrania* Spuler + *Eriocrania* Zeller (node 11; BP = 98, nt123) to the exclusion of *Eriocraniella* Viette. This high support is somewhat surprising, as the findings from the only published attempt (morphology-based) at elucidating intra-family phylogeny retrieved a sister-group relationship between *Dyseriocrania* and other eriocraniids (Davis, 1978a). This pairing is supported by an additional remarkable apomorphy in the male postabdomen of non-*Dyseriocrania* species: a cut-off part of the gonopod base, dorsally produced into a prominent seta-bearing process.

Neopseustoidea

The unexpected grouping of Neopseustidae and Acanthopteroctetidae (node 25) was also reported by Mutanen *et al.* (2010). Both the monophyly of this clade and relationships within are tentative in our analyses. The two Neopseustidae are never united, as one or the other is always closer to *Acanthopteroctetes* Braun but with bootstrap values < 60 (node 26). It is possible that the dearth of sequence obtainable for the neopseustid genus *Apoplania* Davis (3639 bp; Table S1) contributed to this apparent anomaly. But it is noteworthy that when *Aenigmatinea* is included, support for the group comprising all three taxa (and with *Aenigmatinea* and neopseustids being sister groups) is much stronger (Kristensen *et al.*, 2015).

A few morphological specializations shared between Acanthopteroctetidae and Neopseustidae have, in fact, been found, mainly in the antenna: the smooth intercalary sclerotization and the alignment of antennal scale sockets in longitudinal rows. Also, the prominent peg-and-socket type of neopseustid scapo-pedicellar articulation is to some degree approached in *Acanthopteroctetes* (Kristensen *et al.*, 2013). The narrowed labrum, which is present in *Acanthopteroctetes* and *Neopseustis* Meyrick, can with some certainty be considered a parallelism, as the neopseustids *Apoplania* and *Synempora* Davis & Nielsen have the ancestral, broader and more pentagonal type, and, importantly, the overall generalized neopseustid *Nematocentropus* Hwang also has a broad labrum (Davis, 1975b; Kristensen *et al.*, 2013; N.P. Kristensen, unpublished data). Accepting a monophyletic Acanthopteroctetidae + Neopseustidae would necessitate a different interpretation of the evolution of complex characters that have so far been considered as synapomorphies of Myoglossata and Neolepidoptera. Nonetheless, the findings arguably reopen the question of whether Neopseustidae alone might be the sister group of Heteroneura, as first proposed by Küppers & Speidel (1980), referring to their shared jugum reduction and proboscis linking with ventral 'secondary' ligulae. The independent development of the latter is at least not now as obvious, as previously stated by Krenn & Kristensen (2000: 193). This relationship would also explain two seemingly noteworthy neopseustid-heteroneuran similarities in thoracic structure (Nielsen & Kristensen, 1996), the presence of a prothoracic precoxal (pleurosternal) bridge and the anteriorly markedly produced meso-basisternum, which reaches the prospinasternum. The anterior extension of the mesobasisternum in lophocoronids + exoporians would, in this case, have to be considered independently evolved, rather than as steps in a transformation series of which the neopseustid and heteroneuran conditions are end points. Although labral retractor muscles were previously believed to have been lost just once in adult Lepidoptera (in the stem lineage of all Glossata except eriocraniids and acanthopteroctetids), three independent losses must now be postulated: in Lophocoronidae + Exoporia, in *Aenigmatinea* + Neopseustidae and in Heteroneura.

Given the strong molecular support for the monophyly of a clade comprising Acanthopteroctetidae plus Neopseustidae and Aenigmatineidae that emerged after the discovery of the latter (Kristensen *et al.*, 2015), the option of including them all in a single superfamily (to which Neopseustoidea based on the oldest family-group name should then be applied) deserves serious attention. On balance we have decided to adopt this arrangement (see Table 1) rather than retaining three small monobasic superfamilies, even though no certain morphological autapomorphies of the newly circumscribed Neopseustoidea are identified.

Hepialoidea

Within Exoporia (node 14), there is consistent strong support for monophyly of Hepialoidea (node 15; BP = 100) and of Hepialidae sensu stricto (node 18; BP = 100, nt123). The evidence for other relationships within Hepialoidea is, however, unusually complex, with multiple disagreements between analyses (see Fig. 3). Under degen1 analysis (Fig. 3B), the 'primitive hepialid' *Gazoryctra* Hübner is sister to Hepialidae sensu stricto, making Hepialidae sensu lato also monophyletic (node 17), but support is very weak (BP = 53, degen1). This grouping is very weakly contradicted by nt123 (Fig. 3A), under which *Prototheora* Meyrick (Prototheoridae) moves into Hepialidae sensu lato as sister to *Gazoryctra*. The evidence for relationships among the three hepialoid families sampled is also complex. Degen1 groups *Ogygioses* Issiki & Stringer with Hepialidae, but with very weak support (node 16; BP = 60). In contrast, nt123 (Fig. 3A) unites hepialids and *Prototheora* with very strong support (BP = 94). Preliminary morphological studies support the monophyly of Palaeosetidae + Hepialidae sensu lato, excluding Prototheoridae (T.J. Simonsen, unpublished data). The first two of these families show a posterior displacement of the forewing Rs2 vein that is not shared by other Exoporia. A monophyletic Hepialidae sensu lato, although not strongly supported here, is also supported by the most comprehensive phylogeny of Hepialidae to date (Grehan, 2012); all genera in Hepialidae sensu lato appear to share a unique synapomorphy in the male genitalia – the presence of the so-called intermediate sclerite (Nielsen & Kristensen, 1989). The preliminary study by Simonsen also indicates that all the hepialoid taxa included here constitute a monophyletic group which excludes the two hepialoid families not sequenced (Neotheoridae and Anomosetidae).

Within Hepialidae sensu stricto, there are two strongly supported pairs of genera: *Elhamma* Walker + *Oxycanus* Walker, both Australian (node 23; BP = 94), and *Korscheltellus* Börner + *Sthenopis* Packard, which are Holarctic and North American, respectively (node 21; BP = 100, nt123). The Australian genus *Trictena* Meyrick is consistently grouped with or near *Elhamma* + *Oxycanus*. However, the positions of the two other genera (both relatively long-branch under nt123; not shown) are unstable and/or in conflict between data sets. Under degen1 (Fig. 3B), the South American *Callipielus* Butler is the first to diverge within Hepialidae sensu stricto, but this position is very weakly supported. In contrast, under nt123 (Fig. 3A), *Callipielus* is grouped strongly with the Australian genera (BP = 97), with moderate support as subordinate within that clade (BP = 72) and with very weak support (BP < 50) as sister group to *Elhamma*. Moderate signal in degen1 (BP = 72) places the Holarctic genus *Phymatopus* Wallengren as sister group to *Korscheltellus* + *Sthenopis*, but nt123 very weakly places this genus as sister group to all other Hepialidae sensu stricto. The close relationship between *Elhamma* and *Oxycanus* robustly supported by the molecular data is also well supported by morphology, as these two genera (together with other genera not sampled here – see Dugdale, 1994) share the so-called 'oxycanine' branching of the forewing radial sector veins, in which the Rs3 vein arises from the stem of Rs1 + 2, and not from the discal cell. Grehan (2012) also found moderate support for this 'oxycanine' clade (based on more taxa), but did not find any evidence for a close relationship between this group and *Trictena*. While the 'oxycanine' genera probably comprise a monophyletic group, a more detailed phylogenetic study of Hepialidae sensu stricto is needed to determine whether this group should have subfamily status as suggested by Dumbleton (1966), but rejected by subsequent authors (i. e. Common, 1990).

At least some of the instability of relationships within Hepialoidea is probably a result of contradictory phylogenetic signal among loci. For example, in the five-gene degen1 analysis (not shown) there is 80% bootstrap support for inclusion of *Prototheora* in a subset of Hepialidae sensu stricto that excludes *Callipielus*. In contrast, the 19-gene degen1 analysis (Fig. 3B) excludes *Prototheora* from Hepialidae sensu stricto with bootstrap support of 60%. The complexity of the evidence and our limited taxon sampling (seven of 52 genera) leave us reluctant to draw firm conclusions about relationships within Hepialoidea beyond the several strongly supported groupings previously identified. Resolving the relationships between the major hepialoid lineages as well as the genera within Hepialidae sensu stricto will require much denser taxon sampling in the future.

Given the strong molecular and morphological support for the monophyly of Mnesarchaeoidea + Hepialoidea, we think that there is little need for two superfamily names and suggest that Mnesarchaeoidea should be synonymized with Hepialoidea (**syn.n.**, Table 1). This makes the name Exoporia redundant and the diagnostic characters for the redefined Hepialoidea are the same as for Exoporia.

Heteroneura: Nepticuloidea

Within Heteroneura (node 27), the molecular data support a basal split between Nepticuloidea (node 28; BP = 100) and Eulepidoptera (node 37; BP = 100). Within Nepticuloidea, monophyly is strongly supported for each of the two families, Nepticulidae (node 31; BP = 100) and Opostegidae (node 29; BP = 100). Within Nepticulidae, the molecular data strongly favour a basal split between Trifurculini (van Nieukerken, 1986) as represented here (node 32; BP = 99) and a clade consisting of Nepticulini plus *Pectinivalva* Scoble (node 34; BP = 100). The latter clade as sampled here is also supported by a synapomorphy of wing scale ultrastructure: *Enteucha* Meyrick, *Stigmella* Schrank, and *Pectinivalva* all have cover scales with numerous micropores, in irregular rows between ridges (Simonsen, 2001). Microtrichia also show a progressive reduction within this clade (Simonsen, 2001). This result contradicts the earlier division of Nepticulidae into the Australian subfamily Pectinivalvinae versus Nepticulinae (Scoble, 1983; van Nieukerken, 1986; Hoare, 2000). Although a suite of characters supports the combination of the two pectinivalvine genera, *Pectinivalva* and *Roscidotoga* Hoare, morphological support for Nepticulinae was not very strong and is partly based on reductions, e.g. of the valval pectinifer and of the number of antennal segments in the larva (two or three in *Pectinivalva*, one in other Nepticulidae). More recently, it has been found that the number of larval antennal segments is also variable within *Pectinivalva* (Hoare & van Nieukerken, 2013). The pectinifer character was based on the assumption that the pecten in *Pectinivalva* is homologous to pectens in Opostegidae and Adeloidea (Scoble, 1982). The nepticulid pecten deviates from that in other families, however, by not being stalked and its homology remains questionable. In addition, similar pectens occur as a derived condition in the trifurculine genus *Acalyptris* Meyrick. A molecular analysis with fewer genes but a large taxon sample from Nepticulidae also supports the subordinate position of *Pectinivalva* plus *Roscidotoga* in the *Stigmella* clade (E. van Nieukerken *et al.*, unpublished data). Within Trifurculini, there is strong evidence for the grouping of *Ectoedemia* Busck sensu stricto + *Ectoedemia* (*Fomoria*) Beirne to the exclusion of *Trifurcula* Zeller (node 33; BP = 96, nt123), a finding that is also supported by morphological characters (van Nieukerken, 1986).

Within the nepticuline lineage (node 34), the two *Enteucha* species are strongly grouped (node 36; BP = 100) to the exclusion of *Pectinivalva* and *Stigmella*, but the branching order of the latter two genera conflicts between nt123 and degen1 and is weakly supported in each case (BP = 53 vs. BP = 52). The grouping of *Pectinivalva* and *Enteucha* is supported by at least one morphological character: the tubular form of the so-called 'cathrema', a structure that surrounds the opening of the ejaculatory duct (van Nieukerken, 1986; Hoare & van Nieukerken, 2013). These observations provide further evidence that the division of Nepticulidae into Pectinivalvinae versus Nepticulinae can no longer be maintained. It could reasonably be replaced by a division into Nepticulinae and Trifurculinae, as suggested by Puplesis (1994).

Eulepidoptera

Within Eulepidoptera (node 37), the basal split is between Palaephatidae + Tischeriidae + Ditrysia (node 53; BP = 98, degen1) and Andesianidae + Adeloidea (node 38; BP = 74, nt123). This position for Andesianidae, although never more than moderately supported, is consistent across all analyses. The same position for *Andesiana* Gentili was found by Mutanen *et al.* (2010) with stronger support (BP = 84; Fig. 1). However, we cannot completely rule out the possibility that *Andesiana* is instead the sister group to Ditrysia + Palaephatidae + Tischeriidae; this arrangement has the next-highest level of bootstrap support (BP = 22% for both degen1 and nt123). The latter hypothesis accords somewhat better with evidence from wing vestiture, which provides a possible synapomorphy linking Andesianidae, Tischeriidae and Ditrysia (Simonsen, 2009).

Within Adeloidea (node 39; BP = 100), our analyses provide very strong support for relationships among most families. Remarkably, the branching order is nearly identical to that resulting from the morphological cladistic analysis of Nielsen & Davis (1985; see Fig. 1F), except that the root is placed at the opposite end of the tree. The source of the difference may lie in the differing approaches taken to estimating the ground plan. In the molecular analysis, character polarity was inferred secondarily, through inclusion of outgroups, whereas in the morphological study, polarity was inferred a priori on the basis of character state distribution in taxa related to Adeloidea and no outgroups were included in the analysis.

The molecular data strongly support a basal split between Cecidosidae (node 40; BP = 100) and all other families (node 41; BP = 100, nt123). Within the latter clade (node 41), the basal divergence, also strongly supported, is between Prodoxidae sensu stricto (node 42; BP = 100) and the remaining families (node 44; BP = 100, degen1). The next divergence, likewise very strongly supported, separates the aberrant prodoxid *Tridentaforma* Davis from the remaining families (node 45; BP = 98, degen1). This result confirms earlier findings about the difficulty of placing *Tridentaforma* (Nielsen & Davis, 1985; Davis, 1998; Friedlander *et al.*, 2000) and strongly implies that this monotypic genus, now firmly excluded from all other lepidopteran families as currently defined, but securely placed as a separate lineage in adeloid phylogeny, merits elevation to family status. Accordingly, we provide a formal description for Tridentaformidae **fam.n.** in a later section.

