INTRODUCTION

With over 16,000 described species, Pyraloidea represent one of the most diverse lineages of Lepidoptera (Nuss et al., 2003–2020). The adults bear paired tympanal organs in the second abdominal segment consisting of two tympanic chambers supporting a tympanum. This feature allows detecting the echolocation sounds of hunting bats and plays a role in acoustic communication during mating (Greenfield, 2014 and references therein). Pyraloids exhibit an unprecedented spectrum of ecological adaptations in larval life habits, including adaptations to freshwater habitats (Acentropinae) or extreme dry environments such as deserts (some Phycitinae). The larval food spectrum spans from detritus, lichens and mosses over lycopods and ferns to conifers and mono- and eudicotyledonous plants. A number of species are known as pests of Poaceae (e.g. in the genera Chilo Zincken, 1817, Cnaphalocrocis Lederer, 1863, Diatraea Guiding, 1828, Marasmia Lederer, 1863, Ostrinia Hübner, 1825, Scirpophaga Treitschke, 1832), Brassicaceae (Hylina Guenée, 1854) and Solanaceae (Duponchellia Zeller, 1847, Hynenia Hübner, 1825, Lineodini, Spodalea Guenée, 1854) (Capinera, 2001; Hill, 1987, 2008; Khan et al., 1991; Landry & Roque-Albelo, 2008; Mally et al., 2019; Solis & Adamski, 1998). Mutualistic relationships with bees, ants and sloths, or parasitism on other Lepidoptera or Hymenoptera larvae have been reported for some taxa, for example Chalcoela Zeller, 1872, Cryptoses Dyar, 1908, Dicytomolomia...
Zeller, 1872, *Galleria* Fabricius, 1798 and *Niphopyralis* Hampson, 1893 (Kenner, 1923; Nacko & Henderson, 2017; Pauli et al., 2014; Rau, 1941; Roepe, 1916).

Morphological differences in the tympanal organ led authors to recognize two main groups designated as Crambidae and Pyralidae (Börner, 1925; Minet, 1982, 1983, 1985). The Crambidae are characterized by a tympanal organ of the ‘open type’, that is with a broad anteromedial opening, the presence of a praecinctorium, and the conjunctiva and tympanum not in the same plane (Minet, 1982). A further synapomorphy lies in the presence of one or two L setae in the abdominal segment 9 of the larvae (Hasenfuß, 1960). Different hypotheses regarding the phylogeny of the Crambidae flourished during the second half of the 20th century. Roesler (1978) presented hypotheses about their relationships based on adult and immature characters. Kuznetsov and Stekolnikov (1979) formulated a hypothesis on the Crambidae phylogeny based on the muscular anatomy of the male genitalia. Minet (1982, 1985) characterized several subfamilies based on the examination of the tympanal organ. Yoshiyasu (1985) postulated a partly resolved phylogeny based on adult and immature characters for the Japanese Acentropinae (formerly Nymphulinae) and Musotiminae. The first cladistic analysis of Crambidae was that of Solis and Maes (2002), based on 33 morphological characters assembled from previous studies. Their study, however, did not resolve relationships among subfamilies, and no convincing phylogeny was known in the early 2000s. Mutanen et al. (2010) and Regier et al. (2009) provided the first molecular phylogenies of Lepidoptera including a significant number of Pyraloidea subfamilies (10 and 17, respectively). They confirmed the monophyly of both Crambidae and Pyralidae, forming together the monophyletic Pyraloidea, the subfamilies Cathariinae, Cybalomiinae and Linostinae were never included in previous studies, and so far, no supported phylogenetic placements were obtained for Heliothelinae (Léger et al., 2019) or Lathrocallinae (Mally et al., 2019). This study aims to investigate the phylogenetic placement of Cathariinae, Cybalomiinae, Heliothelinae, Lathrocallinae and Linostinae within Crambidae. A brief summary of these five subfamilies is provided hereafter.

### 1.1 Cathariinae Minet, 1982

These small, blackishly winged moths are found in the alpine areas of the Alps and the Pyrenees. Male genitalia lack a gnathos, and females have a reduced tympanal organ. Depending on the taxonomic concept, one or two species are recognized (Leraut, 1997). Larvae are reported feeding on *Cerastium pedunculatum*, *Silene acaulis* (Caryophyllaceae), *Saxifraga aphylla* and *S. oppositifolia* (Saxifragaceae) (Schmid, 2019). *Catha* was originally placed in the Odontiinae (Munroe, 1961) or Pyraustinae (Marion, 1962), before Minet (1982) erected a subfamily to accommodate the genus based on the reduction of the gnathos and tympanal organ. Leraut (1997), however, treated Cathariinae as synonym of Odontiinae.

### 1.2 Cybalomiinae Marion, 1955

Cybalomiine moths display yellow to brownish forewings similar to those of some Glaphyriinae. The adult Cybalomiinae exhibit a characteristic fovea between Rs 2 + 3 and Rs 4 on the forewing, and lateral indentations of abdominal sternite 2 (Luquet & Minet, 1982). Larvae are reported to feed on Brassicaceae and Capparaceae (Chrétien, 1911; Lhomme, 1935; Robinson et al., 2010). Marion (1955) described the tribe Cybalomiini as part of the Scopariinae, and Munroe (1959) raised it to the subfamily level. Regier et al. (2012) suspected this subfamily to belong to the Glaphyriinae based on the shared use of Brassicales as larval host plant. The subfamily currently counts 113 species classified in 19 genera, which are predominantly found in dry regions of Southern Europe, Africa, Asia and Australia, and North and South America (Nuss et al., 2003–2020).

### 1.3 Heliothelinae Amsel, 1961

This subfamily comprises two tribes, Heliothelini and Hoploscopini, that share the presence of a spine in the corpus
bursae of the female genitalia (Nuss, 1998). The Heliothelini are small dark-winged moths with yellow to orange coloration on the hindwings in many species. These diurnal moths are found in dry habitats of the Old World. In contrast, the Hoploscopini display reddish-brown forewings with yellow to red markings. They fly at night and are found in tropical mountains of the Oriental and Australasian regions. Larvae of *Heliothela wulfeniana* (Scopoli, 1763) feed on Lamiaceae and Violaceae (Schütze, 1931), while larvae of Hoploscopini are reported from ferns (Mally et al., 2017). Heliotheline genera are still a matter of debate, treated by some authors as subgroup of Scopariinae (Hannemann, 1964; Leraut, 1980; Munroe & Solis, 1998; Robinson et al., 1994), while others advocate two separate lineages (Minet, 1982; Nuss, 1998, 1999). Heliotheline genera were not recovered as monophyletic by Léger et al. (2019), but among-subfamily relationships were poorly supported, precluding the inference of meaningful conclusions. The three Heliothelini and two Hoploscopini genera encompass 76 described species (Nuss et al., 2003–2020), with an estimated 30 species awaiting description in Hoploscopini (Léger et al., 2020; Robinson et al., 1994).

