Abstract

Compared to the leaf-miners and stem-miners on flowering plants, the miners on ferns (including both Lycopodiophyta and Polypodiophyta in the broad sense) are less known. Knowledge of miners and their host plants is essential to fully understand plant-insect interactions. Although there are many scattered records on fern miners, a worldwide checklist has not been reported.

We provide a preliminary checklist of fern-mining insects and their host plants worldwide. Altogether, we found records for 128 species and 18 families of fern miners, mainly that feed on Dennstaedtiaceae, Equisetaceae, Polypodiaceae and Aspleniaceae. Fern miners belonged to four orders: Diptera (51 species; 39.8%), Coleoptera (33 species; 25.8%), Lepidoptera (28 species; 21.9%) and Hymenoptera (16 species; 12.5%). They are primarily known from the Palaearctic Region, Nearctic Region, Neotropical Region and Oriental Region.

Keywords

fern, leaf miner, host plant, plant-insect interactions, plant apparency hypothesis
Introduction

Leaf/stem miners are endophagous insects whose larvae feed on parenchyma or epidermal cells and form visually distinctive feeding tunnels, i.e. ‘mines’ on the leaves or stems (Dai et al. 2018, Eiseman 2020b, Liu et al. 2015, Sinclair and Hughes 2010). The mines can provide useful hints on insect species identities, insect life histories, insect behaviour and insect-plant interactions (Dai et al. 2018). Fewer miner groups (e.g. gracillariid moths, agromyzid flies and leaf-mining chrysomelids) can utilise over 100 plant families (Dai et al. 2017, De Prins and De Prins 2020, Santiago-Blay 2004, Spencer 1990), which are mainly angiosperm families, such as Fabaceae and Myrtaceae (Dai et al. 2018).

Ferns (Pteridophyta, including both Lycopsidophyta and Polypodophyta in the broad sense) are the second largest group of vascular plants, just after angiosperms (Dai et al. 2020, Schneider et al. 2004). With lower nutrition, higher defensive chemicals and no flowers, the interspecific associations between ferns and insects are often overlooked (Mehltreter et al. 2010, Weintraub et al. 1995). However, ferns used to be the primary food resource for insects before the thriving of angiosperms (Mehltreter et al. 2010). In fact, fossil records indicate that ferns and insects have co-evolved for at least 300 myr (Chandra and Srivastava 2003). Some ferns have nectaries and domatia, which could attract ants to be bodyguards (Mehltreter et al. 2010). Moreover, some insects mimic the soral crypsis of ferns to escape from their natural enemies (Barker et al. 2005, Patra et al. 2008). Some researchers hypothesise that fern-feeding insects should have fewer species, genera and families than those of seed plants (Weintraub et al. 1995), while others suggest that the richness of fern-feeding insects is largely underestimated (Auerbach and Hendrix 1980, Mehltreter et al. 2010). The possible underestimation might be deduced from the following facts: (1) many fewer investigations have been performed for wild ferns than for cultivated ferns or invasive ferns (Fountain-Jones et al. 2012); (2) many more fern herbivores have been discovered in the comprehensive screening of bio-control agents for pest ferns (Mehltreter et al. 2010); (3) no noticeable difference has been found between leaf herbivory loss of ferns and that of seed plants (Chandra and Srivastava 2003); and (4) the possible biases of plant apparency (i.e. body size, distribution range and individual numbers (Dai et al. 2017)) are not considered for phytophagous insects on ferns in comparison to those on seed plants (Auerbach and Hendrix 1980).

Fern-feeding insects could be classified as generalists and specialists. Most fern-feeding generalists tend to be classified as leaf-chewing or sap-sucking, while most specialists are classified as leaf-mining, gall-forming or spore-feeding (Mehltreter et al. 2010). By far, the miners on ferns are much less known than those on seed plants; although there are scattered records on publications and websites (De Prins and De Prins 2020, Edmunds et al. 2020, Ellis 2020, Eiseman 2020b, Pitkin et al. 2019, Santiago-Blay 2004, Spencer 1990), few comprehensive reviews on fern miners have been provided and a worldwide checklist has not been reported. In this study, we will compile a preliminary checklist of fern-mining insects and their host plants throughout the world, which could provide meaningful information to the study of plant-insect–environment interactions.
Material and methods

The names and hosts of fern miners were obtained from websites, books and articles. Most publications were retrieved from the Web of Science (https://www.webofknowledge.com) and Google Scholar (https://scholar.google.com), while the others were obtained from reference lists of the websites and retrieved publications. According to the Taxonomic Name Resolution Service (http://tnrs.iplantcollaborative.org/TNRSapp.html), the host fern's scientific names were verified and corrected. The number of species in a fern family was obtained from the Catalogue of Life (http://www.catalogueoflife.org/). Based on two recent mega-trees (Smith and Brown 2018, Zanne et al. 2014), 'GBOTB.extended.tre' is the latest and largest dated phylogenetic tree for vascular plants, with 74533 species, 10587 genera and all extant 479 families (Jin and Qian 2019). The R package 'V. PhyloMaker' (Jin and Qian 2019) can bind undetermined plant taxa to the backbone phylogeny of 'GBOTB.extended.tre' and generates the customised tree we needed (Dai et al. 2020). Here, we obtained the phylogenetic tree of our host fern families using the above method. Bivariate linear regression was fitted with Past 4.04 (Hammer et al. 2001).

Both leaf-miners and stem-borers have been found in the same insect family (e.g. Buprestidae, Cossidae and Blastocotomidae) or even in the same genus (e.g. Amauromyza, Melanagromyza, Phytomyza and Zygoneura) (Eiseman 2020b, Hering 1951, Scherbakov 2006, Woodley and Janzen 1995). Occasionally, the same species could change their feeding habits from leaf-mining to stem-mining or stem-boring, when the younger larvae transform into the older larvae, when the leaf is too small to offer enough food or when leaves and stems do not differ significantly (Eiseman 2020b, Hering 1951). Such phenomena can be found in Heliozela hammoniella (= Heliozela betulae) (Heliozelidae), Marmara spp. (Gracillariidae), Ophiomyia spp. (Agromyzidae), Phyllocnistis spp. (Gracillariidae), Scaptomyza graminum (= Scaptomyzella incana) (Drosophilidae), Zygoneura calthella (Sciaridae), Temnosira czurhini (Pallopteridae) and many other species (Eiseman 2020b, Ellis 2020, Hering 1951, Kato 2002). There are transitions amongst leaf-mining, stem-mining, leaf-boring and stem boring (Hering 1951). Moreover, most ferns are herbaceous, with developed parenchyma in the stems (Crang et al. 2018). Therefore, we incorporated fern borers into fern miners for this article (Suppl. material 1). Some suspected insect species are not included in this study (e.g. Correia et al. 2020, Santiago-Blay 2004).

