

Damage from species of leafminer flies (Agromyzidae: Diptera) on their plant host(s) is caused mostly by internal larval feeding, but also from female oviposition and feeding punctures, which results in structural damage, the vectoring of viruses and pathogenic fungi, and the exposure of tissue to secondary infection. Many plants of agricultural and ornamental importance are attacked in the field and in glasshouses, and while fly populations are normally kept in check by hymenopterous parasitoids, they sometimes occur in large enough numbers to affect yield and may destroy entire crops. Species affecting crops may be specialists on one host or a larger number of related hosts, but only 16 species of *Liriomyza*, *Phytomyza* and *Tropicomyia* are truly polyphagous. The threat of these flies is compounded by increasing insecticide resistance and the ease by which polyphagous species can multiply on weeds around growing areas or on alternate crops. All species are also readily spread through trade on their host plant or in soil, causing some species to become globally invasive, with some being of quarantine concern. An overview of agromyzid biology, ecology and agricultural importance is provided, and detailed consideration is given for 26 major pests of special concern. For each of these species, an overview of contemporary knowledge is provided for identification and diagnosis, global distribution, hosts plant(s), host damage, biology, and means of dispersal. To aid in their control, early warning systems, and means of field monitoring and management are provided.



Agromyzidae (Diptera) Plant Pests

Edited by O. Lonsdale, S.T. Murphy & S.J. Scheffer

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Species depicted: *Liriomyza sativae* Blanchard, male.

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Agromyzidae (Diptera) Plant Pests

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Abstract

Damage from species of Agromyzidae (Diptera) on their plant host(s) is caused mostly by internal larval feeding, but additional damage can arise from female oviposition and feeding punctures, which results in structural damage, the vectoring of viruses and pathogenic fungi, and the exposure of tissue to secondary infection. Many plants of agricultural and ornamental importance are attacked in the field and in glasshouses, and while fly populations are normally kept in check by hymenopterous parasitoids, they sometimes occur in large enough numbers to affect yield and may destroy entire crops. Species affecting crops may be specialists on one host or a larger number of related hosts, but only 16 species in the genera *Liriomyza* Mik, *Phytomyza* Fallén and *Tropicomyia* Spencer are polyphagous, occurring on many hosts in a wide range of families. The threat of these flies is compounded by increasing insecticide resistance and the ease by which polyphagous species can multiply on weeds around growing areas or on alternate crops. All species are also readily spread through trade on their host plant or in soil, causing some species to become globally invasive, with some being of quarantine concern. Since understanding these pests is integral to their control, the objective of the present study is to provide an overview of agromyzid biology, ecology and agricultural importance. Detailed consideration is additionally provided for 26 major pests of special concern. These include eight species of the subfamily Agromyzinae [*Agromyza frontella* (Rondani); *A. megalopsis* Hering; *A. parvicornis* Loew; *Melanagromyza sojae* (Zehntner), *Ophiomyia phaseoli* (Tyron), *O. simplex* (Loew), *O. spencerella* (Greathead), and *Tropicomyia theae* (Cotes)] and 18 species of the subfamily Phytomyzinae [*Amauromyza flavifrons* (Meigen), *Liriomyza brassicae* (Riley), *L. bryoniae* (Kaltenbach), *L. chinensis* (Kato), *L. congesta* (Becker), *L. huidobrensis* (Blanchard), *L. langei* Frick, *L. sativae* Blanchard, *L. strigata* (Meigen), *L. trifolii* (Burgess), *Phytobia cambii* (Hendel), *Phytomyza gymnostoma* Loew, *P. horticola* Goureau, *P. ilicicola* Loew, *P. ilicis* Curtis, *P. nigra* Meigen, *P. rufipes* Meigen, and *P. syngenesiae* (Hardy)]. For each of these species, an overview of contemporary knowledge is provided for identification and diagnosis, global distribution, hosts plant(s), host damage, biology, and means of movement and dispersal. To aid in control, early warning systems, and means of field monitoring and management are provided.

Introduction

Larvae of species in the family Agromyzidae (Diptera) all live and feed in the living tissue of their host plants. The family occurs globally in all biogeographic regions, is sometimes abundant, and has been reared from 140 families of monocots, dicots, horsetails, ferns and liverworts (Hering 1957, 1966; Spencer 1990; Scheffer et al. 2007). Not surprisingly, a number of species occur on plant species of agricultural or

ornamental importance and are of great concern because of the harm they inflict, either through loss of production via damage to plant tissue on agricultural crops, or reduction of product quality and marketability by more modest (or even minor) feeding on ornamental and agricultural species. The most serious pests are polyphagous and occur on hundreds of different crops. These species can be quite difficult to control because populations often evolve insecticide resistance, easily multiply on weeds around growing areas or on alternate crops and are frequently spread through trade (Parrella 1987; Weintraub et al. 2017). True polyphagy, where a species regularly feeds and reproduces on hosts in different orders or subclasses, is uncommon in the Agromyzidae, being restricted to an estimated 16 species (Spencer 1990) of the more than 3,000 described in the family.

The standard reference for information on pest Agromyzidae is Spencer's 1973 "Agromyzidae (Diptera) of Economic Importance". In this seminal work, Spencer aggregated most of the information known at the time on many dozens of severe and modest pests, as well as species of lesser or occasional concern. The present work is not intended as a replacement for this book, but will provide updated, in-depth treatments for 26 major agromyzid pest species, incorporating literature available since 1973. Over recent decades there has been valuable advances in the understanding of a range of important and diverse areas in agromyzid research which needs to be brought together; for example, the identification of possible cryptic taxa or host races within some of the polyphagous *Liriomyza* species, the opportunities for biological control and in the compatibility of modern insecticides in the IPM of agromyzid pests. Most of the species covered in this work are known to consistently cause economic problems regionally or globally, primarily on crops used for food production. While the impact of more regionally important or less frequently pestiferous species should not be overlooked, this work is necessarily restricted in scope and not intended to be exhaustive.

Also provided is a brief global overview of life history and host use by agromyzid pest species, and host use patterns in each genus are highlighted. The idea for the present work evolved out of a separate and much larger book project in what was to be "The Encyclopedia of Plant Pests", a compendium of economically important plant pest species of invertebrates, but this project was abandoned.

Most genera that include pest species can be identified using the key in Lonsdale (2021), which is a manual to Nearctic Agromyzidae. This work also provides the most up-to-date summary of agromyzid classification available, and a description of all Nearctic genera from a taxonomic perspective. The only genus discussed here that cannot be identified using that key is *Tropicomyia*, since it is exclusively Old World in distribution. This genus can be keyed using the chapter on Afrotropical Agromyzidae in Lonsdale & von Tschirnhaus (2021), however, and all polyphagous and economically important species are extensively discussed in Spencer (1973).

Of those 26 species receiving focused treatments here, eight are species of the subfamily Agromyzinae [*Agromyza frontella* (Rondani); *A. megalopsis* Hering; *A. parvicornis* Loew; *Melanagromyza sojae* (Zehntner), *Ophiomyia phaseoli* (Tyron), *O. simplex* (Loew), *O. spencerella* (Greathead), and *Tropicomyia theae* (Cotes)]; and 18 are species of the subfamily Phytomyzinae [*Amauromyza flavifrons* (Meigen), *Liriomyza brassicae* (Riley), *L. bryoniae* (Kaltenbach), *L. chinensis* (Kato), *L. congesta* (Becker), *L. huidobrensis* (Blanchard), *L. langei* Frick, *L. sativae* Blanchard, *L. strigata* (Meigen), *L. trifolii* (Burgess), *Phytobia cambii* (Hendel), *Phytomyza gymnostoma* Loew, *P. horticola* Goureau, *P. ilicicola* Loew, *P. ilicis* Curtis, *P. nigra* Meigen, *P. rufipes* Meigen, and *P. syngenesiae* (Hardy)]. A few of these are not considered major pests at the present time but are discussed because their oligophagous or polyphagous diet increases the likelihood of introductions to new regions through trade. The species entries are organized into the following format: i) Identification and diagnosis; ii) Distribution, listing countries by biogeographic region; iii) Hosts, listing genera by plant family; iv) Damage; v) Biology; vi) Movement and Dispersal; and vii) Management, including early detection (fact sheets, monitoring and forecasting) and control methods. Common names are provided when available. In addition to these entries, the the biology and ecology of the family is summarized, including their broader impacts on human agriculture and commerce.

