Evolution of larval life mode of Oecophoridae (Lepidoptera: Gelechioidea) inferred from molecular phylogeny

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Abstract

Phylogenetic relationships within family Oecophoridae have been poorly understood. Consequently the subfamily and genus level classifications with this family problematic. A comprehensive phylogenetic analysis of Oecophoridae, the concealer moths, was performed based on analysis of 4,444 base pairs of mitochondrial COI, nuclear ribosomal RNA genes (18S and 28S) and nuclear protein coding genes (IDH, MDH, Rps5, EF1a and wingless) for 82 taxa. Data were analyzed using maximum likelihood (ML), parsimony (MP) and Bayesian (BP) phylogenetic frameworks.

Phylogenetic analyses indicated that i) genera *Casmara*, *Tyrolimnas* and *Pseudodoxia* did not belong to Oecophoridae, suggesting that Oecophoridae s. authors was not monophyletic; ii) other oecophorids comprising two subfamilies, Pleurotinae and Oecophorinae, were nested within the same clade, iii) *Martyringa*, *Acryptolechia* and Periacmini were clustered with core Xyloryctidae. They appeared to be sister lineage with core Oecophoridae.

BayesTraits were implemented to explore the ancestral character states to infer historical microhabitat patterns and sheltering strategy of larvae. Reconstruction of ancestral microhabitat of oecophorids indicated that oecophorids might have evolved from dried plant feeders and further convergently specialized. The ancestral larva sheltering strategy of oecophorids might have used a silk tube by making itself, shifting from mining leaves.

Key words: Oecophoridae, concealer moths, phylogeny, ancestral character states, Bayes traits

1. Introduction

Oecophoridae (Lepidoptera: Gelechioidea) is one of the most species-rich microlepidopteran family with worldwide distribution. It comprises more than 3000 described species and numerous undescribed ones (Nieukerken et al., 2011). The highest diversity is in Australia with estimated over 3,000 endemic species (Common, 1990; 1994; 1997; 2000). Oecophorids comprise tiny to large sized moths with wingspan ranging from 7 to 35 mm. The majority of oecophorid larvae are concealed feeders, sheltering themselves, within their feeding substrate or with a dense silken shelter.

1.1. Phylogenetic relationships

Historically, Oecophoridae has been variably delineated, and considered to comprise two to seven subfamilies by different authors (Table 1). Lack of a well resolved phylogeny for the whole Gelechioidea has long been one cause for the variable concept. So far, relationships of family level or subfamily level of Oecophoridae have only recently been dealt within analytical phylogenetic works of the whole Gelechioidea (Hodges, 1998; Kaila, 2004; [Bucheli and Wenzel, 2005](#); Kaila et al., 2011; Heikkilä et al., 2014). Although these works have been focused on Gelechioidea as a whole, the internally heterogeneous Oecophoridae has not been exhaustively represented. The lack of a detailed exploration of the Oecophoridae has left its internal relationships partly obscure.

In the first phylogenetic analysis of Gelechioidea using parsimony with 38 morphological characters, Hodges (1998) restricted the family Oecophoridae to include two subfamilies, Oecophorinae and Stathmopodinae (Fig. 1, a), based on the lack of an articulation between gnathos and tegumen in male genitalia. He excluded the (sub) families, Deuterogoniinae (Oecophoridae in Toll, 1964; Hodges, 1978), Depressariinae (Oecophoridae in Toll, 1964; Hodges, 1974, 1978; Common, 1990), Stenomatinae (Oecophoridae in Hodges, 1978;

Common 1990), Ethmiinae (Oecophoridae in Hodges, 1978) to Elachistidae, Amphisbatini/Amphisbatinae (Oecophoridae in Toll, 1964; Hodges, 1974), Chimabachinae (Oecophoridae in Hodges, 1974, 1978), Peleopodinae (Oecophoridae in Hodges, 1974, 1978; Common, 1990), and Autostichinae (Oecophoridae in Hodges, 1978; Common, 1990). Despite limited number of morphological characters and problematic methodology, his work was accepted as a major rearrangement of family and subfamily concepts.

In an analysis using 143 taxa with 193 morphological characters, and species as terminals instead of larger units, Kaila (2004) suggested that Gelechioidea should to be divided into two main lineages, ‘gelechiid lineage’ and ‘oecophorid lineage’ (Fig. 1, b). Stathmopodinae was clustered with ‘batrachedrid taxa’ and Coleophoridae in the ‘gelechiid lineage’. Oecophorinae were divided into two groups: i) three New Zealand genera, i.e. *Hierodoris*, *Izatha* and *Phaeosaces*, were grouped to ‘xyloryctid assemblage’; ii) the New Zealand genus *Tingena* and a number of other genera, i.e. *Palimmeces*, *Pleurota*, *Philobota*, *Prionocris*, *Phryganeutis*, *Borkhausenia*, *Hofmannophila*, *Oecophora*, *Harpella*, *Denisia*, *Bisigna*, *Promalactis* and *Polix*, formed the ‘Oecophoridae s.s.’, with a sister-group relationship with Amphisbatidae s.s., Carcinidae, Stenomatid[n/d]ae, Chimabachidae and Elachistidae. However, *Martyringa* (Oecophoridae: Oecophorinae in Hodges, 1998), with deficient data, was not settled in any group removing all basal resolution between Oecophorinae and the xyloryctid assemblage in the strict consensus tree of Kaila (2004). He excluded it from the final analysis. Lvovsky (2009) presented a non-analytical cladogram (Fig. 1, c) of Oecophoridae s.s., including Oecophorinae, Pleurotinae and Deuterogoniinae based on characters of adult and larva feeding mode. He considered them to be separated from his other “broad winged” gelechioids, i.e. Chimabachidae, Amphisbatidae and Depressariidae. Kaila et al. (2011) performed a large-scale molecular phylogeny of Gelechioidea. The results (Fig. 1, d) support the finding that the clade with core Xyloryctidae and New Zealandian genera *Hierodoris*,

Gymnobathra, and *Izatha* is monophyletic as shown by Kaila (2004). A significant difference between the results of Kaila (2004) and Kaila et al. (2011) was the placement of *Phaeosaces*. In the Kaila (2004), it was grouped in Xyloryctidae s.l. however, in the Kaila et al. (2011), it was associated with the 'Elachistid s. l.' clade. Hoare (2005) tentatively accepted the position of *Phaeosaces* in the *Hierodoris* group following Kaila (2004) with reservations. However, there are doubts about such placement because *Phaeosaces* shares the typical characters of Oecophoridae s. s. (Common 1994, 1997, 2000).

Bucheli & Wenzel (2005) were the first to apply molecular approach to gelechioid phylogeny. They used Hodges's (1998) morphological data as the basis, and supplemented it with molecular data derived from mitochondrial COI and COII. Oecophorinae was found polyphyletic, and it clustered with Amphisbatinae, Symmocinae and Blasobasinae. This work was, however, based on limited taxon sampling. In Kaila et al. (2011), Oecophoridae s. s. was delineated largely similarly as Oecophorinae *sensu* Hodges (1998), but with the exclusion of Coelopoetinae which grouped with Pterolonchidae. Deuteroniinae was grouped within the core Oecophoridae as in Tokár et al. (2005), Saito (2005), and Wang (2006). Stathmopodinae was grouped as a sister-group of Blastobasidae. Due to several conflicting results, the classification of Oecophoridae remained unclear as noted by Kaila et al. (2011). Heikkilä et al. (2014) implemented the most comprehensive phylogeny of Gelechioidea so far based on combined morphological and molecular data. Their results closely corroborate with the molecular-based work by Kaila et al. (2011). Heikkilä et al. (2014) (Fig. 1, e) suggested that the monophyly of Oecophoridae s.s. comprise Pleurotinae and Oecophorinae, with the exclusion of *Martyringa* and *Hierodoris* group. Sohn et al. (2016) performed the most recent phylogenetic work on Gelechioidea based on 19 nuclear genes, yet excluding morphology. In their work, Oecophoridae was positioned between Ethmiinae and a clade consisting of Xyloryctidae, Symmocidae and Lecithoceridae. The subfamily or genus divisions of

Oecophoridae were not resolved because of limited number of taxa of Oecophoridae included.

The aim of this study was to perform a molecular phylogeny study for Oecophoridae with global samples to comprehensively encompass the diversity of the family. Our focus was to test the monophyly of Oecophoridae and clarify the relationships of its constituent subfamilies or genera. In addition, phylogenetic hypothesis obtained was used to infer the evolution and life history patterns of different constituent groups. The classification of Heikkilä et al. (2014) is used as background classification below, being based on the most robust phylogenetic analysis so far. Even though the analysis of Sohn et al. (2016) was based on much larger molecular data, they had considerably sparser taxon sampling than in Heikkilä et al. (2014) (77 versus 155 core gelechioid taxa), and had no morphological data included (253 characters utilized by Heikkilä et al., 2014). If the species is not listed in this reference, other recent sources are used.

1.2. Biological diversity of Oecophoridae

Trophic associations of lepidopteran larvae have been formed from a long period of evolution (Powell, 1980; Powell et al., 1998; specifically for Oecophoridae in Lvovsky, 2009). Within Gelechioidea, they appear to be tightly related to biological characters such as larval feeding substrate, habitat, and behavior (Powell et al., 1998; Kaila et al., 2011; Sohn et al., 2016).

For Oecophoridae, the vernacular name, ‘concealer moths’ has often been used. The larva of Oecophoridae can keep being concealed with several strategies. They may be sheltered within a web or hidden under bark or dead wood, or inside leaves rolled by them. Sometimes they bore stem or trunk or burrow under bark or hide in soil. In addition to these diverse sheltering strategies, oecophorids can also be found in very diverse and specialized microhabitats. For example, *Bisigna procerella* and *Callimodes heringii* feed on lichens, *Oecophora bractella*

and *Harpella forficella* consume fungi growing on tree trunks (Schütze, 1931; Toll, 1964; Harper et al., 2002; Lvovsky, 2006). Larvae of *Borkhausenia fuscescens*, *Endrosis sarcitrella* and *Hofmannophila pseudospretella* have even been found in bird's nest (Waters, 1929; Ford, 1949; Klimesch, 1961; Lvovsky, 2009). *Deuterogonia pudorina* has been reported from oak galls evoked by Cynipidae (Hymenoptera) (Toll, 1964). They can also feed on bast and mouldering wood under tree barks or lichens (Schütze, 1931; Toll, 1964; Harper et al., 2002; Lvovsky, 2006). Therefore, another objective of this study was to assess the ancestral character state of microhabitat and larva sheltering strategy within the phylogenetic relationship of Oecophoridae to understand their evolutionary transition and the adaptation of larva to microhabitats using sheltering strategies.

2. Materials and methods

2.1. Taxon sampling

A total of 82 taxa comprising 80 ingroup terminals and two outgroup taxa, one from Cossoidea and one from Thyridoidea as in Mutanen et al. (2010) and Kaila et al. (2011) were included in this study (Table 3). Considering the vast biogeographical radiation of Oecophoridae, 43 putative 'core' species were selected to clarify the delimitation of family Oecophoridae. A total of 37 other species, either formerly considered as Oecophoridae or closely clustered with them in the comprehensive phylogeny works of Gelechioidea by Hodges (1998), Kaila (2004), Lvovsky (2009), Kaila et al. (2011) and Heikkilä et al. (2014) were also added including *Deuterogonia*; Xyloryctid assemblage forming the 'core' Xyloryctidae, so-called New Zealandian genera, and Blastobasinae; Depressariidae (Aeolanthinae, Cryptolechiinae, Depressariinae, Ethmiinae, Hypertrophinae and

Stenomatinae); Lypusidae (Lypusinae and Chimabachinae), and Stathmopodidae.

We also included the following previously untested or problematic species: i) *Martyringa* was not dealt by Kaila et al. (2011), and found not to be close to the core Oecophoridae in Heikkilä et al. (2014); ii) *Acryptolechia* and Periacmini (*Periacma* and *Ripeacma*) were not dealt in any analytical study to date. They have traditionally been treated as genera of Oecophoridae in Asia (Saito et al., 1992; Wang 2006), but recently, *Acryptolechia* has been separated from other cryptolechiids (Lvovsky, 2009). Periacmini has been transferred to Cryptolechiidae/ Periacminae (Lvovsky, 2012); iii) *Orophia ferrugella* was closely associated with Depressariinae in Kaila et al. (2011) and Hodges (1998), and **was** included in Depressariidae in Heikkilä et al. (2014). The identity and composition of Cryptolechiinae (or Cryptolechiidae), even the nominate genus *Cryptolechia* is, however, unclear. Therefore the systematics of the taxa here included and considered as representatives of Cryptolechiinae should be taken with caution.