### 1.4 Lathrotelinae Clarke, 1971

Clarke (1971) described the Lathrotelidae from a single female specimen of *Lathroteles obscura* Clarke, 1971, collected on Rapa Island (French Polynesia). The specimen lacked a tympanic organ but displayed other characters typical for Pyraloidea, so that the author considered it to be closely related to Pyraloidea (‘Pyralidae’ s. l.). Minet (1991) found strongly reduced tympanic organs of the ‘crambid type’ when examining a male specimen of *L. obscura* and synonymized Lathrotelidae with Nymphulinae based on their similarities in the tympanic organs. The same author reinstated the Lathrotelinae to accommodate this genus, along with *Diplopseustis* Meyrick, 1884, *Diplopseustoides* Guillermet, 2013 and *Sufetula* Walker, 1859, and suggested the two or three lunules on the forewing costa as a synapomorphy for the group (Minet, 2015). This pantropical subfamily currently hosts five genera encompassing 42 species (Nuss et al., 2003–2020). All known host-plant associations are with monocotyledons (Genty & Mariau, 1975; Hayden, 2013; Seín, 1930; Solis et al., 2019).

### 1.5 Linostinae Amsel, 1956

Linostine moths display snow-white forewings with finely marked black median and subterminal lines. The subfamily was described by Amsel (1956) to host the genus *Linosta* Möschler, 1882, which includes four neotropical species. The subfamily was revised by Munroe (1959).

## 2 MATERIALS AND METHODS

### 2.1 Taxon sampling

Samples were collected as adult moths by light trapping or at day with a net and preserved either dried or in alcohol. A number of specimens were obtained through loans and donations from colleagues (see Acknowledgments). Specimens were identified based on wing pattern and genitalia, and identification was cross-checked by DNA barcoding with help of the Identification Engine in BOLD (Ratnasingham & Hebert, 2007; http://boldsystems.org/). Dried specimens collected less than two years prior to DNA extraction were considered suitable for molecular genetic analyses. All Crambidae subfamilies were included, with Cathariinae (1 species), Cybalomiinae (4 species) and Linostinae (1 species) represented for the first time in a molecular phylogeny. PCR-generated molecular sequences from studies of Mutanen et al. (2010) (16 taxa), Regier et al. (2012) (41 taxa) and Heikkilä et al. (2015) (1 taxon) were downloaded from GenBank and added to our molecular data set. A representative subset of the taxa from phylogenetic studies of Léger et al. (2019) and Mally et al. (2019) were also included. Sequences of interest were retrieved from published transcriptomes of *Cnaphalocrocis medinalis* (Guenée, 1854), *Myelobia smerintha* (Hübner, 1821) (Kawahara & Breinholt, 2014) and *Scirpophaga incertulas* (Walker, 1863) (Renuka et al., 2017), and from the whole genomes of *Amyelois transitella* (Walker, 1863) and *Chilo suppressalis* (Walker, 1863) on the LepBase interface (Challis et al., 2016; ensembl.lepbase.org). Taxon sampling is summarized in Table S1.

### 2.2 Molecular work

DNA was extracted with the NucleoSpin Tissue kit (Macherey-Nagel) from abdomens following the non-destructive method of Knölke et al. (2004). Seven genes (total = 5,592 bp) from the sampling of Mutanen et al. (2010) were initially considered for amplification: CAD (792 bp), EF-1a (1,071 bp), GAPDH (654 bp), IDH (657 bp), RpS5 (576 bp), wingless (402 bp) and the mitochondrial COI (1,440 bp). The data set of Regier et al. (2012) includes 1 species), Cybalomiinae (4 species) and Linostinae (1 species) represented for the first time in a molecular phylogeny. PCR-generated molecular sequences from studies of Mutanen et al. (2010) (16 taxa), Regier et al. (2012) (41 taxa) and Heikkilä et al. (2015) (1 taxon) were downloaded from GenBank and added to our molecular data set. A representative subset of the taxa from phylogenetic studies of Léger et al. (2019) and Mally et al. (2019) were also included. Sequences of interest were retrieved from published transcriptomes of *Cnaphalocrocis medinalis* (Guenée, 1854), *Myelobia smerintha* (Hübner, 1821) (Kawahara & Breinholt, 2014) and *Scirpophaga incertulas* (Walker, 1863) (Renuka et al., 2017), and from the whole genomes of *Amyelois transitella* (Walker, 1863) and *Chilo suppressalis* (Walker, 1863) on the LepBase interface (Challis et al., 2016; ensembl.lepbase.org). Taxon sampling is summarized in Table S1.

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introns in the first part of CAD, as well as in DDC, enolase and period render their amplification from genomic DNA cumbersome. In order to increase the overlap of the Regier data set with our own molecular data set and the Mutanen data set, we investigated the intron–exon structure for suitable regions to amplify in the CAD, DDC, enolase and period genes from annotated genomes of *Chilo suppressalis* and *Amyelois transitella* available from LepBase (Challis et al., 2016). The 4th CAD and 5th DDC exons (3,142 and 726 bp, respectively) were considered for primer design. Eighty per cent consensus sequences of the Regier gene data sets were generated via GeneFisher2 (Giegerich et al., 1996). Primers were designed by eye on conserved regions and subsequently checked for melting temperature, 3’ complementarity, self-annealing and potential hairpin formation on the online platform OligoCalc (www.basic.northwestern.edu/biotools/OligoCalc.html). Two pairs of primers were tested to amplify the first part of the 4th CAD exon in two fragments of 827 and 793 bp, respectively. The second fragment was successfully amplified in most of the samples, while amplification of first fragment proved to be difficult and was abandoned in the course of the study. A pair of primers was designed for the amplification of a 547 bp fragment of the 5th DDC exon (Table S2). BIO-X-ACT Short DNA Polymerase (Bioline) was used following the PCR protocol of Wahlberg and Wheat (2008) (as in Léger et al. (2019). Hi-Spec Additive (Bioline) was added to samples with lower yields. PCR programmes from Wahlberg and Wheat (2008) with the annealing temperature optimized for each primer set or the TouchDown PCR programme (Regier, 2007) were used as in Léger et al. (2019). Amplification success was checked by electrophoresis on 1% or 2% agarose gels subsequently stained with GelRed and visualized under UV light. For PCR products with weak or multiple bands, bands of interest were excised from the gel and DNA was extracted using Macherey-Nagel’s PCR clean-up gel extraction kit. PCR products were cleaned by adding 0.3 µl ExoSAP-IT (USB) and 1 µl H2O to 10 µl of PCR product, then following the manufacturer’s protocol. Cleaned PCR products were forward-sequenced by Macrogen (Netherlands) or alternatively at the SMTD on a 3730 DNA Analyzer (Applied Biosystems) using the T7 sequencing primer or PCR primers. Reverse sequencing with the T3 sequencing primer or PCR primers was performed for poor quality samples. Samples with ZMBN voucher code (see Table S1) were processed according to the protocol of Mally et al. (2019).