The remaining adeloid families divide into two strongly supported sister clades, one comprising Incurvariidae, including the monotypic Crinopteriginae (node 46; BP = 100), and the other comprising Adelidae + Heliozelidae (node 48, BP = 99, degen1). Within Adelidae + Heliozelidae (node 48), the subfamily Adelinae is strongly supported as monophyletic to the exclusion of Nematopogoninae (node 51; BP = 100). Among our three adeline exemplars, *Adela* Latreille and *Cauchas* Zeller are strongly grouped to the exclusion of *Nemophora* Illiger & Hoffmannsegg (node 52; BP = 100). The two exemplars of Heliozelidae included here are also strongly grouped (node 50; BP = 100 nt123). There is marked conflict, however, regarding the position of the remaining adelids. Degen1 strongly supports a basal divergence between *Nematopogon* Zeller (Adelidae) and all other taxa (node 49; BP = 87), rendering Adelidae paraphyletic with respect to Heliozelidae. In contrast, under nt123, *Nematopogon* joins the other Adelidae with strong support (BP = 85), as shown by the dotted line in Fig. 2. We looked into this striking conflict in some detail (analysis not shown), concluding that, unlike an apparently similar result in Tineoidea (Regier *et al.*, 2013), the synonymous/nonsynonymous conflict in this case does not represent compositional heterogeneity in nt123; the weight of the evidence favours adelid monophyly. Nielsen (1980) listed three synapomorphies for Adelidae: the long antenna; the narrow and slender cloaca in the female; and the high number of ovarioles per ovary. However, ovariole number is not known for Heliozelidae. Further possible synapomorphies include larval feeding mode. After the initial instars, both Nematopogoninae and Adelinae feed on the ground, on leaf litter and sometimes on withering leaves, from the larval case. In contrast, Heliozelidae are mostly, and probably ancestrally, leaf miners throughout larval development, although some apparently secondary departures from this pattern are known. It should be noted, however, that evidence from wing vestiture supports the degen1 topology (Simonsen, 2001). *Nematopogon* and *Heliozela* Herrich-Schäffer both have typical nonditrysian Heteroneura wing vestiture, including well-developed ridge dimorphism and perforations (if small) on the forewing cover scales (both are more prominent in *Nematopogon*). In contrast, *Adela* and *Cauchas* have less well-developed ridge dimorphism and no perforations (only small depressions) on the cover scales, an apparently derived condition. *Nematopogon* is also the only taxon of the four that has typical, well-developed microtrichia on the forewing upper surface. The other three share the reduction of the microtrichia; in the two adeline genera they are greatly reduced, whereas *Heliozela* lacks them completely.

Euheteroneura

The morphology-based clade Palaephatidae + Tischeriidae + Ditrysia (node 53; BP = 98, degen1) is strongly corroborated in all of our analyses and is also a constant feature of previous molecular studies. It is further supported by a derived tRNA gene order in the mitochondrial genome (Timmermans *et al.*, 2014). We propose the new name Euheteroneura for this group. Although monophyly for Euheteroneura seems secure, the evidence on basal divergences within this clade is complex and contradictory. In the 483-taxon study of Regier *et al.* (2013), the very strongly supported basal split lies between Ditrysia + *Palaephatus* and a group consisting of Tischeriidae plus the two Australian genera currently assigned to Palaephatidae. The same topology holds for the 86-taxon data set in the present study (Fig. 2), although support for *Palaephatus* as sister group to Ditrysia is somewhat reduced (BP = 75/90 for degen1/nt123 vs 92/ 97 in the 483-taxa study), possibly as a result of reduced taxon sampling in Ditrysia. The picture changes still further with the post hoc addition of about 1200 bp each for two further species of *Palaephatus* and for *M. ochraceus*, plus 14 more genes (8.1 bp) for *P. luteolus* (Fig. 4). In all analyses in which 19 genes are scored for *P. luteolus*, including reanalyses of the 483-taxon data set (not shown), nt123 continues to group *Palaephatus* and Ditrysia but with much weaker support (BP ≤ 65), while degen1 now weakly identifies the tischeriid/Australian palaephatid clade instead as the closest relative to Ditrysia (BP ≤ 50). The difference between this and the earlier 86-taxon results almost surely reflects inter-gene conflict between the five- and 19-gene sets. The broader consequence is that we are unable to confidently identify the exact sister group to Ditrysia and this will remain a topic for further investigation.

Although the new data fail to resolve the Ditrysia sister group problem, they reinforce the molecular evidence for nonmonophyly of Palaephatidae as presently defined. In the 89-taxon analyses (Fig. 4), the additional *Palaephatus* species group strongly with *P. luteolus*, despite their paucity of sequence data. Bootstrap support uniting the Australian palaephatid genera with Tischeriidae remains strong, although it is somewhat lower due to the conflicting signal for the South American palaephatid *Metaphatus*. The latter groups with *Palaephatus* under degen1 analysis, but with the Australian palaephatids (specifically *Azaleodes* Turner) plus Tischeriidae under nt123 (Fig. 4). The difference appears to reflect conflict between the only two gene sequences obtained for *Metaphatus*. Although more data will be needed to settle the position of *Metaphatus*, the molecular data argue strongly for removing the Australian genera from Palaephatidae.

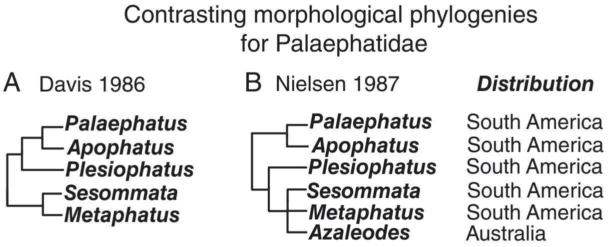


Fig. 5. Alternative morphological phylogenies for the genera of Palaephatidae. (A) Relationships according to Davis (1986); (B) relationships according to Nielsen (1987).

The morphological evidence, however, disagrees. The family Palaephatidae was established by Davis (1986), who recognized five genera, all in southern South America. Nielsen (1987) and Robinson & Nielsen (1993) subsequently assigned the Australian genera *Azaleodes* and *Ptyssoptera* Turner to this family. Davis hypothesized the relationships among the South American genera shown in Fig. 5A. Nielsen proposed a phylogeny (Fig. 5B) conflicting with that of Davis only in the position of *Plesiophatus* Davis and showing *Azaleodes* nested in a clade consisting otherwise of South American genera, including *Metaphatus*, that is defined by a well-developed colliculum (= antrum) in the female genitalia. Davis (1986) listed the presence on the female oviscapt of a medial sensory ridge, richly populated with campaniform sensilla, as the sole strong autapomorphy for the Palaephatidae. This ridge is especially prominent in *Palaephatus* and *Apophatus* Davis, resulting in a very produced apex to the oviscapt. A similar raised medial area on A10 is present in Tischeriidae but lacks campaniform sensilla. It was regarded as a parallelism by Davis, who hypothesized that Tischeriidae is more closely related to Nepticulidae than to Palaephatidae. If we accept the monophyly of Euheteroneura, it becomes equally parsimonious to interpret the joint possession of a median ridge as a ground plan trait subsequently lost in Ditrysia, but no homoplasy beyond that previously postulated is required. Accepting nonmonophyly of Palaephatidae, however, would require multiple gains or multiple losses of the distinctive population of campaniform sensilla on the median ridge, a considerable departure from previous hypotheses and one for which, to our knowledge, there is no supporting morphological evidence. For this reason, combined with the still very incomplete taxon sampling and the internal conflict seen in the molecular data set, we decline at present to alter the classification of Palaephatidae. Due to their potential bearing on the origins and early evolution of the Ditrysia, the basal divergences and family composition in Euheteroneura are deserving of much further study.

If Palaephatidae as currently delimited are in the future shown definitively to be paraphyletic, the nonditrysian Euheteroneura will constitute a notable instance of unequal rates of morphological evolution. The adults of *Palaephatus* and *Azaleodes* are closely similar in morphology, especially with regard to their generalized head and wing structure, whereas larvae of some species also share biological features in being leaf tiers on Proteaceae. No synapomorphies are yet known that would corroborate the strong molecular support for grouping only the Australian palaephatids with Tischeriidae. Tischeriidae, by contrast, have evolved a more derived, reduced body morphology, including many synapomorphies that distinguish them from all genera of Palaephatidae. Among the latter are: (i) third antennal segment greatly elongated; (ii) antennal sensilla trichodea greatly elongated and recurved; (iii) pilifers elongated; (iv) maxillary palpi reduced to one to three segments; (v) distal half of haustellum with scutiform, sclerotized plates externally; (vi) wing venation reduced with medial and cubital veins of hindwing usually unbranched and discal cell not closed; and (vii) metathorax with furcal apophysis joined to secondary arms of metafurcasternum. There also exist morphological differences between the larvae of the two families, which largely reflect the leafmining specializations within Tischeriidae.

Early evolution of phytophagy in Lepidoptera: overview

The Lepidoptera are arguably the largest single radiation of predominantly phytophagous insects, and exemplify a broader hypothesized association between the adoption of higher plant feeding and enhanced diversification (Southwood, 1973; Mitter *et al.*, 1988). To fully explain these observations, we will need to better understand how lepidopteran phytophagy arose and how its evolution might contribute to diversification, topics on which the nonditrysian lineages provide critical evidence. In this section we first provide a synopsis of what is known about the diversity, distribution, life history and larval feeding habits of the extant nonditrysian families, updating the review by Powell *et al.* (1998). This account is accompanied by illustrations of the adult habitus and, where available, the larva and feeding mode, for each family treated (Figs 6–9). Although some of these synopses are lengthy, we include them here to provide one of the most extensive compilations available on nonditrysian biology, including important previously unpublished observations. Much of the content is summarized in Fig. 10. Family and higher rank names of angiosperms used below follow the APG III classification (APG III, 2009). In a subsequent section, we use the updated phylogeny and life-history information to reassess previous ideas on the early evolution of lepidopteran phytophagy (e.g., Kristensen, 1997; Powell *et al.*, 1998; Menken *et al.*, 2010).

Early evolution of phytophagy in Lepidoptera: synopsis of diversity, distribution, life history and larval feeding habits for nonditrysian families

Micropterigidae (Fig. 6A)

There are 165 described species in 23 genera, with more than 100 additional undescribed species recognized (van Nieukerken *et al.* 2011a). Accumulating evidence shows that micropterigids are nearly cosmopolitan, with two newly discovered genera from Costa Rica providing some of the first records from lowland tropical rainforest (Davis & Landry, 2012; Wagner & Davis, 2015). Still unnamed Micropterigidae have also been collected at relatively low elevations in Madagascar (Aberlenc *et al.*, 2007). Adult micropterigids feed on pollen from a broad range of angiosperm families (Zeller-Lukashort *et al.*, 2007). Members of some groups have also been observed to feed on fern spores (Davis & Landry, 2012; Gibbs & Lees, 2014; Wagner & Davis, 2015). Micropterigidae are found in humid habitats, with the larvae typically living on, near or below the soil surface, sometimes in rotting wood (Gibbs, 2010) The larvae of many genera and species feed on liverworts, as is particularly well documented in the hypothesized clade (Gibbs *et al.*, 2004; Gibbs, 2010; Gibbs & Lees, 2014) consisting of the North American genus *Epimartyria* (three species; Davis & Landry, 2012) plus the genera *Paramartyria* Issiki, *Palaeomicroides* Issiki, *Issikiomartyria* Hashimoto, *Kurokopterix* Hashimoto and *Neomicropterix* Issiki, which are endemic to Japan and Taiwan (Hashimoto, 2006; Imada *et al.*, 2011). The latter five genera exhibit a remarkable degree of host specificity: all 24 species feed on the liverwort *Conocephalum conicum* Dumortier, despite the availability of many other liverworts in the same habitat (Imada *et al.*, 2011). Some micropterigids in other clades have other habits. Heath (1976) reported larvae of *Micropterix* Hübner at depths down to 10 cm in loose soil. Occasionally, fresh as well as decaying angiosperm leaves may be consumed by larval *Micropterix*. Lorenz (1961) reared larvae of *Micropterix calthella* (L.) on both plant detritus and fresh angiosperm leaves, whereas successful rearing of two species of *Micropterix* was shown to require fresh, photosynthetic angiosperm tissue (Carter & Dugdale, 1982).

Agathiphagidae (Fig. 6B)

Members of this family are markedly larger than other nonglossatan moths. The larger of the two species of *Agathiphaga* (*Agathiphaga vitiensis* Dumbleton) may have a wing span exceeding 25 mm. Adults are nocturnal and have only on very few occasions been observed in nature; their mandibles are devoid of teeth/cusps, and they are probably nonfeeding. The larvae are seed miners in Kauri pines (Araucariaceae) and renowned for their capacity to undergo very extended (> 10 years) diapause. Females have long, extensible 'probing' oviscapts, and the eggs are believed to be positioned on the seeds while these are still in the cone (Kristensen, 1998a; Hünefeld & Kristensen, 2010).

Heterobathmiidae (Figs 6C, 8A)

There is a single genus, *Heterobathmia* Kristensen & Nielsen, in which 10 species are recognized, although only five have been described. All are restricted to southern South America, where the diurnal adults feed on the flowers of southern beeches (*Nothophagus* Blume), of which the larvae mine the leaves, apparently on deciduous species only. Adults are superficially similar to many Eriocraniidae, and like the latter are active in early spring. Larval biology is also similar: both form large blotch mines on leaves of Fagales trees; in the closely examined instances, heterobathmiid mines start as narrow galleries. However, their eggs are not inserted into the leaves, but deposited on the surface, covered by a secretion. Also, the larvae have retained a generalized trunk morphology with well-developed thoracic legs, and they are capable of leaving the mine to form a new one in another leaf. Indeed, their postcephalic body design may be closer to the lepidopteran ground pattern than that of any other extant moth family (Kristensen, 1998a; Hünefeld & Kristensen, 2012; Dupont, 2013; Ramos & Parra, 2013).