2.2. Specimen vouchering, DNA extraction, PCR amplification, and sequencing

Before DNA extraction, all specimens were examined for identification under microscope (DM 4000B, Leica Microsystems, Wetzlar, Germany) and **photographed** (18.3 Three Shot Color, Diagnostic Instruments, Sterling Heights, MI, USA). Mounted slides of genitalia were made.

Total genomic DNA was extracted by grinding up usually legs of alcohol vouchers or whole body except abdomen of dried specimens using DNeasy® Blood and Tissue kit (QIAGEN, Inc) according to the manufacturer's protocols. Remaining parts of specimens were preserved as vouchers. Genes previously used in Lepidoptera systematics were chosen. One mitochondrial protein coding gene, cytochrome oxidase subunit I gene (COI) (Folmer et al.,

1994, Simon et al., 1994; Aubert et al., 1999; Martin et al., 2002; Zakharov et al., 2004; Hundsdoerfer et al., 2005; Bucheli and Wenzel, 2005; Katoh et al., 2005, Kaila et al., 2011), two nuclear ribosomal RNA genes, 18S rRNA (18S) (Wiegmann et al., 2000) and 28S rRNA (28S) (Abraham et al., 2001; Brady et al., 2006; Niehuis et al., 2006; Yamamoto et al., 2007) and five nuclear protein coding genes, Ribosomal protein S5 (Rps5), Isocitrate dehydrogenase (IDH), the Cytosolic malate dehydrogenase (MDH), elongation factor-1 α (EF1 α) and wingless were selected (Wahlberg and Wheat, 2008; Kaila et al., 2011). We also tried to amplify the mitochondrial 16S rRNA (16S) and two nuclear protein coding genes, Carbamoylphosphate synthase domain protein (CAD) and Glyceral-dehyde-3-phosphate dehydrogenase (GAPDH). However, we achieved very low success rate. Therefore, they were discontinued from our further analysis. Each gene region used for PCR amplification is summarized in Table 4. PCRs were performed using Advantage PCR II Taq polymerase (BD Advantage™) and the reactions were performed in 20 μ L volumes containing 0.4 μ M of each primer, 200 μ M dNTPs, 2.5 μ M MgCl₂, and 0.05 μ g genomic DNA template. The thermal cycling program consisted of 95°C/ 5 min, 38-40 cycles of 95°C/ 30 sec, 72°/ 60 sec followed by a final extension at 72°C/ 10 min. The annealing temperature was adjusted accordingly to each gene (Table 4). PCR products were cleaned using a QIAquick® PCR purification kit (QIAGEN, Inc.) and directly sequenced at Macrogen, Inc (Geumcheon–Gu, Seoul, Republic of Korea).

2.3. Alignment and characterization of gene fragments

The character set used for analysis included 1,355 bp of COI, 579 bp of 18S rRNA, 272 bp of 28S rRNA, 369 bp of EF1 α , 657 bp of IDH, 313 bp of MDH, 553 bp of Rps5, and 346 bp of wingless. Therefore, a total of 4,444 bp of sequences were used.

We also retrieved GenBank reference sequences for the six genes, COI, RpS5, MDH, IDH, EF1 α , and wingless (Kaila et al., 2011), to analyze our sequences. Raw sequences were assembled and edited using SeqManTMII (version 5.01, 2001; DNA-starTM). Multiple sequence alignments were conducted using MAFFT (<http://mafft.cbrc.jp/alignment/server/>, version 7; Katoh et al., 2002; Katoh et al., 2005). FFT-NS-i (approximate group-to-group alignment algorithm) for mitochondrial COI, and Q-INS-i (CONTRAFold algorithm) for rRNA genes, 18S and 28S, and nuclear EF1 α , RpS5, MDH, IDH, and wingless were setting for strategy (Katoh and Toh, 2008). During the alignment, severely contaminated or very short sequences were excluded to minimize the risk of any kind of confusion and errors. Sequence data were combined using SequenceMatrix windows ver. 1.7.8. (Vaidya et al., 2010).

For phylogenetic resolution, maximum parsimony, Bayesian, and maximum likelihood analyses were used for the combined data sets.

2.4. Phylogenetic analyses

Maximum parsimony (MP) analysis was implemented in PAUP*4.0b10 (Swofford, 1998) using a heuristic search procedure, tree bisection reconnection (TBR) branch swapping, and 1000 random sequence additions with 10 trees held at each pseudoreplicate. All characters were treated as unordered and equally weighted for MP analysis. One thousand MP bootstrap replicates were performed using a heuristic search procedure, with a maximum tree setting of 200. Decay index values (Bremer, 1988) were calculated to determine branch support using TreeRot v3 (Sorenson and Farnzosa, 2007). Partition-homogeneity test (Farris et al., 1994) was performed to test any significant phylogenetic conflict between gene fragments in PAUP*.

For maximum likelihood (ML) analysis, MODELTEST version 3.06 (Posada and Crandall, 1998) was used to select the best-fitting nucleotide substitution model. PAUP* settings were optimized using data of the selected model before searching. ML analyses were performed using RAxML 7.2.6. (Stamatakis, 2006) at CIPRES Web portal (Miller et al., 2009). Supports for nodes were evaluated with 1000 bootstrap replicates.

Bayesian phylogenetic (BP) analysis was implemented in MrBayes (version 3.1.2; Ronquist and Huelsenbeck, 2003) using combined datasets. We analyzed the combined dataset using partitioned Bayesian analysis, in which the data were partitioned by 18S, 28S, COI, EF1a, RpS5, MDH, IDH, and wingless segments. BP was performed using a partition scheme to maximize the likelihood based on GTR + I + G model with specific model scores estimated by the MODELTEST for each gene region. For BP analyses, four chains (three heated and one cold) were run, starting from a random tree and proceeding for 10 million Markov chain Monte Carlo (MCMC) generations, sampling the chains every 100th cycle. To ensure that the distribution was stabilized, Tracer version 1.4.1. (Rambaut and Drummond, 2008) was used to view the graphical representation of MCMC chain mixing. Burn-in was set at 15% of the sampled number of trees. Convergence was confirmed by monitoring likelihood values graphically. A 50% majority-rule consensus tree was constructed from the remaining trees to estimate posterior probabilities (PP).

2.5. Reconstruction of ancestral character states

The information of microhabitats and larva sheltering types of Oecophoridae was collected from literature (Table 5). Microhabitat types were coded for the following: (A) on foliage; (B) live shrub or tree; (C) flowers or fruit capsule; (D) lichen; (E) leaf litter; (F) decaying wood or dead tree; (G) under bark; (H) on fungi; (I) bird's nest; and (J) dried plant (including stored

grain). Larval sheltering strategy types were coded in the following: (A) not shelter; (B) leaf mine; (C) tied or folded or rolled leaves; (D) boring seeds, fruits or buds; (E) boring other insect's gall or frass or eggs; (F) boring stem or trunk; (G) burrowing under bark or in soil; (H) make a silk web on leaf or flowers or stem; and (I) make a silk tube (silk + live or dried materials). In some cases, two or three types were coded for the same taxon, while some taxa were coded as 'unknown' due to the lack of information.

Bayesian ancestral-state reconstruction methods were implemented using BayesTraits v.1.0 (Pagel et al., 2004; Pagel and Meade, 2007) to reconstruct ancestral feeding microhabitat and larva sheltering character states for selected nodes in molecular phylogeny. BayesTraits uses reversible-jump MCMC methods to derive posterior probabilities and values of traits at ancestral nodes of the phylogeny (Pagel et al., 2004). BayesMultiState was selected as the model of evolution and MCMC were used as the method of analysis. Considering that some taxa had mixed microhabitat or larva sheltering strategies, we used multiple character-state option for BayesMultistate. First, we constructed the phylogenetic tree using maximum likelihood analysis and topology in the BayesMultistate analysis. The rate deviation was set at 30. A hyperprior approach was employed with an exponential prior seeded from a uniform prior in an interval of 0–10. Acceptance rates were achieved in the preferred range of 20–40% (Pagel et al., 2004; Pagel and Meade, 2007). A total of 50 million iterations were run for each analysis with the first 1 million samples discarded as burn-in while sampling every 1000th generation. Because the posterior probabilities for ancestral patterns of single runs differed slightly, we calculated the arithmetic mean of all samples used for the reconstruction of ancestral types.

3. Results

3.1.Characteristics of the eight gene fragments

The alignment results of each gene region used in this study using the eight aligning programs were almost identical to each other.

The mitochondrial COI dataset comprised of 1,355 aligned base pairs (bp). Of them, 620 bp were variable and 533 bp were parsimony informative. The average of uncorrected sequence divergence among taxa for COI was 12.0 % with an average proportion of T:C:A:G of 41:15:31:14. The nuclear 18S rRNA dataset comprised 579 bp of aligned sequences. Some ambiguous sites were excluded using GBLOCK 0.91b with half-option, resulting in. 531 bp, of which 26 bp were variable and 10 bp were parsimony informative. The average of uncorrected sequence divergence among taxa for 18S rRNA was 1.0 % with an average proportion of T:C:A:G of 21: 29: 25: 26. For nuclear 28S rRNA data set, 272 aligned bp of sequences were aligned. After one site was excluded using GBLOCK 0.91b with the half-option, a total of 271 bp remained, of which, 28 bp were variable and 8 bp were parsimony informative. The average uncorrected sequence divergence of the 28S gene among taxa was 2.0 % with an average proportion of T:C:A:G of 21:26:19:34. The mitochondrial COI sequences were AT rich, in consistent with previous reports on insect mitochondrial DNA sequences (Tautz et al., 1988; Crozier and Crozier, 1993; Yamamoto et al., 2007). Nuclear ribosomal RNA genes had more even base compositions for AT and GC. Nuclear protein coding Rps5 dataset comprised 553 aligned base pairs (bp), of which 220 bp were variable and 202 bp were parsimony informative. The average of uncorrected sequence divergence among taxa for Rps5 was 12.0 % with an average proportion of T:C:A:G of 25:24:26:26. Nuclear protein coding gene IDH dataset comprised 657bp, of which 355 bp were variable and 295 bp were parsimony informative. The average of uncorrected sequence divergence among taxa for IDH was 15% with an average proportion of T:C:A:G of 27: 20: 31: 22. Of a

total 313 aligned base pairs (bp) of the nuclear protein coding gene MDH dataset, 168 bp were variable and 142 bp were parsimony informative. The average of uncorrected sequence divergence among taxa for MDH was 16.0 %. The average proportion of T:C:A:G was 24:24:28:24. Nuclear EF1 α comprised 369 bp, of which 135 bp were variable and 122 bp were parsimony informative. The average of uncorrected sequence divergence among taxa for EF1 α was 8.0 % with an average proportion of T:C:A:G of 23:30:25:23. The nuclear wingless dataset comprised 346 aligned base pairs (bp), of which 200 bp were variable and 151 bp were parsimony informative. The average of uncorrected sequence divergence among taxa for wingless was 13.0 % with an average proportion of T:C:A:G of 15:33:21:31.

In the nuclear protein coding gene sequences, Rps5, IDH, and MDH were AT rich as in mitochondrial COI sequences. However, EF1 α and the wingless were CG rich as in nuclear ribosomal RNA genes, 18S and 28S.

3.2. Tree topology from combined dataset

Results of parsimony (MP), Bayesian (BP), and maximum-likelihood (ML) analyses using combined datasets for mitochondrial and nuclear genes are shown in Fig. 2. The MP analysis produced four equally parsimonious trees with a tree length of 17,945. The parsimony bootstrap values and decay index (DI) values for strict consensus cladogram of the four most parsimonious trees are shown in Fig. 2, a. Posterior probabilities of BP and bootstrap values of ML tree ($-\ln/L = 76245.013186$) are shown in Fig. 2, b, c.

The parsimony topology was different from those estimated from BP (Fig. 2, b) and ML (Fig. 2, c) regarding the position of Stathmopodidae, Blastobasidae and Lycopodiidae. The clade of Blastobasidae + Stathmopodidae was not with Depressariidae in the BP and ML, but was nested within the Depressariidae s.l. in the MP. The BP topology was almost identical to ML

topology regarding the position of oecophorids. However, the position of Aeolanthinae clade was different between the two topologies.

Monophyly of Oecophoridae was supported in BP and ML analyses, including Oecophoridae sensu Heikkilä et al. (2014) (symbols at the terminals of branches ‘Oe’, Oecophorinae + ‘P’, Pleurotinae in Fig. 2) and Oecophoridae sensu from other sources (symbols at the terminals of branches ‘O’, Oecophoridae), but not including *Casmara*, *Tyrolimnas* and *Pseudodoxia*. Xyloryctidae sensu Heikkilä et al. (2014) was closely clustered with *Acryptolechia*, Periacmini and *Pseudodoxia* in all analyses. Polyphyly of cryptolechiids was strongly supported *Cacochroa*, *Orophia* and *Eutorna* being separated from *Acryptolechia* and Periacmini in all analyses. Monophyly of *Promalactis* was well supported in all analyses.