The miners' biogeographical regions followed Juan J. Morrone’s system (Morrone 2002). For detailed information about fern miners associated with each host plant species, the original sources should be consulted.
Results

We recorded 128 species and 18 families of fern miners (Table 1; Suppl. material 2), including Agromyzidae, Anthomyiidae, Drosophilidae, Chironomidae, Pallopteridae, Buprestidae, Chrysomelidae, Curculionidae, Crambidae, Noctuidae, Tineidae, Tortricidae, Cosmopterigidae, Gelechiidae, Hepialidae, Psychidae, Blasticotomidae and Tenthredinidae. They were primarily distributed in the Palaeartic Region, Nearctic Region and Oriental Region of the Northern Hemisphere and the Neotropical Region between the Tropic of Cancer and the Tropic of Capricorn (Table 1). One explanation for this distribution pattern could be that the land area in the Northern Hemisphere is almost double that of the Southern Hemisphere. Another reason might be that the investigations on leaf-mining insects and their host plants are more thorough in the Northern than in the Southern Hemisphere (Sinclair and Hughes 2008, Sinclair and Hughes 2008, Sinclair and Hughes 2010).

Table 1.
A preliminary world checklist of fern miners and their biological information.

| Miner family | Miner species | Host fern | Biogeographical regions | References |
|--------------|---------------|-----------|-------------------------|------------|
| Diptera      |               |           |                         |            |
| Agromyzidae  | *Chromatomyia* |           |                         |            |
|              | *cheilanthus*  |           |                         |            |
|              | Garg*         |           |                         |            |
|              | *virga-aure*  |           |                         |            |
|              |               |           | Oriental Region         | Spencer 1990 |
| Agromyzidae  | *Chromatomyia* |           |                         |            |
|              | *dorsata*     |           |                         |            |
|              | Hendel²       |           |                         |            |
|              | Asplenium     |           |                         |            |
|              | ceterach      |           | Palaeartic Region       | Ellis 2020, Spencer 1990 |
| Agromyzidae  | *Chromatomyia* |           |                         |            |
|              | *dryoptericola*|           |                         |            |
|              | Sasakawa³     |           |                         |            |
|              | Lepisorus      |           |                         |            |
|              | *thunbergianus*|           | Palaeartic Region       | Sasakawa 2010, Spencer 1990 |
| Agromyzidae  | *Chromatomyia* |           |                         |            |
|              | *dryoptericola*|           |                         |            |
|              | Sasakawa      |           |                         |            |
|              | Asplenium     |           |                         |            |
|              | pinnaatifidum |           | Palaeartic Region       |            |
| Agromyzidae  | *Chromatomyia* |           |                         |            |
|              | *dryoptericola*|           |                         |            |
|              | Sasakawa      |           |                         |            |
|              | Lepisorus      |           |                         |            |
|              | thunbergianus |           | Palaeartic Region       | Sasakawa 2010 |
| Agromyzidae  | *Chromatomyia* |           |                         |            |
|              | masumiae      |           |                         |            |
|              | Sasakawa      |           |                         |            |
|              | Lepisorus      |           |                         |            |
|              | thunbergianus |           | Palaeartic Region       | Sasakawa 2010 |
| Agromyzidae  | *Chromatomyia* |           |                         |            |
|              | scolopendri   |           |                         |            |
|              | Robineau      |           |                         |            |
|              | Desvoi.dy⁴    |           |                         |            |
|              | Asplenium     |           |                         |            |
|              | ruta-muraria  |           | Palaeartic Region       | Civelek 2002, Dempewolf 2001, Ellis 2020, Sasakawa 2010, Spencer 1990 |
| Agromyzidae  | *Chromatomyia* |           |                         |            |
|              | scolopendri   |           |                         |            |
|              | Robineau      |           |                         |            |
|              | Desvoi.dy     |           |                         |            |
|              | Asplenium     |           |                         |            |
|              | scolopendrium |           | Palaeartic Region       |            |
| Agromyzidae  | *Chromatomyia* |           |                         |            |
|              | scolopendri   |           |                         |            |
|              | Robineau      |           |                         |            |
|              | Desvoi.dy     |           |                         |            |
|              | Asplenium     |           |                         |            |
|              | septentrionale|           | Palaeartic Region       |            |
| Miner family | Miner species          | Host fern      | Biogeographical regions   | References                      |
|--------------|------------------------|----------------|--------------------------|---------------------------------|
| Agromyzidae  | *Chromatomyia* scolopendri Robineau Desvoidy | *Polypodium vulgare* | Palaeartic Region | Eiseman 2020b, Ellis 2020, George 2014, Lonsdale 2017, Spencer 1990 |
| Agromyzidae  | *Liriomyza equiseti* de Meijere⁵ | *Equisetum arvense* | Nearctic and Palaeartic Regions | Eiseman 2020b, George 2014, Spencer 1990 |
| Agromyzidae  | *Liriomyza occipitalis* Hende⁶ | *Equisetum arvense* | Palaeartic Region | Eiseman 2020b |
| Agromyzidae  | *Liriomyza nordica* Spencer* | *Equisetum sp.* | Nearctic Region | Eiseman 2020b |
| Agromyzidae  | *Liriomyza virgo* Zetterstedt⁷ | *Equisetum fluviatile* | Nearctic and Palaeartic Regions | Eiseman 2020b, George 2014, Lonsdale 2017, Spencer 1990 |
| Agromyzidae  | *Liriomyza virgo* Zetterstedt | *Equisetum palustre* | Nearctic and Palaeartic Regions | Eiseman 2020b, George 2014, Lonsdale 2017, Spencer 1990 |
| Agromyzidae  | *Liriomyza virgula* Frey⁸ | *Equisetum arvense* | Palaeartic Regain | George 2014 |
| Agromyzidae  | *Phytoliriomyza clara* Melander | *Pteridium aquilinum* | Nearctic Region | Eiseman 2020b, Spencer 1990 |
| Agromyzidae  | *Phytoliriomyza cyatheae* Spencer | *Cyathea dealbata* | Neozelandic Region | Spencer 1976, Spencer 1990 |
| Agromyzidae  | *Phytoliriomyza cyatheae* Spencer | *Cyathea smithii* | Neozelandic Region | Spencer 1990 |
| Agromyzidae  | *Phytoliriomyza diplazii* Sasakawa | *Diplazium* | Oriental Region | Spencer 1990 |
| Agromyzidae  | *Phytoliriomyza felti* Malloch | *Asplenium pinnatifidum* | Nearctic Region | Eiseman 2020b, Spencer 1990 |
| Agromyzidae  | *Phytoliriomyza felti* Malloch | *Asplenium platyneuron* | Nearctic Region | Eiseman 2020b, Spencer 1990 |
| Agromyzidae  | *Phytoliriomyza felti* Malloch | *Pellaea atropurpurea* | Nearctic Region | Eiseman 2020b, Spencer 1990 |
| Agromyzidae  | *Phytoliriomyza felti* Malloch | *Pellaea glabella* | Nearctic Region | Eiseman 2020b, Spencer 1990 |
| Agromyzidae  | *Phytoliriomyza felti* Malloch | *Asplenium rhizophyllum* | Nearctic Region | Eiseman 2020b, Spencer 1990 |
| Agromyzidae  | *Phytoliriomyza felti* Malloch | *Woodsia obtusa* | Nearctic Region | Eiseman 2020b, Spencer 1990 |
| Agromyzidae  | *Phytoliriomyza flavopleura* Watt | *Microsorum* | Neozelandic Region | Spencer 1990 |
| Agromyzidae  | *Phytoliriomyza flavopleura* Watt | *Notogrammitis billardierel* | Neozelandic Region | Spencer 1990 |
| Miner family | Miner species | Host fern | Biogeographical regions | References |
|--------------|--------------|-----------|-------------------------|------------|
| Agromyzidae  | Phytoliriomyza flavopleura Watt | Asplenium flaccidum | Neozelandic Region | Ellis 2020, Lawton 1982, Lawton 1976, MacGarvin et al. 1986, Rigby and Lawton 1981, Spencer 1990 |
| Agromyzidae  | Phytoliriomyza flavopleura Watt | Asplenium oblongifolium | Neozelandic Region | |
| Agromyzidae  | Phytoliriomyza hilarella Zetterstedt | Asplenium | Palaeartic Region | Ellis 2020, Lawton 1982, Lawton 1976, MacGarvin et al. 1986, Rigby and Lawton 1981, Spencer 1990 |
| Agromyzidae  | Phytoliriomyza hilarella Zetterstedt | Pteridium aquilinum | Palaeartic Region | |
| Agromyzidae  | Phytoliriomyza hilarella Zetterstedt | Polypodium | Palaeartic Region | |
| Agromyzidae  | Phytoliriomyza kuscheli Spencer | Histiopteris | Oriental Region | Spencer 1990 |
| Agromyzidae  | Phytoliriomyza pteridii Spencer | Pteridium aquilinum | Palaeartic Region | Gerson 1979, Mcgavin and Brown 1986, MacGarvin et al. 1986, Spencer 1990 |
| Agromyzidae  | Phytoliriomyza pulchella Spencer* | Pteridium aquilinum | Nearctic Region | Eiseman 2020b |
| Agromyzidae  | Phytoliriomyza sp1 | Marattia* | Oriental Region | Spencer 1990 |
| Agromyzidae  | Phytoliriomyza sp2 | Cyathea | Neotropical and Andean Regions | Spencer 1990 |
| Agromyzidae  | Phytoliriomyza tearohensis Spencer | Cyathea dealbata | unknown | Spencer 1976, Spencer 1990 |
| Agromyzidae  | Tropicomyia angiopterica Shiao | Angiopteris lygodifolia | Palaeartic Region | Shiao and Wu 2005 |
| Agromyzidae  | Tropicomyia polyphaga Spencer | Nephrolepis | Oriental Region | Spencer 1990, Shiao and Wu 2005 |
| Agromyzidae  | Tropicomyia sp1 | Pleopeltis | Afrotropical Region | Spencer 1990 |
| Agromyzidae  | Tropicomyia sp1 | Asplenium auriculatum | Afrotropical Region | |
| Agromyzidae  | Tropicomyia sp2 | Angiopteris evecta* | Oriental Region | Spencer 1990 |
| Anthomyiidae | Chirosia albilfons Tiens | Pteridium aquilinum | Palaeartic Region | Lawton 1976, MacGarvin et al. 1986 |
| Anthomyiidae | Chirosia albitaris Zetterstedt | Pteridium aquilinum | Palaeartic and Oriental Regions | Ellis 2020, Gerson 1979, Lawton 1976, Mcgavin and Brown 1986, Suwa 1984, Suwa 1999 |
| Anthomyiidae | Chirosia asperistilata Suwa | Dryopteris monticola | Palaeartic Region | Suwa 1999, Suwa 2005 |
| Anthomyiidae | Chirosia asperistilata Suwa | Dryopteris crassirhizoma | Palaeartic Region | |