Eriocraniidae (Figs 6D, 8B)

This is a relatively homogeneous family (both morphologically and biologically) of small, primarily diurnal moths restricted to the Holarctic Region. Although descriptions of a few additional East Asian taxa are forthcoming (T. Hirowatari, personal communication), at present a mere 30 named species are recognized in seven genera, with several of the latter being of questionable status. The larvae are mostly whitish in colour,

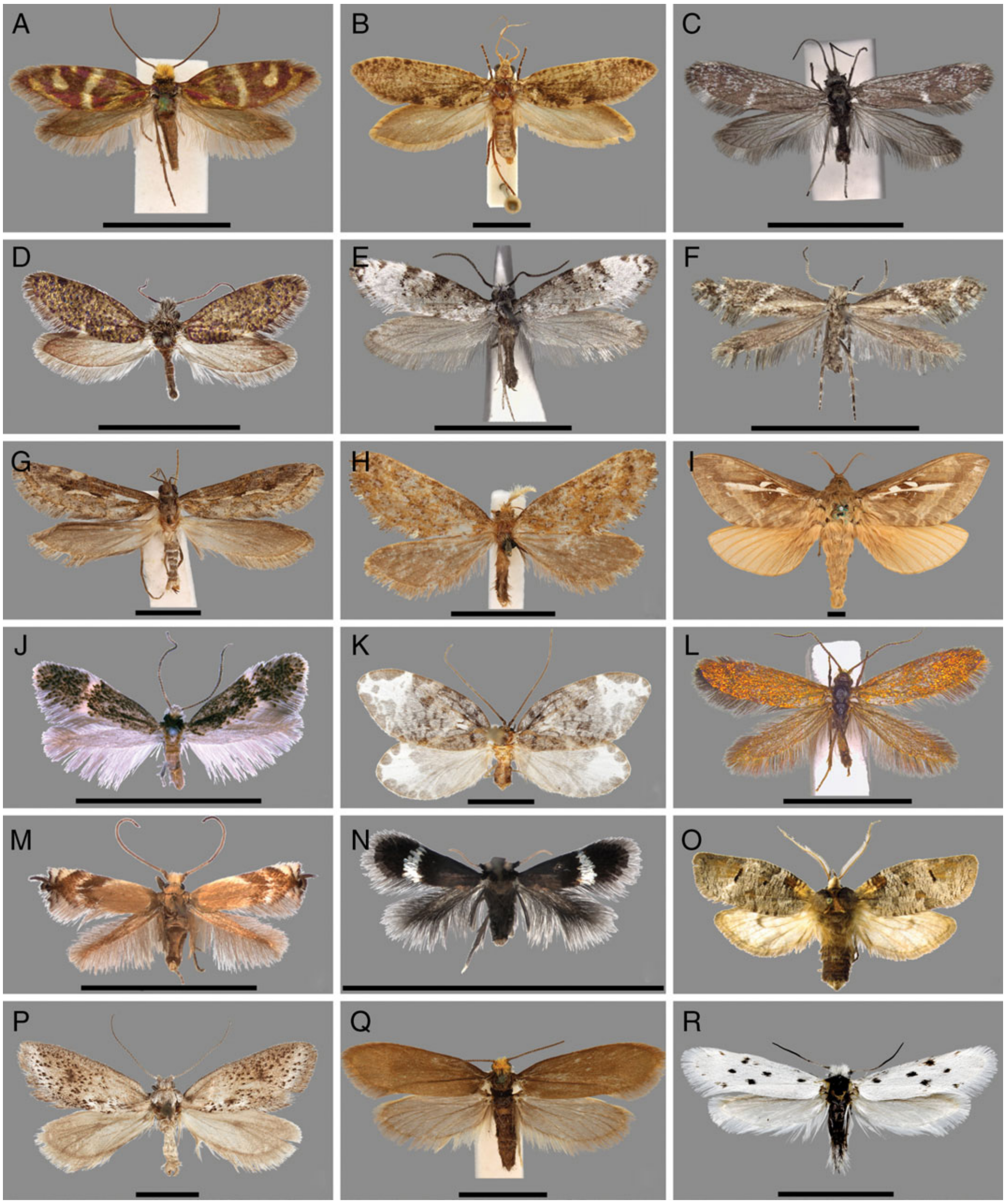


Fig. 6. Adult habitus of representatives of families treated, part 1. Scale bar = 5 mm. (A) *Micropterix schaefferi* Heath (Micropterigidae), no locality data (Europe); (B) *Agathiphaga vitiensis* Dumbleton (Agathiphagidae), New Hebrides; (C) *Heterobathmia pseuderiocrania* Kristensen & Nielsen (Heterobathmiidae), Argentina; (D) *Dyseriocrania griseocapitella* (Walsingham) (Eriocraniidae), USA; (E) *Lophocorona pediasia* Common (Lophocoronidae), Australia; (F) *Mnesarchaea paracosma* Meyrick (Mnesarchaeidae), New Zealand; (G) *Prototheora petrosema* Meyrick (Hepialidae), South Africa; (H) *Ogygioses caliginosa* Issiki & Stringer (Hepialidae), Taiwan; (I) *Oxycanus australis* Walker (Hepialidae), Australia; (J) *Acanthopteroctetes unifascia* Davis (Acanthopteroctetidae), USA; (K) *Neopseustis meyricki* Hering (Neopseustidae), Taiwan; (L) *Aenigmatinea glatzella* Kristensen & Edwards (Aenigmatineidae), Australia; (M) *Pseudopostega* **sp.n.**, (Opostegidae), Turkey; (N) *Stigmella* **sp.n.** (Nepticulidae), USA; (O) *Andesiana lamellata* Gentili (Andesianidae), Chile, wingspan = 45 mm; (P) *Cecidoses eremita* Curtis (Cecidosidae), Brazil; (Q) *Lampronia pubicornis* (Haworth) (Prodoxidae 1), France; (R) *Prodoxus quinquepunctella* (Chambers) (Prodoxidae 1), USA.

near-cylindrical (somewhat tapering posteriorly) in outline, and lack both thoracic legs and abdominal prolegs. The total length usually does not exceed 11 mm. The larvae are leaf miners, nearly all on Betulaceae and Fagaceae (Fagales) (Davis, 1978a; Zagulajev, 1998). The entire life cycle of these moths is synchronized with the production of new, tender leaves. The highly modified piercing oviscapt enables the adult female to insert the egg under the leaf epidermis. The first-instar larva initiates a narrow serpentine mine near the outer margin of the developing leaf. Subsequently, the mine enlarges to form an

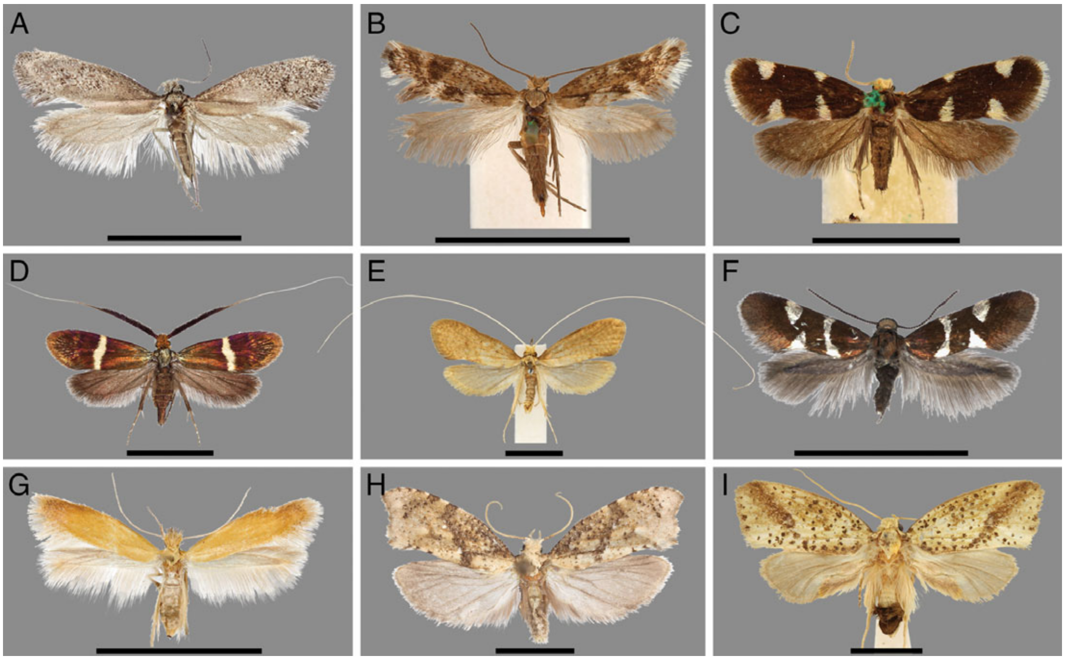


Fig. 7. Adult habitus of representatives of families treated, part 2. Scale bar = 5 mm. (A) *Tridentaforma fuscoleuca* (Braun) (Tridentaformidae), USA; (B) *Crinopteryx familiella* Peyerimhoff (Incurvariidae), France; (C) *Incurvaria praelatella* (Denis & Schiffermüller) (Incurvariidae), no label data (Europe); (D) *Adela australis* (Herrich-Schäffer) (Adelidae 1), Italy; (E) *Nematopogon metaxella* (Hübner) (Adelidae 2), no label data; (F) *Antispila metallella* (Denis & Schiffermüller) (Heliozelidae), the Netherlands; (G) *Coptotriche zelleriella* (Clemens) (Tischeriidae), USA; (H) *Palaephatus falsus* Butler (Palaephatidae 1), Argentina; (I) *Azaleodes micronipha* Turner (Palaephatidae 2), Australia.

irregular, translucent, full-depth blotch, within which all of the parenchyma has been eaten. Larval development is rapid and may be complete before the leaf has fully expanded. The larva cuts a small slit in the leaf epidermis, drops to the ground, digs into the soil, creates an earthen cell and spins a cocoon. Pupal emergence from the cocoon is accomplished with the aid of the greatly enlarged and partially functional mandibles.

Lophocoronidae (Fig. 6E)

This family consists of six species in the genus *Lophocorona* Common, all endemic to southern and western Australia. The larvae have not been discovered, but have been surmised to be leaf miners because the adult female has an apparent piercing oviscapt resembling that of other nonditrysians known to be leaf miners, such as Eriocraniidae and Acanthopteroctetidae (Nielsen & Kristensen, 1996).

Mnesarchaeidae (Fig. 6F)

This family comprises 14 species (half of them undescribed) of small moths (wingspan 8–12 mm) in the genus *Mnesarchaea* Meyrick, all endemic to New Zealand. They typically occur in moist sheltered situations in forests. Adults are weak fliers, active largely by day, but never in strong sunlight. Their proboscis is well developed, but although they have been observed drinking water from wet leaf surfaces, they are not encountered in flowers. The larvae live in silk galleries constructed within the layer of mosses and liverworts that cover the damp forest floor, feeding on fern sporangia, fungal spores and algae in addition to mosses and liverworts (Gibbs, 1979; G. Gibbs and N.P. Kristensen, unpublished data).

Hepialoidea

The superfamily Hepialoidea (Figs 6G–I, 8C, D) currently comprises 629 species in 69 genera. Five taxa have so far mostly been treated as distinct families (Neotheoridae, Anomosetidae, Prototheoridae, Hepialidae and Palaeosetidae), while the genera *Afrotheora* Nielsen & Scoble, *Antihepialus* Janse (both sub-Saharan Africa), *Fraus* Walker (Australian) and *Gazoryctra* Hübner (Holarctic) have been classified as 'primitive Hepialidae' without certain family assignment (Nielsen & Scoble, 1986; Nielsen *et al.*, 2000). Neotheoridae (South America) and Anomosetidae (Australian) have been considered monobasic (additional species in the former are now known, however) and both are poorly known. Prototheoridae, with 12 species in the genus *Prototheora*, are the largest nonhepialid hepialoid family and are restricted to southern Africa. Palaeosetidae are a geographically disjunct family comprising four small genera: *Palaeoses* Turner with one known species from Australia; *Osrhoes* Druce with one rarely collected (and morphologically unique) species from Colombia; and two closely related genera *Genustes* Issiki & Stringer (one species) from the Assam region and *Ogygioses* Issiki & Stringer (four species) from Taiwan and Thailand (Common, 1990; Kristensen & Nielsen, 1994; Davis *et al.*, 1995; Davis, 1996; Kristensen, 1998b; Nielsen *et al.*, 2000). Hepialidae sensu lato comprise the