Biology and ecology of Agromyzidae

Most agromyzid species with known host plant associations are leafminers, having larvae that feed on mesophyll located between the epidermal layers of leaves. Other agromyzid species feed in seeds, stems, or roots, but the diversity of such species is unknown as these feeding locations are highly cryptic and have been poorly sampled. Host plant species and feeding location are known for fewer than half of all agromyzid species (Spencer 1990; Benavent-Corai et al. 2005). Current records indicate that most agromyzids are highly host plant-specific, feeding on one or a few host species in the same or closely related genera or families (Spencer 1990; Winkler et al. 2009). However, the extreme host specificity of many of the species may be an artifact of the paucity of host data, as increased collecting often uncovers additional host plant affiliations of species that were previously considered to be monophagous (e.g. Eiseman and Lonsdale 2018; Scheffer et al. 2021). While it may be that some seemingly monophagous species are, in fact, oligophagous, the converse may also be true. Multiple molecular studies of genetic structure within several oligophagous species have shown the presence of highly specialized, monophagous, host races and/or cryptic species (Scheffer and Hawthorne 2007; Hebert et al. 2016; Mlynarek and Heard 2018; Scheffer et al. 2021). The large range in dietary breadth, from polyphagy to monophagous host races/cryptic species, suggests that dietary specialization is somewhat labile within the Agromyzidae. Recent phylogenetic study of *Liriomyza* corroborates lability in diet breadth in this genus (Xuan et al. 2022).

Presence of the host plant is generally believed necessary for courtship and copulation of agromyzids. In dense populations, adult agromyzids may be seen feeding, courting, and mating on their host plants. Courtship within the Agromyzidae involves both pheromonal and vibratory (including acoustic) communication (Carrière and McNeil 1988, 1990; Ge et al. 2019b; Wicker-Thomas 2007). Head/body pumping and wing vibrations are commonly observed during agromyzid courtship (Carrière and McNeil 1988; Ge et al. 2019b). All *Agromyza* and the males of some species of *Liriomyza* have an abdominal “stridulatory organ”, although the organ is a narrow band along the lateral margins of tergite 1+2 in *Agromyza* (Fig. 18, arrow), and a raised, ill-defined patch on the lateral abdominal membrane in *Liriomyza* (Fig. 55).

Female agromyzids possess a telescoping ovipositor with which they puncture the host plant tissue for oviposition. In the case of leafminers, punctures are made from either the upper or lower leaf surfaces. Many punctures do not contain eggs and are used for feeding on plant sap by both males and females (Potter and Kimmerer 1986; Parrella 1987; Ge et al. 2019a). A study by Bethke and Parella (1985) on *Liriomyza trifolii* found that while females backed over all leaf punctures to feed, the ones made specifically for feeding were fan-shaped, while those made for egg deposition were cylindrical in shape and required fewer abdominal thrusts. It may be that these punctures also play a role in female assessment of leaf suitability or quality for oviposition. Eggs are typically laid singly, although many can be laid on the same leaf with the mines coalescing into what appears to be a single mine with multiple larvae. Oviposition behavior, fecundity, and adult longevity are greatly influenced by nutrition and temperature (e.g. Saito 1988; Minkenberg and Helderman 1990; Scheirs et al. 2001). Survival and development of juvenile life stages are also heavily affected by temperature, which may limit the geographic distributions of some species (Minkenberg 1988; Mujica et al. 2017). Agromyzid species have a single generation a year (univoltine) or multiple generations a year (multivoltine). Parthenogenesis is uncommon in the family, being known only from two related *Phytomyza* Fallén found on Plantaginaceae: *P. plantaginis* Robineau-Desvoidy, a widespread species with bisexual populations in the Palaearctic and Australia, and *P. crassiseta* Zetterstedt, a north temperate species also occurring in Argentina and Chile that also has bisexual populations (Coquilleau et al. 2021).

Unlike some other leafmining taxa, agromyzid leafminers typically cannot exit a leaf and enter a new one, nor, in most cases, do they move between leaves via the petioles. Exceptions occur with some stem miners that oviposit into leaf tissue with the resulting larvae moving through the leaf petiole to the stem (eg. see *Ophiomyia phaseoli* below). In most cases, pupariation occurs after the mature larva makes a characteristic hemispherical exit slit at the end of the mine and drops to the soil. In some agromyzids, pupariation takes place within the leaf, in or adjacent to the actual mine. In most of these cases, the larva pupariates with its

anterior spiracles projecting from the leaf epidermis. This allows the mature fly to use its balloon-like head structure (ptilinum) to push open the operculum of the puparium to exit the mine as if through a trap door. In a few species, the larva appears to have exited the leaf, but instead has tunneled without removing leaf tissue in order to pupate very cryptically a centimeter or so beyond what appears to be the end of the mine. These pupae can be easily overlooked by collectors and presumably by some parasitic wasps who use mine characteristics to locate their hosts. An excellent summary of these strategies is presented in Eiseman (2021).

For any particular agromyzid species, the shape and location of leafmines on a given host species may be consistent and seemingly species-specific (Spencer and Steyskal 1986; Eiseman 2021; Scheffer et al. 2021). Such consistency may be due to selective feeding on or avoidance of particular leaf regions by the larvae (Kimmerer and Potter 1987; Scheirs et al. 2001; Ayabe 2010). There is evidence that leafmine shape, location and degree of contrast with the surrounding leaf surface can influence parasitoid attack (Salvo and Valladares 2004). It is not, however, always the case that leafmines are species-specific on a single host as leaf quality and/or season may influence both mine shape and mine location (Scheffer et al. 2021). Additionally, the leafmines of many species are not especially remarkable. Multiple species of agromyzids may form similar mines on the same host plant species and cannot be differentiated. This is particularly a problem in agricultural ecosystems where polyphagous pests, such as *Liriomyza sativae* and *L. trifolii*, co-occur. The mines of these and other species are not distinguishable across dozens or hundreds of crops they attack, often in the same crops at the same time. Truly definitive identification of all agromyzids must be through dissection of male genitalia or from molecular sequence data.

Detailed studies on movement and dispersal of adult agromyzid pest species have mostly been done on the polyphagous *Liriomyza* species, and these suggest that the flies remain close to their host crops and only move short distances, such as between plants (for example, see Zehnder and Trumble 1984a). Given that several other adult pest agromyzids are similar in size and morphology to *Liriomyza* species, the dispersal behavior of these species is probably similar. However, more generally, adult agromyzids are likely to move over much longer distances aided by wind; for example, Spencer and Stegmaier (1973) suggested that agromyzid adults have moved between islands around Florida in the USA by wind movements. Further to this, and for some species, both adult and immature agromyzids are known to have been moved around the globe with the development of trade and transport. Further information about the movement and dispersal of specific species, where this is known, is included in the species accounts below.