*Note: The table is incomplete and may require further review for accuracy.
| Miner family | Miner species | Host fern | Biogeographical regions | References |
|--------------|---------------|-----------|-------------------------|------------|
| Anthomyiidae | *Chirosia cinerosa* Zetterstedt<sup>9</sup> | *Pteridium aquilinum* | Palaearctic Region | Ellis 2020, Kwon and Suh 1982, Suwa 1999 |
| Anthomyiidae | *Chirosia cinerosa* Zetterstedt | *Matteuccia struthiopteris* | Palaearctic Region | Brown and McGavin 2007, Ellis 2020, Gerson 1979, Lawton 1976, Mcgavin and Brown 1986 |
| Anthomyiidae | *Chirosia cinerosa* Zetterstedt | *Athyrium filix-femina* | Palaearctic Region | Brown and McGavin 2007, Ellis 2020, Gerson 1979, Lawton 1976, Mcgavin and Brown 1986 |
| Anthomyiidae | *Chirosia crassiseta* Stein | *Pteridium aquilinum* | Palaearctic Region | Brown and McGavin 2007, Ellis 2020, Gerson 1979, Lawton 1976, Suwa 2013 |
| Anthomyiidae | *Chirosia filicis* Huckett | *Osmunda claytoniana* | Nearctic Region | Eiseman 2018, Eiseman 2020b |
| Anthomyiidae | *Chirosia filicis* Huckett | *Osmundastrum cinnamomeum* | Nearctic Region | Eiseman 2018, Eiseman 2020b |
| Anthomyiidae | *Chirosia flavipennis* Fallen | *Pteridium aquilinum* | Nearctic and Palaearctic Regions | Eiseman 2018, Lawton 1976, Suwa 2013 |
| Anthomyiidae | *Chirosia gleniensis* Huckett | *Onoclea sensibilis* | Nearctic Region | Eiseman 2020, Eiseman 2020a |
| Anthomyiidae | *Chirosia gleniensis* Huckett | *Woodsia areolata* | Nearctic Region | Eiseman 2020, Eiseman 2020a |
| Anthomyiidae | *Chirosia gleniensis* Huckett | *Woodsia virginica* | Nearctic Region | Eiseman 2020, Eiseman 2020a |
| Anthomyiidae | *Chirosia griseifrons* Séguy | *Dryopteris* | Palaearctic Region | Brown and McGavin 2007, Ellis 2020, Gerson 1979, Lawton 1976, Mcgavin and Brown 1986, Suwa 1999 |
| Anthomyiidae | *Chirosia griseifrons* Séguy | *Athyrium filix-femina* | Palaearctic Region | Brown and McGavin 2007, Ellis 2020, Gerson 1979, Lawton 1976, Mcgavin and Brown 1986, Suwa 1999 |
| Anthomyiidae | *Chirosia grossicauda* Strobl<sup>10</sup> | *Asplenium* | Palaearctic Region | Lawton 1976, Mcgavin and Brown 1986, Suwa 1999 |
| Anthomyiidae | *Chirosia grossicauda* Strobl | *Pteridium aquilinum* | Palaearctic Region | Lawton 1976, Mcgavin and Brown 1986, Suwa 1999 |
| Anthomyiidae | *Chirosia grossicauda* Strobl | *Dryopteris* | Palaearctic Region | Lawton 1976, Mcgavin and Brown 1986, Suwa 1999 |
| Anthomyiidae | *Chirosia histricina* Rondani<sup>11</sup> | *Osmunda regalis* | Nearctic and Palaearctic Regions | Brown and McGavin 2007, Ellis 2020, Gerson 1979, Lawton 1976, Mcgavin and Brown 1986, Suwa 1999 |
| Anthomyiidae | *Chirosia histricina* Rondani | *Asplenium* | Nearctic and Palaearctic Regions | Brown and McGavin 2007, Ellis 2020, Gerson 1979, Lawton 1976, Mcgavin and Brown 1986, Suwa 1999 |
| Anthomyiidae | *Chirosia histricina* Rondani | *Blechnum spicant* | Nearctic and Palaearctic Regions | Brown and McGavin 2007, Ellis 2020, Gerson 1979, Lawton 1976, Mcgavin and Brown 1986, Suwa 1999 |
| Anthomyiidae | *Chirosia histricina* Rondani | *Pteridium aquilinum* | Nearctic and Palaearctic Regions | Brown and McGavin 2007, Ellis 2020, Gerson 1979, Lawton 1976, Mcgavin and Brown 1986, Suwa 1999 |
| Anthomyiidae | *Chirosia histricina* Rondani | *Dryopteris filix-mas* | Nearctic and Palaearctic Regions | Brown and McGavin 2007, Ellis 2020, Gerson 1979, Lawton 1976, Mcgavin and Brown 1986, Suwa 1999 |
| Miner family   | Miner species                  | Host fern         | Biogeographical regions                  | References               |
|----------------|--------------------------------|-------------------|------------------------------------------|--------------------------|
| Anthomyiidae   | *Chirosia histricina* Rondani  | Matteuccia struthiopteris | Nearctic and Palaearctic Regions         |                          |
| Anthomyiidae   | *Chirosia histricina* Rondani  | Polypodium         | Nearctic and Palaearctic Regions         |                          |
| Anthomyiidae   | *Chirosia histricina* Rondani  | Athyrium filix-femina | Nearctic and Palaearctic Regions         |                          |
| Anthomyiidae   | *Chirosia histricina* Rondani  | Cystopteris fragilis | Nearctic and Palaearctic Regions         |                          |
| Anthomyiidae   | *Chirosia montana* Pokorny     | Cystopteris fragilis | Nearctic and Palaearctic Regions         | Eiseman 2020b, Eiseman 2018 |
| Anthomyiidae   | *Chirosia nigripes* Bezzi      | Pteridium aquilinum | Palaearctic Region                       | Ellis 2020, Suwa 1999    |
| Anthomyiidae   | *Chirosia pusillans* Huckett   | Athyrium filix-femina | Nearctic Region                          | Eiseman 2018, Eiseman 2020a, Eiseman 2020b |
| Anthomyiidae   | *Chirosia pusillans* Huckett   | Matteuccia struthiopteris | Nearctic Region                         |                          |
| Anthomyiidae   | *Chirosia spinosissima* Malloch | Pteridium aquilinum | Nearctic and Palaearctic Regions         | Eiseman 2020b, Eiseman 2020a |
| Anthomyiidae   | *Pegomya cedrica* Huckett      | Equisetum hyemale  | Nearctic Region                          | Michelsen and Palmer 2020 |
| Anthomyiidae   | *Pegomya disticha* Griffiths   | Equisetum hyemale  | Nearctic Region                          | Michelsen and Palmer 2020 |
| Anthomyiidae   | *Pegomya glabra* Stein         | Equisetum          | Nearctic Region                          | Michelsen and Palmer 2020 |
| Drosophilidae  | *Drosophila apicipuncta* Hardy  | Sadleria           | Nearctic Region                          | Magnacca et al. 2008, Magnacca and O’Grady 2014, Maunsell et al. 2016 |
| Drosophilidae  | *Drosophila diminuens* Hardy*  | Sadleria           | Nearctic Region                          | Magnacca and O’Grady 2014 |
| Drosophilidae  | *Drosophila sadleria* Bryan    | Sadleria           | Nearctic Region                          | Magnacca et al. 2008    |
| Drosophilidae  | *Scaptodrosophila notha* Bock  | Pteridium aquilinum | Australotropical and Australotemperate Regions | Maunsell et al. 2016 |
| Drosophilidae  | *Scaptodrosophila sp.*         | Parablechnum wattsii | Australotropical and Australotemperate Regions | Maunsell et al. 2016 |
| Chironomidae    | *Bryophaeonocladius furcatus* Kieffer | Adiantum         | Nearctic and Palaearctic Regions         | Eiseman 2020b           |
| Pallopteridae   | *Temnosira czurhini* Ozerov    | Huperzia serrata  | Palaearctic Region                       | Kato 2002               |