Fig. 8. Larval feeding habits of selected nonditrysian Lepidoptera, part 1. (A) *Heterobathmia pseuderiocrania* Kristensen & Nielsen (Heterobathmiidae), larval mines and larva on *Nothofagus* Blume (Nothofagaceae), Chile (photograph: R.A. Ramos); (B) *Eriocrania semipurpurella* (Stephens) (Eriocraniidae), larval mines with larvae inside on *Betula* (Betulaceae), the Netherlands, Steenbergen (photograph: K. Boele); (C) *Ogygioses eurata* Issiki and Stringer (Palaeosetidae), feeding on moss, pupal case shown, Taiwan (photograph: L.C. Shih); (D) *Zelotypia stacyi* Scott (Hepialidae), frass plugs in the mouth of the mine on *Eucalyptus saligna* Sm. (Myrtaceae), southeastern New South Wales, Australia (photograph: T.J. Simonsen); (E) *Acanthopteroctetes cf. bimaculata* Davis (Acanthopteroctetidae), larval mine and larva on *Ribes* L. sp. (Grossulariaceae), USA, Oregon (photograph: C. Eiseman); (F) *Pseudopostega auritella* (Hübner) (Opostegidae) larval mines and young larva in stem mines on *Lycopus europaeus* L. (Lamiaceae) after removal of epidermis (larva visible in upper half), the Netherlands, Callantsoog; (G) *Ectoedemia* (*Fomoria*) *jubae* (Walsingham) (Nepticulidae), larva in leaf mine on *Euphorbia regis-jubae* (Euphorbiaceae), Spain, Gran Canaria; (H) *Cecidoses eremita* Curtis (Cecidosidae), live galls (note the lower circular ring of the future exit hole; arrow) and old galls (inset) showing the exit holes on *Schinus* L. sp. (Anacardiaceae) (photographs: German San Blas); (I) *Diacranoses capsulifex* Kieffer & Jörgensen (Cecidosidae), tubular galls (photograph: German San Blas); (J) *Antispila metallella* (Denis & Schiffermüller) (Heliozelidae), larva cutting out its case on *Cornus sericea* L. (Cornaceae), the Netherlands, Oegstgeest.

remaining species and genera, including the earlier-mentioned four ‘primitive Hepialidae’ genera. This assemblage is found in all major biogeographical regions, except, rather surprisingly, Madagascar. Hepialids are found in virtually all terrestrial habitats, but are remarkable among relatively species-rich glossatan families in being most diverse outside the tropics, with the major centres of diversity being Australia and New Zealand, southern Africa and southern South America (Grehan, 1989; Nielsen *et al.*, 2000). Scoble (1992) included all hepialoids in the single family Hepialidae, and we now adopt this arrangement, as ongoing morphological work (T.J. Simonsen, unpublished data) indicates that a consistent cladistic systematization of this assemblage might otherwise require an unwieldy proliferation of little-distinctive hepialoid families. As a corollary, and

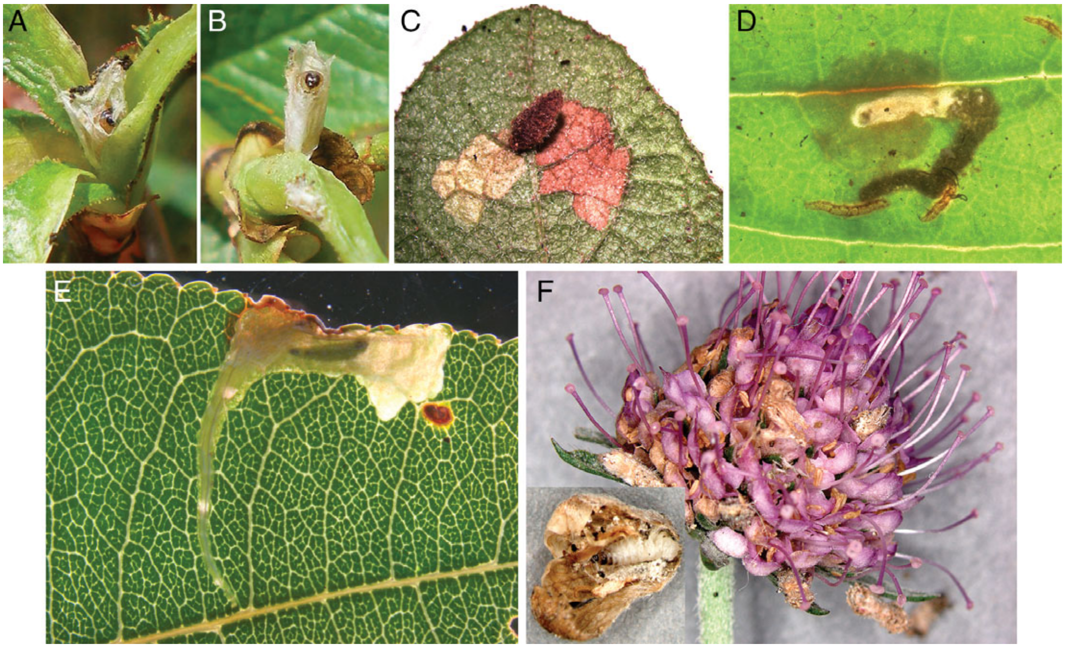
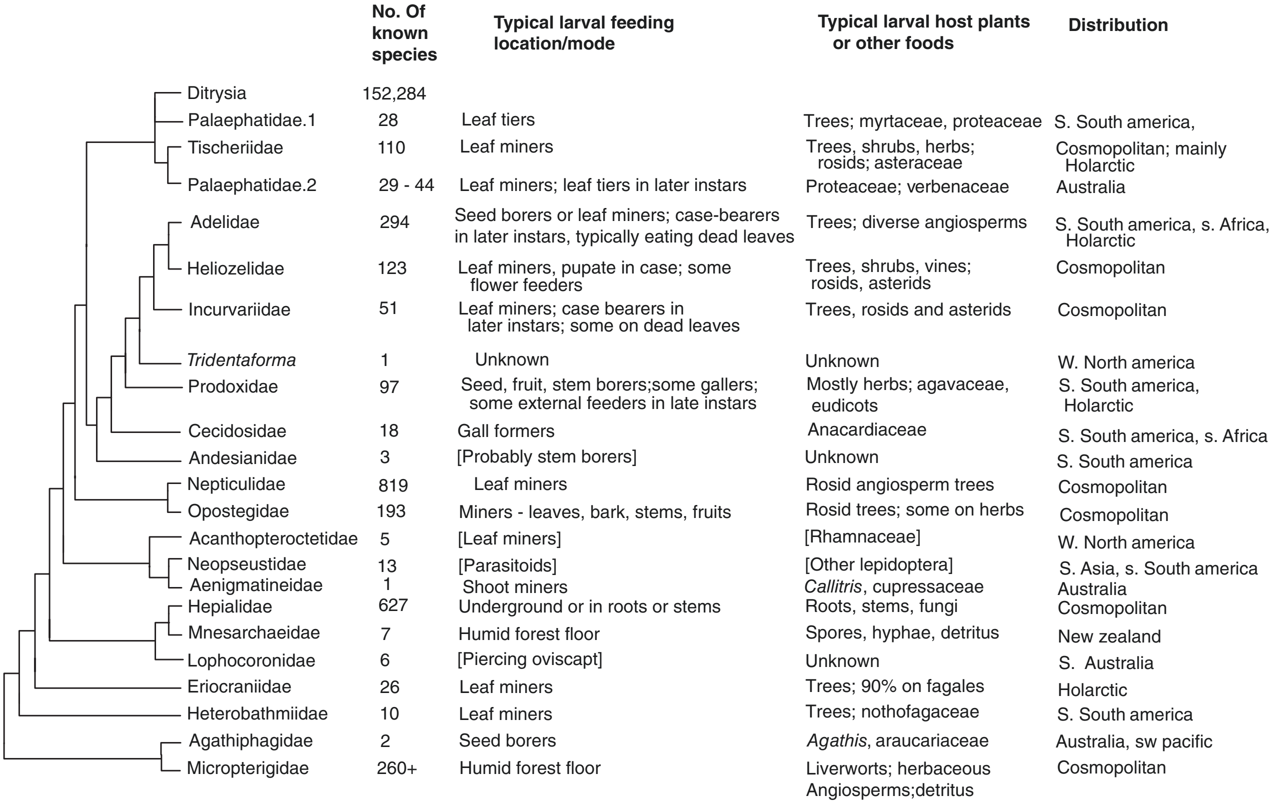


Fig. 9. Larval feeding habits of selected nonditrysian Lepidoptera, part 2. (A, B) *Lampronia morosa* (Zeller) (Prodoxidae), larva in young shoots of *Rosa* L. (Rosaceae), the Netherlands, Monster (photographs: J. Scheffers); (C) *Crinopteryx familiella* Peyerimhoff (Incurvariidae), larval mine on *Tuberaria lignosa* (Sweet) Samp. (Cistaceae), Portugal, Algarve (the small mine) and (D) larva in case and mine on *Cistus salvifolius* L. (Cistaceae), Spain, Huelva; (E) *Coptotriche gaunacella* (Duponchel) (Tischeriidae), larva in mine on *Prunus dulcis* (Mill.) D.A. Webb (Rosaceae), Greece, Arkadia; (F) *Nemophora* cf. *minimella* (Denis & Schiffermüller) (Adelidae), larvae in flowers of *Succisa pratensis* Moench (Caprifoliaceae) (inset: larva in opened flower), the Netherlands, Denekamp.

as the superfamily concept is consistently applied throughout Lepidoptera, we then widen the circumscription of the Hepialoidea to include the small, long-tongued and slender-winged mnesarchaeids, whose sister-group relationship to the hepialids is so strongly corroborated in our analyses; the name Exoporia thus becomes redundant. Hepialidae sensu lato display one of the greatest size ranges in any Lepidoptera family, with a forewing length of *c.* 6 mm in members of the *Palaeoses* group, while exceeding 100 mm in the Australian genera *Zelotypia* Scott (> 120 mm), *Trictena* and *Abantiades* Herrich-Schäffer and the South American *Trichophassus* Le Cerf.

Anomoses Turner has been reared from a 'rotten log' (ABRS, 2009), indicating that it might be mycophagous, but although the first larval stage has been described from *Ogygioses*, and *Prototheora* has been reared from pupae (Davis *et al.*, 1995; Davis, 1996), general life-history and larval feeding strategies otherwise remain unknown for all taxa previously included in separate families. Larval feeding behaviour is also relatively poorly known in 'core' Hepialidae; the following account is based primarily on Grehan (1989), which is the still most comprehensive review of larval feeding strategies and behaviours in the group. He recognized three functional groups: leaf feeders, stem feeders/borers, and root feeders. This grouping reflects the fact that Hepialidae are often highly polyphagous, but almost always restricted to only one of the feeding types. For example, Grehan listed 30 different plant taxa in 15 families as recorded hosts for the root-feeding *Korscheltellus lupulina* L. He also mentioned that the wood-borer *Endoclita excrescens* Butler may feed on as many as 103 different species in 43 families, including several gymnosperms, whereas *E. signifer* Walker has been recorded from 72 plants, including 22 gymnosperms, as well as *Cycas* L. and *Ginkgo* L. Regardless of feeding strategy, hepialid larvae are always concealed feeders living in silken lined tunnels: excavated in the host; burrowed in the ground; or as exposed silk tubes on the ground, or amongst leaf litter or moss. Leaf feeders (which include a number of serious pasture and agricultural pests) either burrow tunnels into the ground or live in such exposed silk tubes, and emerge to feed on herbs and grasses close to the tunnel entrance at night. Root feeders excavate tunnels in the ground where they feed on the roots of various herbaceous and woody hosts. In some large species, such as the Australian *Trictena*, the tunnels may be several metres long. Stem feeders bore into the stem of generally woody hosts; the opening of the tunnel is usually concealed by a mixture of silk webbing, sawdust and frass. Some genera such as the Australo-New Zealand *Aenetus* Herrich-Schäffer and the East and South East Asian *Endoclita* Felder mostly feed on callus growth close to the tunnel opening, but others, such as the South African *Leto venus* Cramer, feed on the tissue of the host. Some species of both leaf feeders and stem borers are known to be fungus feeders or mycophagous in the early larval stages before moving to either leaf feeding or stem boring in later life stages. Specialized mycophagy has only been recorded from a few hepialids such as *Zenophassus* Christoph,



	No. Of known species	Typical larval feeding location/mode	Typical larval host plants or other foods	Distribution
Ditrysia	152,284			
Palaephatidae.1	28	Leaf tiers	Trees; myrtaceae, proteaceae	S. South america,
Tischeriidae	110	Leaf miners	Trees, shrubs, herbs; rosids; asteraceae	Cosmopolitan; mainly Holarctic
Palaephatidae.2	29 - 44	Leaf miners; leaf tiers in later instars	Proteaceae; verbenaceae	Australia
Adelidae	294	Seed borers or leaf miners; case-bearers in later instars, typically eating dead leaves	Trees; diverse angiosperms	S. South america, s. Africa, Holarctic
Heliozelidae	123	Leaf miners, pupate in case; some flower feeders	Trees, shrubs, vines; rosids, asterids	Cosmopolitan
Incurvariidae	51	Leaf miners; case bearers in later instars; some on dead leaves	Trees, rosids and asterids	Cosmopolitan
Tridentaforma	1	Unknown	Unknown	W. North america
Prodoxidae	97	Seed, fruit, stem borers;some gallers; some external feeders in late instars	Mostly herbs; agavaceae, eudicots	S. South america, Holarctic
Cecidosidae	18	Gall formers	Anacardiaceae	S. South america, s. Africa
Andesianidae	3	[Probably stem borers]	Unknown	S. South america
Nepticulidae	819	Leaf miners	Rosid angiosperm trees	Cosmopolitan
Opostegidae	193	Miners - leaves, bark, stems, fruits	Rosid trees; some on herbs	Cosmopolitan
Acanthopteroctetidae	5	[Leaf miners]	[Rhamnaceae]	W. North america
Neopseustidae	13	[Parasitoids]	[Other lepidoptera]	S. Asia, s. South america
Aenigmatineidae	1	Shoot miners	*Callitris*, cupressaceae	Australia
Hepialidae	627	Underground or in roots or stems	Roots, stems, fungi	Cosmopolitan
Mnesarchaeidae	7	Humid forest floor	Spores, hyphae, detritus	New zealand
Lophocoronidae	6	[Piercing oviscapt]	Unknown	S. Australia
Eriocraniidae	26	Leaf miners	Trees; 90% on fagales	Holarctic
Heterobathmiidae	10	Leaf miners	Trees; nothofagaceae	S. South america
Agathiphagidae	2	Seed borers	*Agathis*, araucariaceae	Australia, sw pacific
Micropterigidae	260+	Humid forest floor	Liverworts; herbaceous Angiosperms;detritus	Cosmopolitan

Fig. 10. Synopsis of species diversity, distribution and larval feeding habits of the families of nonditrysian Lepidoptera nonditrysian lineages, superimposed on family relationships extracted from the molecular phylogeny of Fig. 2. The variable numbers of species given for the two lineages of Palaephatidae reflect uncertainty about the placement of all genera except those included in Fig. 2: in each case, the lower number counts only the genera sequenced, and the higher number reflects the possibility that all the genera not sequenced belong to that lineage.

but mycophagy (both specialist and partial, as described earlier) could well be under-recorded in Hepialidae (Grehan, 1989; Scoble, 1992).