As larvae, agromyzids suffer from numerous sources of mortality, with losses due to parasitism by hymenopteran wasps being among the most important, often reaching levels above 50% in both natural and agricultural ecosystems (Salvo and Valladares 1998). Attack by parasitoids appears to be largely responsible for keeping natural as well as agricultural agromyzid populations at low to moderate levels (Hidayani et al. 2005; Reitz et al. 2013). The primary families of parasitoids attacking agromyzids are Braconidae, Eulophidae, Pteromalidae and Figitidae, with a few additional families being rarely reported (Spencer 1970; Johnson and Hara 1987; Salvo and Valladares 1998; Valladares et al. 2001). The parasitoids attacking agromyzids may be either host-specialists or host-generalists. Those attacking oligophagous agromyzids also can vary in levels of specialization to host plant species and may differentially attack their leafminer host on different plant species (Johnson and Hara 1987; Salvo and Valladares 1997; Tran et al. 2006).

Parasitoid wasps that attack agromyzids typically exhibit one of two broad life history categories, as described in Godfray (1994). Within some mines, the agromyzid larva is or appears to be dead within the unfinished mine, and a smaller parasitoid larva or pupa may be attached or nearby. These parasitoids are ‘idiobionts’ - wasps whose females paralyze a host larva with a sting and then oviposit on the living but immobile larva. The wasp larva consumes the larva and pupates within the mine near or within the larval fly remains. In contrast, ‘koinobionts’ oviposit into a host larva (or for some wasp species, an egg) but do not paralyze it. In this case, the agromyzid larva continues to feed and develop until it pupariates, at which point the wasp larva consumes the contents of the developing fly pupa. Regardless of the lifestyle of the wasps, the newly eclosed wasp adults exit the leafmine or the fly puparium by chewing a small, perfectly circular hole through which they climb out.

Molecular identifications of agromyzids can be made by sequencing the mitochondrial COI “barcode” (or other) DNA region and comparing that sequence to equivalent sequence data of morphologically identified specimens (e.g., Scheffer and Lewis 2005, 2006; Scheffer et al. 2006; Amin et al. 2014; Scheffer et al. 2021). Sequence databases currently hold tens of thousands of sequences from many hundreds of agromyzid species. Agriculturally important agromyzid species are usually accurately represented in these databases, particularly those represented by multiple sequences.

Agricultural importance of Agromyzidae

Agromyzids of economic importance predominantly attack vegetable and floriculture crops. Damage to plants by agromyzids is primarily caused by direct removal of leaf mesophyll due to larval feeding activity (Spencer 1973). In some cases, the oviposition and feeding punctures made by females can also significantly damage host plants by injuring, deforming, and disfiguring leaves, leading to reduced photosynthetic rates (Johnson et al. 1983; Parrella et al. 1985). Oviposition and feeding punctures may also vector viruses and pathogenic fungi and expose tissue to secondary fungal infection (Zitter et al. 1977; Richard and Guibord 1980; Parrella 1987; Bishop et al. 2004; Simoglou et al. 2008; CABI 2015a; PaDIL 2016).

In agricultural crops, extensive leafmining damage can cause reduced growth rates and loss of yield (Spencer 1973; Parrella 1987; Weintraub et al. 2017). In addition to direct loss of photosynthetic tissue to larval feeding, other common effects of heavy leafmining include leaf dropping, withering, disfiguration and discolouration, all of which affect leaf function and general plant vigor (Parrella 1987). Although adult plants can usually tolerate low levels of leafmining damage with negligible impact on output (Levins et al. 1975; Parrella 1987), young plants can be affected by even low levels of leafmining and may be killed (Hofsvang et al. 2005). Outbreak levels of leafminers on crops of any age can lead to severely reduced yields, even total crop loss (Sheppard and Braun 1998; Weintraub et al. 2017). In the case of food and ornamental crops, visible damage of leafmining impacts marketability and leads to economic losses; crops for which low levels of leafmining affect value include those for consumption such as celery (*Apium graveolens* L.) and lettuce (*Lactuca sativa* L.), as well as ornamentals, such as *Chrysanthemum* L. and holly (*Ilex* L.). Further economic damage can occur from losses due to quarantine restrictions placed on exports of infested produce or plants, including possible requirements of phytosanitary measures (Parrella 1987; Reitz et al. 2013).

Detection and control

Here we mention some general points about detection and control that have arisen from studies of specific species; these points may be applicable to other pest agromyzids where there is no specific information available.

The early detection of a leafminer incursion into a crop using sticky traps has commonly been employed for species that attack vegetable and ornamental crops (see the species accounts section). Also, for these species, the first appearance of feeding and oviposition punctures can be used as a sign of attack (Collins and Anderson 2016).

Although many methods have been used to control agromyzid pest populations, the use of insecticides has predominated despite questionable long-term success. The efficacy of many insecticides is limited because the eggs and larvae of agromyzids are protected within the plant. The development of translaminar insecticides, such as abamectin, cryomazine, and spinosyns, has improved chemical control as these can reach juvenile stages within the host (Reitz et al. 2013). However, some pest agromyzids, such as *L. trifolii*, have shown an ability for the rapid development of insecticide resistance (Leibee 1981; Parrella 1987; Ferguson 2004). Also of importance in the management of agromyzids is that applications of insecticides typically inflict more harm on the parasitoid wasp populations than on leafminer populations, resulting in the collapse of natural control dynam-

ics, often leading to devastating outbreaks (Oatman and Kennedy 1976; Johnson et al. 1980a; Parrella 1987; Hidrayani et al. 2005). This can occur even when the leafminers are not the primary target of an insecticide program; in fact, agromyzids are notorious for secondary pest outbreaks where spraying for a different insect pest reduces populations of parasitoid wasps and results in a relatively minor agromyzid pest population growing to often unmanageable levels (Weintraub and Horowitz 1995; Reitz et al. 2013; Weintraub et al. 2017).

Biological control through the use of insect parasitoids has been commonly researched and used in the management of agromyzid pest populations (Salvo and Valladares 2007; Liu et al. 2009), although some work has been done on the potential of other groups of natural enemies, for example, entomopathogenic nematodes (Hara et al. 1993; Liu et al. 2009). Within the native ranges of some agromyzid leafminers parasitoid species diversity can be high and, as mentioned, in some circumstances, these can cause significant mortality of the agromyzid host (Murphy and LaSalle 1999; Mujica and Kroschel 2011; Reitz et al. 2013). A number of classical biological control programmes (i.e., through the introduction of non-indigenous parasitoids in their host's advenive range) have been undertaken, with some notable successes, although most of these have been against the highly polyphagous *Liriomyza* species that attack field vegetable crops (Drea and Hendrickson 1986; Johnson 1993; Liu et al. 2009). Further to this, the use of parasitoids in integrated pest management (IPM) programs, either through the conservation of native species or the introduction of non-indigenous species, has been applied where parasitoids have been combined with targeted insecticide applications and other measures, but this has mostly been in the Americas (Trumble and Alvarado 1993; Mujica and Cisneros 1997). The use of parasitoids for the biological control of agromyzids that attack greenhouse crops has also received much attention in several countries but these programs have resulted in varying degrees of success (Trumble 1985; Parella 1985; van der Linden 2004; Liu et al. 2009) and some species are now available commercially (Liu et al. 2009).

Cultural control through the removal of crop residues has been considered an important component of some agromyzid control programs for annual crop plants. This is because some leafminers may be able complete their life-cycle in the residues (Bosio 1994; Velez et al. 1980; Ridland 2009). With small infestations, it may be possible to remove and destroy leaves containing larvae prior to adult emergence (Virginia Cooperative Extension 2021). Other approaches to agromyzid control include chemical soil treatment (Larew et al. 1985) and the development of agromyzid resistant plant cultivars (Nkhata et al. 2019; Fujito et al. 2021). Guidance on controls for the polyphagous *Liriomyza* Mik species and other major agromyzid pests is available in the Plantwise database (Plantwise 2023).