**Lepidoptera**
| Miner family | Miner species | Host fern | Biogeographical regions | References |
|--------------|---------------|-----------|-------------------------|------------|
| Crambidae    | Albusambia elaphoglossumae Solis & Davis | Elaphoglossum conspersum | Nearctic Region | Solis et al. 2005a |
| Crambidae    | Albusambia elaphoglossumae Solis & Davis | Elaphoglossum biolleyi | Nearctic Region | |
| Crambidae    | Eudonia zophocaena Meyrick | Pyrrosia eleagnifolia | Neozelandic Region | Patrick 2015 |
| Crambidae    | Scoparia illota Philpott | Pyrrosia eleagnifolia | Neozelandic Region | Patrick 2015 |
| Crambidae    | Scoparia molifera Meyrick | Pyrrosia eleagnifolia | Neozelandic Region | Patrick 2015 |
| Crambidae    | Siamusotima aranea Solis & Yen | Lygodium flexuorum | Oriental Region | Solis et al. 2005b |
| Crambidae    | Siamusotima disrupta Solis | Lygodium | Palaeartic Region | Solis et al. 2017 |
| Crambidae    | Undulambia polystichalis Capps | Rumohra adiantiformis | Nearctic Region | Gerson 1979 |
| Noctuidae    | Hydraecia micacea Esper | Equisetum | Palearctic Region | Ellis 2020 |
| Noctuidae    | Papaipema inquaesita Grote & Robinson | Onoclea sensibilis | Nearctic Region | Bird 2012 |
| Noctuidae    | Papaipema pterisii Bird | Pteridium aquilinum | Nearctic Region | Bird 2012, Hinz and Zahniser 2015, Schweitzer 2012 |
| Noctuidae    | Papaipema pterisii Bird | Matteuccia struthiopteris* | Nearctic Region | |
| Noctuidae    | Papaipema speciosissima Grote & Robinson | Osmunda regalis | Nearctic Region | Hinz and Zahniser 2015, Lafontaine and Schmidt 2010, Oppenheim et al. 2018 |
| Noctuidae    | Papaipema speciosissima Grote & Robinson | Osmundastrum cinnamomeum | Nearctic Region | |
| Noctuidae    | Papaipema stenocelis Dyar | Woodwardia virginica | Nearctic Region | Chaloux, Andrea 2012 |
| Noctuidae    | Pseudobryomima fallax Hampson | Pellaea andromedifolia | Nearctic Region | Eiseman 2020b |
| Noctuidae    | Pseudobryomima muscosa Hampson | Polypodium californicum | Nearctic Region | Eiseman 2020b |
| Tineidae     | Psychoides filicivora Meyrick | Asplenium adiantum-nigrum | Palaeartic Region | Gaedike 2019, Kim and Bae 2007 |
| Miner family | Miner species | Host fern | Biogeographical regions | References |
|--------------|---------------|-----------|-------------------------|------------|
| Tineidae     | Psychoides ficicivora Meyrick | Asplenium ceterach | Palaeartic Region |            |
| Tineidae     | Psychoides ficicivora Meyrick | Asplenium scolopendrium | Palaeartic Region |            |
| Tineidae     | Psychoides ficicivora Meyrick | Asplenium trichomanes | Palaeartic Region |            |
| Tineidae     | Psychoides ficicivora Meyrick | Dryopteris filix-mas | Palaeartic Region |            |
| Tineidae     | Psychoides ficicivora Meyrick | Dryopteris aculeata | Palaeartic Region |            |
| Tineidae     | Psychoides ficicivora Meyrick | Polystichum setiferum | Palaeartic Region |            |
| Tineidae     | Psychoides gosari Kim & Bae | Athyrium yokoscense | Oriental and Palaeartic Regions | Kim and Bae 2007 |
| Tineidae     | Psychoides gosari Kim & Bae | Dryopteris setosa | Oriental and Palaeartic Region |            |
| Tineidae     | Psychoides gosari Kim & Bae | Dryopteris chinensis | Oriental and Palaeartic Regions |            |
| Tineidae     | Psychoides gosari Kim & Bae | Dryopteris crassirhizoma | Oriental and Palaeartic Regions |            |
| Tineidae     | Psychoides gosari Kim & Bae | Dryopteris saxifraga | Oriental and Palaeartic Regions |            |
| Tineidae     | Psychoides phaedrospora Meyrick | Aspleniaceae | Palaeartic and Oriental Regions | Gaedike 2019, Kim and Bae 2007 |
| Tineidae     | Psychoides verhuella Bruand | Asplenium ceterach | Palaeartic Region | Ellis 2020, Gaedike 2019, Heckford 2004, Kim and Bae 2007, Muus 2015 |
| Tineidae     | Psychoides verhuella Bruand | Asplenium ruta-muraria | Palaeartic Region |            |
| Tineidae     | Psychoides verhuella Bruand | Asplenium scolopendrium | Palaeartic Region |            |
| Tineidae     | Psychoides verhuella Bruand | Asplenium trichomanes | Palaeartic Region |            |
| Tineidae     | Psychoides verhuella Bruand | Pteridium aquilinum | Palaeartic Region |            |
| Tortricidae  | Apoctena taipana Felder & Rogenhofer | Pyrrosia eleagnifolia | Neozelandic Region | Patrick 2015 |
| Tortricidae  | Celypha tiedemannianna Zeller | Equisetum | Palaeartic Region | Ellis 2020 |
| Tortricidae  | Philocryptica polypodii Watt | Pyrrosia eleagnifolia | Neozelandic Region | Patrick 2015 |
| Miner family   | Miner species                        | Host fern         | Biogeographical regions | References                  |
|---------------|--------------------------------------|-------------------|-------------------------|-----------------------------|
| Cosmopterigidae | **Hyposmocoma** *(Euperissus) ekaha* Swezey | **Asplenium nidus** | Oriental Region         | Kawahara et al. 2011        |
| Cosmopterigidae | **Hyposmocoma** *(Euperissus) trivitella* Swezey | **Elaphoglossum aemulum** | Oriental Region         | Kawahara et al. 2011        |
| Cosmopterigidae | **Hyposmocoma** *(Euperissus) trivitella* Swezey | **Elaphoglossum gorgoneum** | Oriental Region         |                             |
| Cosmopterigidae | **Hyposmocoma** *(Euperissus) trivitella* Swezey | **Elaphoglossum crassifolium** | Oriental Region         |                             |
| Cosmopterigidae | **Hyposmocoma** *(Euperissus) trivitella* Swezey | **Elaphoglossum reticulatum** | Oriental Region         |                             |
| Gelechiidae   | **Monochroa harrisonella** Busck      | **Pteridium aquilinum** | Nearctic Region         | Eiseman 2020b                |
| Gelechiidae   | **Paltodora cytisella** Curti*       | **Pteridium aquilinum** | Palaeartic Region       | Lawton 1976, Rigby and Lawton 1981 |
| Hepialidae    | **Endoclista excrescens** Butler*     | **Equisetum arvense** | Palaeartic Region       | Correia et al. 2020, Grehan 1989 |
| Hepialidae    | **Triodia sylvina** Linnaeus*         | **Equisetum arvense** | Palaeartic Region       | Correia et al. 2020, Grehan 1989 |
| Psychidae     | **Apterona helicoidella** Vallot      | **Polypodium**     | unknown                 | Alders and Gielis 1999      |
| **Hymenoptera** |                                      |                   |                         |                             |
| Blasticotomidae | **Blasticotoma atra** Zholochovtsev   | unknown           | unknown                 | Taeger et al. 2010, Wikipedia 2019 |
| Blasticotomidae | **Blasticotoma filiceti** Klug        | **Pteridium aquilinum** | Palaeartic Region       | Ellis 2020, Liston 2007, Novgorodova and Biryukova 2011, Shcherbakov 2006, Shcherbakov 2008, Taeger et al. 2010, Wikipedia 2019 |
| Blasticotomidae | **Blasticotoma filiceti** Klug        | **Dryopteris**     | Palaeartic Region       |                             |