The adults of *Ogygioses* are known to be diurnal (Kuroko, 1990; Davis *et al.*, 1995) and strongly associated with a habitat type dominated by *Dicrapteris* fern growing on very wet moss substrate in Taiwan, Thailand, Vietnam and China (S.-H. Yen and L.C. Shih, unpublished data). Like those of most hepialids, the eggs of *Ogygioses* are white when laid, but become black within a few hours (S.-H. Yen and L.C. Shih, unpublished data). The first record of an *Ogygioses* larva was documented by Heppner *et al.* (1995). The first-instar larva of *Ogygioses caliginosa* Issiki & Stringer is characterized by having a prognathous head with a clypeus protruded over the labrum, stemmata numbering only 3, and compact antennae recessed into circular cavities plus the circular spiracles with encircling rings. S.-H. Yen and L.C. Shih (unpublished data) reared out two species of *Ogygioses* from mosses collected from northeastern and central Taiwan, respectively. The larvae make silky tunnels across the leaflets of mosses. This behaviour is similar to that of some moss-feeding Crambinae species, but *Ogygioses* larvae never make tunnels under the moss layer. Pupation occurs within moss and the pupa is enclosed by leaflets of moss.

Mating behaviour and egg laying are highly specialized in Hepialoidea. Males in many species initially attract females visually, sometimes lekking at dusk low over the vegetation in flocks ranging from a few individuals to several hundreds or even thousands of males (Mallet, 1984; Grehan, 1989; Davis *et al.*, 1995; Kaaber *et al.*, 2009; Turner, 2015). As recently reported by Turner (2015) in a study of lekking behaviour in the European Gold Swift, *Phymatopus hecta* (Linnaeus), this behaviour can be highly plastic even within a single species depending on the conditions. Once females have approached a lek, males may employ short-range pheromones to further attract them. In some species females actively seek out a single male in a lek, which then follows her to nearby vegetation where mating occurs (Mallet, 1984). In other species, males may literally knock females out of the air and mate with them on the ground below (Grehan, 1989). Lekking behaviour is triggered by falling light levels below a certain threshold (Mallet, 1984; Davis *et al.*, 1995). Female Hepialidae are known to produce the largest number of eggs of any Lepidoptera, with some species producing more than 30 000 eggs (Kristensen, 1998b), which are often just scattered in flight. This somewhat haphazard behaviour is undoubtedly closely linked to the polyphagous habits of the larva.

Acanthopteroctetidae (Figs 6J, 8E)

There are two described genera in this family. *Acanthopteroctetes* includes four species in western North America (Davis, 1978a), an undescribed species from montane Peru, and the recently discovered *Acanthopteroctetes nepticuloides* Mey from South Africa (Mey, 2011). *Catapterix* Zagulajev and Sinev contains the single species *Catapterix crimea* Zagulajev & Sinev, from the Crimean region of Ukraine (Zagulajev & Sinev, 1988). Another undescribed member of this family is known to occur in China. The only described larva is that of the North American *Acanthopteroctetes unifascia* Davis. It is a full-depth blotch leaf miner in the leaves of *Ceanothus* Linnaeus (Rhamnaceae) in California. The eggs are inserted into the upper (adaxial) epidermis of the leaf by the piercing oviscapt of the female. Larval feeding is extended, beginning in summer (July) and continuing into fall with the half-grown larva overwintering. Nearly all larval growth occurs in late winter–early spring. The relatively large frass pellets are packed into the older portions of the mine. Feeding continues the following spring until maturity, at which time the larva exits through the lower epidermis and constructs a cocoon in debris beneath the host plant. Recently a larva from a leaf mine on *Ribes* (Grossulariaceae) was identified as *Acanthopteroctetes* cf. *bimaculata* Davis (Eiseman, 2015) (Fig. 8E).

Neopseustidae (Fig. 6K)

This family currently consists of two genera, *Nematocentropus* Hwang (two species) and *Neopseustis* (seven species), of the Oriental Region, from northern Sichuan, China, and Assam, India, south to Burma and Taiwan; and two genera, *Apoplania* (three species) and *Synempora* Davis & Nielsen (one species), endemic to austral South America (Argentina and Chile). The moths range in wingspan from 14 to 27 mm (Davis, 1975b). The proboscis is scaled, with a unique double-tube structure, the inner wall of each galea being strongly concave and forming by itself a functionally closed tube (Kristensen & Nielsen, 1981). The larvae were long surmised to be endophagous (Davis & Nielsen, 1980), because the adult female has an apparent piercing oviscapt resembling that of other nonditrysians known to be internal feeders (Davis, 1975b; Nielsen & Kristensen, 1996; Powell *et al.*, 1998). Schisandraceae Blume was considered as a candidate host plant family, due not only to its relatively basal position in angiosperm phylogeny, but also its disjunct geographical distribution between East Asia and South America, which is similar to that of Neopseustidae. Quite remarkably, an individual of *Neopseustis meyricki* Hering has recently been reared by one of us (S.H.Y.) out of a larva of *Microleon* Butler (Limacodidae), collected from northeastern Taiwan in 2010, strongly suggesting that the species is instead an endoparasitoid, and therefore that the piercing oviscapt is more likely to be used to drill through the hard cuticle of the limacodid larva. The *Microleon* larva was found feeding on a *Rubus* leaf. It immediately made a cocoon and pupated after being brought back to the laboratory. When the adult of *N. meyricki* emerged, S.H.Y. pulled out the pupal skin within the limacodid cocoon and examined the morphological characters. All the appendages are separable from the abdomen, and the head sheath morphology agreed with that of the adult *Neopseustis*. Meanwhile, a head capsule of *Microleon* was found within the cocoon, excluding the possibility that the larva collected was *Neopseustis* and feeding on *Rubus* L. More rearings of *Neopseustis* need to be conducted to corroborate this surprising observation.

Aenigmatineidae (Fig. 6L)

This family, recently described for the single species *A. glatzella*, is so far known only from Kangaroo Island (Australia). Adults are of the same size as several heterobathmiids, eriocraniids and small adeloids, to which they have a superficial similarity. They fly in spring (October) and have greatly reduced mouthparts. They are surely nonfeeding (but may drink water), while the larvae are miners in shoots of *Callitris* Vent. (Cupressaceae). They form a cell just below the bark and supposedly feed on phloem or callus tissue; pupation takes place in this cell (Kristensen *et al.*, 2015).

Opostegidae (Figs 6M, 8F)

Currently seven genera and 194 species are recognized (van Nieukerken *et al.*, 2011a; van Nieukerken, 2014). More than three-quarters of the known species occur in subtropical or tropical regions. Of these, 84 are restricted to the Neotropical Region (Davis & Stonis, 2007), but the African and Australian faunas have not been revised recently and are expected to be rich as well. *Notiopostega* Davis, the possible sister group to all other Opostegidae, consists of a single species from the Valdivian forests of southern Chile. This is the largest of all opostegids, with females reaching a wingspan of 16 mm. The highly apomorphic *Pseudopostega* Kozlov is by far the most species-rich genus in both hemispheres, comprising more than half the known diversity.

Adult opostegids have wingspans ranging from about 3.5 to 16 mm. Similar to the sister group Nepticulidae, the female does not have a piercing oviscapt. Opostegid larvae are whitish in colour, extremely slender, 8–25 mm long, and apodous. Little is known about the biology of this family. Leaf mining seems to be rare and has been reported from the endemic Hawaiian *Paralopostega* Davis, of which the six species mine the leaves of *Melicope* J.Forster & G. Forster (Rutaceae), whereas the Indian *Pseudopostega myxodes* Meyrick is a leaf miner of *Cordia* L. (Boraginaceae; Fletcher, 1920). Probably most Opostegidae have a more concealed lifestyle, mining in cambium of trees and stems of herbs and shrubs. *Notiopostega atrata* Davis makes very long mines in the cambium of *Nothofagus dombeyi* (Mirb.) Oerst. in Chile (Davis, 1989), resulting in damage to the trees. Also, two species of *Opostegoides* Kozlov are known to make mines in the cambium, resulting in so-called pith flecks: the North American *O. scioterma* Meyrick makes such mines in *Ribes* L. (Grossulariaceae) and the East Asian *O. minodensis* Kuroko likewise mines cambium of *Betula* L. (Kumata, 1984; Davis, 1989). The Palearctic *Opostega spatulella* Herrich-Schäffer is probably a leaf-stem miner on *Salix* L. (Salicaceae) (Puplesis & Diškus, 2003). The other common European species, *O. salaciella* Treitschke, has been reared from *Rumex* L. (Polygonaceae; van Nieukerken, 1990).

The three European *Pseudopostega* species are associated with herbaceous or shrubby Lamiaceae: *Pseudopostega auritella* Hübner is a miner in the stems of *Lycopus europaeus* L. (van Nieukerken, 1990); *Pseudopostega crepusculella* Zeller likewise tunnels or mines in stems of *Mentha* L. (mines observed in 2013, E. van Nieukerken, personal communication); and *Pseudopostega chalcopepla* Walsingham is associated with *Rosmarinus* L. (van Nieukerken *et al.*, 2004a). Pupation occurs in a tough, silken, lenticular cocoon outside the mine, usually in leaf litter.

Nepticulidae (Figs 6N, 8G)

Currently 852 extant species are recognized in 12 genera, making this by far the largest nonditrysian family (van Nieukerken *et al.*, 2011a; van Nieukerken, 2014). Nepticulids are found in all major biogeographic regions. They also occur on some remote islands in the Pacific but are absent from many others, such as Hawaii (van Nieukerken & van den Berg, 2003). Areas with a high diversity include the Mediterranean region, with diverse faunas of *Trifurcula*, *Parafomoria* Borkowski and *Ectoedemia*; East and South East Asia, with most species belonging to *Stigmella*, *Ectoedemia* and *Acalyptris*, the last with a more tropical distribution; and Australia, with a largely undescribed fauna of 250+ species, including the near-endemic *Pectinivalva* and the endemic *Roscidotoga*. Other tropical areas are potentially very rich, but undersampled.

Nepticulids are very small moths, with forewing lengths of only 1.5 to *c.* 5 mm. Females have a nonpiercing oviscapt; and eggs are deposited on the plant surface and covered by a secretion from the colleterial glands (van Nieukerken *et al.*, 1990). The larvae are miners in all instars, usually in leaves, sometimes in other plant parts, and probably bore directly from the egg into the plant tissue. A few species scattered through the family make galls, such as the North American *Ectoedemia populella* Busck in the petiole of aspen (*Populus tremuloides*, Salicaceae) (Busck, 1907) and the European *Trifurcula pallidella* (Duponchel), which makes spindle-shaped galls in stems of *Chamaecytisus* Link and *Lembotropis* Griseb. species (Fabaceae) (van Nieukerken *et al.*, 2004b). Interestingly, both are type species of large genera that otherwise consist of miners. The mines are typically slender and serpentine, with a median frass trail, but many variations on this pattern are known. Larvae are not normally able to change mines. Pupation usually occurs in a flat cocoon outside the mine, in leaf litter, on trunks or occasionally in the leaf mine. The host plants are in most cases trees or shrubs, but some are specialized on herbs, such as many Polygonaceae for *Enteucha* and Plumbaginaceae for some *Acalyptris*. Individual species are typically host-specific at the plant genus or family level, but collectively the family ranges across the major lineages of eudicots, with a small minority in two genera feeding on monocots, namely Cyperaceae and Poaceae, and very few on more primitive dicots. The Australian (and one Indonesian) *Pectinivalva* species almost all feed on Myrtaceae, with one exception on Paracryphiaceae (Hoare & van Nieukerken, 2013), whereas the Australian *Roscidotoga* all feed on Oxalidales (van Nieukerken *et al.*, 2011b). The widespread genus *Enteucha* is confined to Polygonaceae, with a considerable number of unnamed species in East Asia. Species of the Mediterranean genus *Parafomoria* all feed on Cistaceae. The larger genera have a wide host range, the top five host families being Rosaceae, Fagaceae, Fabaceae, Myrtaceae and Rhamnaceae (Menken *et al.*, 2010).

Andesianidae (Fig. 6O)

This small family consists of only the genus *Andesiana* with three species known from a very restricted region within the Valdivian forests of southern Argentina and Chile. Adults have a forewing length of between 12 and 26 mm, making this family the only large-sized lower Heteroneura. Major synapomorphies of the family include labial palpi with elongate second segment and hindtibiae of male with a basal, eversible pouch, which at rest contains a tip of elongate hair pencil arising from the inner subapical surface of hind femur. The antennae of *Andesiana* are unusual in being sexually dimorphic, with males possessing broadly bipectinate antennae, a condition previously known among monotrysian moths in only a few Incurvariinae. The male frenulum consists of a single stout spine. The female frenulum is composed of four to six smaller, well-spaced spines along the costal margin of the hindwing. The female oviscapt is nonpiercing and largely enclosed within the eighth abdominal segment. The sister group Adeloidea, in contrast, possess a piercing oviscapt. The cloaca is broad and extremely short. Adults fly from spring to early summer and are readily attracted to UV light. The larval biology of this family is unknown; the larvae may be stem borers (Davis & Gentili, 2003).