2.3 | Generation of molecular data sets

Targeted genes were retrieved from transcriptomes using reciprocal blasting with BLASTn 2.6 and from whole genomes using the blast tool as provided by the LepBase interface (Challis et al., 2016; ensembl.lepbase.org). DNA sequences from closely related taxa were used as query for both sequence searches. RAxML analysis for each single gene data set was performed in order to identify and remove potential paralogues. Alignment of most sequence data sets was straightforward and was done by eye in PhyDE 0.9971 (Müller et al., 2005). Due to high occurrence of indels, the period gene was aligned using MAFFT (Katoh & Standley, 2013) as provided online by the European Molecular Biology Laboratory (EMBL, www.ebi.ac.uk). Single gene files were concatenated using a bash script. Conspecific sequences from different data sets were combined for the following taxa: *Chilo suppressalis* (CsuOGS1.0 and MAS-92-1001-1), *Pyralis farinalis* (Linnaeus, 1758) (MM00051 and CWM-08-2331), *Scirpophaga incertulas* (MAS-92-1003 & SRR1613323) and *Syntonarcha iriastis* Meyrick, 1890 (MTDLEP3002 and AZ-07-2650). Codon positions with undergoing synonymous substitutions tend to evolve faster and have a heterogeneous base composition (Cho et al., 2011; Regier et al., 2009, 2012). Following the approach described in previous studies (Regier et al., 2010, 2012, 2013), we used a bash script to generate an additional data set ‘no-syn’ with all synonymous substitutions at third codon positions discarded. The size of the final data sets was 11,247 bp.

2.4 | Identification of rogue taxa

A taxon is identified as ‘rogue’ when its topological position varies greatly in the comparison of similar tree reconstructions (Aberer et al., 2013; Wilkinson, 1994). RogueNaRok (Aberer et al., 2013) was used to identify rogue taxa using the following options: majority-rule search, support optimized, maximum dropset size = 2, algorithm = roguenarok.

2.5 | Phylogenetic analyses

The molecular data set was analysed for the best partitioning scheme using PartitionFinder 2 (Lanfear et al., 2017) with the AICc model selection and the ‘greedy’ algorithm (Lanfear et al., 2012). The best model merged the second codon position of CAD, DDC, IDH in a subset and the second codon position of EF-1alpha, GAPDH and RpS5 in another subset, with all other codon position representing their own partition. Maximum-likelihood (ML) analyses were performed on RAxML (Stamatakis, 2006), with the data set partitioned according to the best PartitionFinder model. Branch support was estimated with 1,000 rapid bootstrap inferences with the GTR + CAT algorithm, and the best
tree was estimated with the GTR + GAMMA algorithm. Bayesian inferences (BI) were performed under MrBayes v.3.2.6 (Huelsenbeck & Ronquist, 2001) with the data set partitioned according to the best PartitionFinder model. The following settings were used: prset revmatpr = dirichlet (1,2,1,1,1) [assuming a transition frequency twice as high as transversions] pinvarpr = uniform(0,1), ratepr = variable, brlenspr = unconstrained: exponential (1,0), parameters revmat, tratio, statefreq, shape set unlink. Number of generations was set to 100,000,000, with burn-in set to 0.25. The degree of mixing of the Markov chain Monte Carlo (MCMC) was assessed by visualizing the effective sample size in Tracer (Rambaut et al., 2018). Effective sample sizes (ESS) over 200 indicated sufficient sampling. ML and BI analyses were conducted on the CIPRES Portal (Miller et al., 2010).

3 | RESULTS AND DISCUSSION

3.1 | Rogue taxa

Hendecasis apicefulva Hampson, 1916 (sample MM13885) is highlighted as most unstable taxon (RogueNaRok raw improvement = 2.514), followed by Niphopyralis chionesis (sample ANIC002674) together with Udea ferrugalis (Hübner, 1796) (sample MTDLEP870) (raw improvement = 1.279), and Ancylolomia inornata (Staudinger, 1870) (sample MTDLEP1634; raw improvement = 0.806). Excluding the rogue taxon H. apicefulva from our data set greatly improves the support for the wet-habitat clade (bootstrap support (BS) = 35% versus 71% after removal) and the clade Acentropinae + Schoenobiinae (BS = 67% versus 91%). Similarly, removing A. inornata from our data set recovers the ‘open-cell clade’ (sensu Léger et al., 2019) with great support (BS = 31% versus 93%). Niphopyralis chionesis (Spilomelinae) was already known to be problematic by Mally et al. (2019) and Regier et al. (2012) due to its very long terminal branch in the phylogenetic trees. This taxon was accommodated in its own subfamily Wurthiinae before Regier et al. (2012) synonymized the subfamily with Spilomelinae. These peculiar pyraloid moths resemble limacodid moths, and their larvae develop in nests of leafcutter ants. Interestingly, a previous study on the ditrysian phylogeny found several unstable taxa to be internal feeders (Heikkilä et al., 2015), suggesting that the shift in larval life habit potentially resulted in rapid genetic evolution in these taxa. More generally, parasitic life habits in invertebrates have been shown repeatedly to be associated with high evolutionary rates, translating into strongly diverging DNA sequences and long branches in phylogenies (Bernt et al., 2013; Pentinsaari et al., 2016). Adaptation for the parasitic life in Niphopyralis is thus a possible explanation to the long branch observed in the phylogenetic tree.

3.2 | Phylogenetic analyses

ML and BI (Figure 1) provide largely congruent relationships among subfamilies. Topological incongruences between the ML and the BI analysis show poor support in both analyses. The positions of Linosta (Linostinae) and Erupa Walker, 1864 (Erupini) differ in both analyses, but none of these placements are strongly supported. 65% of among-subfamily relationships and 81% of infra-subfamilies relationships show substantial support (BS > 70%). The analysis of the no-syn data set (Figure S2) shows overall lower node support, with substantial support (BS > 70%) recovered for 58% of among-subfamily relationships and 60% of infra-subfamilies relationships. The topology recovered from the no-syn data set shows ten nodes in discordance with the ML analysis of the standard data set, and some alternative groupings are recovered with substantial support: Rupela (Schoenobiinae) branches at the base of the Acentropinae (BS = 77%), as recovered in Regier et al. (2012), and Erupa groups with Hoploscopia Meyrick, 1886 (BS = 77%). These phylogenetic incongruences are discussed in the ‘Section 3.4’ below.