3.3. Ancestral microhabitat analysis

The ancestral microhabitat of Oecophoridae and related higher taxa within Gelechioidea were estimated for the 18 nodes shown in the Maximum likelihood tree (Fig. 3). BayesMultistate analyses allowed for free rates of microhabitat type exchange within the 10 types coded for each species (Table 5). The analysis suggested that the microhabitat type coded as D (lichen in Fig. 3, node A) at the root of Gelechioidea in this study had a reconstructed probability of greater than 99 % compared to alternative microhabitat types. The ancestral microhabitat types were reconstructed as types D + J, ‘lichen’ + ‘dried plant’ at the root of Lypusidae, Depressariidae, Xyloryctidae and Oecophoridae (Fig. 3, node C) with the reconstructed probabilities of more than 99 %, whereas each ancestral states of Aeolanthinae (Fig. 3, node H) and Blastobasidae + Stathmopodidae (Fig. 3, node I) were mainly reconstructed as ‘on foliage’ (with a probability 71%) and ‘flowers or fruit capsule’ (with a probability 89%). The origin of microhabitat type for Lypusidae + Depressariidae (Fig. 3, node K, including

Tyrolimnas), was reconstructed as ‘on foliage’ + ‘lichen’ with a probability of more than 95% (on foliage 71 % + lichen 27%), whereas the ancestral microhabitat type for Xyloryctidae + Oecophoridae (Fig. 3, node D) was reconstructed as ‘dried plant’ with a probability of 95 %. The ancestral microhabitat of Oecophoridae also yielded ‘dried plant’ with a probability of 89%. Within Oecophoridae, ancestral microhabitat types were reconstructed as types G + H, ‘under bark’ + ‘on fungi’ at the nodes representing *Deuterogonia*, *Callimodes*, *Oecophora*, *Harpella* and *Promalactis* (Fig. 3, node F) with probabilities of more than 90 % (under bark 56 % + on fungi 39 %).

The common ancestral microhabitat of Xyloryctidae (Fig. 3, node O) was reconstructed as ‘dried plant’ with a probability of more than 90 %. However, the ancestral microhabitat for ‘core’ Xyloryctidae (Fig. 3, node N) was reconstructed as ‘live shrub or tree’ with a probability of 86 %. Within the Xyloryctidae, diverse microhabitats were yielded as ancestral states. ‘Decaying wood or dead tree’ + ‘on fungi’ with probability of 91% was reconstructed at node of *Gymnobathra* and *Izatha* (Fig. 3, node P). ‘Decaying wood or dead tree’ + ‘on fungi’ + ‘birds’ nest’ with a probability of more than 80 % was reconstructed at node of *Martyringa*, *Pseudodoxia*, *Periacma*, *Ripeacma* and *Acryptolechia* (Fig. 3, node Q). The common ancestral microhabitat at the node of Oecophoridae, including the pest species *Endrosis sarcitrella*, *Borkhausenia fuscescens* and *Hofmannophila pseudospretella*, (Fig. 3, node R) was reconstructed as ‘bird’s nest’ with a probability of 89 %, although constituent *Wingia aurata* feeds on live plants was coded as ‘on foliage’.

3.4. Ancestral larva sheltering strategy analysis

The ancestral larva sheltering strategy of Oecophoridae and related higher taxa within Gelechioidea for the 18 nodes in the Maximum likelihood tree is shown in Fig. 4.

BayesMultistate analyses allowed free rates of larva sheltering type exchange within the 9 types coded for each species (Table 5). The larva sheltering type coded as B (mine leaf in Fig. 4, node a) at the root of Gelechioidea had a reconstructed probability of greater than 90 % compared to alternative larva sheltering types. The common ancestral larva sheltering type was reconstructed as type B + I ('mine leaf' + 'a silk tube') at the root representing Lypusidae, Depressariidae, Xyloryctidae and Oecophoridae (Fig. 4, node c) with the reconstructed probabilities of 95 %. However, the ancestral states of Aeolanthinae (Fig. 4, node h) and Blastobasidae + Stathmopodidae (Fig. 4, node i) were mainly reconstructed as 'tied or folded or rolled leaves' with a probability 81% and 'boring seed or fruits or bud' with a probability 73%. The origin of larva sheltering strategy type for Lypusidae + Depressariidae (Fig. 4, node k, including *Tyrolimnas*) was reconstructed as 'mine leaf' + 'open habit' with a probability of 86 % (mine leaf 50 % + open habit 36 %).

The ancestral state type for Xyloryctidae + Oecophoridae (Fig. 4, node d) was reconstructed as 'make a silk tube' with a probability of more than 99 %, but transferred to different types by each constituent group. The ancestral type of Xyloryctidae was reconstructed to mixed types ('tied or folded or rolled leaves' + 'boring stem or trunk') at the 'core' Xyloryctidae (Fig. 4, node, n) with a probability of 85 % (tied or folded or rolled leaves 69 % + boring stem or trunk 16 %). The 'boring stem or trunk' was reconstructed at node p (Fig. 4) with *Gymnobathra* and *Izatha*, with a probability of 96%. 'Making a silk web on leaf or flowers or stem' + 'boring other insect's gall or frass or eggs' were reconstructed at node q (Fig. 4) representing genera *Martyringa*, *Pseudodoxia*, *Periacma*, *Ripeacma* and *Acryptolechia* with a probability of 76 %. Within Oecophoridae, the origin of larva sheltering strategy types for the nodes f and g (Fig. 4) representing *Deuteroгония*, *Callimodes*, *Oecophora*, *Harpella* and *Promalactis* were mainly reconstructed as 'burrowing under bark or soil' with a probability of more than 79% each, whereas that for node r (Fig. 4) representing *Wingia*, *Endrosis*,

Borkhausenia, *Palimmeces*, *Philobota*, *Hofmannophila* and *Tingena* was reconstructed as ‘make a silk tube’ with a probability of 96%.

4. Discussion

4.1. Phylogenetic relationship of oecophorids and discussion on morphological characters

We acknowledge that our taxon sampling appears somewhat biased towards East Asia. However, a number of relevant representatives from other biogeographical areas were included as well. Even though numerically it would seem that our taxon sampling of putative core Oecophoridae was restricted, it is not necessarily quite so.

Although Oecophoridae comprises more than 3000 species, more than 2300 species are endemic and are associated with eucalypt forests or woodlands in Australia, and a large section of the Australian Oecophorids are related to genus *Wingia* (Common, 1990). We included in our sampling some congeneric species and their relatives. It would have been most intriguing to increase the taxon sampling to better represent taxa particular to other geographic areas as well. Unfortunately, the current literature does not cover areas such as South America too well, so detection of taxa of particular interest is difficult. Even if such are found in literature, their biology, essential for this study, seldom is known. Moreover, if such taxa meeting these traits were detected, obtaining material suitable for DNA studies was found next to impossible. Admittedly, inclusion of such taxa would have had a potential to strengthen our hypotheses.

We deliberately also included a wide variety of taxa formerly often considered to belong to

Oecophoridae. The placement of them in the present study was largely in concordance with other recent studies, like the separation of Stathmopodidae from Oecophoridae. On the other hand, *Deuteronia*, traditionally considered separated from core Oecophoridae was found to belong there as has been suggested by other, recent molecular studies, (Kaila et al., 2011; Heikkilä et al., 2014; Sohn et al., 2016). Some taxa supposed to belong to core Oecophoridae, like Periacmini and *Casmara*, apparently do not belong there. These patterns obtained reduced the remaining core oecophorid taxa in our results – an intriguing result itself. Interrelationships of taxa here grouped with Xyloryctidae should be considered with particular caution, as no representatives of core Lecithorceridae or Austostichidae were included. These families appear closely related to Xyloryctidae (Kaila et al., 2011; Heikkilä et al., 2014; Sohn et al., 2016). To better understand the position of, e.g., Periacmini, these groups should be included. However, interrelationships within Xyloryctidae are not the focus of the present study.

Even though interrelationships of taxa vary to some extent between different analyses, they largely agree. What is most important, the agreement is evident regarding the interrelationships of, and within, Oecophoridae that was our focal group. We take the general agreement of analyses itself as support that at least to some extent overweighs the low support values obtained in, e.g. ML analysis (see Supplementary file 3). Nevertheless, due caution must be taken when interpreting our results and the discussion below.

4.1.1. Genus *Casmara*

The genus *Casmara* was assigned **close to** the family Stathmopodidae (node I in Fig. 5). They **both** were clustered with Blastobasidae at node H. This result **is** inconsistent with earlier suggestions (Wang, 2006; Wang et al., 2012; Byun et al., 2012) that *Casmara* should belong

to core Oecophoridae. It is a little known genus comprising approximately 15 species or more worldwide, with highest diversity in Southeast Asia (Robinson et al. 1994). Its constituent species are characterized by large-sized and distinct tufts on hind tibia (Fig. 6, a), similar to those of Stathmopodidae s. authors. The morphologically allied genera *Ashinaga*, *Lactistica* and *Aeolarcha* (Lvovsky, 2007b) are likely to be close to Stathmopodidae as well. The inclusion of *Casmara* in Oecophoridae has already been questioned by Lvovsky (2007a), since they have features in common with Stathmopodidae, such as the hind tibia scale tufts and the presence of a row of stout scales along the posterior margins of abdominal tergites. The latter character has been used as a key character to distinguish Stathmopodinae from Oecophorinae by Hodges (1998) and Wang (2006). Therefore, the systematic position of *Ashinaga*, *Lactistica* and *Aeolarcha* should also be re-considered.

4.1.2. Genus *Tyrolimnas*

Tyrolimnas was not associated with Oecophoridae (node E in Fig. 5). However, it was clustered with *Machimia* + *Carcina* (node N in Fig. 5). *Tyrolimnas* could be distinguished from core Oecophoridae by the absence of vein R₅ in the forewing which is present in all core oecophorids (Fig. 7).

4.1.3. Genus *Phaeosaces*

All our analyses supported that *Phaeosaces* spp. belong to Depressariidae (node O in Fig. 5), as in Kaila et al. (2011) and Heikkilä et al. (2014). The systematic position of *Phaeosaces* has earlier been unstable. This genus, erected by Meyrick (1885) was synonymized to *Cryptolechia* by Meyrick (1922), but reinstated by Dugdale (1988) because the New

Zealandian congeneric species did not match the type species of *Cryptolechia*. Only four species of *Phaeosaces* are currently known. They are all endemic to New Zealand (Dugdale, 1988). The present topology suggested that *Phaeosaces* spp. were not close to *Acryptolechia* spp. (node U in Fig. 5) or other presumed Cryptolechiinae spp. (node K in Fig. 5).

4.1.4. Genus *Pseudodoxia*

The genus *Pseudodoxia* was nested in the family Xyloryctidae (node Q in Fig. 5). It was clustered with *Martyringa* in node S, *Acryptolechia*, *Periacma* and *Ripeacma* in node T, however, was not clustered with core Oecophoridae. *Pseudodoxia* mostly occurs in oriental region, mainly Sri Lanka and South India, and comprises approximately forty species (Wang, 2006). Its constituent species are characterized by broad wings with dot-like markings in adults and sclerotized saccular margin with processus in the male genitalia. Its antrum has distinct shaped caudal margin in female genitalia. These key characters are also present in *Martyringa* (Fig. 8).

4.1.5. Oecophoridae

The core Oecophoridae is equivalent to node E (Fig. 5). The basally arising *Pleurota* (node V in Fig. 5) is characterized by erect labial palpi which, [though](#), is a fairly homoplastic character. The male genitalia in the species of Pleurotinae have characteristic narrow and elongate posterior lobes of the juxta. Our results supports the opinion of Toll (1964), Lvovsky (2009), and Heikkilä et al. (2014) that *Pleurota* should be regarded as a subfamily by itself.

The next branch [includes the](#) genera *Wingia*, *Endrosis*, *Borkhausenia*, *Palimmeces*, *Philobota*, *Hofmannophila* and *Tingena* (node W, Fig. 5). A great majority of the core Oecophoridae

species have characteristic beak-shaped gnathos with dorsal scobination.