Cecidosidae (Figs 6P, 8H, I)

This family consists of 16 primarily gall-forming species restricted to the southern hemisphere. Of the six genera, four [*Cecidoses* Curtis – one species, *Dicranoses* Kieffer & Jörgensen – two species (San Blas & Davis, 2013), *Eucecidoses* Brethes – one species, *Oliera* Brethes – one species (Moreira *et al.*, 2012)] have been described from southern South America; one, *Scyrothis* Meyrick (10 species), from South Africa (Mey, 2007, 2011); and *Xanadoses* Hoare & Dugdale (one species) from New Zealand (Hoare & Dugdale, 2003). Except for two gall-producing species of Prodoxidae and at least one species of Heliozelidae, Cecidosidae are the only Adeloidea with this habit. Together with Prodoxinae and a few Adelidae, Cecidosidae are also the only adeloids to have adapted to arid and semi-arid environments, a recurring correlate of galling among insects (e.g., Stone & Schönrogge, 2003). Adult cecidosids range in forewing length from 3.5 to 13 mm. The female has a piercing oviscapt. The larvae of most species are univoltine and cecidogenic, developing within galls on *Rhus* L. and *Schinus* L. (Anacardiaceae). Larvae are varying shades of greenish-yellow, up to 11 mm long, with thoracic legs reduced to circular, minute, unsegmented tubercules. Galls of the South American *Cecidoses* and *Eucecidoses*, termed ‘pyxidiocecidea’, develop as hard, thick-walled, sessile spheres up to 18 mm in diameter on the woody, terminal branches of *Schinus* (Davis, 1998). Pyxidial galls are characterized by the presence of a cap-like covering, or operculum, the formation of which is sometimes unclear. In

Cecidoses, operculum formation is largely independent of larval development: past a certain developmental stage, the operculum forms even if the young larva dies or is surgically removed (Wille, 1926). Pupation takes place inside the gall. Prior to emergence, the pharate adult easily forces open the operculum. *Oliera* and *Dicranoses* form colonies of much smaller, elliptical to spindle-shaped galls enclosed within swollen stems of *Schinus* (Davis, 1998). Stems infested by *Dicranoses* eventually rupture, exposing the galls inside. The larvae of the South African *Scyrothis* form similar galls on *Rhus*, but these galls eventually dehisce and fall to the ground. While on the ground and probably as a means of avoiding excessive heat from the sun, the very active pupa is capable of propelling the gall for distances of up to 30 cm (Mey, 2007). Because of this unusual habit, the galls of this species have been referred to locally as 'jumping beans'. The New Zealand species *Xanadoses nielseni* Hoare & Dugdale, considered sister to all other Cecidosidae (Hoare & Dugdale, 2003), forms the only exception to the cecidogenic habit: it makes scribble mines of up to 2.1 m in length in the smooth bark of trees of several unrelated families, including Cunoniaceae, Nothofagaceae, Myrsinaceae and Escalloniaceae.

Prodoxidae (Figs 6Q, R, 9A, B)

Eight genera and 97 species are currently recognized (van Nieukerken *et al.*, 2011a). Except for a single monotypic genus in southern South America, Prodoxidae are confined to the Holarctic. They are most diverse in North America. Only the genus *Lampronia* Stephens, with 27 species, is widespread in the Holarctic. The adult moths are small, with forewing length ranging from 4 to 16 mm. The female has a piercing oviscapt and lays the eggs inside plant tissue. The larvae are endophagous, at least in the early instars, boring into seeds, fruits, stems, shoots or leaves and, in some cases, causing galls. The larval stage typically overwinters. Larval host plant associations are of two broad types. The probable plesiomorphic condition is association with rosid and (less often) asterid angiosperms, including Saxifragales, Rosales, Fagales and Apiales. A large subclade of prodoxids, however, is restricted to the monocot family Agavaceae. The 23 species of *Prodoxus* Riley, the so-called 'bogus yucca moths', feed in other plant parts than the seeds, such as other parts of the fruit, or the inflorescence stalks and one species mines the leaves (Wagner & Powell, 1988; Pellmyr *et al.*, 2006, 2009). The sister group of *Prodoxus* is formed by the 'true Yucca moths', with the genera *Parategeticula* Davis (five species) and *Tegeticula* Zeller (20 species), which have evolved an obligate pollination mutualism with *Yucca* in which the adult female deliberately pollinates the host plant flowers while the larvae feed in the seeds. This case is often presented as a textbook example of coevolution (Thompson, 2005), although the data do not provide evident examples of co-speciation (Pellmyr, 2003). There are also cases of reversal of mutualism, where the insect no longer pollinates the plant, the so-called 'cheater' moths.

Tridentaformidae (Figs 7A, 10)

This new family (see description later) consists of a single western North American species, *Tridentaforma fuscoleuca*, with unknown life history.

Incurvariidae (Figs 7C, 9C, D)

The family presently contains 51 described species in 12 genera. It is best represented in Australia (endemic genus *Perthida* Common and several undescribed genera and species; Nielsen & Common, 1991) and in the Palearctic with seven genera (Davis, 1998). It is poorly represented in Africa (one species), South America (two endemic monotypic genera), and North America (three endemic species and the Holarctic species *Phylloporia bistrigella* Haworth and *Incurvaria vetulella* Zetterstedt; Davis, 1998). Incurvariid adults are small, with forewing length ranging from 3.5 to 9.0 mm, and usually diurnal. The female has a serrated, piercing type of oviscapt. Typically, the eggs are inserted into the underside of the host leaf, where the first instar develops an irregular blotch mine. The larva has well-developed thoracic legs, but the prolegs are greatly reduced. When the mine is complete, most larvae construct an oval case constructed from pieces cut out from the leaf epidermal layers and held together by silk. Often many mines occur together in a leaf, and the many circular holes that remain form an easily recognizable pattern of damage. After constructing the case, the larva either continues to feed externally or feeds on dead or partially withered leaves on the ground (e.g. *Incurvaria* Haworth). The growing larva enlarges its case by adding oval sections from leaves to the top and bottom of the older case. A few genera (e.g. *Perthida*, *Phylloporia* Heinemann) continue to mine throughout development and do not abandon the mine to construct a case until ready to pupate, rather similar to Heliozelidae. The larva of *Crinopteryx familiella* constructs a case, but continues feeding by mining in a similar fashion as Coleophoridae (Gelechioidea). Pupation occurs within the larval case, either attached to the host or on the ground in leaf litter. The host plants are typically woody eudicots, with recorded host families including Adoxaceae, Betulaceae, Cistaceae, Clethraceae, Cornaceae, Ericaceae, Fagaceae, Myrtaceae, Proteaceae, Rosaceae and Sapindaceae (Davis, 1998). A few species are polyphagous. Species of *Perthida* are important pests of *Eucalyptus* species (Nielsen, 1996).

Adelidae (Figs 7D, E, 9F)

The family consists of nearly 300 species in five genera and occurs on all continents except Antarctica; it is also missing from New Zealand. In addition, a large number of unnamed species of *Nemophora* from the tropics are known in collections and their description is under way (M. Kozlov, personal communication). Two subfamilies have been proposed (Küppers, 1980): Adelinae (maxillary palpi two- to three-segmented, male valvae without pectinifers), including *Adela*, *Cauchas* and *Nemophora*; and Nematopogoninae (maxillary palpi usually four- to five-segmented; male valvae usually with pectinifers), including *Ceromitia* Zeller and *Nematopogon*. Adult adelids are small, with forewing length ranging from 3.5 to 12 mm. The chief synapomorphy for the family is the elongate antenna, particularly in the male, which is usually longer than the forewing in both sexes. The pupae of some genera with elongate antennae are also known to have the antennae form one to four coils around the caudal end of the pupal abdomen (Kuroko, 1961). Most Nematopogoninae are drab in colour and crepuscular or nocturnal. By contrast, the adults of Adelinae are often metallic and predominantly diurnal. The males of many species of *Adela* and *Nemophora* swarm, usually near the host plant or oviposition site. The enlarged compound eyes in these males are an adaptation for swarming (McAlpine & Munroe, 1968; Downes, 1969). The development of specialized, spinose setae and scales near the base of the antennae of swarming males may be further adaptations associated with this courtship behaviour (Nielsen, 1980), possibly for use in sound production or visual signalling (Bland, 1977).

Largely because of the secretive and sometimes omnivorous feeding habits of the larva, surprisingly little is known about the biology of most adelid species. The adelid female has a piercing oviscapt and the eggs are typically inserted singly into plant tissue, but the larva may or may not feed on that plant (Heath & Pelham-Clinton, 1976; Nielsen, 1985). According to Chrétien (1894), during late spring and early summer, the eggs of *Nematopogon metaxella* Hübner are inserted into any convenient herbaceous plant. Upon hatching, the larva immediately drops to the ground where it constructs a flattened, oval case from soil particles and eventually dead leaves. The larva feeds on both living and dead plants and does not complete its development until the following spring. Kuroko (1961) reports a somewhat different life history for *Nemophora raddei* Rebel, which may more closely approximate the univoltine norm for the family. In this species, the eggs are inserted into the ovaries of *Salix sieboldiana* Blume in spring. The first-instar larva feeds on the ovules as well as the ovary wall. After moulting, it constructs a small, oval case and descends on a silken thread to the ground where it prefers to feed on dead leaves of the host *Salix* and of *Castanea crenata* Siebold & Zucc. The mature larva (sixth instar) pupates near the end of October, with the adult emerging the following spring. Several European *Nemophora* species also oviposit in flowers or flower buds, but after constructing a case, the larva keeps feeding for some time in the flowers or flowerheads of Dipsacaceae or Gentianaceae (photos in Huisman *et al.*, 2009). The eggs of most *Adela* are inserted into the flower ovary of their host wherein the first-instar larvae feed on the developing seeds. From the second instar on, the larvae become case-bearers and feed on the lower or fallen leaves of their host (Heath & Pelham-Clinton, 1976). First-instar larvae of some Adelidae may mine leaves (Common, 1990). Over 20 families of angiosperms and one of gymnosperms (Pinaceae) have been reported as hosts (Küppers, 1980). Pupation typically takes place inside the larval case with the pupal exuvium partially extruded.

Heliozelidae (Fig. 7F)

Twelve genera and 124 species are currently recognized (van Nieukerken *et al.*, 2011a, 2012), reported collectively from every major biogeographic region except New Zealand. Because of their minute size (forewing length ranging from 1.7 to 7.0 mm) and diurnal habit, adult Heliozelidae are seldom collected, even though they can be very abundant. More knowledge derives from adults reared from the leaf mines. The diversity is highest in Australia, where 28 named species are known, but the real number probably exceeds 100 (D. Hilton, personal communication). Also, the Nearctic fauna is comparatively rich, with 30 known species. All tropical faunas are poorly known, with just three species described from Africa, although collections contain several more. The putative sister group to the remaining genera, *Plesiozela* Karsholt & Kristensen, is endemic to temperate austral South America (Karsholt & Kristensen, 2003). The largest diversity in Australia is in a separate clade with the genera *Hoplophanes* Meyrick (20 named species), *Pseliastis* Meyrick (three species) and possibly new genera (D. Hilton, personal communication). Most of the species elsewhere in the world are contained in *Heliozela*, *Antispila* and *Coptodisca*, but *Antispila* Hübner is a composite 'waste basket' taxon, and several species need to be removed to the previously monotypic *Holocacista* Walsingham & Durrant (van Nieukerken & Geertsema, 2015). *Coptodisca* Walsingham is restricted to North and Central America (Bernardo *et al.*, 2015). The adult female has a piercing oviscapt, and the larvae are usually leaf miners, with prolegs absent or nearly so and thoracic legs usually absent, although these are well developed and five-segmented in some *Heliozela* (Davis, 1987). The larvae reach 4–6 mm in length. Most first-instar larvae begin a short, serpentine mine, which is – often abruptly – enlarged into a small, full-depth blotch with the frass retained inside the mine. All instars mine except the last, which constructs a flat, oval case by cutting sections from the upper and lower epidermis of the mine and joining them with silk. The lenticular shape of the case, which is either carried or dragged by the larva, provides the origin of this family's common name, the 'shield bearers'. The mature larva typically spins a silk strand by which it lowers itself to the ground to pupate, inside the case, amongst leaf litter, and does not feed thereafter. Many species in *Coptodisca* and *Holocacista*, however, attach the cases to the bark or leaves of the host plant. Abandoned mines with small oval holes are characteristic of the leaf damage caused by these insects. The species in the Australian clade of *Hoplophanes* Meyrick do not make mines, but probably oviposit in flowers of various angiosperm families. Some *Heliozela* mine twigs, petioles, or leaf ribs, and *Heliozela aesella* initiates galls on grapevine (Davis, 1998). Individual species are typically host-specific to at least the plant genus or family level. The genus *Antispilina* Hering feeds on herbaceous Polygonaceae, whereas most others feed on woody plants. Most *Heliozela* species feed on Fagales or Myrtales. Most species of *Antispila* sensu stricto feed on Cornaceae and Vitaceae, and *Holocacista* species on Vitaceae, Rubiaceae and several other families. Vitaceae are hosts for several genera, and recently some pest species have been identified from grapevine, such as *Antispila uenoi* Kuroko in Japan and the North American *A. oinophylla* van Nieukerken & Wagner after introduction into Italy (van Nieukerken *et al.*, 2012).