| Blasticotomidae | **Blasticotoma filiceti** Klug        | **Polystichum**    | Palaeartic Region       |                             |
| Blasticotomidae | **Blasticotoma filiceti** Klug        | **Matteuccia struthiopteris** | Palaeartic Region |                             |
| Blasticotomidae | **Blasticotoma filiceti** Klug        | **Athyrium alpestre** | Palaeartic Region       |                             |
| Blasticotomidae | **Blasticotoma filiceti** Klug        | **Athyrium filix-femina** | Palaeartic Region       |                             |
| Blasticotomidae | **Blasticotoma filiceti** var. pacificus Malaise | unknown           | unknown                 | Taeger et al. 2010, Wikipedia 2019 |
| Miner family       | Miner species                  | Host fern          | Biogeographical regions | References                      |
|-------------------|--------------------------------|--------------------|-------------------------|---------------------------------|
| Blasticotomidae   | Blasticotoma nipponica         | unknown            | unknown                 | Wikipedia 2019, Taeger et al. 2010 |
|                   | Takeuchi                       |                    |                         |                                 |
| Blasticotomidae   | Blasticotoma smithi            | unknown            | unknown                 | Taeger et al. 2010, Wikipedia 2019 |
|                   | Shinohara                      |                    |                         |                                 |
| Blasticotomidae   | Blasticotoma warabii           | unknown            | unknown                 | Taeger et al. 2010, Wikipedia 2019 |
|                   | Togashi                        |                    |                         |                                 |
| Blasticotomidae   | Bohea abrupta                  | unknown            | unknown                 | Taeger et al. 2010, Wikipedia 2019 |
|                   | Maa                             |                    |                         |                                 |
| Blasticotomidae   | Paremphytus ostentus           | unknown            | unknown                 | Taeger et al. 2010, Wikipedia 2019 |
|                   | Brues                          |                    |                         |                                 |
| Blasticotomidae   | Runaria flavipes               | unknown            | unknown                 | Taeger et al. 2010, Wikipedia 2019 |
|                   | Takeuchi                       |                    |                         |                                 |
| Blasticotomidae   | Runaria hunannica              | unknown            | unknown                 | Taeger et al. 2010, Wikipedia 2019 |
|                   | Wei in Wei & Nie               |                    |                         |                                 |
| Blasticotomidae   | Runaria punctata               | unknown            | unknown                 | Taeger et al. 2010, Wikipedia 2019 |
|                   | Wei in Wei & Nie               |                    |                         |                                 |
| Blasticotomidae   | Runaria shaanxinica            | unknown            | unknown                 | Taeger et al. 2010, Wikipedia 2019 |
|                   | Wei in Wei & Nie               |                    |                         |                                 |
| Blasticotomidae   | Runaria taiwana                | unknown            | unknown                 | Taeger et al. 2010, Wikipedia 2019 |
|                   | Shinohara                      |                    |                         |                                 |
| Tenthredinidae    | Aneugmenus coronatus           | Pteridium aquilinum| Palaeartic Region       | Beneš 2014, Ellis 2020, Schwarz 2005 |
|                   | Klug                           |                    |                         |                                 |
| Tenthredinidae    | Aneugmenus coronatus           | Dryopteris filix-mas| Palaeartic Region       |                                 |
|                   | Klug                           |                    |                         |                                 |
| Tenthredinidae    | Aneugmenus coronatus           | Polystichum setiferum| Palaeartic Region       |                                 |
|                   | Klug                           |                    |                         |                                 |
| Tenthredinidae    | Aneugmenus coronatus           | Athyrium filix-femina| Palaeartic Region       |                                 |
|                   | Klug                           |                    |                         |                                 |
| Tenthredinidae    | Heptamelus dahlbomi            | Athyrium filix-femina| Nearctic and Palaeartic Regions | Vikberg and Liston 2009 |
|                   | Thomson                        |                    |                         |                                 |
| Tenthredinidae    | Heptamelus ochroleucus         | Blechnum spicant   | Nearctic and Palaeartic Regions | Ellis 2020, Shcherbakov 2008, Vikberg 2017, Vikberg and Liston 2009 |
|                   | Stephens 16                    |                    |                         |                                 |
| Tenthredinidae    | Heptamelus ochroleucus         | Matteuccia struthiopteris| Nearctic and Palaeartic Regions |                                 |
|                   | Stephens                       |                    |                         |                                 |
| Tenthredinidae    | Heptamelus ochroleucus         | Dryopteris dilatata| Nearctic and Palaeartic Regions |                                 |
|                   | Stephens                       |                    |                         |                                 |
| Tenthredinidae    | Heptamelus ochroleucus         | Polypodium vulgare | Nearctic and Palaeartic Regions |                                 |
|                   | Stephens                       |                    |                         |                                 |
| Tenthredinidae    | Heptamelus ochroleucus         | Athyrium filix-femina| Nearctic and Palaeartic Regions |                                 |
|                   | Stephens                       |                    |                         |                                 |
| Coleoptera        |                                |                    |                         |                                 |
| Miner family | Miner species | Host fern | Biogeographical regions | References |
|--------------|---------------|-----------|--------------------------|------------|
| Buprestidae  | *Endelus bakerianus* Obenberger | Lygodium microphyllum | Oriental Region | Kalashian 2013, Goolsby et al. 2003, Mehltreter et al. 2010 |