3.3 | Missing data

Our approach of combining data sets from different studies aims to expand gene and taxon sampling. However, merging data sets with different gene samplings may result in blocks of missing data that can result in misleading phylogenetic reconstructions (Lemmon et al., 2009; Simmons, 2012). The analysis excluding the Regier data set (not shown) does not show any discrepancies compared to the analysis of the complete data set, but several deep nodes within the Crambidae show a decrease in support. This observation is in line with a previous study analysing the effect of missing data when combining different data sets (Cho et al., 2011).

3.4 | Phylogenetic relationships

Our analyses confirm the basal split of Pyraloidea into Crambidae and Pyralidae, which is well supported by morphological and molecular evidence (Minet, 1982; Mutanen et al., 2010; Regier et al., 2012). Relationships among the five subfamilies of Pyralidae are widely concordant with the findings of Regier et al. (2012) and are strongly supported (BS > 95%). One exception is the clade including Galleriinae and Chrysauginae, which is supported only in half of the analyses of Regier et al. (2012). In our analyses, it is either recovered with strong support (BS = 96%) or with weak support in the analysis of the conc10genes_nosyn data set. Chrysauginae
are recovered monophyletic, but only BI provides substantial support for it (posterior probability (pp) = 1.00, BS = 56%). Chrysauginae were found paraphyletic with respect to Gallerinae in Regier et al. (2012), and the authors raised doubt regarding the monophyly of this group. Solis and Mitter (1992) proposed a sclerotized ring around the base of the larval SD1 seta as apomorphy for the group, while characters of the male forewing venation are suspected to be apomorphic.

Crambidae are recovered monophyletic with maximum support (BS = 100%) and show a basal dichotomy into the ‘PS clade’ comprising Pyraustinae and Spilomelinae (BS = 100%), and another moderately supported ‘non-PS clade’ including all remaining Crambidae (BS = 88%), in line with the results from Regier et al. (2012). Relationships within the Spilomelinae are surprisingly poorly resolved, with only the clade referred to as ‘Euspliophinae’ in Mally et al. (2019) showing substantial support (BS = 85). The broad taxon sampling and the integration of morphological characters in the Bayesian reconstruction possibly explain the better branch support observed in Mally et al. (2019).

We find the non-PS clade of Regier et al. (2012), comprising Acentropinae, Crambinae, Glaphyriinae, Midilinae,
Musotiminae, Odontiinae, Schoenobiinae and Scopariinae, to also include Cathariniinae, Cybalomiinae, Heliotheliniinae, Hoploascopinae stat. n., Lathrotelinae and Linostinae, with moderate support (BS = 88%) in the ML analysis. Basal relationships among Cathariniinae, Cybalomiinae, Glaphyriinae, Linostinae, Odontiinae and the CAMMSS clade do not show significant support (BS < 50%). Linostinae are found to be sister to Glaphyriinae + Cybalomiinae + Cathariniinae without significant support in the ML analysis, while in the BI they are placed as sister to the CAMMSS clade (pp = 0.84). The absence of a proboscis and ocelli and the reduced labial palpi supported the sister relationship of Linosta and Niphopyralis in Solis and Maes (2002), but this relationship was questioned by the authors due to the nature of the character changes (three losses) and the different geographical occurrences of these lineages (Neotropics and Oriental-Australasian, respectively). The position of Niphopyralis within Spilolomelinae (Figure S1) is in line with Mally et al. (2019) and Regier et al. (2012), while Linosta is recovered in the ‘non-PS clade’ (with as of yet unresolved sister-group relationship). The reductions in the morphological characters thus appear to be convergent in the light of these results.

Our analysis recovers Linostinae, Cathariniinae and Cybalomiinae in the Odontiinae + Glaphyriinae clade (‘OG clade’) of Regier et al. (2012), although with low support (BS = 53%, pp = 0.99; BS = 73% in analysis of all taxa). When Linosta is excluded from the analysis (not shown), the OG clade shows strong support (BS = 98), confirming the rogue behaviour of Linosta in our analyses. Both analyses recover a clade comprising Cathariniinae, Cybalomiinae and Glaphyriinae, but only BI provides strong support for this grouping (pp = 0.98; BS = 50% when Linosta excluded). Glaphyriinae are separated in two clades: Cosmopteris + (Crocidolomia + (Trischistognatha + Evergestis) (BS = 100%), and Noorda + (Hellula + (Dichogama + (Chalcoela + Dicumolomia))) (BS = 82%, pp = 0.95). Cathariniinae are sister to the first clade (BS = 60%, pp = 1.00; BS = 73% when Linosta excluded). The absence of a gnathos in Cathariniinae is also reported in many Glaphyriinae, but this character was shown to vary greatly in this group (Monro, 1972; Regier et al., 2012; Solis & Adamski, 1998). However, Catharia pyrenaearis larvae feed on Heliosperma alpestre (Caryophyllaceae; Krone, 1905) and were also found feeding on Saxifraga oppositifolia, S. aphylla (Saxifragaceae), Cerastium pedunculatum (Caryophyllaceae) and Silene acaulis (Caryophyllaceae) (Schmid, 2019). Cathariniinae hence do not share the Brassicales-feeding in larval instars with Glaphyriinae and Cybalomiinae. Catharia inhabits a high-alpine habitat where shelter offered by the host plant might be of high importance. Cybalomiinae, here represented by four genera, are recovered monophyletic (BS = 100%) and are found nested within Glaphyriinae, however with low support. Larvae of this subfamily almost exclusively feed on Brassicales, a trait shared with most Glaphyriinae, which suggests a common origin of this feeding habit in the two groups. Our results suggest a broad concept of Glaphyriinae including Cathariniinae syn. n. and Cybalomiinae syn. n. The latter two are here synonymized with Glaphyriinae due to the overall topology and basal support of the OG clade.

The ‘CAMMSS clade’ sensu Regier et al. (2012), comprising Acentropinae, Crambinae, Midilinae, Musotiminae, Schoenobiinae and Scopariinae, includes here also the Erupininae stat. n., Hoploascopinae stat. n., Heliotheliniinae s. str., and Lathrotelinae (BS = 92%). Basal relationships between Lathrotelinae, Musotiminae, the ‘wet-habitat clade’ of Regier et al. (2012) comprising the Acentropinae, Midilinae and Schoenobiinae, and the clade including Crambinae, Erupini, Heliothelini, Hoploascopini and Scopariinae do not show substantial support in the ML analysis, while BI supports a clade comprising the Lathrotelinae and Musotiminae as sister to all other lineages of the CAMMSS clade.