Tischeriidae (Figs 7G, 9E)

At present, three genera and 112 species are recognized (Puplesis & Diškus, 2003; van Nieukerken *et al.*, 2011a, updated). The genus *Astrotischeria* is confined to the New World, whereas *Tischeria* Zeller and *Coptotriche* Walsingham are widespread, although unknown from Australia, New Zealand and Pacific Islands. *Coptotriche* was recently recorded from Madagascar (Lees & Stonis, 2007). The diversity is highest in North America, with 65 species known. There is also a largely undescribed diversity in East Asia. Adult tischeriids are very small, with forewing length ranging from 2.7 to 5 mm. The female oviscapt is not of the piercing type. Nonetheless, tischeriid larvae are all leaf miners through all instars. They make blister-like mines from which the very mobile larva ejects the frass through a hole. The larva pupates inside the mine in a circular cocoon. The larvae appear to be monophagous or oligophagous, restricted to a single host plant family or subset thereof (Puplesis & Diškus, 2003). Tischeriid food plant use shows a striking discontinuity in host taxon and growth form. Nearly all records for *Tischeria* and *Coptotriche* are from woody members of the angiosperm clade fabids and malvids (APG III, 2009), especially Fagacaeae, Rosaceae, Rhamnaceae and Malvaceae, but in the tropics, a few more families, such as Hypericaceae, Combretaceae, Theaceae and Anacardiaceae, are used. In contrast, *Astrotischeria* species appear restricted to herbaceous Asteraceae and some Malvaceae.

Palaephatidae (Fig. 7H, I)

Currently 57 species are recognized, equally divided between southern South America (Davis, 1986) and Australia (Nielsen, 1987; Common, 1990). Five genera (*Sesommata* Davis, six species; *Metaphatus*,six species; *Plesiophatus*, one species; *Palaephatus*, 13 species; and *Apophatus*, two species) have been described from South America, and two genera (*Azaleodes*, four species; *Ptyssoptera*, 25 species) have been described from Australia. In South America this family occurs in eight major biotic regions (Davis, 1986) of southern Argentina and Chile between approximately 32°S and 55°S latitudes. The greatest species concentration occurs in regions characterized by a cool, moist climate and temperate forests dominated by *Nothofagus* and associated vegetation, namely, the Northern Valdivian forest, Valdivian forest and Valdivian Cordillera. Nielsen (1987) reported *Azaleodes* to occur in two disparate areas along the east coast of Australia: in northern Queensland between Cooktown and Paluma, and between Barrington Tops (New South Wales) and Wollongong (Victoria).

Palaephatid adults are small, with forewing length ranging from 3.8 to 16 mm. The female oviscapt is short and nonpiercing. The immature stages have been described for few species. O. Karsholt (personal communication to Davis, 1986) reared a single larva of *Sesommata holocapna* in Argentina, which had spun together small twigs of its host shrub, *Diostea juncea* Miers (Verbenaceae). Parra & Ibarra-Vidal (1994) reported observations on *M. ochraceus* in southern Chile. Oviposition occurs in late winter or spring on the new leaves of the host plant, *Embothrium cocciniuum* J.R. Forst. & G. Forst. (Proteaceae). The early-stage larva folds over the edge of a leaf or ties together two overlapping leaves, and feeds within the resulting gallery, skeletonizing the leaf. A similar behaviour has been observed in *Palaephatus albicerus* by A. Aguilera and D.R. Davis (unpublished data) feeding on 'murta' (Myrtaceae) in Chile, and in *Ptyssoptera* in Australia (Nielsen & Common, 1991; ABRS, 2009), for which there are food plant reports on six species in Robinson *et al.* (2010), from a total of four genera of Proteaceae.

Early evolution of phytophagy in Lepidoptera: reassessment of hypotheses

In this section, we revisit some of the main questions that have been posed about the early history of lepidopteran phytophagy. First, when and how often did phytophagy arise in Lepidoptera? In the ecological scenario for early Lepidoptera proposed by Kristensen (1997), based on the morphological phylogeny (Fig. 1A), feeding on vascular plants is hypothesized to have a single origin, from a soil-dwelling ancestor that fed, like extant Micropterigidae, on nonvascular plants, detritus or fungi. The arboreal feeding typical of most early-arising families, including Agathiphagidae, Heterobathmiidae, Eriocraniidae and others, is taken to reflect common ancestry. The soil-dwelling habits of Hepialoidea as here redefined, which somewhat resemble those of Micropterigidae, are taken to represent a reversal. Although the molecular phylogeny presented here departs in several ways from the morphological hypothesis (Fig. 1A), it remains largely consistent with Kristensen's (1997) scenario. The major departure stems from the molecular finding, supported weakly in our tree (Fig. 2) but strongly in Kristensen *et al.* (2015) that Agathiphagidae and Micropterigidae may be sister groups (Fig. 10). In that case, it seems equally parsimonious to suppose either that Agathiphagidae represent an independent origin of vascular plant phytophagy or that Micropterigidae represent an independent reversion to an ancestral antliophoran soil-dwelling larval life history.

How to choose between these alternatives is unclear. Further study of micropterigids might help. Over the past two decades it has become clearer that larval habits vary distinctly among subclades in this family. Some micropterigids, such as *Micropterix* species, seem to be detritivores or general feeders, using decaying angiosperms, though sometimes living plant tissue as well. Others, however, are restricted to living nonvascular plants. Most notably, the clade of five genera and 30 species of Japanese micropterigids studied by Imada *et al.* (2011) all feed on the same species of liverwort, an association to which Imada *et al.* (2011) assigned a tentative age of over 30 Ma. Thus, at least two features broadly characteristic of more typical lepidopteran phytophagy – host specificity and long-conserved association with particular plant taxa – are present in Micropterigidae as well. It is conceivable that host-specific liverwort feeding is ancestral for micropterigids, which would imply that phytophagy of a sort was ancestral for Lepidoptera as a whole. Testing this hypothesis will require improved understanding of both feeding habits and deep phylogeny in the family.

Micropterigidae are host-specific within nonvascular plants, whereas in our tree the closest relatives of Micropterigidae and most other lepidopteran lineages show host specificity solely for vascular plants. Why is there such a clear division? One plausible hypothesis, compatible with our phylogeny, is that micropterigids simply never evolved a potential 'key innovation' that may have been essential to the colonization of vascular plants by other early lepidopteran lineages, namely, adult oviposition and larval feeding on trees. All known micropterigid larvae feed at or below ground level. By contrast, the two earliest-originating lineages of Angiospermivora, i.e. Heterobathmiidae and Eriocraniidae, are entirely arboreal feeders, as are a vast majority of the remaining nonditrysians. Arboreality might have promoted the origin of vascular plant feeding if ancestral Lepidoptera, like their early-diverging extant descendants, lived in forest habitats in which the bulk of nutrient-rich vascular plant resources lay in the canopy.

Likewise, it is uncertain how the switch from ground feeding to arboreal feeding occurred, i.e. what the intermediate evolutionary steps might have been. Our topology is at least consistent with a hypothesis put forward by Menken *et al.* (2010), who speculate that specialization on the leaf litter of single dominant forest tree species by an ancestral angiospermivoran could have been a precursor to leaf-mining on attached living leaves, by fostering acquisition of the ability to digest the more nutritious cell contents in freshly fallen leaves. This adaptation, in turn, they hypothesized, could have been promoted by the evolution of cytokinin-like hormones for creating so-called 'green islands' (Engelbrecht *et al.*, 1969; Giron *et al.*, 2007). A similar conjecture about transition to the canopy could be made for the early diverging Agathiphagidae, in which the eggs appear to be laid on Agathis seeds while they are still in the cone on the tree, but the larvae develop mainly after the cones have fallen (Kristensen, 1997).

A second focal question about the evolutionary history of Lepidoptera has been the degree to which the diversification of lepidopterans has temporally overlapped, and thus potentially influenced and been influenced by that of their main food plants, the angiosperms (Kristensen & Skalski, 1998; Menken *et al.*, 2010; Wahlberg *et al.*, 2013). To answer this question will require robust estimates of divergence dates for both Lepidoptera and flowering plants. Broad-scale dating analyses across the Lepidoptera, based on molecular chronograms calibrated with fossils, have only recently started to appear, and the variation in age estimates is still great, as two examples will show. The most extensive study so far is that of Wahlberg *et al.* (2013), who used the molecular data of Mutanen *et al.* (2010; 350 taxa, eight genes) in conjunction with six fossils. These authors date the crown group Lepidoptera (= the first split between extant lineages) at 215 Ma (late Triassic), the origin of Ditrysia at about 160 Ma (late Jurassic), and the origin of Apoditrysia at about 140 Ma (early Cretaceous). More recently, Misof *et al.* (2014) included four nonditrysian and six ditrysian lepidopterans, plus three lepidopteran fossils, in a phylogenomic/dating study of all the insect orders (1478 genes, > 100 taxa). This study pushed back the origins for insects overall, but yielded dates for early divergences in Lepidoptera about 60 Ma younger than those of Wahlberg *et al.* (2013), namely ~ 140 Ma (early Cretaceous) for the basal split within extant Lepidoptera, ~ 100 Ma (early late Cretaceous) for the origin of Ditrysia, and ~ 80 Ma for the origin of Apoditrysia (late Cretaceous). Both studies can be criticized on the grounds of fossil number and selection, and it is to be hoped that further work will lead to better consensus on divergence times.

Comparable variation is evident in recent dating studies of angiosperms. For example, Bell *et al.* (2010) and Smith *et al.* (2010) used similar methodologies but reached age estimates for crown group angiosperms of 147–183 Ma (depending on the dating prior; Jurassic) and 217 Ma (late Triassic), respectively. Both are older than the oldest angiosperm fossils. The variation in estimates is important as under some combinations of these dates, such as late Triassic origin of extant nonditrysian lepidopterans and late Jurassic origins of crown group angiosperms, early lepidopteran lineages could not have fed on angiosperms at all. At the opposite extreme, such as Triassic origin of crown group angiosperms and early Cretaceous origin of extant nonditrysians, the early diversification of Lepidoptera would have taken place against a background of already diversified angiosperms. To distinguish such alternatives will require more definitive results from molecular dating studies.

Uncertainty about ages also produces uncertainty in the interpretation of present-day distributions of nonditrysian lineages across plant taxa, in particular the degree to which they might reflect long-conserved interactions from the past. For example, among extant Micropterigidae, larval feeding on liverworts and adult feeding on conifer pollen or fern spores could represent establishment of feeding habits before angiosperms were available. Similarly, the specialization of Agathiphagidae on seeds of the coniferous genus *Agathis* Salisb. could reflect either a habit established before angiosperm hosts were available or a shift from earlier association with angiosperms. In both cases, the critical evidence is the relative ages of hosts and herbivores.

The subsequent branchings in Fig. 10 lead to two leaf-mining groups, the nonglossatan Heterobathmiidae, larvae feeding on *Nothofagus* (Nothofagaceae) and the glossatan Eriocraniidae, feeding on various Fagales (Betulaceae, Fagaceae) and some Rosaceae (Davis, 1978a; Imada *et al.*, 2011). The related orders Fagales and Rosales also form a major component of the host lists of other leaf-mining nonditrysian families, such as Nepticulidae and Tischeriidae (e.g. Menken *et al.*, 2010), and indeed of most nonditrysian families. It is therefore tempting to consider feeding on (woody) rosids to be an ancient trait in Lepidoptera, possibly ancestral to most other host associations. Such a conclusion would require, however, that the rosid clade be as old as, or older than, the nonditrysian lineages that feed on them. If separation among the nonditrysian lineages were complete before rosids arose, the prevalence of rosids in the diets of nonditrysians would be better explained by parallelism. Some dating estimates for the rosids (125 Ma; Bell *et al.*, 2010) would make them comparable to some estimates for the ages of nonditrysian lineages (Misof *et al.*, 2014), but much younger than others (Wahlberg *et al.*, 2013). Additional doubt about the hypothesis of an ancestral association of most Lepidoptera with rosids is raised by host records of fossil leaf mines, allegedly belonging to Nepticulidae, which suggest a wider host range, including earlier, nonrosid angiosperm lineages such as Laurales, Proteales and Saxifragales (Kozlov, 1988; Labandeira *et al.*, 1994). Recent Jurassic age finds of additional extinct, probably lepidopteran lineages (Huang *et al.*, 2010; Zhang *et al.*, 2013) further suggest that the early history of Lepidoptera and their feeding habits is more complicated than might be inferred from extant taxa alone. On the other hand, it seems safe to conclude that most extant Lepidoptera are descended from an ancestor that fed on vascular plants of some kind, as these plants as a whole are much older than the Lepidoptera.

A final often-raised question about the early history of lepidopteran phytophagy is concerned with the mode and location of larval feeding. Our molecular phylogeny supports the conclusion that the ancestral angiospermivoran (Fig. 10), at the least, was an internal feeder. Apart from Hepialoidea, internal feeding is ubiquitous in the nonheteroneurous families. Moreover, it remains a reasonable conjecture, although not definitively established, due in part to uncertainty about basal divergences in Glossata, that this ancestor was a leaf miner. In our phylogeny (Fig. 8), leaf mining characterizes the first two families diverging successively within Angiospermivora, Heterobathmiidae and Eriocraniidae, as well as early-diverging families of Coelolepida (Fig. 2, node 12), such as Acanthopteroctetidae (so far as known) and Nepticulidae.

The potential evolutionary advantages to leaf mining seem obvious: the larva is living in a protected habitat and can survive drought more easily than an externally feeding larva. However, these advantages also apply to other forms of internal feeding, including root boring, cambium mining and galling. In fact, we see a combination of these modes of larval feeding in several nonditrysian groups. For instance, in Opostegidae, leaf mining is rare, whereas both stem mining in herbs and cambium mining in trees are common. Also in nepticulids transitions between leaf mining and stem mining are common (Ivinskis *et al.*, 2012). It is therefore plausible that evolutionary changes of internal feeding modes between wood boring, stem mining and leaf mining have occurred frequently.