| Buprestidae  | *Neotrichys bellamyi* Hespenheide | Gleichenia glauca | Neotropical Region | Hespenheide 2006 |
| Buprestidae  | *Neotrichys bicolor* Hespenheide | Cnemidaria petiolata | Neotropical Region | Hespenheide 1982 |
| Buprestidae  | *Neotrichys bordoni* Cobos | Cyatheaceae | Neotropical Region | Hespenheide 1982 |
| Buprestidae  | *Neotrichys caerulea* Hespenheide | Cyatheaceae | Neotropical Region | Hespenheide 1982 |
| Buprestidae  | *Neotrichys concinna* Fisher | Cyatheaceae | Neotropical Region | Hespenheide 1982, Hespenheide 2006 |
| Buprestidae  | *Neotrichys cyanipennis* Fisher | Cyatheaceae | Neotropical Region | Hespenheide 2006 |
| Buprestidae  | *Neotrichys estebana* Kerremans* | Dicranopteris | Neotropical Region | Hespenheide 1982 |
| Buprestidae  | *Neotrichys fennahi* Thery | Cyatheaceae | Neotropical Region | Hespenheide 1980 |
| Buprestidae  | *Neotrichys gleicheniae* Hespenheide | Gleichenia | Neotropical Region | Hespenheide 1982 |
| Buprestidae  | *Neotrichys hoffmani* Fisher | Cyatheaceae | Neotropical Region | Hespenheide 1980, Hespenheide 1982 |
| Buprestidae  | *Neotrichys mariae* Hespenheide | Gleichenia | Neotropical Region | Hespenheide 2006 |
| Buprestidae  | *Neotrichys resplendens* Hespenheide | Cyatheaceae | Neotropical Region | Hespenheide 1982 |
| Buprestidae  | *Neotrichys segregata* Waterhouse | Gleicheniaceae* | Neotropical Region | Hespenheide 1982 |
| Buprestidae  | *Neotrichys solisi* Hespenheide | Gleichenia | Neotropical Region | Hespenheide 2006 |
| Chrysomelidae | *Febra insularis* Bryant | Acrostichum aureum | Oriental Region | Samuelson 1973, Santiago-Blay 2004 |
| Chrysomelidae | *Febra ovata* Bryant | Angiopteris evecta | Oriental Region | Samuelson 1973, Nadein 2013, Jolivet 1991 |
| Miner family | Miner species | Host fern | Biogeographical regions | References |
|-------------|--------------|-----------|-------------------------|------------|
| Chrysomelidae | *Febra venusta* Clark | *Nephrolepis* | Oriental Region | Samuelson 1973, Santiago-Blay 2004 |
| Chrysomelidae | *Halticorcus bhaumiki* Basu et Sengupta \(^17\) | *Pteris vittata* | Palaeartic and Oriental Regions | Isowa and Kojima 2011, Konstantinov and Prathapan 2008, Patra and Bera 2007 |
| Chrysomelidae | *Halticorcus bhaumiki* Basu et Sengupta | *Ampelopteris prolifera* | Palaeartic and Oriental Regions | |
| Chrysomelidae | *Halticorcus bhaumiki* Basu et Sengupta | *Cyclosorus* | Palaeartic and Oriental Regions | |
| Chrysomelidae | *Halticorcus bhaumiki* Basu et Sengupta | *Christella dentata* | Palaeartic and Oriental Regions | |
| Chrysomelidae | *Halticorcus bhaumiki* Basu et Sengupta | *Nephrolepis cordifolia* | Palaeartic and Oriental Regions | |
| Chrysomelidae | *Halticorcus bhaumiki* Basu et Sengupta | *Adiantum lunulatum* | Palaeartic and Oriental Regions | |
| Chrysomelidae | *Halticorcus bhaumiki* Basu et Sengupta | *Drynaria propinqua* | Palaeartic and Oriental Regions | |
| Chrysomelidae | *Halticorcus bhaumiki* Basu et Sengupta | *Pyrosera adnascens* | Palaeartic and Oriental Regions | |
| Chrysomelidae | *Halticorcus bhaumiki* Basu et Sengupta | *Microsorum scolopendria* | Palaeartic and Oriental Regions | |
| Chrysomelidae | *Halticorcus hiranoi* Takizawa \(^18\) | *Lemmaphyllum microphyllum* | Palaeartic Region | Kato 1991, Santiago-Blay 2004 |
| Chrysomelidae | *Halticorcus hiranoi* Takizawa | *Loxogramme salicifolia* \(^*\) | Palaeartic Region | |
| Chrysomelidae | *Halticorcus kasuga* Nakane | *Lepisorus thunbergianus* | Palaeartic Region | Isowa and Kojima 2011 |
| Chrysomelidae | *Halticorcus kasuga* Nakane | *Lepisorus onoei* | Palaeartic Region | |
| Chrysomelidae | *Halticorcus kasuga* Nakane | *Lemmaphyllum microphyllum* | Palaeartic Region | |
| Chrysomelidae | *Halticorcus kasuga* Nakane | *Pyrosera linearifolia* | Palaeartic Region | |
| Chrysomelidae | *Halticorcus platycerii* Lea | *Platycerium alcicorne* | Australotropical, Australotemperate and Palaeartic Regions | Hawkeswood 2003, Isowa and Kojima 2011, Sinclair and Hughes 2010 |
| Chrysomelidae | *Halticorcus platycerii* Lea | *Asplenium nidus* | Australotropical, Australotemperate and Palaeartic Regions | |
| Chrysomelidae | *Halticorcus sauteri* Chen \(^19\) | *Colysis elliptica* | Palaeartic Region | Kato 1991, Santiago-Blay 2004 |
| Miner family | Miner species | Host fern | Biogeographical regions | References |
|--------------|---------------|-----------|------------------------|------------|
| Chrysomelidae | Halticorus sauteri Chen | Leptochilus ellipticus | Palaeartic Region | Correia et al. 2020, Poinar 2014 |
| Chrysomelidae | Hippuriphila babai Chujo* | Equisetum | Palaeartic Region | Correia et al. 2020, Poinar 2014 |
| Chrysomelidae | Hippuriphila canadensis Brown* | Equisetum arvense | Nearctic Region | Correia et al. 2020, Poinar 2014 |
| Chrysomelidae | Hippuriphila catherinae Barr* | Equisetum | Neotropical Region | Correia et al. 2020, Poinar 2014 |
| Chrysomelidae | Hippuriphila equiseti Beller et Hatch* | Equisetum arvense | Nearctic Region | Correia et al. 2020, Poinar 2014 |
| Chrysomelidae | Hippuriphila modeeri Linnaeus | Equisetum arvense | Palaeartic Region | Biological Records Centre 2020, Ellis 2020, Santiago-Blay 2004 |
| Chrysomelidae | Hippuriphila modeeri Linnaeus | Equisetum fluviatile | Palaeartic Region | Biological Records Centre 2020, Ellis 2020, Santiago-Blay 2004 |
| Chrysomelidae | Hippuriphila modeeri Linnaeus | Equisetum palustre | Palaeartic Region | Correia et al. 2020, Poinar 2014 |
| Curculionidae | Bagous claudicans Boheman | Equisetum fluviatile | except for Central and South America, all the world | Ellis 2020, Gosik et al. 2019 |
| Curculionidae | Bagous lutulentus Gyllenhal* | Equisetum fluviatile | except for Central and South America, all the world | Ellis 2020, Gosik 2009, Gosik et al. 2019, Gosik and Wanat 2014 |
| Curculionidae | Grypus brunniostris Fabricius*21 | Equisetum arvense | Nearctic Region | Ellis 2020, George 2014 |
| Curculionidae | Grypus brunniostris Fabricius | Equisetum fluviatile | Nearctic Region | Ellis 2020, George 2014 |
| Curculionidae | Grypus brunniostris Fabricius | Equisetum ramosissimum | Nearctic Region | Ellis 2020, George 2014 |
| Curculionidae | Grypus equiseti Fabricius*22 | Equisetum arvense | Nearctic and Palaearctic Regions | Ellis 2020, George 2014, Gosik et al. 2019 |
| Curculionidae | Grypus equiseti Fabricius | Equisetum palustre | Nearctic and Palaearctic Regions | Ellis 2020, George 2014 |
| Curculionidae | Grypus equiseti Fabricius | Equisetum pratense | Nearctic and Palaearctic Regions | Ellis 2020, George 2014 |
| Curculionidae | Grypus equiseti Fabricius | Equisetum sylvaticum | Nearctic and Palaearctic Regions | Ellis 2020, George 2014 |
| Curculionidae | Stenopelmus rufinasus Gyllenhal | Azolla | Nearctic, Afrotropical and Palaearctic Regions | Center et al. 2002, Hill and Cilliers 1999, Richerson and Grigarick 1967 |