Polyphagous species

Many pestiferous Agromyzidae target only a highly restricted set of agricultural or ornamental crops, however, the most severe global pests are polyphagous. The 16 polyphagous species of Agromyzidae occur on a wide range of host families, with *L. huidobrensis* now recorded from 49 plant families (Weintraub et al. 2017). Polyphagous species are unsurprisingly found on a spectrum of agriculturally significant crops, occurring with regularity in growing regions and greenhouses. Populations easily accumulate on weeds in and around growing areas or alternate crops, and they are readily dispersed globally through trade within plant tissue and potting soil. Half of the polyphagous Agromyzidae are species of *Liriomyza*, with *Phytomyza* and *Tropicomyia* Spencer making up the rest. Most of these species are treated briefly below and more thoroughly in the Species Treatment section.

The subfamily Phytomyzinae contains the majority of polyphagous species in the genera *Liriomyza* and *Phytomyza*. When comparing the two genera, polyphagy in *Liriomyza* appears to have evolved independently at least four times, and speciation often coincides with major host shifts, while in *Phytomyza*, most polyphagous species appear to be closely related, and major shifts to new host families or genera is far less frequent (Winkler et al. 2009; Xuan et al. 2022). The globally invasive *L. huidobrensis* (Fig. 69), *L. sativae* (Fig. 81) and *L. trifolii* (Fig. 87) are well-understood to be the most problematic and damaging of all polyphagous species in

the family (Parrella 1987; Weintraub et al. 2017). All of these are of New World origin and are now distributed on most continents with the exception of Australia, although quite recently, *L. trifolii* has entered the north of Queensland and Western Australia, and *L. sativae* was found in the Torres Strait islands (Queensland, Australia) (Blacket et al. 2015) and northern Australia (Ridland et al. 2020).

Liriomyza huidobrensis is closely related to a number of polyphagous species. *Liriomyza langei* Frick (Fig. 75) is the likely sister species to *L. huidobrensis*; its distribution is limited to the western United States, primarily in California where it is an important polyphagous pest, although having a much smaller host range than *L. huidobrensis* (Lonsdale 2011). Other polyphagous species related to *L. huidobrensis* include *L. bryoniae* (Kaltenbach) (Fig. 43) and *L. strigata* (Meigen) (Fig. 49). These species are mostly Palaearctic in distribution, with the former extending into the Orient; these attack numerous food and ornamental crops in 112 genera in 29 families and over 200 genera in 35 families, respectively, but mostly occur on Asteraceae and Brassicaceae.

Liriomyza sativae and *L. trifolii* are two New World species that have readily been transported to other parts of the globe via trade and are now essentially ubiquitous. Both species have very broad and partially overlapping host ranges, and each comprise multiple distinct mitochondrial genetic lineages that differ in global distribution and possibly in host use (Scheffer and Lewis 2005, 2006). Currently, the significance of these lineages and whether they represent cryptic species has yet to be determined. *Liriomyza sativae* has hosts in 32 families, preferring a number of ornamentals in the family Asteraceae, and food plants in the families Cucurbitaceae (including cantaloupe (*Cucumis melo* L.), cucumber (*C. sativus* L.) and squash (*Cucurbita* L.)), Fabaceae (beans) and Solanaceae (pepper (*Capsicum* L.), tomato (*Solanum lycopersicum* L.), eggplant (*Solanum melongena* L.) and potato (*Solanum tuberosum* L.)); it is considered a major quarantine pest globally (OEPP/EPPPO 1990). *Liriomyza trifolii* is a smaller, paler pest species often intercepted on *Chrysanthemum*, and is known to attack a wide diversity of ornamental and food crops in 41 families (mostly dicots, but also some monocots), with major hosts in 50 genera of Asteraceae; on *Chrysanthemum* alone, this species resulted in a loss of US\$93m to the industry over five years in the early 1980s (Parrella 1987); it is a common tropical and subtropical pest, but in temperate countries it regularly occurs in greenhouses. In developing nations, these species and *L. huidobrensis* cause enormous economic damage where they are introduced, and climate change is likely to amplify and widen their impact as their range spreads within and between countries (Pratt et al. 2017). The potential of these and other species being spread globally through the cut flower pathway may be minimized considering that these primarily end up in homes where hosts senesce more rapidly and emerged puparia are less likely to complete their life cycle, although those in unsold or discarded/composted hosts may fare better.

There are two additional *Liriomyza* species having broad host ranges. *Liriomyza brassicae* (Fig. 35) is of unknown origin, but it has a nearly cosmopolitan distribution; it occurs regularly on brassicaceous crops, including *Brassica oleracea* L. (especially cabbage, cauliflower and broccoli), but also beans, *Tropaeolum* L. (Spencer 1973; Ipe and Sadaruddin 1984; Gil-Ortiz et al. 2009; Lonsdale 2011) and a handful of genera in at least eight other families. *Liriomyza congesta* (Becker) (Fig. 62) is mostly Palaearctic in distribution, attacking a variety of Fabaceae in 27 genera.

Polyphagous species of *Phytomyza* are the closely related, primarily Old World, *P. horticola* [Palaearctic, Oriental, Afrotropical and Australasian Regions] (Fig. 138) and *P. syngenesiae* [global temperate regions, including the Canary Islands] (Fig. 147). These two species are treated as *Chromatomyia* Hardy in a number of publications, but that genus is now known to be a synonym of *Phytomyza* (Winkler et al. 2009; Lonsdale and Eiseman 2021). *Phytomyza horticola* is highly polyphagous, occurring on at least 237 plant genera, mostly Apiaceae, Asteraceae, Boraginaceae, Brassicaceae, Fabaceae and Lamiaceae (Benavent-Corai et al. 2005; Ortiz 2009; CABI 2016a); this polyphagy, combined with high rates of fecundity (females can lay 100–500 eggs a day for 50 days; Dempewolf 2004) make this a serious pest prone to outbreaks that is likely to be introduced into the New World. *Phytomyza syngenesiae* mostly occurs on Asteraceae, but also Apiaceae and Fabaceae, and is known to be problematic in greenhouses (Dempewolf 2004; Benavent-Corai et al. 2005).

In the subfamily Agromyzinae, polyphagy is uncommon and largely restricted to *Tropicomyia*, which includes a number of known pests: *T. flacourtiiae* Séguy (Africa), *T. polyphaga* (Spencer) (Oriental), *T. polyphyta* (Klein-

schmidt) (Australian), *T. styricicola* (Sasakawa) (Palearctic), *T. theae* (Cotes) (Fig. 172) and *T. vigneae* (Séguy) (Africa). Lists of hosts are available from Spencer (1973), Dempewolf (2004) and Benavent-Corai et al. (2005). Major crops attacked by these species include coffee (*Coffea* L.), tea (*Camellia sinensis* (L.) Kuntze), legumes, *Citrus* L. and cotton (*Gossypium* L.), but problems uncommonly occur due to high rates of parasitism (Spencer 1973).

Currently, it is only the New World species *Liriomyza huidobrensis*, *L. trifolii*, and *L. sativae* that are invasive at a global scale, and even now are continuing to spread. It is not known why other polyphagous and sometimes related species are not presently invasive despite often being abundant and highly damaging where they are present. It is critical that vigilance be maintained in ensuring that these species are not given the opportunity to establish outside of their current ranges, as it is certain that many countries provide conditions highly favourable to their development.