Lathrotelinae are recovered monophyletic (BS = 100%) and they are confirmed as part of the CAMMSS clade (BS = 92%) as hypothesized by Minet (2015) based on the shared use of monocotyledons as larval host plants. The author discussed morphological characters shared with Acentropinae, for example the dorsal position of the lobulus (= tympanic crest) and the presence of well-developed venulae secundae. The latter character has however been shown to vary greatly in Crambidae (Léger et al., 2019). Lathrotelinae are found sister to Musotiminae, although without significant support in the ML analysis (BS = 42%, pp = 1.00). The lathroteline genus Sufetula shares with Musotiminae the undulating wing margin and the absence of chaetosemata and ocelli. In contrast, Musotiminae lack the CuP in the forewings, which are present in Lathrotelinae, and males bear a gnathos and display secondary sexual characters (both absent in Lathrotelinae) (Hayden, 2013). Musotiminae are recovered monophyletic with maximal support.

The clade comprising Acentropinae, Midilinae and Schoenobiinae referred to as the ‘wet-habitat clade’ by Regier et al. (2012) is recovered monophyletic, however with weak support in the ML analysis (BS = 71%, pp = 1.00). Hendecasis, flagged as rogue taxon, is recovered within the wet-habitat clade as sister to Midilinae (Figure S1), however without significant support (BS = 35%). This genus is currently placed in Cybalomiinae, although wing shape and pattern resemble those of musotimine moths. Our analysis refutes this placement and shows Hendecasis to belong to the ‘CAMMSS clade’. Acentropinae and Schoenobiinae form a sister group with strong support (BS = 94%). This clade is one of the few relationships within Crambidae which is well supported by morphological evidence (Martinez, 2010; Passoa, 1988; Yoshiyasu, 1985). Monophyly of Acentropinae is well supported (BP = 97%), while monophyly of Schoenobiinae shows moderate support (BS = 84%, pp = 1.00). However, analysis of the no-syn data...
set recovers *Rupela* as nested in the Acentropinae (BP = 79%). This result is similar to that of Regier et al. (2012), where *Rupela* was recovered as sister to Acentropinae in analyses of their 19-gene data set, rendering Schoenobiinae paraphyletic. They argued that this position is due to large portions of missing data in their 19-gene data set. Indeed, nine morphological characters support the monophyly of Schoenobiinae including *Rupela* (Common, 1960; Lewvanich, 1981; Martínez, 2010; Passoa, 1988), while no synapomorphy shared by *Rupela* and Acentropinae is known (Regier et al., 2012). We assume that the weak number of informative sites in the no-syn data set explains this ambiguous grouping.

The clade including the Crambinae and Scopariinae in Regier et al. (2012) is confirmed here and also includes the Erupinae stat. n. and the Heliolothelinae, with maximum support (BS = 100%). The Heliolothelinae s. l. are polyphyletic: Hoploscopini are recovered as sister to the remaining groups of this clade (BS = 84%), while Heliolothelini are found sister to Scopariinae (BS = 95%). The sclerotized thorn invaginated into the corpus bursae in female genitalia, considered as apomorphic for this group by Nuss (1998), now appears homoplastic in the light of these results. Hoploscopini were found sister to Musotiminae by Léger et al. (2019), a position only supported by BI and by the sharing of ferns (Pteridophyta) as larval host plants. Larval morphology of the Hoploscopini suggests close relationship either to Crambinae or to Acentropinae + Schoenobiinae (Mally et al., 2017). The sister relationship between Heliolothelinae s. str. and Scopariinae finds echo in the morphology: Minet (1982) showed the Heliolothelinae and Scopariinae to have a similar tympanal organ and wing venation, while he recognized substantial differences in male and female genitalia. Nuss (1998) justified the separation of Heliolothelinae s. l. from the Scopariinae by the presence of a thor in the female corpus bursae (absent in Scopariinae) and the lack of an appendix bursae (present in Scopariinae). The latter one is however absent in all basal lineages of Scopariinae and does not represent an apomorphy for this group (Léger et al., 2019). Heliolothelinae s. str. also lack the median discoidal X-shaped stigma suggested as synapomorphy for Scopariinae (Nuss, 1999). Habitat and biology of Heliolothelinae s. str. and Scopariinae also differ from each other. Heliolothelinae s. str. occur in warm and dry lowlands of the Old word and Australia, and their larvae are endophagous on Violaceae. In contrast, Scopariinae occur predominantly in moist habitats and their larvae are moss feeders. The present topology leaves us with a choice of considering Heliolothelinae as a separate subfamily or as part of the Scopariinae. Due to morphological and ecological differences of the two taxa, we decide here to keep Heliolothelinae s. str. and Scopariinae as separate taxa. As Hoploscopini are recovered as sister to Heliolothelinae, Scopariinae and Crambinae, it is raised here to subfamily rank, that is Hoploscopini stat. n. The position of Erupini in this clade remains ambiguous. *Erupa* was alternatively placed in Schoenobiinae (Bleszynski, 1966), Crambinae (Lewvanich, 1981; Munroe, 1995), and later in Midilinae (Hayden, 2012). *Erupa* was recovered as sister to Crambinae by Léger et al. (2019), but only BI provided strong support for this topology. Current analyses refute a placement of *Erupa* in Midilinae, and we consequently remove Erupini from Midilinae as Erupinae stat. n. However, the detailed relationships remain obscure due to lack of support. Interestingly, the analysis of the no-syn data set (Figure S2) pairs *Hoploscopa* with *Erupa* (BS = 77%). This relationship is recovered here for the first time and is in conflict with the topology resulting from the analysis of the main data set (i.e. including synonymous substitutions at the third codon position). Analysis of the morphology in both groups did not reveal any possible synapomorphy. Inclusion of further taxa such as *Neerupa* Hampson, 1919, *Schoenerupa* Hampson, 1919 (Erupinae) and *Perimecta* Turner, 1915 (Hoploscopinae) might shed more light onto the placement of Erupinae.

### 3.5 Host-plant utilization

The inclusion of five new subfamily-level lineages in a phylogenetic frame sheds additional light into host-plant evolution in Crambidae. In the following, we treat feeding habits in Crambidae by plant group.

**Eudicotyledons.** Eudicotyledons represent the bulk of the almost 300,000 species of angiosperm (Christenhusz & Byng, 2016). Pyraustinae and Spilomelininae (PS clade), as well as Odontiinae feed on a broad spectrum of eudicotyledons (Mally et al., 2019; Munroe & Solis, 1998; Robinson et al., 2010), and Glaphyriinae (together with Odontiinae forming the OG clade) are specialists on Brassicales. Larvae are leaf folders, leaf tiers, or bore in fruits or stems (Munroe & Solis, 1998). The dominance of eudicotyledons in the host-plant spectrum of the ‘PS’ and the ‘OG clade’, the two basal-most groups in Crambidae, suggests them as the likely ancestral host-plant group of the Crambidae. Shifts to host plants belonging to monocotyledons, pteridophytes or bryophytes are considered secondary.