* possible host fern or miner
Fern miners belong to four orders: Diptera (51 species; 39.8%), Coleoptera (33 species; 25.8%), Lepidoptera (28 species; 21.9%) and Hymenoptera (16 species; 12.5%) (Fig. 1; Suppl. material 2). In general, dipteran leaf miners are dominant in herbaceous plants while lepidopteran leaf miners are dominant in woody plants (De Prins and De Prins 2020, Edmunds et al. 2020, Eiseman 2020b, Ellis 2020, Pitkin et al. 2019, Spencer 1990). The life form of most extant ferns is herbaceous, which could explain why nearly half of fern-mining species are dipteran flies.
Amongst the 18 fern-mining insect families, Agromyzidae, Anthomyiidae, Buprestidae, Chrysomelidae and Blasticotomidae had the highest numbers of species (20.3%, 14.1%, 11.7%, 10.2% and 10.2%, respectively), while the other 13 families accounted for 33.5% only (Fig. 1; Suppl. material 2).

The fern families with highest numbers of host species were Dryopteridaceae (19), Polypodiaceae (18) and Aspleniaceae (15) (Fig. 2; Suppl. material 3). The fern families with the highest numbers of miner species were Dennstaedtiaceae (21), Equisetaceae (21), Polypodiaceae (20) and Aspleniaceae (14) (Fig. 2; Suppl. material 3). With 82 species and 12 families of host ferns and 67 species of fern miners, Polypodiales was the dominant host order of fern-mining insects (Suppl. material 3).