Consistent with other recent studies (Saito, 2005; Kaila et al., 2011; Heikkilä et al., 2014), our results also support the placement of *Deuterogonia* within Oecophorinae (node X in Fig. 5). So far, the taxonomical status of *Deuterogonia* (Fig. 10) has been unstable, largely owing to the lack of the gnathos whose shape is often informative. The genus was considered as a subfamily Deuterogoniinae of Oecophoridae by Toll (1964), Saito (2005), Lvovsky (2009), and Nieuwerkerken et al. (2011). However, it was considered as Elachistidae by Hodges (1998), and Oecophorinae by Heikkilä et al., (2014) who considered the lack of male gnathos as a variation. Within the node F (Fig. 5), *Deuterogonia* was closely clustered with node X, including the genera *Callimodes*, *Oecophora*, *Harpella* and *Promalactis*. They all have bright yellow to yellowish brown forewing ground color with distinct markings, such as metallic, white or fuscous scales and pattern. Among them, *Promalactis*, one of the largest genera of Oecophoridae with global distribution, ranging from Palearctic and Oriental Regions to Nearctic and Afrotropical Regions (Adamski et al., 2009; Vári and Kroon, 1986), is monophyletic (node Y in Fig. 5).

4.2. Notes on phylogenetic results

4.2.1. Xyloryctidae

The ‘core’ Xyloryctidae was the most basally arising node (node P in Fig. 5) of the Xyloryctidae (node Q in Fig. 5), and the next branch (node Q in Fig. 5) included the New Zealandian *Hierodoris* clustering with *Gymnobathra* and *Izatha* as in Kaila et al. (2011). According to Kaila (2004), they have the following two homoplastic characteristics: the presence of a submental pit as sclerotized pair of grooves, and a ring-shaped pinaculum on

SD1 leaving a non-sclerotized area around the seta at A1-8 in larva morphology.

4.2.2. Genus *Martyringa*

Martyringa was recently transferred to Lecithoceridae from Oecophoridae (Heikkilä et al., 2014). In this study, this genus was nested within Xyloryctidae (node S in Fig. 5). However, Lecithoceridae was not included in the present study so the position of *Martyringa* remains untested. *Martyringa* has the following characteristics: i) 2nd segment of labial palpi with rough scales; ii) fuscous dot-like markings of forewing; iii) tongue-shaped gnathos and sclerotized sacculus margin of male genitalia; iv) large lamella postvaginalis with setose and distinct shaped at the caudal margin of antrum of female genitalia, in common with the genus *Pseudodoxia* (Fig. 8). The characteristics of male and female genitalia are also similar to those of *Periacma*, *Ripeacma* and *Acryptolechia*.

4.2.3. *Cryptolechiidae* s. authors

Palearctic and Oriental genera of *Cryptolechiidae* sensu Lvovsky (2012), *Acryptolechia* (*Cryptolechiinae*), *Periacma* and *Ripeacma* (*Periacminae*), were nested within the family Xyloryctidae (node Q in Fig. 5). They were close to the clades of *Gymnobathra* and *Izatha*, with negligible support (node R in Fig. 5).

All our analyses revealed that *Cryptolechiinae* s. authors were polyphyletic (node K, U in Fig. 5). *Acryptolechia* spp. (node U in Fig. 5.) were nested in Xyloryctidae with *Pseudodoxia*, *Periacma* and *Ripeacma* (node T in Fig. 5). *Cacochroa*, *Orophia* and *Eutorna* were grouped with *Depressariidae* (node K in Fig. 5). These four genera have in common the scape of antenna without a pecten, a developed sacculus in the male genitalia, and a distinctly

developed lamella postvaginalis in the female genitalia (Fig. 9).

4.3 Evolutionary history of larva host plant preference, microhabitat, and sheltering strategy of Oecophoridae and related taxa

4.3.1. Genus *Casmara*

Species of *Casmara* are stem borers of, e.g., *Camellia sinensis*, *C. oleifera* (Theaceae) and *Murraya paniculata* (Rutaceae) (Chao et al, 2007; Diakonoff, 1966) like larvae of many Blastobasidae and some Stathmopodidae (Wang, 2006; Adamski et al., 2010; Kaila et al., 2011). They appear to have evolved to live on live shrubs or trees and hide inside seeds, fruits, or bud by boring (each node, I and i in Fig. 11). Thus, also the biology of *Casmara* is closer to Stathmopodidae than Oecophoridae.

4.3.2. Genus *Tyrolimnas*

The biology of *Tyrolimnasis* currently unknown. Its putatively close relatives *Machimia* and *Carcina* have similar feeding behavior and larvae preference for host plants. They are known as leaf tiers or rollers (not sheltering) on oak (*Quercus*) and other deciduous plants (Hodges, 1974). Further studies are merited to find out whether its biology is also similar to that of *Machimia* and *Carcina*.

4.3.3. Genus *Phaeosaces*

Phaeosaces were nested within Depressariidae (nodes, O and o in Fig. 11). Unlike the almost

universally green plant feeding species of Depressariidae, the larvae of *Phaeosaces coarctatella* live on lichens on branches and burrow old wood as borers (http://en.wikipedia.org/wiki/Phaeosaces_coarctatella). Pupae of another species, *P. compsotropa* have been found in thin-shelled almond (Davies, 1990). The larvae of *Phaeosaces* might feed on lichens during the initial stages and bore to the bark of trees for pupation or hibernation. The pattern of lichenivorous groups among the majority of green plant feeders is typical in Lepidoptera. It has been reported that lichenivorous Lepidoptera such as some glaphyrines of Pyraloidea, lithosiine Arctiinae, Lycaenidae and Geometridae, have derived from phytophagous groups (Powell, 1980; Scoble, 1992).

4.3.4. Oecophoridae

Species within the Oecophoridae (each node, E and e in Fig. 11) appear to have shifted from two mixed microhabitats (pie chart of node E in Fig. 11), dried plant + lichen, to three various microhabitats (pie chart of node G in Fig. 11). Those ancestor sheltering strategy is also evolved from the silk tube sheltering type to more than three other sheltering types.

Pleurota bicostella, the sister of other Oecophoridae has been collected from white web on stems of heather, and other *Pleurota* spp., i.e., *P. pyropella* and *P. schlaegeriella*, have been found on *Salvia officinalis* L. near the neck of plant root of various herbs (Toll, 1964). Our result suggests that *Pleurota* species have evolved from dried plant + lichen feeders to live on living plants.

The common ancestor of the next branch (each node, R and r in Fig. 11) including *Wingia*, *Endrosis*, *Borkhausenia*, *Palimmeces*, *Philobota*, *Hofmannophila*, and *Tingena* has perhaps shifted to feed on miscellaneous detritus in a silk tube. *Wingia*, *Palimmeces* and *Philobota* are also associated with eucalypt forests or woodlands (Common, 1990). Larvae of

W. aurata live in strong silk shelter amongst green yet old leaves of *Eucalyptus*. *Philobota* spp. live on dead eucalypt leaves and burrow into soil (Common, 1990). Eucalypt leaves, especially when dead, are exceptionally low in nitrogen and high in tannins. They do not break down rapidly in a relatively dry climate. Common (1990) observed that Australian oecophorids have ability to utilize these leaves even under very dry conditions.

Of the other three species, *Endrosis sarcitrella*, *Borkhausenia fuscescens* and *Hofmannophila pseudospretella*, *E. sarcitrella* and *H. pseudospretella* are very widespread and known as pests, in addition of being observed in birds' nest in nature (Waters, 1929; Ford, 1949; Klimesch, 1961). The larvae of *E. sarcitrella* mainly feed on a wide variety of dried plant materials such as grains and seeds by boring (<http://museumpests.net>). The larva of *H. pseudospretella* is a common omnivorous scavenger and is known, e.g., as textile pest in dwellings (Cole, 1962). It also lives on various seeds in storages or dry leaves and can make a silk web around several seeds by constructing a sack (Toll, 1964). *B. fuscescens* lives and feeds on fungi growing on tree trunks (Schütze, 1931; Toll, 1964; Harper et al., 2002; Lvovsky, 2006), and fallen leaves (Heckford 1999). In our phylogeny, these three species are nested within Australian species inhabiting dry environments. This would suggest that these species many have adapted from dry to moister environments.

The common ancestor of nodes F and f in Fig. 11 appears to have lived under bark and sheltered there by burrowing under the bark or soil. *Deuteronia pudorina* is known to be able to live under bark and on lichens, and has also been bred from oak galls evoked by Cynipidae (Toll, 1964). Usually, galls are rich in resins and tannic acid. The larvae in galls probably have used these materials for sustenance. Species in the next branch, *Callimodes zelleri*, *Oecophora bractella* and *Harpella forficella*, live underbark of decaying trees and shelter by burrowing under bark or soil (Toll, 1964). *C. zelleri* also feed on lichens. *O. bractella* and *H. forficella* live on other fungi (Schätze, 1931; Harper et al., 2002; Lvovsky,

2006).

The common ancestor of *Promalactis* (nodes G and g in Fig. 7) shifted from living on dried plant and lichen to living under bark and decaying wood or dead tree. The sheltering strategy of its larvae has also shifted from silk tube to burrowing under bark or soil, rarely to boring stems or trunks. Among *Promalactis*, larvae of *P. suzukiella* have been found under bark of rotting logs of chokecherry (*Prunus virginiana* L.) and oak (*Quercus* sp.) in USA (Adamski et al., 2009). They have been collected under bark of peach, *Prunus persica* (L.) (Park, 1981) and also been from shiitake mushroom plantation (observation and collection by this author, S. Kim).

4.3.5. Xyloryctidae

The common ancestor of Xyloryctidae (nodes O and o in Fig. 11) lived in dried plants with making a silk tube for sheltering, but its descendants shifted to different microhabitats and sheltering strategies. The ancestor of core Xyloryctidae (nodes N and n in Fig. 11) shifted to live shrubs or trees by tying, folding, or rolling leaves for shelter.

Hierodoris atychioides has gregarious larvae that are moderately polyphagous on Gymnospermae. They not only feed on live shrub or tree, i.e., *Kunzea* and *Leptospermum* of Myrtaceae and *Ozothamnus* of Asteraceae, but also consume leaf litter. Additionally, they roll dead leaves and bore woody stem, sometimes galls (Hoare, 2005). The next branch includes *Gymnobathra* and *Izatha*. They live on bark, dead wood, or leaf litter and make silken nests covered with frass and leaf fragments. *Izatha* are also found from dead wood (Hoare, 2005). Their ancestral microhabitats has shifted from ‘dried plant’ to ‘decaying wood or dead tree’ + ‘leaf litter’ and their ancestral sheltering strategy has changed from ‘making a silk tube’ to ‘boring stem or trunk’. These New Zealand genera are clustered with *Martyringa*,

Pseudodoxia, *Periacma*, *Ripeacma* and *Acryptolechia*. The descendants of their common ancestor apparently have evolved to various microhabitats and sheltering strategies, but have mainly lived on decaying wood or tree and make a silk web on leaf or flowers or stem. It should, however, be noted that the biology of *Acryptolechia*, *Periacma* and *Ripeacma* is currently unknown.

Martyringa xeraula, a polytrophic pest using various dry food in houses and storages, damages carpets and leather goods by boring (Zagulajev, 1965; Lvovsky, 1994). The larvae of *Pseudodoxia achlyphanes* have been found from leaf litter without sheltering (Saito, 1976).

The biology of *Acryptolechia* spp. is unknown. Leraut (1993) excluded *Cacochroa* and *Orophia* from Oecophoridae, due to the fact that their larvae feed on living plants. *Cacochroa* and *Orophia* were merged to Depressariinae (Depressariidae) by Hodges (1998) and Lvovsky (2002, 2009). Therefore, *Acryptolechia* spp. (nodes, Q and q in Fig. 11), may not feed on living plants. It is feasible to suggest that it may have similar biology as its close relatives *Pseudodoxia*, *Periacma* and *Ripeacma*,

4.2.6. *Lypusidae* + *Depressariidae*

The common ancestor of *Lypusidae* + *Depressariidae* (each node K and k in Fig. 11) changed the habitat from lichens mainly to living plants. In accordance with this changes, the ancestral leaf miner began to have various sheltering strategies. They do not only mine inside live leaves, but also bore other insects' galls or frass or eggs or do not shelter at all. Lypusid ancestor (each node J and j in Fig. 11) expanded its habitat from lichens to dry plants material. Extant lyusid larvae usually shelter by mining, tying, folding or rolling leaves.

4.2.7. *Blastobasidae* + *Stathmopodidae*

The ancestors of Blastobasidae + Stathmopodidae (nodes I and i in Fig. 11) has evolved from leaf miners to seed, fruits, or bud borers. They probably lived on flowers or fruit capsule by boring them or sometimes by tying, folding, or rolling leaves.