Other pestiferous Phytomyzinae

The European *P. gymnostoma* Loew (Fig. 129) is newly established in northeastern North America (Barringer et al. 2018); it attacks *Allium* L. species by mining in the leaves and sometimes the bulb, especially on leek (*Allium ampeloprasum* L.) and chives (*A. schoenoprasum* L.) (Coman and Cean 2009). The Holarctic *P. fuscula* Zetterstedt and *P. nigra* Meigen (Fig. 157) occur on a number of cereal crops such as corn (*Zea mays* L.), barley (*Hordeum* L.), rye (*Secale cereale* L.) and wheat (*Triticum* L.), but are uncommonly pestiferous despite their broad occurrence and host use (Spencer 1973; Griffiths 1980; Benavent-Corai et al. 2005). *Phytomyza petoei* Hering, 1924 is a Palearctic species that has recently been introduced into North America on *Mentha* L. (Boucher 2009). Damage to ornamental hollies (*Ilex*) are caused by a number of native species in eastern North America, most notably *P. ilicicola* Loew (Lonsdale and Scheffer 2011; Scheffer et al. 2021) (Fig. 153). The European holly leafminer, *P. ilicis* Curtis (Fig. 148) is present in North America on its host, European holly, which was introduced as an ornamental and is now itself invasive in the Pacific Northwest (Jones and Reichard 2009). *Phytomyza krygeri* Hering is a Palearctic species newly invasive in North America on the ornamental species *Aquilegia vulgaris* L., where the larvae feed on seeds and may affect commercial production; the species is already widespread in North America and attacking native columbine (Lonsdale 2017; Eiseman et al. 2021).

Two species of the subgenus *Ptochomyza* Hering are known on asparagus (*Asparagus officinalis* L.) – *P. asparagi* (Hering) (Europe, Palearctic China) and *P. asparagivora* Spencer (southern Europe, Pakistan and Africa) (Lonsdale 2015) - but these are considered to be of little economic importance (Dempewolf 2004).

Other pestiferous Phytomyzinae include *Amauromyza flavifrons* (Fig. 27), another Palearctic introduction to North America (Spencer and Steyskal 1986; Boucher 2012b) that may attack beets (*Beta vulgaris* L.) and spinach (*Spinacia oleracea* L.), but prefers hosts in the family Caryophyllaceae (Scheffer 1999; Dempewolf 2004), including many ornamentals. *Phytobia* Liroy species (Fig. 125) can be occasional pests in tree nurseries, impacting wood strength and appearance, as well as reducing market value (Greene 1914; Spencer 1973; Ylloja et al. 1998). Two widespread species of *Nemorimyza* Frey are oligophagous on Asteraceae, *N. posticata* (Meigen) and *N. maculosa* (Malloch), and while the latter is reported to have caused damage on *Chrysanthemum*, other ornamentals and lettuce, there have been few serious outbreaks (EFSA Panel on Plant Health et al. 2020b; CABI 2021).

Other pestiferous Agromyzinae

Within *Agromyza*, one diverse lineage of Poaceae-feeding *Agromyza* contains several pests of cereal crops, including the Holarctic *A. albipennis* Meigen, the New World *A. parvicornis* (Fig. 18), and the Palearctic *A. megalopsis* (Fig. 9), of which only the latter is usually considered to occur in numbers large enough to be a problem (Dempewolf 2004). These grass crops are usually considered resistant to heavy feeding unless com-

bined with other biotic factors and poor growing conditions, and pests are usually kept to low numbers by parasitoids (Spencer 1973; Wright 1998; also see below). On dicots, some *Agromyza* mine the leaves of non-tree fruit crops – such as *Agromyza fragariae* Malloch (*Fragaria* L.) and *A. idaeiana* Hardy (*Fragaria*, *Rubus* L.), among others – but these are not known to cause appreciable damage (Spencer 1973).

In *Japanagromyza*, *J. tristella* (Thomson) occurs in the Oriental Region into Nepal and parts of Oceania; it forms blotch mines on the upper surface of leaves and leaflets on soybean and several *Pueraria* DC species, with younger plants being more severely affected (Spencer 1973; Dempewolf 2004). *Japanagromyza tokunagai* (Sasakawa) attacks a number of orchid species and can reduce seed production by 96–100%, making it a serious potential threat to commercial production (Suetsugu and Nakahama 2019).

Most species of *Ophiomyia* and *Melanagromyza* engage in stem and seed boring, and a number of these attack legumes, causing considerable damage to major food crops, mostly in Old World tropical and subtropical countries. *Ophiomyia phaseoli* (the “bean fly” - Fig. 100) is a highly important pest of legumes in the Old World tropics, attacking a number of crop species. It is most frequently problematic on the common bean (*Phaseolus vulgaris* L.), but other crops such as soybean (*Glycine max* (L.) Merr.), black gram (*Vigna mungo* (L.) Hepper), mung bean (*V. radiata* (L.) R. Wilczek) and pea (*Pisum sativum* L.) are sometimes hard hit regionally. The damage inflicted by larval feeding of *O. phaseoli* is devastating in many parts of the Old World, especially in tropical and subtropical regions where beans are a staple crop and a key source of dietary protein, leading Spencer (1973) to describe it as “the most serious of all Agromyzid pests”. In an excellent review by Ojwang et al. (2011a), which focused on breeding and genetic resistance of *Phaseolus vulgaris* to the bean fly, the species was determined to be the most important insect pest limiting bean production in sub-Saharan Africa. The bean fly can be especially serious in regions where farmers use traditional pest management practices in marginal conditions, and where there is limited access to chemical insecticides, fertilizers and quality seed. Larvae first mine in the leaves, preferably the cotyledon, and then move to the petiole via the closest vein, sometimes even travelling to the stem and root (Talekar 1990). Larval mining may cause high mortality among plants, especially seedlings and younger, more vulnerable individuals, resulting in severe loss of crop yield that is not much limited by the controlling effects of parasitoids (Dempewolf 2004).

The African *Ophiomyia spencerella* (Greathead) (Fig. 116) is similar to *O. phaseolus* in morphology and larval activity (see details in Greathead (1968) and Dempewolf (2004)); hosts are *Lablab purpureus* (L.) Sweet, *Vigna mungo*, *V. umbellata* (Thunb.) Ohwi & H. Ohashi and *V. unguiculata* (L.) Walp., *Phaseolus lunatus* L. and *P. vulgaris*, with the latter being preferred (Dempewolf 2004). A review by Abate et al. (2000) notes the African endemic *O. spencerella* favours cooler and wetter habitats at higher altitudes, while *O. phaseoli* and *O. centrosematis* (De Meijere) which are more widespread in the Old World tropics, prefer warmer mid-altitude regions; *O. spencerella* also appears to be more problematic in late-sown crops, and *O. phaseoli* is more common early in the season.

Ophiomyia centrosematis occurs in Japan, Africa, Micronesia and the Oriental Region, where it mines in stems and sometimes seed pods, but not the seeds themselves; it attacks numerous Fabaceae and appears to prefer *Pisum sativum*, soy and several *Phaseolus* L. species (Dempewolf 2004; Singh et al. 1981); it is often found alongside *O. phaseoli* and *O. spencerella*, but it is the least serious of the three pests, occurring less frequently and in smaller numbers (Abate et al. 2000).