Figure 1. Percentage distribution of the fern-mining species into the four orders and the 18 families.

Figure 2. The dated phylogenetic tree of host fern families generated with the R package ‘V. PhyloMaker’ (Jin and Qian 2019). The first number after the fern family is the number of host fern species and the second is the number of fern miner species. The length of each branch is also shown and the scale bar unit is 100 myr.
The number of host species was significantly and positively correlated with the total number of fern species at the family level ($R^2 = 0.614$, $t = 5.352$, $P < 0.001$; Fig. 3a), but the number of miner species was not significantly correlated with the total number of fern species at the family level ($R^2 = 0.110$, $t = 1.495$, $P = 0.152$; Fig. 3b).

Discussion

In this paper, we provide a preliminary checklist about fern miners and their host plants worldwide. Table 1 summarises this checklist in terms of published information to date. However, there is also more information available on some fern-mining groups and this is summarised here:

1. Diptera: In Anthomyiidae, there is an unknown *Chiro sia* species with *Deparia acrostichoides* as host in the Nearctic Region (Eisman 2020b), while *C. similata* could be a possible Nearctic *Pteridium* borer (Eisman 2018). In Drosophilidae, the Fuscoamoeba subgroup has many species that have been reared from rotting fern rachises (Magnacca et al. 2008). For *Chromatomyia* species in Agromyzidae, Kahanpää (2014) separates *Chromatomyia* and *Napomyza* as different genera (Kahanpää 2014) and Spencer (1990) considers that *C. cheilanthus* should belong to the genus *Ptochomyza* (Spencer 1990). Molecular phylogeny suggests that the genus of *Phytomyza* should include all species of *Phytomyza*, *Chromatomyia*, *Napomyza* and *Ptochomyza* (Winkler et al. 2009). However, only one fern-feeding *Chromatomyia* species is included in the above molecular analysis. Moreover, no *Phytomyza* s. s. species has previously been found as fern-mining. In this article, we rather kept the genus name of *Chromatomyia* and listed the *Phytomyza* species as the synonym of the corresponding *Chromatomyia* species in .

**Figure 3.**
Linear regressions between (a) the number of host species in each fern family; (b) the number of miner species for each fern family and the total number of fern species in the corresponding family. Families without any host species were not included.
(2) Lepidoptera: In Tineidae, early instar larvae of the subfamily Teichobinae are leaf miners, while their later instars feed on sporangia from a loose portable case (Gaedike 2019). An unknown species of Pyralidae has two hosts (Lygodium microphyllum and L. flexuosum) in the Oriental Region (Goolsby et al. 2003). There is an unknown moth in the Nearctic Region, which mines the leaves of Pteridium aquilinum (Eiseman 2020b), but the species name could not be confirmed. In Gelechiidae, Monochroa placidella larvae make gall-like deformities on the fronds of the bracken (P. aquilinum) (Eiseman 2020b). Eiseman (personal observations) believes that the deformities are caused by internal feeding; he has also reared an undetermined Monochroa species from larvae that similarly bored in the terminal part of the rachis and caused a gall-like deformity.

(3) Hymenoptera: In Tenthredinidae, the genus Heptamelus has 36 species in the Palaearctic and Oriental Regions and their larvae are internal feeders and all probably use ferns as larva hosts (Vikberg and Liston 2009), but we cannot know with certainty which species of Heptamelus is involved, except for H. ochroleucus on Athyrium filix-femina (Vikberg 2017). With only 13 species and 3 tribes in Eurasia's temperate region, Blasticotomidae is a small family in the Hymenoptera and their larvae are stem borers on ferns (Taeger et al. 2010, Wikipedia 2019, Santiago-Blay 2004).

(4) Coleoptera: In Buprestidae, both Neotrachys and Endelus have fern-mining habits (Xiao 2018, Bellamy 1997). Most Neotrachys feed on the ferns of Cyatheaceae and Gleicheniaceae (Hespenheide 1980, Hespenheide 1982, Hespenheide 2006). However, some Neotrachys larvae may mine other non-fern plants. For example, N. dominicanus feeds on Arthrostylidium (Poaceae) (Meurgey 2017). The genus Leiopleura is morphologically similar and sometimes confused with Neotrachys, but Leiopleura feeds on Moraceae and Apocynaceae (Hespenheide 1991). Fern-feeding or not could be a clue to distinguish Neotrachys and its related genera. Although there are many publications on Endelus, only very few mention its host plants (Kalashian 2013).

Dominant plant groups generally are rich in leaf miners and rich in host plants, which could be explained by the ‘plant apparency hypothesis’ (Feeny 1976). Such phenomena have been found in several other leaf-mining insects (Dai et al. 2017, Dai et al. 2018). Apart from species richness in a fern taxonomic group, the distribution range should also be considered as an important component of ‘plant apparency’ (Dai et al. 2017). Equisetaceae has 39 species and eight host species, and Dennstaedtiaceae has 245 species and two host species, but both families host 21 miner species, which is the highest amongst all fern families (Fig. 2; Suppl. material 3). It is Equisetaceae and Dennstaedtiaceae that strongly affected the significance of the correlation in Fig. 3b. In particular, the bracken fern (Pteridium aquilinum), one species in Dennstaedtiaceae, had 20 miner species (Suppl. material 3), which is not less than many dominant flowering plants. The bracken fern might be the only globally distributed fern and one of the most widespread vascular plants, which occurs in temperate and subtropical regions in both hemispheres (Flora of North America Editorial Committee 1993). It is used as vegetable, food or feed in many places. It is also a common invasive plant in disturbed areas (Flora of North America Editorial Committee 1993). The above features of the bracken fern make it highly attractive to both miners and researchers, thus the high number of mining species might be the combined effects of
plant apparency and sampling effects. Dryopteridaceae has 2257 species (Suppl. material 3) and also a cosmopolitan distribution, with many cultivated ornamental species (Olsen and Olsen 2007). Aspleniaceae has 855 species (Suppl. material 3) and also a worldwide distribution (POWO 2019). Polypodiaceae has 1667 species (Suppl. material 3) and is distributed nearly worldwide, but mainly in tropical areas, with some cultivated species (Simpson 2010). Both high species richness and wide geographical distribution could explain why the three families have large numbers of both host fern species and miner species. Besides *P. aquilinum*, *Equisetum arvense* (Equisetaceae), *Athyrium filix-femina* (Athyriaceae) and *Matteuccia struthiopteris* (Onocleaceae) also have a high richness of miners (10, 8 and 6 species, respectively) (Suppl. material 3). The common horsetail (*E. arvense*) is native throughout the Arctic and temperate regions in the Northern Hemisphere (Schaffner 1930). *E. arvense* becomes an invasive plant in New Zealand and a systematic evaluation of its potential biocontrol agents including miners and borers has been performed (Paynter and Barton 2008). The common lady-fern (*A. filix-femina*) is one of the most abundant fern species in the temperate regions in the Northern Hemisphere (Adam 1995). The ostrich fern (*M. struthiopteris*) is widely distributed in the temperate regions of the Northern Hemisphere (Kimura et al. 2004). However, since the checklist of fern-mining insects and the corresponding host fern species is preliminary, these patterns need further verification.

As the sampling of fern miners and their hosts are insufficient in many places and some sampled records might be inaccessible, this study was only a preliminary list. We hope that this basic list can serve as an initial reference for future inventories and research on fern-mining insects.

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Supplementary materials

**Suppl. material 1: The feeding mode and feeding plant organ of each fern miner**

**Authors:** Jie Yang, Xiaohua Dai  
**Data type:** Feeding habits  
**Download file** (16.21 kb)

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Suppl. material 2: The number of fern-miners in each insect family and each insect order

Authors: Jie Yang, Xiaohua Dai
Data type: Number of species
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Suppl. material 3: The number of miners on each fern species, each fern family and each fern order

Authors: Jie Yang, Xiaohua Dai
Data type: Number of species
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