Although the earlier-diverging lepidopterans are nearly all strictly internal feeders, the heteroneuran subclade Eulepidoptera (Fig. 2, node 37) shows a strong trend toward greater flexibility of habits. Within Adeloidea, for example, the larvae of Cecidosidae and Prodoxidae are, respectively, gallers and flower or seed feeders, whereas many larvae in the clade consisting of Incurvariidae, Heliozelidae and Adelidae start larval life as leaf miners. Although many Incurvariidae and most Heliozelidae continue as leaf miners, most incurvariids and adelids in later instars build a portable case from leaf pieces and leave the leaf or flower to pupate or to feed in the leaf litter. In some Palaephatidae, finally, early instars have been reported to fold and tie the leaf edge, or tie two overlapping leaves together and feed within the resulting gallery. In this way, the palaephatids presage the later radiation of Ditrysia, many or perhaps most families of which show analogous forms of concealed external feeding, although the earliest-diverging ditrysians, Tineoidea, seem to have returned to fungal and/or detritus feeding (Regier *et al.*, 2015).

Although we have sketched a plausible hypothesis of how the evolution of larval feeding mode generally proceeded, there are some striking deviations from this pattern. For example, the apparent parasitoid habit of *N. meyricki*, here reported for the first time and needing further confirmation, is unexpected. Further study is needed of this rare family, which may be the only instance of endoparasitoidism in Lepidoptera. It is hard to understand how this habit could have evolved from angiosperm feeding, but as multiple, more advanced (ditrysian) species are carnivores or ectoparasites, the potential for shifting to a carnivorous diet is clearly widespread (Pierce, 1995). Similarly, whereas simple flower or fruit feeding can potentially easily evolve from other means of internal feeding, specialized flower and seed feeding resulting in active pollination and close mutualism, as in some Prodoxidae and their host Agavaceae, appears to be very rare. In the Agavaceae-feeding Prodoxidae, all kinds of transitions between various modes of internal feeding occur within the same plant family. This group may therefore illustrate, on a small scale, what might have happened during long-term evolution of lepidopteran feeding modes. In Australian Heliozelidae, there is another group of potential flower and seed feeders (around the genus *Hoplophanes* Meyrick; Meyrick, 1897), which deserve closer study to see whether mutualistic relationships also occur there.

Taxonomy

Description of Tridentaformidae, fam.n.

Tridentaformidae Davis, **fam.n.**

Type genus: *Tridentaforma* Davis, 1978.

Adult (Figs 7A, 11). Small, slender-bodied moths with moderately slender wings; wing expanse 8.5–20.5 mm. Basal one-fifth of haustellum covered with broad, appressed scales dorsally. Venation heteroneurous; microtrichia generally distributed over all wing surfaces. Primary arms of metafurcasternum free, not fused to secondary arms. Male with a single stout frenular bristle; female with four to five stout frenular bristles basal to a more distal row of 10–14 smaller, costal spines. Eighth segment of female reduced, normally enclosed within enlarged seventh segment; female reproductive system of the monotrysian type, with a single genital opening and ventral oviduct; oviscapt elongate; posterior apophysis acute, seemingly specialized for piercing plant tissue; cloaca slender, elongate, nearly half the length of posterior apophysis.

Head (Fig. 11A, B). Vestiture rough; frons and vertex densely covered by long, piliform scales with acute apices. Antenna 40–49 segmented, simple, approximately 0.50–0.55× the length of forewing; basal 0.6–0.7 of flagellum with a single annulus of broad, flattened scales over each flagellomere; distal portion of flagellum mostly devoid of scales, densely pubescent; scape with a pecten consisting of an anterior row of seven to 10 long, brown bristles. Ocelli absent. Compound eye moderately large, interocular index (Davis, 1975a) approximately 1.0–1.1;

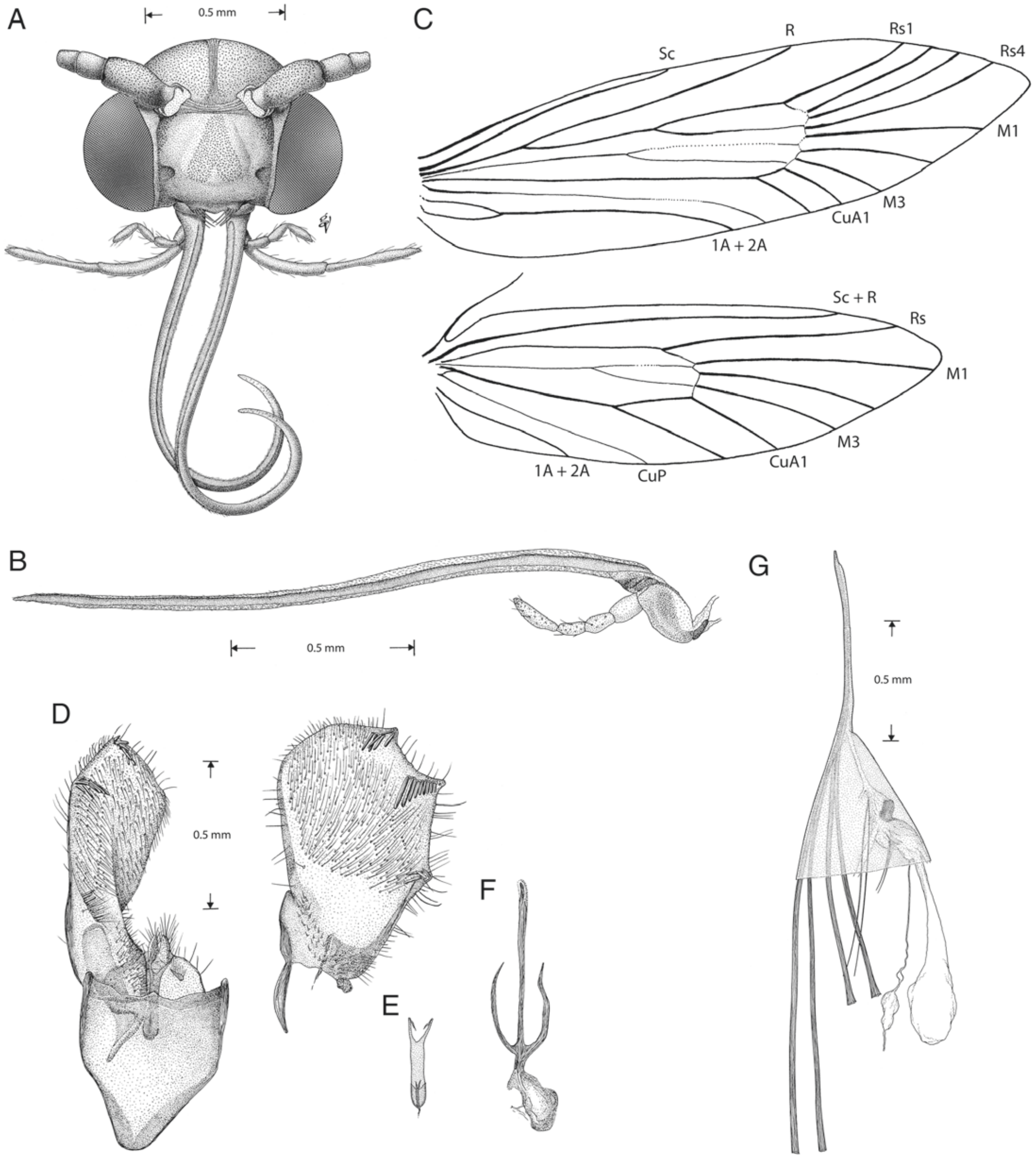


Fig. 11. Adult morphology, *Tridentaforma fuscoleuca* (Braun). (A) Head, anterior view; (B) Haustellum, maxilla; (C) wing venation; (D) male genitalia, ventral view with mesal view of valva; (E) juxta; (F) phallus; (G) female genitalia, lateral view.

microtrichia few, widely scattered over eye. Mandible vestigial. Maxillary palpus moderately long, approximately 0.5–0.6× the length of labial palpus, four-segmented, all segments relatively short; apical (fourth) segment slightly longer (~1.5× the length of third). Haustellum elongate, over 4× the length of maxillary palpus and about 2× the length of labial palpus. Labial palpus three-segmented, with apical segment elongate and equalling length of second; second segment with four to five stout bristles arising laterally at apex.

Thorax (Fig. 11C). Foretibia with pectinate epiphysis arising from middle, extending approximately halfway to apex of tibia. Forewing relatively narrow; forewing L/W ratio: ~3.5–3.7, with 10 veins arising usually separately from discal cell; R arising near basal third of cell; Rs1 from apex of accessory cell; Rs2 rarely stalked with Rs1; CuA1 about equidistant from M3 and CuA2. Hindwing approximately the same width as forewing, with six veins from cell; M1 and M2 sometimes connate; CuA1 arising from distal third of cell; base of medius forked within cell of both wings.

Abdomen. Unmodified, without specialized setal tufts. Sternum 7 of female 2.4–2.8× the length of sternum 6. Eighth segment of female lightly and uniformly pigmented, without darkly sclerotized areas laterally.

Male genitalia (Fig. 11D–F). Uncus reduced, consisting of two small lobes. Vinculum and saccus well developed, V- or Y-shaped saccus sometimes attenuated; total length 0.6–1.3× the length of valva. Valva varying in width from relatively narrow to extremely broad; an equally spaced series of three pectens situated along ventral margin of cucullus, each pecten consisting of a short, transverse row of five to 10 broad, stout spines. Juxta reduced in size, ~ half the length of median branch of phallus, and slender, gradually tapering anteriorly to a slender, acute apex. Phallus three-branched with slender median branch the longest (approximately 2× the length of lateral branches) and enclosing the vesica; cornuti absent.

Female genitalia (Fig. 11G). Apex of oviscapt very slender, slightly compressed, acute, smooth, without a serrated cutting edge. Anterior and posterior apophyses extremely slender and elongate. Vestibulum relatively small and mostly without heavily thickened walls, but with some thickening evident ventrally near caudal end. Ductus bursae membranous, relatively short, less than one-third the length of posterior apophyses. Corpus bursae entirely membranous, without signa.

Comments. The family relationships of *Tridentaforma* have long been recognized as problematic (Davis, 1998). Originally described in Incurvariidae (Davis, 1978b), it was moved to Prodoxidae by Nielsen & Davis (1985). Morphologically, the genus shares important features with the Adelidae (basally scaled haustellum), Incurvariidae (male valva with rows of broad spines), and the prodoxid genus *Lampronia* (metafurcal apophyses free, lateral cervical sclerites without lateral process). Earlier molecular studies, using mitochondrial DNA (Brown *et al.*, 1994), 18S rDNA (Wiegmann, 1994) and dopa decarboxylase (Friedlander *et al.*, 2000), agreed in excluding *Tridentaforma* from Prodoxidae, but disagreed on where it should go instead. Tridentaformidae may be best recognized morphologically by the apomorphic, tridentiform male phallus, with its slender lateral processes that extend half the length of the central phallus tube, and by the broad valvae bearing three isolated, transverse rows of spines along the ventral margin of the cucullus. The family significance of such genitalic characters, which are often species-specific, is somewhat uncertain in this case, because *Tridentaforma* is currently represented by a single species, *T. fuscoleuca* (Braun), from the western United States. However, the present molecular data firmly exclude *Tridentaforma* from all other families. The molecular analysis also helps to explain the patchwork of characters shared variously between *Tridentaforma* and Prodoxidae, Incurvariidae and Adelidae, by showing that it is closely related to all three: it is the sister group to Incurvariidae + Adelidae + Heliozelidae, and these plus *Tridentaforma* are sister group to Prodoxidae (Fig. 2). Biology and immature stages are unknown.

Hepialoidea

Hepialoidea Stephens **stat. rev.**
Mnesarchaeoidea Eyer, **syn.n.**

Fig. 12. The late Niels Peder Kristensen, a foremost authority on Lepidoptera and insect phylogeny (Bulgaria, 2013).

Diagnosis (following Kristensen, 1998b). Ostium bursae well separated from the ovipore, with no internal connection between the bursa copulatrix and the ovipore; female accessory glands lost; apodemal apophyses in the female genitalia lost; phallus membranous and devoid of retractor and protractor muscles; segment X with strongly developed supra- and subrectal transverse muscles.

Given the emerging morphological (Grehan, 2012; T.J. Simonsen, unpublished data) and molecular evidence, we further suggest following Scoble's (1992) proposal that all 'classical' Hepialoidea families be included in Hepialidae. Consequently, we treat Neotheoridae, Anomosetidae, Prototheoridae and Palaeosetidae as synonyms of Hepialidae (**stat. rev.**).

Hepialidae Stephens **stat. rev.**
Neotheoridae Kristensen, **stat. rev.**
Anomosetidae Tillyard, **stat. rev.**
Prototheoridae Meyrick, **stat. rev.**
Palaeosetidae Turner, **stat. rev.**

Diagnosis (following Kristensen, 1998b). Strong reduction of the proboscis; intercalary sclerite between scape and pedicle elongate and partly lowered into a membranous pocket; Rs3 displaced backwards, reaching wing margin posterior to apex; male genitalia with hinged juxta-truellum sclerites.

In memoriam: Niels Peder Kristensen

Niels Kristensen (Fig. 12) was a prolific and influential scholar of insect systematics, especially Lepidoptera. He spent his entire career as a curator and scientist at the Zoological Museum of the University of Copenhagen, Denmark. He authored many influential research papers on Lepidoptera morphology and phylogeny, especially the basal Lepidoptera. He edited several books, including the Handbook of Zoology volumes on Lepidoptera (Kristensen, 1998c, 2003b), which have served as the primary manuals for every lepidopterist. Niels was a great mentor, friend and father figure to many lepidopterists, including the present authors. One of the leaders of Lepidoptera research has passed away, leaving behind a legacy that will influence our science for many years to come.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12129

Figure S1. ML topology and bootstraps for nt123, 86 taxa, 19 genes.

Figure S2. ML topology and bootstraps for nt123, 86 taxa, five genes.

Figure S3. ML topology and bootstraps for degen1, 86 taxa, five genes.

File S1. Additional palaephatid sequences.

Table S1. Specimens sequenced, accession numbers, Genbank numbers.

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