Ophiomyia kwansonis Sasakawa, a recent invasive to the United States from east Asia, mines in leaves of the ornamental *Hemerocallis* L., reducing market value (Williams and Steck 2011, 2014); populations have also expanded into Canada in the last few years (Lonsdale, unpublished). *Ophiomyia simplex* (Fig. 106) is a Holarctic species introduced to North America that attacks asparagus, an \$89.7m industry in the United States alone (NASS 2016), with sometimes up to nine individuals per plant (Chittenden 1907) that girdle the stalk to crack the epidermis, resulting in plant discoloration, rot and death (Spencer 1973).

Melanagromyza obtusa (Malloch) is an Oriental and east Palaearctic species that is also present in South America, the Caribbean, and Florida (United States). The feeding activities of this species differ from those of the other *Ophiomyia* legume-feeders, described above, in that after a *M. obtusa* egg hatches, the larva first feeds in the surface layers of the seed before it moves deeper into the embryo. A second seed is sometimes sub-

sequently attacked. Additional legumes can serve as hosts, but the primary host is *Cajanus cajan* (L.) Millsp., where damage can reduce crop yield by 5–30%; okra (*Abelmoschus esculentus* (L.) Moench) is sometimes also a host, where the larva bores in the stem and petiole (Venugopal and Venkataramani 1954; Patel and Verma 1974; Sharma and Singh 1984; Rajmohana 1999; Dempewolf 2004).

Some Agromyzidae contribute positively to agriculture in the control of weeds. *Lantana camara* L. is an especially common and noxious weed impacting ecosystems; over 200 biocontrol agents have been released, with the Central American *Ophiomyia lantanae* (Froggart) becoming one of the most widely established (CABI 2016b); *O. camarae* Spencer and *Calycomyza lantanae* (Frick) have also been released as control agents for this plant (Baars and Heystek 2003). Investigations into other stem and seed head-mining Agromyzinae have been conducted, but results are either preliminary or unpromising (Greathead and Milner 1971; Greathead 1984; CABI 1987; Hattendorf et al. 2006; Cortat et al. 2013). The use of *Phytomyza vitalbae* Kaltenbach against *Clematis vitalba* L. in New Zealand appears unpromising (Paynter et al. 2006), as does the use of *Calycomyza eupatorivora* against the widespread weed *Chromolaena odorata* (L.) R.M. King & H. Rob. (Nzama et al. 2014). *Phytomyza orobanchia* Kaltenbach has been successful against *Orobancha* L. in Russia (Spencer 1973), is the main method of biocontrol for this weed in Egypt (Abu-Shall and Al-Eryan 2014) and is establishing elsewhere in regions where *Orobancha* is problematic such as India (Kannan and Pathak 2014). The control of *Tecoma stans* (L.) Juss. ex Kunth involves an undescribed species of *Pseudonapomyza* Hendel from Argentina (Madire, Simelane and Waladde 2010).

Species treatments

Agromyza frontella (Rondani)

“Alfalfa Blotch Leafminer”

(Figs 1–8)

IDENTIFICATION & DIAGNOSIS. As in other *Agromyza*, *A. frontella* has one pair of prescutellar acrostichal setae (Fig. 2) and a stridulatory file on fused syntergites 1+2. It can be differentiated from congeners by having a costa that extends only slightly past vein R_{4+5} (Fig. 3), at least 4 fronto-orbital setae, a reddish to yellowish frons that becomes more yellow anteriorly, and has the orbital plate and ocellar triangle dark, a reddish to yellowish parafacial, gena, scape and pedicel, a dark brown, long-haired male first flagellomere (Figs 1–3; only pubescent anterodorsally in female), 4 long, well-developed dorsocentral setae, a dark brown, lightly pruinose notum and a clypter with the margin and hairs dark. There are several spines along the surstylus, which is shallow and extensively fused to the epandrium (Fig. 5), and the apex of the phallus is divided into two short, cylindrical sections, the basal mesophallus and apical distiphallus, the latter of which is bent downwards and apically membranous (Figs 7, 8); the similar species *A. drepanura* Hering has the distiphallus straight, not bent downwards, the surstylus has 9–10 spines (not 4), and the venter of the mesophallus is produced as a narrower process (see Zlobin (2000: figs 4–8)). Wing length 1.6–2.2 mm. The larva has 8–12 pores on the anterior spiracle and 3 on the posterior spiracle.

DISTRIBUTION. *Agromyza frontella* is relatively widespread in Europe and likely has a broad western to central Palaearctic distribution, with specimens also known from Afghanistan, Israel, Morocco and Tunisia (Spencer 1973; Zlobin 2000; Černý and Merz 2006; Loumerem et al. 2007; Martinez 2013).

It was introduced into eastern North America by at least 1968 when it was found in Massachusetts, and was soon thereafter detected in Ontario, Quebec and other Midwestern states, as discussed in Miller and Jensen (1970) and Venette et al. (1999). It is now known from much of northeastern North America from West Virginia and the Canadian Maritimes to Illinois, west to North Dakota and Alberta (Thompson 1974; Hendrickson and Barth 1978; Plummer and Byers 1981; MacCollom et al. 1982; Spencer and Steyskal 1986; Hutchison et al. 1997; Lundgren et al. 2003; Soroka and Otani 2011), although its actual distribution is likely much broader.

•**Nearctic Region:** Canada (Alberta Manitoba, New Brunswick, Nova Scotia, Ontario, PEI(?), Quebec, Saskatchewan), USA (Connecticut, Illinois, Massachusetts, Minnesota, New Jersey, New York, North Dakota, Ohio, Pennsylvania, Vermont, West Virginia, Wisconsin).

•**Palaearctic Region:** Afghanistan, Austria, Belarus, Czech Republic, Denmark, France, Germany, Hungary, Israel, Italy, Lithuania, Morocco, Netherlands, Norway, Poland, Russia, Slovakia, Spain, Sweden, Switzerland, Tunisia, Turkey, United Kingdom, former Yugoslavia.

HOSTS. *Agromyza frontella* is a leafminer that most often occurs on *Medicago* L., including *M. sativa falcata* (L.) Arcang. (alfalfa) and *M. lupulina* L. (Spencer 1990), but it is also found on *Melilotus* Mill. and *Trifolium* L. (Benavent-Corai et al. 2005), all of which are Fabaceae species in the tribe Trifolieae.

DAMAGE. If larval feeding is partial, leaflets are retained, but more extensive damage causes loss of leaflets and weakening of the plant (Hendrickson and Barth 1978).

Female feeding punctures, which may exceed 250 per leaflet and up to several thousand during the lifetime of the adult (Hendrickson and Barth 1978), also causes the leaf to become brittle, further reducing yield (Soroka and Otani 2011). Oviposition, larval activity and damage caused by female feeding punctures also aids in secondary infection by spring black stem - the fungal pathogen *Ascochyta medicaginicola* Qian Chen & L. Cai [as "*Phoma medicaginis* var. *medicaginis* Malbr. & Roum." - see Richard and Guibord (1980)] - which causes black crown and root rotting in alfalfa (Rodriguez et al. 1990).

In Europe, this species infrequently causes appreciable damage, but it has been highly problematic in North America following its introduction, where alfalfa is widely grown as a forage crop. In North America, reductions in alfalfa yield have been estimated at 7–20%, and in some fields, over 70% of leaflets have been observed with larvae (Venette et al. 1999).