4.2.8. *Aeolanthinae*

Aeolanthinae spp. basally positioned in nodes H and h (Fig. 11), evolved from leaf miners. They live on living plants and shelter by tying, folding, or rolling leaves.

5. Conclusions

Our results support the findings of other recent studies that Oecophoridae in the traditional sense are not monophyletic. Our findings are generally in accordance with the classification by Heikkilä et al. (2014). The sister group of Oecophoridae is found to be Xyloryctidae as in Heikkilä et al. (2014). Within Oecophoridae, the two subfamilies Pleurotinae and Oecophorinae are again recognized based on morphology, genetic relationship, and evolutionary transitions in microhabitats and sheltering strategies. *Casmara*, *Tyrolimnas*, *Pseudodoxia*, *Martyringa*, *Acryptolechia* and Periacmini are found to not belong to Oecophoridae, but, an assemblage of Xyloryctidae.

The larval feeding mode of Oecophoridae is hypothesized to have evolved from dried plant feeding to broad range of different feeding and sheltering strategies in numerous microhabitats, such as under bark or fungi, decaying wood, dead tree, and bird's nest. The ancestral oecophorids evolved from taxa whose larvae could construct silk tube to various specific strategies. They probably adapted to their living environments according to their

demands. Xyloryctidae have evolved from dried plants to other microhabitats. Species not only live on live plant substrates, but also on decaying wood or dead trees. Some can live on leaf litter, such as oecophorids. The ancestral sheltering strategy of Xyloryctidae is suggested to have been a silk tube, further evolving towards diverse strategies, such as tying, folding, or rolling leaves or boring stems or trunks.

Acryptolechia spp. have little similarities with the type species of Cryptolechiinae, *Cryptolechia straminella*. Therefore, the systematic position of *Acryptolechia* and numerous Chinese ‘so-called’ *Cryptolechia* is likely presently wrong. Based on our results, they likely belonging to Xyloryctidae + Autostichidae + Lecithoceridae clade.

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Figure captions

Fig. 1. Current hypotheses of family relationships within the superfamily Gelechioidea

(a) cladogram after Hodges (1998), and the classification system; (b) cladogram after Kaila (2004), and the classification system; (c) cladogram after Lvovsky (2009); (d) cladogram after Kaila et al. (2011) and the classification system; (e) cladogram after Heikkilä et al., (2014) and the classification system.

Fig. 2. Phylogenetic trees resulting from the combined data of all mitochondrial and nuclear genes

(a) Strict consensus tree of 4 shortest trees resulting from parsimony analysis (consistency index [CI] = 0.1700; retention index [RI] = 0.3584). The numbers below the branches are

bootstrap percentages/ Decay index [DI]). (b) Fifty percent majority consensus tree resulting from Bayesian analysis. The numbers below the branches are posterior probability values (%). (c) Maximum likelihood tree (-lnL= 76245.013186). The numbers below the branches are bootstrap percentages. Symbols at the terminals of branches indicate subfamilies/ families): A, Aeolanthinae; B, Blastobasidae; C, Cryptolechiidae; Cr, Cryptolechiinae; D, Depressariinae; De, Depressariidae; E, Ethmiinae; Hp, Hypertrophinae; Hc, Hypercallinae; L, Lypusidae; Le, Lecithoceridae; O, Oecophoridae; Oe, Oecophorinae; P, Peleopodinae; Pl, Pleurotinae; S, Stathmopodidae; St, Stenomatinae; X, Xyloryctidae. The family and subfamily names in parentheses follow Heikkilä et al. (2014). If the species is not listed in this reference, other recent sources were used (e.g. 'C' and 'O' follows other sources).

Fig. 3. BayesMultistate analysis results of ancestral microhabitats type reconstructions inferred from Maximum likelihood analysis

Pie charts under the nodes show the relative likelihoods of each type at respective nodes. The types of each species are color-coded according to the pattern. The family name follows reclassification based on previous phylogenetic results. An asterisk indicates the root of Oecophoridae.

Fig. 4. BayesMultistate analysis results of ancestral larva sheltering strategy type reconstructions inferred from Maximum likelihood analysis

Pie charts under the nodes show the relative likelihoods of each type at respective nodes. The types of each species are color-coded according to the pattern. The family name follows reclassification based on previous phylogenetic results. An asterisk indicates the root of Oecophoridae.

Fig. 5. Phylogenetic relationships inferred from Maximum likelihood analysis

Numbers on the branches are bootstrap percentages (%) from the ML and MP analysis, posterior probabilities (BP) from the Bayesian phylogenetic analysis under the branches. Thick branches indicate nodes also recovered in the other analyses. Capital letters on the nodes refer to nodes discussed in the text. The family and subfamily names in parentheses follows Heikkilä et al. (2014). If the species is not listed in this reference, other recent sources were used. Re-classification by the results indicated the rightmost in column: AE, Aeolanthinae; BL, Blastobasidae; ST, Stathmopodidae; LY, Lypusidae; DE, Depressariidae; XY, Xyloryctidae; OE, Oecophoridae.

Fig. 6. Oecophoridae spp. and related taxa. (a) *Casmara agronoma*; (b) *Stathmopoda masinissa*; (c) *Tyrolimnas anthraconesa*; (d) *Acryptolechia malacobyrsa*; (e) *A. torophanes*; (f) *Periacma delegata*; (g) *Deuteroгония pudorina*; (h) *Callimodes zelleri*; (i) *Promalactis jezonica*. Scale bar: 5mm. An arrow indicates tufts in hind tibia.

Figs. 7. Wing venation of Oecophorid genera.

(a) *Acryptolechia malacobyrsa*; (b) *Cryptolechia* sp.; (c) *Deuteroгония pudorina*; (d) *Callimodes zelleri*; (e) *Periacma delegata*; (f) *Promalactis suzukiella*; (g) *Pseudodoxia achlyphanes*; (h) *Tyrolimnas anthraconesa*

Fig. 8. Morphology of *Martyringa* and *Pseudodoxia*.

(a) adult of *Martyringa xeraula*; (b) wing pattern of *ditto*; (c) labial palpus of *ditto*; (d) adult of *Pseudodoxia achlyphanes*; (e) wing pattern of *ditto*; (f) labial palpus of *ditto*; (g) male genitalia of *Martyringa xeraula*; (h) female genitalia of *ditto*; (i) caudal margin of antrum of *ditto*; (j) male genitalia of *Pseudodoxia achlyphanes*; (k) female genitalia of *ditto*; (l) caudal

margin of antrum of *ditto*. Scale bar: 0.5mm.

Fig. 9. Morphology of *Acryptolechia*.

(a) male genitalia of *Acryptolechia malacobyrs*; (b) aedeagus of *ditto*; (c) male genitalia of *A. torophanes*; (d) aedeagus of *ditto*; (e) female genitalia of *ditto*; (f) lamella postvaginalis and antrum of *ditto* in detail; (g) signum of *ditto* in detail. Scale bar: 0.5mm.

Fig. 10. Morphology of *Deuterogonia*

(a) labial palpus; (b) 5th segment of hind tarsus with tufts; (c) spiniform setae of abdomen; male genitalia; (d) aedeagus; (e) female genitalia; (f) signum in detail. Scale bar: 0.5mm.

Fig. 11. Evolutionary flows of Oecophoridae and related taxa based on ancestral microhabitats (left) and larva sheltering strategy (right) type reconstructions inferred from Maximum likelihood analysis

Pie charts under the nodes show the relative likelihoods of each type at respective nodes. The types of each species are color-coded according to the pattern: eleven types of microhabitats (left) and ten types of larva sheltering strategy (right).

Supplementary file 1. Strict consensus tree of 4 shortest trees resulting from parsimony analysis. Consistency index [CI] = 0.1700; retention index [RI] = 0.3584; the numbers below the branches are bootstrap percentages/ Decay index [DI]; Symbols at the terminals of branches indicate subfamilies/ families): A, Aeolanthinae; B, Blastobasidae; C, Cryptolechiidae; Cr, Cryptolechiinae; D, Depressariinae; De, Depressariidae; E, Ethimiinae; Hp, Hypertrophinae; Hc, Hypercallinae; L, Lypusidae; Le, Lecithoceridae; O, Oecophoridae; Oe, Oecophorinae; P, Peleopodinae; Pl, Pleurotinae; S, Stathmopodidae; St, Stenomatinae; X,

Xyloryctidae. The family and subfamily names in parentheses follow Heikkilä et al. (2014). If the species is not listed in this reference, other recent sources were used (e.g. ‘C’ and ‘O’ follows other sources).

Supplementary file 2. Fifty percent majority consensus tree resulting from Bayesian analysis. The numbers below the branches are posterior probability values (%); Symbols at the terminals of branches indicate subfamilies/ families): A, Aeolanthinae; B, Blastobasidae; C, Cryptolechiidae; Cr, Cryptolechiinae; D, Depressariinae; De, Depressariidae; E, Ethimiinae; Hp, Hypertrophinae; Hc, Hypercallinae; L, Lypusidae; Le, Lecithoceridae; O, Oecophoridae; Oe, Oecophorinae; P, Peleopodinae; Pl, Pleurotinae; S, Stathmopodidae; St, Stenomatinae; X, Xyloryctidae. The family and subfamily names in parentheses follow Heikkilä et al. (2014). If the species is not listed in this reference, other recent sources were used (e.g. ‘C’ and ‘O’ follows other sources).

Supplementary file 3. Maximum likelihood tree. -lnL= 76245.013186; the numbers below the branches are bootstrap percentages; Symbols at the terminals of branches indicate subfamilies/ families): A, Aeolanthinae; B, Blastobasidae; C, Cryptolechiidae; Cr, Cryptolechiinae; D, Depressariinae; De, Depressariidae; E, Ethimiinae; Hp, Hypertrophinae; Hc, Hypercallinae; L, Lypusidae; Le, Lecithoceridae; O, Oecophoridae; Oe, Oecophorinae; P, Peleopodinae; Pl, Pleurotinae; S, Stathmopodidae; St, Stenomatinae; X, Xyloryctidae. The family and subfamily names in parentheses follow Heikkilä et al. (2014). If the species is not listed in this reference, other recent sources were used (e.g. ‘C’ and ‘O’ follows other sources).

Figure 1

Figure 2

Figure 3

Figure 4

- hot shelter (apple habitat)
- stone leaf
- leaf or folded or rolled leaves
- honey seed or fruit or bud
- turning silver insect's gall or frass or eggs or grubs
- honey stem or trunk
- burying under bark or leaf
- making a silk web on soil or flower or stem
- making a silk tube (silk = use or shed material)

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9

Figure 10

Figure 11

Table 1. Exemplars of classification of Oecophoridae since 1960's.

Toll (1964)	Hodges (1974)	Hodges (1998)	Kaila (2004)	Bucheli & Wenzel (2005)
OECOPHORIDAE	OECOPHORIDAE	OECOPHORIDAE		OECOPHORIDAE
Amphisbatinae	Depressariinae	Stathmopodinae	Xyl. assemblage	Blastobasinae
<i>Amphisbatis</i>	Tribe Amphisbatini	<i>Hieromantis</i>	<i>Hierodoris</i>	<i>Hypatopa</i>
Depressariinae	<i>Eupragia</i>	<i>Lactistica</i>	<i>Phaeosaces</i>	<i>Calosima</i>
<i>Agonopteryx</i>	<i>Machimia</i>	<i>Oedematopoda</i>	<i>Izatha</i>	<i>Pigritia</i>
<i>Anchinia</i>	<i>Psilocorsis</i>	<i>Pseudaegeria</i>	Oecophoridae s.s.	<i>Blastobasis</i>
<i>Carcina</i>	Tribe Depressariini	<i>Snellenia</i>	<i>Bisigna</i>	Amphisbatinae
<i>Cryptolecychia</i>	<i>Agonopterix</i>	<i>Stathmopoda</i>	<i>Borkhausenia</i>	<i>Psilocorsis</i>
<i>Depressaria</i>	<i>Apachea</i>	<i>Tortilia</i>	<i>Denisia</i>	Symmocinae
<i>Enicostoma</i>	<i>Bibarrambla</i>	Oecophorinae	<i>Harpella</i>	<i>Oegoconia</i>
<i>Epigraphia</i>	<i>Depressaria</i>	<i>Barea</i>	<i>Hofmannophila</i>	Oecophorinae
<i>Exaeretia</i>	<i>Himmacia</i>	<i>Borkhausenia</i>	<i>Oecophora</i>	<i>Epicallima</i>
<i>Hypercallia</i>	<i>Martyrhilda</i>	<i>Chezala</i>	<i>Palimmeces</i>	<i>Fabiola</i>
<i>Levipalpus</i>	<i>Nites</i>	<i>Chrysonoma</i>	<i>Philobota</i>	<i>Mathildana</i>
<i>Martyrhilda</i>	<i>Semioscopis</i>	<i>Diocosma</i>	<i>Phryganeutis</i>	<i>Decantha</i>
<i>Semioscopis</i>	Oecophorinae	<i>Endrosis</i>	<i>Pleurota</i>	
Oecophorinae	Tribe Oecophorini	<i>Eulechria</i>	<i>Polix</i>	
<i>Alabonia</i>	<i>Batia</i>	<i>Garrha</i>	<i>Prionocris</i>	
<i>Batia</i>	<i>Borkhausenia</i>	<i>Hofmannophila</i>	<i>Promalactis</i>	
<i>Bisigna</i>	<i>Brymblia</i>	<i>Inga</i>	<i>Tingena</i>	
<i>Borkhausenia</i>	<i>Callima</i>	<i>Orophila</i>		
<i>Borkhausenia</i>	<i>Carcina</i>	<i>Oxystola</i>		

Dasycera

Decantha

Endrosis

Fabiola

Harpella

Hofmannophila

Lampros

Metalampra

Oecophora

Schiffermuelleria

Telechrysis

Tichonia

Tubuliferola

Pleurotinae

Aplota

Holoscolia

Macrochila

Pleurota

Toeutis

Deuteroniinae

Deuteronia

Diurneinae

Cheimophila

Diurnea

Herrichiinae

Herrichia

Carolana

Chambersia

Dafa

Decantha

Eido

Endrosis

Esperia

Fabiola

Hormannophila

Inga

Martyringa

Mathildana

Polix

Tribe Pleurotini

Pleurota

Chimabachinae

Tribe Chimabachini

Cheimophoila

Peleopodinae

Tribe Peleopodini

Durrantia

Pseuderotis

Philobota

Pleurota

Tanyzancla

Wingia

Table 1-2. Exemplars of classification of Oecophoridae since 1960's.