**Brassicales.** Brassicales are characterized by the presence of mustard oils or glucosinolates. These chemical compounds form toxic isothiocyanates when they interact with myrosinases stocked in myrosin cells (Halkier & Gershenzon, 2006). The families Brassicaceae, Capparaceae and Cleomaceae form the bulk of the Brassicales diversity. In Crambidae, the Glaphyriinae feed predominantly on Brassicaceae and Capparaceae. Larvae of *Noorda* feed on *Moringa* (Moringaceae), whose species also contain glucosinolates (Fahey et al., 2018). Interestingly, *Trischistognatha* is reported to feed on *Drypetes* (Malpighiales: Putranjivaceae), which is the only family outside the Brassicales exhibiting mustard oil (Hall et al., 2002). The position of *Trischistognatha* nested
within the Glaphyriinae speaks for a host-plant switch from an ancestral Brassicales host plant to Drypetes. A similar host-plant switch to Drypetes is observed in Brassicales-feeding Pieridae (Papilionoidea) (Braby & Trueman, 2006). There are notable exceptions in feeding habits of glaphyriine larvae: a few specialists are reported feeding on Cyperaceae (Braby, 2006). There are few specialists are reported feeding on Cyperaceae (Braby & Trueman, 2006). The process of glucosinolates in their food plants, the Brassicaceae feeders Plutella xylostella (Linnaeus, 1758) (Yponomeutoidea) and Pieris rapae Linnaeus, 1758 (Papilionoidea) use the enzyme glucosinolinate sulfatase (Ratzka et al., 2002), or they hydrolyse them into nitriles (Wittstock et al., 2004). Not much is known about the way Glaphyriinae metabolize glucosinolates, but Crocidolomia pavonana (Fabricius, 1794) appears to be resistant to isothiocyanate, while it is lethal to P. xylostella, suggesting the existence of a different metabolic pathway of processing glucosinolates (Tadle, 2017). In Crambidae, several other taxa are feeding on Brassicales: Styrpholepis and Dolichobela (Mudimilinae) are reported from Capparaceae (Solis et al., 2009), while some species of Chilo and Tals (Crambinae), Loxostege and Ostrinia (Pyraustinae), and Herpetogramma, Nonomphila, Omiodes and Udea (Spilomelinae) have been recorded from Brassicaceae (Robinson et al., 2010). This implies that the ability to metabolize glucosinolates was retained in these taxa, or that it evolved independently.

Monocotyledons. Monocotyledons encompass about 60,000 species and include notably Poaceae, Cyperaceae and Arecaceae used as host plants by a substantial number of Crambidae species. The subfamilies Acentropinae, Crambinae, Lathrotelinae, Mordilinae and Schoenobiinae of the CAMMSS clade are predominantly feeding on monocotyledons. Lathrotelinae are reported feeding on Carex spp., Cyperaceae (Diplotetoides, Arecaceae (Diplotetoides, Sufetula), Poaceae (e.g. S. grumalis, a pest on sugarcane) and recently on Bromeliaceae (S. ananica) (Gaedeke, 2010; Gentry & Mariau, 1975; Patrick, 1994; Robinson et al., 2010; Sein, 1930; Solis et al., 2019). In Mordilinae, Cacographis and Eupanestria are reported boring in roots of some Arecaceae (Caladium, Colocasia, Philodendron), while Dolichobela and Styrpholepis were found feeding on Capparaceae (Caphoris) (Munroe, 1970; Munroe & Solis, 1998). A majority of larvae of Crambinae and Schoenobiinae larvae bore in Cyperaceae and Poaceae, with feeding in roots or at the base of the stems considered derived in Crambinae (Léger et al., 2019). Acentropinae are unique in the adaptation of larvae to live in aquatic habitats. Their foodplants include aquatic monocotyledons alongside with aquatic Pteridophyta and dicotyledons. The recovering of the Lathrotelinae within the CAMMSS clade reinforces the hypothesis of a monocotyledon as ancestral host plant of the group, but pteridophytes are another possible ancestral host plant for this clade. Monocot-feeders outside of the CAMMSS clade are scarce.

In the Spilomelinae, the Cnaphalocrocis/Marasmi group forms a major radiation on monocots (Mally et al., 2019).

Pteridophyta. Ferns are rather uncommon as host plants of insects (Auerbach & Hendrix, 1980). They contain simple phenolic compounds, tannins and several other chemicals that act as defence against bacteria, fungi and herbivores, but they lack compounds like acetylenes or glucosinolates found in angiosperms (Cooper-Driver, 1985). High concentrations of phytocystostroids are found in some fern taxa, for example Polypodiaceae (Lafont et al., 2011). Fern-feeding habits are scarcely represented in lepidopteran lineages, and exclusive or nearly exclusive associations to ferns are observed only in a few lepidopteran lineages, for example Callidulidae, Lithinini (Geometridae), Psychides Bruand, 1853 (Tineidae), Pachyrhabda Meyrick, 1897 (Oecophoridae), Monochroa cystisella (Curtis, 1837) (Gelechiidae) and Callopistria Hübner, 1821 (Noctuidae) (Auerbach & Hendrix, 1980; Karsholt et al., 2013; Weintraub et al., 1995). In Crambidae, lineages predominantly feeding on ferns include the Hoploscopinae (Mally et al., 2017) and the Musotiminae (see Solis et al., 2005 and references therein). These two subfamilies currently include 42 and 194 described species, respectively. Hoploscopinae occur in South-East Asia and Melanesia, where diversity of Pteridophyta is at its highest (Ebihara & Kuo, 2012). Our finding of Hoploscopinae and Musotiminae in different clades speaks in favour for an independent evolution of fern feeding in these two groups. Further cases of fern feeding in Crambidae are known from Diасemiospis ramburialis (Dupochel, 1833), Herpetogramma platycapna (Meyrick, 1897), Samea multiplicaalis (Guénoné, 1854), Udea decrepitalis (Herrich-Schäffer, 1848) (all Spilomelinae) and Phenacodes aleuropus (Lower, 1903) (Glaphyriinae), and from several Acentropinae feeding on aquatic pteridophytes (Farahpour-Haghani et al., 2016; Kirk, 1978; Knopf & Habeck, 1976; Lhomme, 1935; see also Mally et al., 2017 for additional fern-feeding species).