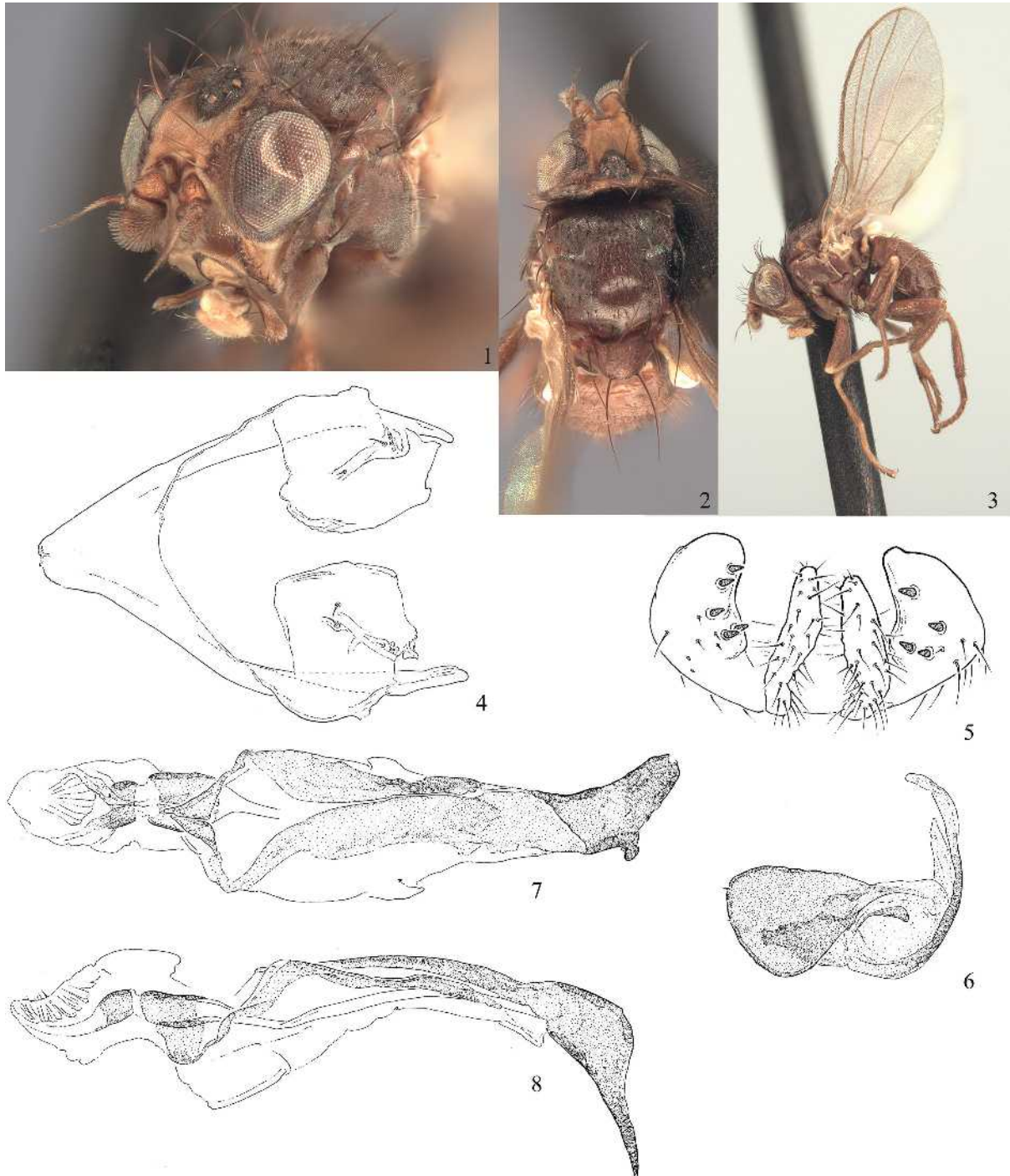
However, Daley and McNeill (1987) from work on alfalfa in Canada, found that overall forage accumulation and net photosynthesis did not differ between plots of uncontrolled and controlled (with insecticides) leafminers, even though the former were at higher densities.

BIOLOGY. This species has a life-cycle typical of leaf-mining agromyzids. Newly emerged females puncture leaflets to feed (Hendrickson and Barth 1978); larval survival is reduced in leaflets with high densities of punctures (Quiring and McNeil 1984a). In alfalfa, the larva is restricted to a single leaflet, where the full-depth mine is initially narrow and linear, following the leaf margin to the apex or sometimes the lateral margin, but then becomes blotch-like as the larva returns to the base via the mid rib (Dempewolf 2004). Many larvae can be found per leaflet and intraspecific competition and cannibalism among first instars is density dependent and results in lower survival rates (Quiring and McNeil 1984b). Pupation is in the soil (Spencer 1973). In Pennsylvania, USA, there are four generations per year (Plummer and Byers 1981).

Mellors and Helgesen (1978) in the USA found the highest immature stage survival at 20°C, but there was little difference in development rates between 20–25°C: the egg stage took 3.5–14 days; the larval stages 5.9–16.4 days; and the pupal stage 15.9–61.5 days. The photoperiod during egg and larval development influenced the initiation of pupal diapause; with a decrease in the light period from 18 to 10 h (tested at 15 and 20°C), diapause increased from less than 5% to greater than 55%. Temperature only affects diapause under a 14 h light period, where more pupae enter diapause if eggs and larvae are reared at 15°C than at 20°C (Therrien et al. 1985).

A female sex pheromone has been reported (Carrière et al. 1988) and there is evidence of an oviposition-detering pheromone produced by females (McNeil and Quiring 1983).

Life table studies of field populations in the USA revealed that the most variable age-specific factors were oviposition and pupal survival of a current season: the former varying between 3–48% of potential oviposition, and the latter from 38–72% in non-diapausing populations. It is suggested that the variation in these factors results from the effects of alfalfa harvests on the environments of the adult and pupal stages (Mellors and Helgesen 1980).



Figures 1–8. *Agromyza frontella* (Rondani), male: **1:** head; **2:** dorsal; **3:** lateral; **4:** hypandrium; **5:** external genitalia, ventral; **6:** pregonite, left lateral; **7:** phallus, ventral; **8:** phallus, left lateral. Note that external genitalia in this and the following images are not to the same scale as the accompanying genitalia images.

MOVEMENT & DISPERSAL. No published information is available, but it is likely that this species shows behaviour typical of leaf mining agromyzids: thus, naturally capable of short distance flights. The transport of infested hosts would facilitate dispersal.

MANAGEMENT. Early detection. General information about this species is provided in a fact sheet produced by University of Wisconsin, Pest Management Program (University of Wisconsin 2016). For

field monitoring, sampling plans for estimating the current egg and larval populations of the leafminer in alfalfa were developed in Canada, including the cost of sampling; recommendations include four leaves taken per stem and 200 stems per field (Harcourt and Binns 1980a). Similar recommendations have been made for the estimation of mature larvae and pupae from soil: the former include the use of 40 pans to catch larvae per field; and the latter, 50 quadrats per field (Harcourt and Binns 1980b). Further to this, temperature-dependent models have been developed to predict the seasonal occurrence of the life stages to facilitate timely management to prevent population outbreaks in Eastern Ontario, Canada (Harcourt et al. 1983).

Control. Early cutting of alfalfa is recommended in Wisconsin, USA (University of Wisconsin 2016). Classical biological control (= introduction biological control) was undertaken in the USA and Canada. Fourteen hymenopterous parasitoids were introduced from Europe in the mid-late 1970s into Delaware, USA, with three species becoming established (Hendrickson and Barth 1979). Pre-parasitism levels before release was 18%, but two of the released species, *Dacnusa dryas* (Nixon) (Braconidae) and *Chrysocharis punctifacies* Delucchi, spread and increased parasitism levels to 72% by the early 1980s, causing leafminer density to fall below economic threshold levels (Drea and Hendrickson 1986; Hendrickson and Plummer 1983). These two parasitoids were distributed to other states in the USA and also into Ontario, Canada in the late 1970s, where similar impacts were recorded (Heimpel and Meloche 2001).