Lvovsky (2009)	Kaila et al. (2011)	Nieukerken et al. (2011)	Heikkilä et al., (2014)	Sohn et al. (2016)
OEOPHORIDAE		OEOPHORIDAE	OEOPHORIDAE S.S.	OEOPHORIDAE
Oecophorinae	Oecophoridae s.l.	Oecophorinae	Oecophorinae	Oecophorinae
Deuterogoniinae	<i>Hierodoris</i>	Deuterogoniinae	<i>Bisigna</i>	<i>Wingia</i>
Pleurotinae	<i>Gymnobathra</i>		<i>Oecophora</i>	<i>Mimobrachyoma</i>
	<i>Izatha</i>		<i>Polix</i>	<i>Deuterogonia</i>
	Oecophorinae		<i>Harpella</i>	<i>Promalactis</i>
	<i>Bisigna</i>		<i>Denisia</i>	<i>Leistarcha</i>
	<i>Harpella</i>		<i>Philobota</i>	
	<i>Oecophora</i>		<i>Tingena</i>	
	<i>Pleurota</i>		<i>Hofmannophila</i>	
	<i>Borkhausenia</i>		<i>Borkhausenia</i>	
	<i>Endrosis</i>		<i>Endrosis</i>	
	<i>Hofmannophila</i>		<i>Garrha</i>	
	<i>Palimmeces</i>		<i>Deuterogonia</i>	
	<i>Philobota</i>		Pleurotinae	
	<i>Tingena</i>		<i>Pleurota</i>	
	<i>Wingia</i>		<i>Wingia</i>	
	Deuterogoniinae			
	<i>Deuterogonia</i>			

Table 2-1. Taxa used in this study with GenBank accession numbers, employing Heikkilä et al., (2014)’s classification. *Note:* Taxa, whose sequence accession number started with KF were sequenced from this research.

Family	Subfamily	Species	Collecting country	Genbank assession number							
				18S rDNA	28S rDNA	COI	IDH	MDH	RPS5	EF1A	WINGLESS
Depressariidae	Peleopodinae	<i>Acria sp.</i>	South Korea	KF377325	KF311806	KF311836	KF311907		KF377379	KF311873	KF311772
Depressariidae	Aeolanthinae	<i>Aeolanthess semiostrina</i>	South Korea	KF377326		KF311837				KF311874	KF311773
Depressariidae	Depressariinae	<i>Agonopterix inigrum</i>	South Korea	KF377327	KF311807	KF311838	KF311908		KF377380	KF311875	KF311774
Statomopodidae		<i>Atrijuglans hetaohei</i>	South Korea	KF377328	KF311808	KF311868	KF311909		KF377381	KF311876	KF311775
Blastobasidae	Blastobasinae	<i>Blastobasis sprotundalis</i>	South Korea	KF377329	KF311809	KF311839	KF311910	KF377354		KF311877	KF311776
Oecophoridae		<i>Casmara agronoma</i>	South Korea	KF377330	KF311810	KF311840	KF311911	KF377355	KF377382	KF311878	KF311777
Depressariidae	Cryptolechiinae	<i>Acryptolechia malacobyrsa</i>	South Korea	KF377331	KF311811	KF311841			KF377383	KF311879	KF311778
Depressariidae	Cryptolechiinae	<i>Acryptolechia torophanes</i>	South Korea	KF377332	KF311812	KF311842	KF311912	KF377356	KF377384	KF311880	KF311779
Oecophoridae		<i>Deuterogonia pudorina</i>	South Korea	KF377333	KF311813	KF311843	KF311913	KF377357	KF377385	KF311881	KF311780
Statomopodidae		<i>Hieromantis kurokoi</i>	South Korea	KF377334	KF311814	KF311844	KF311914		KF377386	KF311882	KF311781
Lecithoceridae		<i>Martyringa xeraula</i>	South Korea	KF377335	KF311815	KF311845	KF311915		KF377387	KF311883	KF311782
Oecophoridae	Oecophorinae	<i>Periacma delegata</i>	South Korea	KF377336	KF311816	KF311846	KF311916	KF377358	KF377388	KF311884	
Oecophoridae	Oecophorinae	<i>Promalactis</i>	Cambodia		KF311817	KF311847	KF311917	KF377359		KF311885	

		<i>albisquama</i>									
Oecophoridae	Oecophorinae	<i>Promalactis</i> <i>atriplagatta</i>	South Korea			KF311848	KF311918	KF377360	KF377389		KF311783
Oecophoridae	Oecophorinae	<i>Promalactis</i> <i>autoclina</i>	South Korea	KF377337	KF311818	KF311849	KF311919	KF377361	KF377390	KF311886	KF311784
Oecophoridae	Oecophorinae	<i>Promalactis</i> <i>bidenscula</i>	Cambodia	KF377338		KF311850	KF311920	KF377362		KF311887	KF311785
Oecophoridae	Oecophorinae	<i>Promalactis</i> <i>enopisema</i>	South Korea	KF377339	KF311819	KF311851	KF311930	KF377363	KF377391	KF311888	KF311786
Oecophoridae	Oecophorinae	<i>Promalactis</i> <i>jezonica</i>	South Korea		KF311820	KF311852	KF311921	KF377364	KF377392	KF311889	KF311787
Oecophoridae	Oecophorinae	<i>Promalactis</i> <i>kuznetzovi</i>	Vietnam			KF311853	KF311922	KF377365	KF377393	KF311890	KF311788
Oecophoridae	Oecophorinae	<i>Promalactis</i> <i>odaiensis</i>	South Korea	KF377340	KF311821	KF311854	KF311923	KF377366	KF377394	KF311891	KF311789
Oecophoridae	Oecophorinae	<i>Promalactis</i> <i>polyspina</i>	Vietnam	KF377341	KF311822	KF311855	KF311924		KF377395	KF311892	
Oecophoridae	Oecophorinae	<i>Promalactis</i> <i>prolixolobi</i>	Cambodia		KF311823	KF311856	KF311925	KF377367	KF377396	KF311893	KF311790
Oecophoridae	Oecophorinae	<i>Promalactis</i> <i>serratusola</i>	Cambodia	KF377342		KF311857	KF311926	KF377368	KF377397	KF311894	KF311791
Oecophoridae	Oecophorinae	<i>Promalactis striola</i>	South Korea	KF377343	KF311824	KF311858		KF377369	KF377398		KF311792
Oecophoridae	Oecophorinae	<i>Promalactis</i> <i>suzukiella</i>	South Korea	KF377344	KF311825	KF311859	KF311927		KF377399	KF311895	KF311793

Oecophoridae	Oecophorinae	<i>Promalactis tamdaoella</i>	Vietnam			KF311860	KF311928		KF377400	KF311896	KF311794
Oecophoridae	Oecophorinae	<i>Promalactis wonjuensis</i>	South Korea	KF377345	KF311826	KF311861	KF311929	KF377370	KF377401	KF311897	KF311795
Oecophoridae	Oecophorinae	<i>Promalctis bitaenia</i>	South Korea			KF311862	KF311931	KF377371	KF377402	KF311898	KF311796
Oecophoridae	Oecophorinae	<i>Pseudodoxia achlyphanes</i>	South Korea	KF377346	KF311827	KF311863	KF311932	KF377372	KF377403		KF311797
Oecophoridae	Oecophorinae	<i>Ripeacma acuminipiptera</i>	South Korea	KF377347	KF311828	KF311864	KF311933	KF377373	KF377404	KF311899	KF311798
Oecophoridae	Oecophorinae	<i>Callimodes zelleri</i>	South Korea	KF377348	KF311829	KF311865	KF311934	KF377374	KF377405	KF311900	KF311799
Statomopodidae		<i>Stathmopoda auriferella</i>	South Korea		KF311830	KF311866	KF311935		KF377406	KF311901	KF311800
Statomopodidae		<i>Stathmopoda masinissa</i>	South Korea	KF377349	KF311831	KF311867	KF311936		KF377407	KF311902	KF311801
Statomopodidae		<i>Stathmopoda opticaspis</i>	South Korea	KF377350	KF311832	KF311869	KF311937	KF377375	KF377408	KF311903	KF311802
Statomopodidae		<i>Stathmopoda sp1</i>	South Korea	KF377351	KF311833	KF311870	KF311938	KF377376	KF377409	KF311904	KF311803
Statomopodidae		<i>Stathmopoda sp2</i>	South Korea	KF377352	KF311834	KF311871	KF311939	KF377377	KF377410	KF311905	KF311804
Oecophoridae	Oecophorinae	<i>Tyrolimnas anthraconesa</i>	South Korea	KF377353	KF311835	KF311872	KF311940	KF377378	KF377411	KF311906	KF311805

Table 2-2. Taxa used in this study with GenBank accession numbers, employing Heikkilä et al., (2014)’s classification. *Note:* Those sequences were from NCBI (Kaila et al., 2011).

Family	Subfamily	Species	Collecting country	Genbank assession number					
				COI	IDH	MDH	RPS5	EF1A	WINGLESS
Chimabachidae		<i>Diurnea fagella</i>	Finland	GU828735/ GU929710	GU830119	GU830437		GU829051/ GU829336	GU829602
Cossidae	Cossinae	<i>Cossus cossus</i>	Finland	GU828604/ GU828403	GU829992	GU830315	GU830615	GU828938/ GU829232	GU829499
Depressariidae	Aeolanthinae	<i>Aeolanthos sp</i>	Vietnam	JF818803	JF818994	JF819062	JF819128	JF818886	JF818641
Depressariidae	Depressariinae	<i>Agonopterix heracliiana</i>	Finland	JF818718	JF818931	JF818996	JF819064	JF818805	JF818574
Depressariidae	Depressariinae	<i>Cacochroa corfuella</i>	Greece	JF818729	JF818937	JF819004	JF819071	JF818815	
Depressariidae	Depressariinae	<i>Orophia ferrugella</i>	Finland	JF818773	JF818969	JF819039	JF819104	JF818857	JF818617
Depressariidae	Depressariinae	<i>Eutorna sp</i>	New Zealand	JF818749		JF819021	JF819084	JF818833	JF818596
Depressariidae	Depressariinae	<i>Exaeretia ciniflonella</i>	Finland	JF818750	JF818950		JF819085	JF818834	JF818597
Depressariidae	Depressariinae	<i>Machimia tentoriferella</i>	USA	JF818766		JF819035		JF818850	JF818611
Depressariidae	Depressariinae	<i>Nymphostola galactina</i>	New Zealand	JF818771	JF818967		JF819102	JF818855	JF818616
Depressariidae	Depressariinae	<i>Proteodes carnifex</i>	New Zealand	JF818782	JF818977		JF819112	JF818866	JF818626
Depressariidae	Depressariinae	<i>Psilocorsis reflexella</i>		JF818783			JF819113	JF818867	JF818627
Depressariidae	Depressariinae	<i>Semioscopis steinkellneriana</i>	Finland	JF818789	JF818982	JF819053	JF819118	JF818872	JF818631
Depressariidae	Depressariinae	<i>Telechrysis tripuncta</i>	Finland	JF818794	JF818986	JF819055	JF819122	JF818877	JF818635
Depressariidae	Ethmiinae	<i>Ethmia clytodoxa</i>	Australia	JF818745	JF818947	JF819018	JF819081	JF818829	JF818594
Depressariidae	Ethmiinae	<i>Ethmia pusiella</i>	Finland	GU828588/ GU828387	GU829977	GU830300	GU830603	GU828924/ GU829220	GU829486
Depressariidae	Hypertrophinae	<i>Anchinia daphnella</i>	Finland	JF818720	JF818933	JF818998	JF819065	JF818807	JF818575
Depressariidae	Hypertrophinae	<i>Hypocallia citrinalis</i>	Finland	GU828596/ GU828395	GU829985	GU830308	GU830608	GU828930/ GU829227	GU829492
Depressariidae	Hypertrophinae	<i>Pedois lewinella</i>	Australia	JF818777	JF818972	JF819043	JF819107	JF818861	JF818621
Depressariidae	Hypertrophinae	<i>Peritropha oligodrachma</i>	Australia	JF818760	JF818959	JF819030	JF819094	JF818844	JF818605