Bryophyta. Bryophytes form a paraphyletic assemblage comprising liverworts, mosses and hornworts (Wickett et al., 2014). In the early-branching crambine lineage Glaucocharis is feeding on mosses, raising the question whether moss-feeding habits observed in Crambinae and Scopariinae are the result of a single origin, or represent convergent evolution. Heliotelha Guenée, 1854, recovered as sister to Scopariinae in this study, is known to feed on Lamiaceae and Violaceae, contrasting with moss-feeding habits of Scopariinae. Host plants of Erupinae are currently unknown, but monocotyledons were suggested by Hayden (2012). Additional host-plant data for Erupinae
as well as for the basal scopariine lineage *Anarpia* Chapman, 1912 (Léger et al., 2019) would shed light on the evolution of moss-feeding habits. Interestingly, the moss-feeding genera *Agriphila*, *Catoptria* (Crambinae) and *Eudonia* Billberg, 1820 (Scopariinae) comprise species feeding on grasses, and some species have been reported feeding on both plant groups (Cowley, 1988; Robinson et al., 2010). Larvae of these feed at the base of grasses, suggesting that spatial proximity rather than phytochemistry led host-plant shifts to mosses in these cases.

The observed phylogenetic specificity of host-plant use is in agreement with the findings of Segar et al. (2017), who modelled caterpillar–host plant interactions in Pyraloidea and Geometridae. The relatively conserved food plant specificity in subgroups of Crambidae allows host predictions for species whose larval stage and its associated biotic environment are currently unknown—a condition that pertains to the majority of known snout moth species. In Macroheterocera, which together with the Mimallonoidea represents the sister group to Pyraloidea (Kawahara et al., 2019) and contains roughly half the currently known species diversity of Lepidoptera (Mitter et al., 2017), host-plant specificity is usually lower. In the more polyphagous Geometridae, host-plant associations are less conserved than in pyraloids (Segar et al., 2017). Similarly, Gelechioidea and Tortricoidea show only a few lineages of host-plant specialisation (Brown et al., 2008; Kaila, Mutanen, & Nyman, 2011).

Larval stages of crambid moths are predominantly endophagous or concealed feeders. Larvae of Acentropinae, some Crambinae, Scopariinae, Pyraustinae and Spilomelinae build silken retreats from where they venture and feed (Mally et al., 2019; Nuss, 2005a; Slamka, 2008; Speidel, 2005a and references therein). Leaf miners are found in Musotiminae, Odontini and young stages of Heliothelini (Slamka, 2006; Solis et al., 2005). Stem and root borers are found in Heliotheliniae, Lathrotiliae, Midiliae, Schoenobiinae, Spilomeliniae and many Crambinae (Hayden, 2012, 2013; Mally et al., 2019; Munroe & Solis, 1998; Nuss, 2005b; Speidel, 2005b). Concealed larval feeding is considered an ancestral trait in Lepidoptera evolution (Menken et al., 2010). Pyraloidea were considered as external feeders by Menken et al. (2010), a statement that does not hold true for many lineages. In this sense, Crambidae larval life habits resemble more those of the lower Apoditrysia than of the Macroheterocera.

The current classification of Pyraloidea (Pyralidae + Crambidae) is as follows:

**Pyraloidea**: (2,117 genera (1,419 syns), 16,379 species (6,491 syns)).

**Pyralidae** (1,100 genera (691 syns), 6,032 species (2,340 syns)).

**Chrysauginae** Lederer, 1863 (131 genera (61 syns), 399 species (130 syns)).

= Bradypodicolinae Spuler, 1906.

= Semniidae Lederer, 1863.

**Epipaschiinae** Meyrick, 1884 (96 genera (70 syns), 721 species (168 syns)).

= Pococerini Hampson, 1918.

**Gallerininae** Zeller, 1848 (63 genera (62 syns), 259 species (119 syns)).

= Macrotheciinae Barnes & McDunnough, 1912.

Cacotherapiini Munroe, 1995.

Gallerini Zeller, 1848.

Joelminetini Speidel & Witt, 2007.

Megalarthridiini Whalley, 1964.

Tirathabini Whalley, 1964.

**Phycitinae** Zeller, 1839 (675 genera (388 syns), 3,386 species (1,533 syns)).

= Anerastiini Ragonot, 1885.

= Hypsotropinae Hampson, 1918.

= Peoriinae Hulst, 1890.

Cabiini Roesler, 1968.

Cryptoblabini Roesler, 1968.

Phycitini Zeller, 1839.

= Acrobasiina Agenjo, 1958.

**Pyralinae** Latreille, 1809 (135 genera (110 syns), 1,268 species (390 syns)).

= Aglossites Blanchard, 1840.

= Asopidae Guenée, 1854.

= Cledeobiinae Blanchard, 1840.

= Homalochroidae Lederer, 1863.

Endotrichini Ragonot, 1890.

Hypotiini Chapman, 1902.

Pyralini Latreille, 1809.

**Crambidae** (1,017 genera (728 syns), 10,347 species (4,151 syns)).

= Acentridae A. Speyer, 1869.

= Acentropodidae Dunning, 1872.

= Aquaticae Hübner, 1796.

= Argyractini Lange, 1956.

= Cataclystae Hübner, 1825.

= Chloephila Guilding, 1830.

= Elophilae Hübner, 1825.

= Kamptoptera Guilding, 1830.

= Nymphulae Hübner, 1825.

= Nymphulites Duponchel, 1845.

= Hydrocampidae Guenée, 1854.

= Parapoynges Hübner, 1825.

**Crambinae** Latreille, 1810 (175 genera (124 syns), 2,066 species (1,095 syns)).

= Crambina Zeller, 1847.

= Tetrachila Hübner, 1818.
Ancylolomiini Ragnot in Joannis & Ragonot, 1889.
= Prionapterygini B. Landry, 1995.
Argyriini Munroe, 1995.
Calamotrophini Gaskin, 1988.
Chiloini Heinemann, 1865.
= Myeloobiini Minet, 1982.
Crambini Latreille, 1810.
= Corynophorini Gaskin, 1975.
Diptychophorini Gaskin, 1972.
Euchromiini Léger et al., 2019.
Haimbachini B. Landry, 1995.
= Haimbachiini Munroe, 1995.

**Erupinae** Munroe, 1995 stat. n. (3 genera (4 syns), 38 species (4 syns)).

**Glaphyrinae** W. T. M. Forbes, 1923 (74 genera (54 syns), 490 species (186 syns)).
= Cathariinae Minet, 1982 syn. n.
= Cybalomiinae Marion, 1955 syn. n.
= Evergestinae Marion, 1952.
= Evergestini Marion, 1952.
= Evergestrinae P. Leraut, 2008.
= Orenaïni P. Leraut, 1997.
= Homophysidae Lederer, 1863.
= Noordinae Minet, 1980.
Dichogamini Amsel, 1956.
Glaphyriini W. T. M. Forbes, 1923.

**Heliothelinae** Amsel, 1961 (3 genera (2 syns), 30 species (13 syns)).

**Hoploscopinae** Robinson et al., 1994 stat. n. (2 genera (4 syns), 46 species (2 syns)).

**Lathrotelinae** J. F. G. Clarke, 1971 (5 genera (7 syns), 42 species (8 syns)).

**Linostinae** Amsel, 1956 (1 genus, 4 species (2 syns)).

**Midilinae** Munroe, 1958 (10 genera (4 syns), 57 species (12 syns)).

**Musotiminae** Meyrick, 1884 (23 genera (8 syns), 201 species (25 syns)).
= Ambiini Munroe, 1972.

**Odontiinae** Guéné, 1854 (88 genera (38 syns), 388 species (143 syns)).
= Hercynites Blanchard, 1840.
Eurrhypini P. Leraut & Luquet, 1983.
Odontii Guéné, 1854.
= Titanii Marion, 1952.

**Pyraustinae** Meyrick, 1890 (171 genera (102 syns), 1,249 species (621 syns)).
= Boydes Blanchard, 1840.
= Ennychites Duponchel, 1845.
Euclastini Popescu-Gorj & Constantinescu, 1977.
Portentomorphini Amsel, 1956.
Pyraustini Meyrick, 1890.

**Schoenobiinae** Duponchel, 1846 (29 genera (17 syns), 239 species (99 syns)).

**Scopariinae** Guéné, 1854 (19 genera (24 syns), 586 species (208 syns)).
= Eudoraecina Selys-Longchamps, 1844.

**Spilomelinae** Guéné, 1854 (340 genera (300 syns), 4,132 species (1,520 syns)).
= Syleptinae Swinhoe, 1900.
Agroterini Aclouque, 1897.
Asciodini Mally et al., 2019.
Herpetogrammatini Mally et al., 2019.
Hydririni Minet, 1982.
Hymeniini Swinhoe, 1900.
Lineodini Amsel, 1956.
Margaroniini Swinhoe & Cotes, 1889.
= Dichocrociinae Swinhoe, 1900.
= Hapaliidae [sic] Swinhoe, 1890.
= Margarodidae² Guéné, 1854.
Nomophiliini Kuznetzov & Sekolnikov, 1979.
Spilomelini Guéné, 1854.
= Siginae Hampson, 1918.
Steniini Guéné, 1854.
Trichaeini Mally et al., 2019.
Udeini Mally et al., 2019.
= Udein³ P. Leraut, 1997.
Wurthiini Roepke, 1916.

### SUMMARY AND OUTLOOK

We provide the first phylogeny comprising all subfamilies of Crambidae and including pyraloid molecular data sets from major previous phylogenetic studies (Heikkilä et al., 2015; Kawahara & Breinholt, 2014; Léger et al., 2019; Mally et al., 2017; Mutanen et al., 2010; Regier et al., 2012), from published genomes or transcriptomes (Challis et al., 2016; Renuka et al., 2017) and our own sequences. Our data set provides placement for Cathariinae, Cybalomiinae and Linostinae, although without well-supported sister relationships. Cathariinae syn. n. and Cybalomiinae syn. n. are recovered in a clade together with the Glaphyriinae, with which the Cybalomiinae share the Brassicales as host plant. The Heliothelinae s. l. are found to be polyphyletic and are therefore split into Heliothelinae s. str. and Hoploscopinae stat. n., and both are recovered in a clade together with Crambinae, Erupinae stat. n. and Scopariinae. The exclusion of synonymous mutations results in a different placement of Erupinae with respect to Hoploscopinae and for Schoenobiinae with respect to Anteropinae, providing alternative hypotheses to be tested with a greater set of molecular characters. Fern-feeding habits, observed in the Musotiminae and recently reported in the Hoploscopinae **stat. n.**, and both are recovered in a clade together with Crambinae, Erupinae **stat. n.** and Scopariinae. The exclusion of synonymous mutations results in a different placement of Erupinae with respect to Hoploscopinae and for Schoenobiinae with respect to Anteropinae, providing alternative hypotheses to be tested with a greater set of molecular characters. Fern-feeding habits, observed in the Musotiminae and recently reported in the Hoploscopinae (Mally et al., 2017), evolved independently in these two lineages. A common origin of moss-feeding habits in Crambinae and Scopariinae is challenged by the sister
relationship of Scopariinae and Heliothelinae, the latter feeding on Violaceae in larval stages.

The hundred taxa included in the present study constitute a tiny fraction of the more than 16,000 described Pyraloidea. Phylogenetic relationships within the large clades Crambinae + Scopariinae and Pyraustinae + Spilomelinae were the scope of two recent studies (Léger et al., 2019; Mally et al., 2019). Further species-rich groups, such as Acentropinae (779 spp.), and the pyralid subfamilies Epipaschiinae (721 spp.), Pyraulae (1,268 spp.) and Phycitinae (3,386 spp.), are in great need of systematic revision and should be the focus of future studies. The ever-decreasing costs of high-throughput sequencing should enable the use of genomic methods, already in use to reconstruct Lepidoptera phylogenies (e.g. Bazinet et al., 2017; Kawahara & Breinholt, 2014; Kawahara et al., 2019; Li et al., 2019), in future projects on pyraloid phylogeny. This holds the promise of a 100-fold increase in the size of data set and the possibility to include museum specimens of rare taxa.

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ENDNOTES

1 Tetrachila Hübner is not nomenclaturally available from 1818 as a genus-group name. Hübner used Tetrachila on pages 23, 28 and 30 in a suprageneric sense for one of the names of his tribes (‘Namen der Stämme’) listed on pages (33) and (34). Hübner listed his genus-group names on pages [35] and [36]. (Fletcher & Nye 1984).

2 The type genus of Margarodidae, Margarodes Guenée, 1854, is a junior homonym of Margarodes Guenée, 1829 (Trans. Linn. Soc. Lond. 16 (1): 118) (Insecta: Hemiptera). According to the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999: article 39), a family-group name is invalid if it is based on a genus that is a junior homonym. The family-group name must be replaced by the next oldest available name, which is Margaroninita Swinhoe & Cotes, 1889, with type genus Margaronia Hübner, 1825.

3 Udeini were proposed by Leraut in 1997 in Pyraustinae, but without a description to differentiate the taxon, a requirement by the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999: article 13.1) for names published after 1930. Therefore, the family-group name Udeini Leraut, 1997 is not available.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.