Depressariidae	Hypertrophinae	<i>Thudaca mimodora</i>	Australia	JF818796	JF818988	JF819057	JF819124	JF818879	
Depressariidae	Stenomatinae	<i>Agriophara axesta</i>	Australia	JF818719	JF818932	JF818997		JF818806	
Depressariidae	Stenomatinae	<i>Antaeotricha leucillana</i>	Canada	JF818722	JF818935	JF819000	JF819067	JF818809	JF818577
Lypusidae		<i>Pseudatemelia josephinae</i>	Finland	GU828593/ GU828392	GU829982	GU830305	GU830606	GU828928/ GU829224	GU829490
Oecophoridae	Oecophorinae	<i>Borkhausenia fuscescens</i>	Finland	JF818728	JF818936	JF819003			JF818581
Oecophoridae	Oecophorinae	<i>Endrosis sarcitrella</i>	Finland	JF818743	JF818945	JF819016	JF819079	JF818827	JF818593
Oecophoridae	Oecophorinae	<i>Harpella forficella</i>	Finland	JF818753	JF818953	JF819024	JF819087	JF818837	JF818600
Oecophoridae	Oecophorinae	<i>Hofmannophila pseudospretella</i>	Finland	JF818756	JF818955	JF819026	JF819090	JF818840	JF818603
Oecophoridae	Oecophorinae	<i>Oecophora bractella</i>	Finland	GU828695/ GU828491	GU830082	GU830400	GU830685	GU829018/ GU829307	
Oecophoridae	Oecophorinae	<i>Palimmeces sp</i>	Australia	JF818774	JF818970	JF819040		JF818858	JF818618
Oecophoridae	Oecophorinae	<i>Philobota sp</i>	Australia	JF818780	JF818975	JF819046	JF819110	JF818864	JF818624
Oecophoridae	Oecophorinae	<i>Pleurota bicostella</i>	Finland	JF818781	JF818976	JF819047	JF819111	JF818865	JF818625
Oecophoridae	Oecophorinae	<i>Tingena armigerella</i>	New Zealand	JF818797	JF818989		JF819125	JF818880	JF818636
Oecophoridae	Oecophorinae	<i>Wingia aurata</i>	Australia	JF818801	JF818992	JF819060	JF819127	JF818884	JF818640
Xyloryctidae		<i>Gymnobathra flavidella</i>	New Zealand	JF818751	JF818951	JF819022		JF818835	JF818598
Xyloryctidae		<i>Gymnobathra omphalota</i>	New Zealand	JF818752	JF818952	JF819023	JF819086	JF818836	JF818599
Xyloryctidae		<i>Hierodoris atychioides</i>	New Zealand	JF818755			JF819089	JF818839	JF818602
Xyloryctidae		<i>Izatha austera</i>	New Zealand	JF818762	JF818961	JF819032	JF819096	JF818846	JF818607
Xyloryctidae		<i>Izatha peroneanella</i>	New Zealand	JF818761	JF818960	JF819031	JF819095	JF818845	JF818606
Oecophoridae		<i>Phaeosaces coarctatella</i>	New Zealand	JF818779	JF818974	JF819045	JF819109	JF818863	JF818623
Oecophoridae		<i>Phaeosaces compsotypa</i>	New Zealand	JF818778	JF818973	JF819044	JF819108	JF818862	JF818622
Depressariidae	Peleopodinae	<i>Carcina quercana</i>	Bulgaria	GU828758/ GU929731	GU830142	GU830458	GU830726	GU829071/ GU829353	GU829620
Thyrididae	Thyridinae	<i>Thyris fenestrella</i>	Bulgaria	GU828761/ GU929735	GU830146	GU830462	GU830728	GU829074/ GU829357	GU829623
Xyloryctidae	Xyloryctinae	<i>Cryptophasa sarcoxantha</i>	Australia	JF818739	GU830159	GU830478	GU830739	GU829367	GU829638
Xyloryctidae	Xyloryctinae	<i>Tymbophora peltastis</i>	Australia	JF818800	JF818991	JF819059		JF818883	JF818639

Table 3. Primers used in the present study.

Gene region	Direction	Primer name	Primer	Annealing temperature	Product length bp	Reference
16SrRNA	Forward	16SgaF	5' GTA TCT TGT GTA TCA GAG TT 3'	50	1011	Yamamoto and Sota, 2007
16SrRNA	Reverse	16SgaR	5' CCT GGC TTA CAC CGG TTT GAA 3'	50		Yamamoto and Sota, 2007
18SrRNA	Forward	18H'	5' GCCCTTCCGTCAATTCCTTTAAGTTTCAGC 3'	55	550	Wiegmann et al., 2000
18SrRNA	Reverse	18L	5' CACCTACGGAAACCTTGTTACGACTT 3'	55		Wiegmann et al., 2000
28SrRNA	Forward	28SD1F	5' GGG GAG GAA AAG AAA CTA AC 3'	61	300	Larsen, 1992
28SrRNA	Reverse	28SD1R	5' CAA CTT TCC CTT ACG GTA CT 3'	61		Larsen, 1992
COI	Forward	LCO	5' GGT CAA CAA ATC ATA AAG ATA TTG G 3'	50	658	Folmer et al., 1994
COI	Reverse	HCO	5' TAA ACT TCA GGG TGA CCA AAA AAT CA 3'	50		Folmer et al., 1994
COI	Forward	Jerry	5' CAA CAY TTA TTT TGA TTT TTT GG 3'	50	829	Simon et al., 1994
COI	Reverse	Pat	5' ATC CAT TAC ATA TAA TCT GCC ATA 3'	50		Simon et al., 1994
EF-1a	Forward	Starsky	5' CAC ATY AAC ATT GTC GTS ATY GG 3'	57	541	Cho et al., 1995
EF-1a	Reverse	Luke	5' CAT RTT GTC KCC GTG CCA KCC 3'	57		Cho et al., 1995
EF-1a	Forward	Cho	5' GTC ACC ATC ATY GAC GC 3'	50	517	Reed and Sperling, 1999
EF-1a	Reverse	Verdi	5' GAT ACC AGT CTC AAC TCT TCC 3'	50		Nazari et al., 2007
EF-1a	Forward	EF51.9	5' CAR GAC GTA TAC AAA ATC GG 3'	50	511	Cho et al., 1995
EF-1a	Reverse	EFrcM4	5' ACA GCV ACK GTY TGY CTC ATR TC 3'	50		Cho et al., 1995
wingless	Forward	LepWg1	5' GAR TGY AAR TGY CAY GGY ATG TCT GG 3'	50	400	Brower and DeSalle, 1998
wingless	Reverse	LepWg2	5' ACT ICG CAR CAC CAR TGG AAT GTR CA 3'	50		Brower and DeSalle, 1998
GAPDH	Forward	Frigga	5' AAR GCT GGR GCT GAA TAT GT 3'	55	691	Wahlberg and Wheat, 2008
GAPDH	Reverse	Burre	5' GWT TGA ATG TAC TTG ATR AGR TC 3'	55		Wahlberg and Wheat, 2008
RpS5	Forward	RpS5f	5' ATG GCN GAR GAR AAY TGG AAY GA 3'	55	617	Wahlberg and Wheat, 2008
RpS5	Reverse	RpS5r	5' CGG TTR GAY TTR GCA ACA CG 3'	55		Wahlberg and Wheat, 2008
MDH	Forward	MDHf	5' GAY ATN GCN CCN ATG ATG GGN GT 3'	55	733	Wahlberg and Wheat, 2008
MDH	Reverse	MDHr	5' AGN CCY TCN ACD ATY TTC CAY TT 3'	55		Wahlberg and Wheat, 2008
CAD	Forward	CAD743f	5' GGN GTN ACN ACN GCN TGY TTY GAR CC 3'	55	850	Wahlberg and Wheat, 2008
CAD	Reverse	CAD1028r	5' TTR TTN GGN ARY TGN CCN CCC AT 3'	55		Wahlberg and Wheat, 2008
IDH	Forward	IDHdeg27F	5' GGW GAY GAR ATG ACN AGR ATH ATH TGG 3'	55	710	Wahlberg and Wheat, 2008
IDH	Reverse	IDHdegR	5' TTY TTR CAI GCC CAN ACR AAN CCN CC 3'	55		Wahlberg and Wheat, 2008

Table 4. Microhabitat, larva sheltering and geography type coding based on references for species sequenced in this study.

Microhabitat types were coded as follows: (A) on foliage; (B) live shrub or tree; (C) flowers or fruit capsule; (D) lichen; (E) leaf litter; (F) decaying wood or dead tree; (G) under bark; (H) on fungi; (I) bird's nest; (J) dried plant (including grain storage space). Larva sheltering strategy types were coded as follows: (A) not shelter; (B) mine leaf; (C) tied or folded or rolled leaves; (D) boring seed or fruits or bud; (E) boring other Insect's gall or frass or eggs; (F) boring stem or trunk; (G) burrowing under bark or soil; (H) making a silk web on leaf or flowers or stem; (I) making a silk tube (silk + live or dried materials). Seven geography types were coded as follows: Afrotropical (AF); Australasian (AU); Nearctic (NE); Neotropical (NEO); Oriental (O); Palaearctic Asia regions (PA); Palaearctic Europe regions (PE).

Family	Subfamily	Species	Type coding			Distribution	References
			micro-habitat	larva sheltering	geography		
Blastobasidae	Blastobasinae	<i>Blastobasis sprotundalis</i>			PA	Korea, Japan, Russia Far East	Park, 1984; Byun et al., 2009
Lypusidae	Chimabachidae	<i>Diurnea fagella</i>	A	C	PE	Europe, Western Russia	Toll, 1964; Karsholt & Razowski, 1996; Lvovsky, 1996; Sinev, 2008
Cossidae	Cossinae	<i>Cossus cossus</i>	B	A	PE, PA	Europe, Russia	Karsholt & Razowski, 1996; Sinev, 2008
Depressariidae	Aeolanthinae	<i>Aeolanthus semiostrina</i>	A	C	PA	Korea, China	Powell, 1973; Park and Shin, 1985; Byun et al., 2009
Depressariidae	Aeolanthinae	<i>Aeolanthus sp</i>	A	C	O	Vietnam	Robinson et al., 1994; Kaila et al., 2011
Depressariidae	Depressariinae	<i>Agonopterix heracliana</i>	AC	B	PE, PA	Europe, Western and Central Russia	Hering, 1957; Toll, 1964; Karsholt & Razowski, 1996; Sinev, 2008
Depressariidae	Depressariinae	<i>Agonopterix inigrum</i>	AC	B	PA	Korea, Japan, Russia	Hering, 1957; Toll, 1964; Park, 1981b; Sinev, 2008; Byun et al., 2009
Depressariidae	Depressariinae	<i>Cacochroa corfuella</i>	A	B	PE	Greece	Hering, 1957; Lvovsky, 2008; Kaila et al., 2011
Depressariidae	Depressariinae	<i>Orophia ferrugella</i>	AC	B	PE	Europe	Toll, 1964; Karsholt & Razowski, 1996; Lvovsky, 1996, 2008
Depressariidae	Depressariinae	<i>Eutorna sp</i>	A	A	AU	New Zealand	Kaila et al., 2011
Depressariidae	Depressariinae	<i>Exaeretia ciniflonella</i>	A	A	PE	Europe	Karsholt & Razowski, 1996; Kaila et al., 2011
Depressariidae	Depressariinae	<i>Machimia tentoriferella</i>	BE	C	NE	USA	Hodges, 1974

Depressariidae	Depressariinae	<i>Nymphostola galactina</i>	A	A	AU	New Zealand	Kaila et al., 2011
Depressariidae	Depressariinae	<i>Proteodes carnifex</i>	A	A	AU	New Zealand	Kaila et al., 2011
Depressariidae	Depressariinae	<i>Psilocorsis reflexella</i>	B	C	NE	USA	Hodges, 1974
Depressariidae	Depressariinae	<i>Semioscopis steinkellneriana</i>	A	C	PE, PA	Europe, Central Russia	Toll, 1964; Karsholt & Razowski, 1996; Sinev, 2008
Depressariidae	Depressariinae	<i>Telechrysis tripuncta</i>	B		PE, PA	Europe, Russia	Karsholt & Razowski, 1996; Lvovsky, 1996; Sinev, 2008
Depressariidae	Ethmiinae	<i>Ethmia clytodoxa</i>	A	H	AU	Australia	Kaila et al., 2011
Depressariidae	Ethmiinae	<i>Ethmia pusiella</i>	A	H	PE	Europe	Karsholt & Razowski, 1996
Depressariidae	Hypertrophinae	<i>Anchinia daphnella</i>	A	C	PE, PA	Europe, Central Russia	Toll, 1964; Karsholt & Razowski, 1996; Lvovsky, 2008; Sinev, 2008
Depressariidae	Hypertrophinae	<i>Hypercallia citrinalis</i>	A	H	PE	Europe	Toll, 1964; Karsholt & Razowski, 1996; Lvovsky, 2008
Depressariidae	Hypertrophinae	<i>Pedois lewinella</i>	A	A	AU	Australia	Kaila et al., 2011
Depressariidae	Hypertrophinae	<i>Periacma delegata</i>			O, PA	Korea, Japan, China, Taiwan, Eastern Russia	Park, 1981b; Saito et al. 1992, Wang 2006; Sinev, 2008
Depressariidae	Hypertrophinae	<i>Thudaca mimodora</i>	A	A	AU	Australia	Kaila et al., 2011
Depressariidae	Stenomatinae	<i>Agriophara axesta</i>	A	A	AU	Australia	Kaila et al., 2011
Depressariidae	Stenomatinae	<i>Antaeotricha leucillana</i>	A	A	NE	Canada	Kaila et al., 2011
Lypusidae	Lypusinae	<i>Pseudatemelia josephinae</i>	F	C	PE	Europe	Karsholt & Razowski, 1996
Depressariidae	Cryptolechiinae	<i>Acryptolechia malacobyrsa</i>			PA	Korea, China, Japan	Saito et al. 1992, Wang 2006, Lvovsky 2009
Depressariidae	Cryptolechiinae	<i>Acryptolechia torophanes</i>			PA	Korea, China	Park 1981b; Wang 2006
Oecophoridae		<i>Deuteronia pudorina</i>	DG	EG	O, PA, PE	Korea, Japan, China, Europe, Russia	Schütze, 1931; Toll, 1964; Park, 1981b; Harper et al., 2002; Lvovsky, 2006; Wang 2006; Sinev, 2008; Byun et al., 2009
Oecophoridae	Oecophorinae	<i>Borkhausenia fuscescens</i>	FGHI	H	PE	Europe, Western Russia	Waters, 1929; Ford, 1949; Klimesch, 1961; Toll, 1964; Karsholt & Razowski, 1996; Lvovsky, 1996; Sinev, 2008; Kaila et al., 2011
Oecophoridae	Oecophorinae	<i>Endrosis sarcitrella</i>	IJ	E	AU, NE, PE, NEO, AF	Europe, US, New Zealand, Chile, Western Russia, South Africa	Waters, 1929; Ford, 1929; Klimesch, 1961; Toll, 1964; Hodges, 1974; Saito et al. 1992; Karsholt & Razowski, 1996; Lvovsky, 1996; Sinev, 2008; http://museumpests.net
Oecophoridae	Oecophorinae	<i>Harpella forficella</i>	FGH	A	PE	Europe, Western Russia	Toll, 1964; Karsholt & Razowski, 1996; Lvovsky, 1996; Sinev, 2008; Kaila et al., 2011
Oecophoridae	Oecophorinae	<i>Hofmannophila pseudospretella</i>	IJ	H	PE, NE, NEO	UK, North America, Western Russia	Waters, 1929; Ford, 1949; Klimesch, 1961; Cole, 1962; Toll, 1964; Hodges, 1974; Saito et al., 1992; Karsholt & Razowski, 1996; Lvovsky, 1996; Sinev, 2008; Lee & Brown, 2009

Lecithoceridae		<i>Martyringa xeraula</i>	J	E	O, PA, NE	Korea, Japan, China, India, Thailand, Eastern Russia, USA	Hodges, 1960, 1974; Zagulajev, 1965; Saito, 1987, 1992; Park 1981b; Lvovsky, 1994; Wang 2006; Heppner, 2007; Sinev, 2008
Oecophoridae	Oecophorinae	<i>Oecophora bractella</i>	FGH	H	PE	Europe, Western Russia	Schütze, 1931; Toll, 1964; Karsholt & Razowski, 1996; Lvovsky, 1996, 2006; Harper et al., 2002; Sinev, 2008; Kaila et al., 2011
Oecophoridae	Oecophorinae	<i>Palimmeces sp</i>	FH	G	AU	Australia	Kaila et al., 2011
Oecophoridae	Oecophorinae	<i>Peritropha oligodrachma</i>	A	A	AU	Australia	Kaila et al., 2011
Oecophoridae	Oecophorinae	<i>Philobota sp</i>	E	G	AU	Australia	Common, 1990; Kaila et al., 2011
Oecophoridae	Pleurotinae	<i>Pleurota bicostella</i>	B	H	PE, PA	Europe, Russia	Toll, 1964; Karsholt & Razowski, 1996; Sinev, 2008; Kaila et al., 2011
Oecophoridae	Oecophorinae	<i>Promalactis albisquama</i>	FG	G	O	Vietnam	Kim et al., 2010
Oecophoridae	Oecophorinae	<i>Promalactis atriplagatta</i>	FG	G	PA	Korea	Park & Park, 1998
Oecophoridae	Oecophorinae	<i>Promalactis autoclina</i>	FG	G	O, PA	Korea, Japan, China	Park, 1981b; Wang 2006
Oecophoridae	Oecophorinae	<i>Promalactis bidenscula</i>	FG	G	O	Cambodia	Kim et al., unpublished
Oecophoridae	Oecophorinae	<i>Promalactis enopisema</i>	FG	G	PA	Korea, Japan, Chian, Russian Far East	Park & Park, 1998
Oecophoridae	Oecophorinae	<i>Promalactis jezonica</i>	FG	G	O, PA	Korea, Japan, China, India, Eastern Russia	Park 1981a; Wang, 2006; Sinev, 2008
Oecophoridae	Oecophorinae	<i>Promalactis kuznetzovi</i>	FG	G	O	Vietnam	Lvovsky, 1988
Oecophoridae	Oecophorinae	<i>Promalactis odaiensis</i>	FG	G	PA	Korea, China	Park & Park, 1998; Wang, 2006
Oecophoridae	Oecophorinae	<i>Promalactis polyspina</i>	FG	G	O	Vietnam	Kim et al., 2012
Oecophoridae	Oecophorinae	<i>Promalactis prolixolobi</i>	FG	G	O	Cambodia	Kim et al., unpublished
Oecophoridae	Oecophorinae	<i>Promalactis serratusola</i>	FG	G	O	Cambodia	Kim et al., unpublished
Oecophoridae	Oecophorinae	<i>Promalactis striola</i>	FG	G	PA	Korea	Park & Park, 1998
Oecophoridae	Oecophorinae	<i>Promalactis suzukiella</i>	BFGH	G	O, PA, NE	Korea, Japan, China, Taiwan, Vietnam, USA	Park & Park, 1981, 1998; Wang 2006; Adamsky et al., 2009
Oecophoridae	Oecophorinae	<i>Promalactis tamdaoella</i>	FG	G	O	Vietnam	Kim et al., 2010
Oecophoridae	Oecophorinae	<i>Promalactis wonjuensis</i>	FG	G	PA	Korea	Park & Park, 1998
Oecophoridae	Oecophorinae	<i>Promalactis bitaenia</i>	FG	G	PA	Korea	Park & Park, 1998
Oecophoridae	Oecophorinae	<i>Pseudodoxia achlyphanes</i>	E	A	PA	Korea, Japan, China	Saito 1976; Wang, 2006
Oecophoridae	Oecophorinae	<i>Ripeacma acuminipiptera</i>			O, PA	Korea, China	This study, Wang, 2006
Oecophoridae	Oecophorinae	<i>Callimodes zelleri</i>	DFG	G	PA	Korea, Japan, Russia	Byun et al., 2009
Oecophoridae	Oecophorinae	<i>Tingena armigerella</i>			AU	New Zealand	Kaila et al., 2011
Oecophoridae	Oecophorinae	<i>Tyrolimnas anthraconesa</i>			PA	Korea, Japan, China	Park 1981b
Oecophoridae	Oecophorinae	<i>Wingia aurata</i>	A	C	AU	Australia	Common, 1990; Kaila et al., 2011
Oecophoridae		<i>Casmara agronoma</i>	B	F	O, PA	Korea, Japan, China, Indonesia	Robinson, 1994; Byun et al., 2012
Xyloryctidae		<i>Gymnobathra flavidella</i>	EFG	I	AU	New Zealand	Hudson, 1928; Dugdale, 1988; Hoare, 2005
Xyloryctidae		<i>Gymnobathra omphalota</i>	EFG	I	AU	New Zealand	Hudson, 1928; Dugdale, 1988; Hoare, 2005
Xyloryctidae		<i>Hierodoris atychioides</i>	BE	CE	AU	New Zealand	Kay, 1980; Dugdale, 1988; Hoare, 2005

Xyloryctidae		<i>Izatha austera</i>	EFG	F	AU	New Zealand	Dugdale, 1988; Hoare, 2005
Xyloryctidae		<i>Izatha peroneanella</i>	EFG	F	AU	New Zealand	Dugdale, 1988; Hoare, 2005
Depressariidae		<i>Phaeosaces coarctatella</i>	BD	AF	AU	New Zealand	Dugdale, 1988; (http://en.wikipedia.org/wiki/Phaeosaces_coarctatella)
Depressariidae		<i>Phaeosaces compsotypa</i>	BD	AF	AU	New Zealand	Dugdale, 1988; Davies, 1990
Depressariidae	Peleopodidae	<i>Acria sp.</i>	B		PA	Korea	This study
Depressariidae	Peleopodidae	<i>Carcina quercana</i>	B	A	PE	Europe, Western Russia	Toll, 1964; Leraut, 1993; Karsholt & Razowski, 1996; Lvovsky, 1996, 2008; Sinev, 2008
Statomopodidae		<i>Atrijuglans hetaohei</i>	B	C	PA	Korea, Japan, China, Russian Far East	Wang, 2006; Sohn, 2007; Byun et al., 2009
Statomopodidae		<i>Hieromantis kurokoi</i>		D	PA	Korea, Japan, China	Robinson et al., 1994; Wang, 2006; Sohn, 2007
Statomopodidae		<i>Stathmopoda auriferella</i>	C	D	PA	Korea	Wang, 2006; Byun et al. 2009
Statomopodidae		<i>Stathmopoda masinissa</i>	BC	D	PA	Korea, Japan, China, Taiwan	Wang, 2006; Byun et al. 2009
Statomopodidae		<i>Stathmopoda opticaspis</i>	C	D	PA	Korea, Japan, China	Wang, 2006; Byun et al. 2009
Statomopodidae		<i>Stathmopoda sp1</i>	C	D	PA	Korea	Wang, 2006; This study
Statomopodidae		<i>Stathmopoda sp2</i>	C	D	PA	Korea	Wang, 2006; This study
Thyrididae	Thyridinae	<i>Thyris fenestrella</i>	B	A	PE, PA	Europe, Russia	Karsholt & Razowski, 1996; Sinev, 2008
Xyloryctidae	Xyloryctinae	<i>Cryptophasa sarcoxantha</i>	B	F	AU	Australia	Robinson et al., 1994; Kaila et al., 2011
Xyloryctidae	Xyloryctinae	<i>Tymbophora peltastis</i>	B	C	AU	Australia	Common, 1990; Kaila et al., 2011

* The patterns of the change of microhabitat and larva sheltering strategy types of Oecophoridae : ● Split 1; ● Split 2; ★ Split 3