Agromyza megalopsis Hering

“Barley Leaf Mining Fly”

(Figs 9–17)

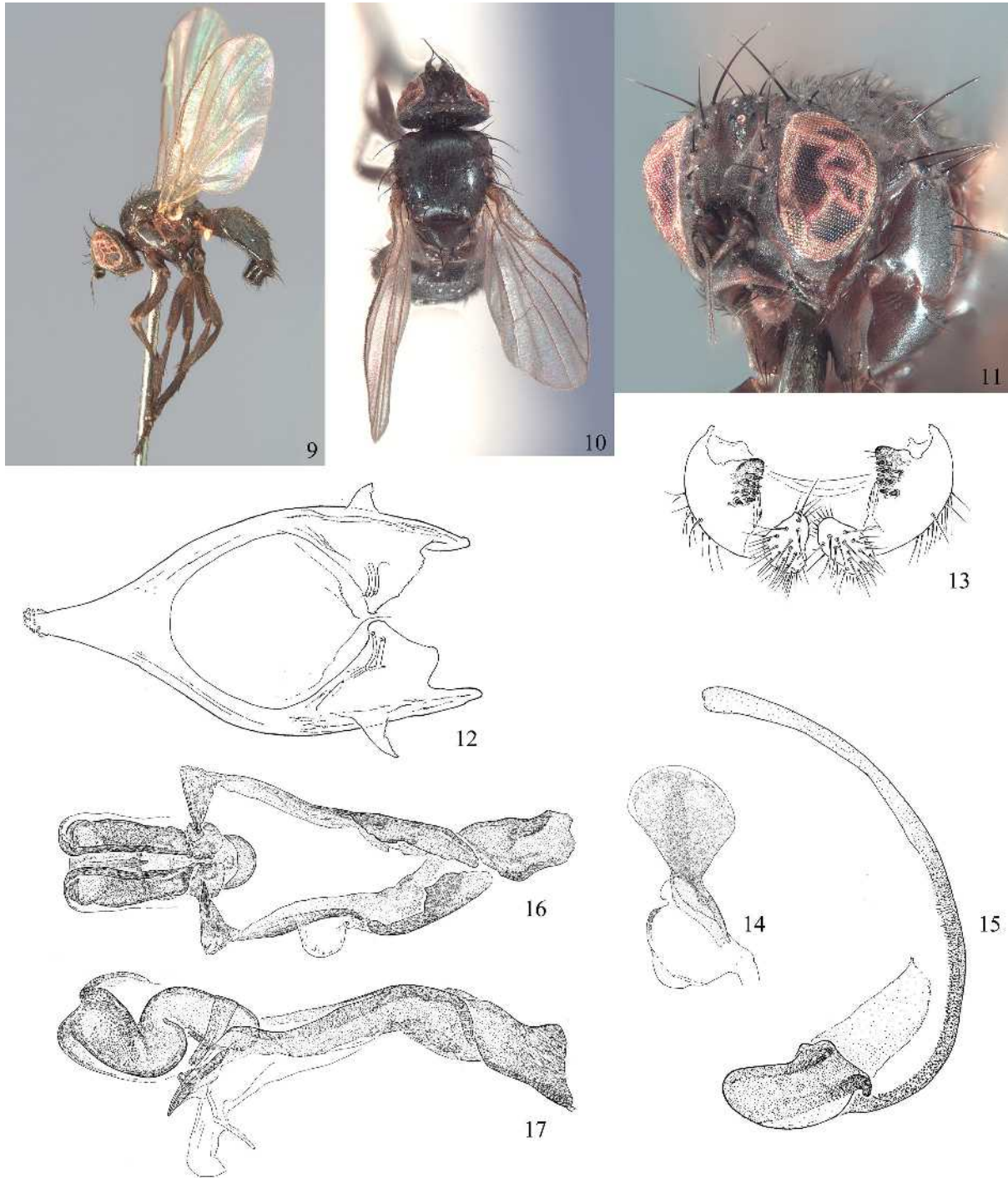
IDENTIFICATION & DIAGNOSIS. Similar to all other *Agromyza*, *A. megalopsis* has one pair of prescutellar setae and a stridulatory file on the lateral margin of abdominal syntergite 1+2 (Fig. 9). Also similar to other grass-feeding species of *Agromyza*, it is mostly brown (Figs 9–11), the male first flagellomere is slightly enlarged and apically haired and the mesophallus+distiphallus is capsule-like and sinuate (Figs 16, 17).

Unlike these other grass-feeders, this species is slightly more shining (Fig. 10), with some specimens almost indistinctly greenish (not green metallic as noted by Dempewolf (2004)), the antenna is black (not brown to dark brown), the parafacial and orbital plate are slightly raised, the costa ends only slightly past vein R_{4+5} (not to M_1), the third dorsocentral is short but well-developed and a fourth and fifth are sometimes obvious, and the apical section of the distiphallus is slightly more elongate. Wing length is 2.5–2.7 mm. The posterior larval spiracles are closely adjoined and with 3 pores (Spencer 1973: fig. 356) – these spiracles are more widely spaced in the highly similar *Agromyza nigrella* (Rondani) (see Spencer (1973: fig. 6)).

DISTRIBUTION. This species is known from the Palearctic Region in much of Europe from Spain to Poland, Turkey and Uzbekistan, as well as Iraq and parts of northern Africa (Spencer 1973; Černý and Merz 2006; Martinez 2013), although is likely more widespread. The known distribution by country is as follows: Bulgaria, Cyprus, Czech Republic, Egypt, Greece (islands), France, Germany, Hungary, Iraq, Poland, Slovakia, Spain (Geigenmüller 1966), Turkey, Uzbekistan, former Yugoslavia.

HOSTS. *Agromyza megalopsis* is a leafminer that likely attacks a number of different Poaceae, but so far it is known from barley (*Hordeum vulgare* L.), and possibly rye (*Secale cereale*) (Spencer 1973).

DAMAGE. *Agromyza megalopsis* is considered the most significant *Agromyza* on cereals in Europe, sometimes co-occurring with other species during outbreaks (Dempewolf 2004). Mined leaves yellow, wilt and sometimes die. Although leaf damage does not always correspond to measurable drops in grain production, yield loss of 27% has been estimated in Bulgaria (Khristov 2000) and 20% in Germany (Spencer 1973).



Figures 9–17. 9–11: *Agromyza megalopsis* Hering, female: **9**: lateral; **10**: dorsal; **11**: head. 12–17: same, male genitalia: **12**: hypandrium; **13**: epandrium, ventral; **14**: ejaculatory apodeme; **15**: pregonite, left lateral; **16**: phallus, ventral; **17**: phallus, left lateral.

BIOLOGY. Spencer (1973) and Dempewolf (2004) referred to studies on the biology of this species (Geigenmüller 1966; Scherney 1966; Weigand 1966; Scherney and Weigand 1967), which has sometimes been referred to incorrectly as *A. nigrella*.

Little recent information is available; most of the following is taken from Spencer (1973). Single females can lay 30–40 eggs. Oviposition is near the leaf base and 30–40 eggs have been recorded from a single leaf.

Individual larvae create a narrow mine to the leaf apex, and then continue back towards the base as a broader, full-depth blotch mine; multiple larvae in one leaf result in merged mines (Ridland 2009). Pupation takes place in the mine but more commonly in the soil. In the former Czechoslovakia, sowing time and the use or absence of fertilizers did not affect the incidence of adults within winter and summer barley (Gallo 1989). In Europe, *A. megalopsis* completes one generation followed by a partial second generation each year; the latter overwinter as pupae (Khristov 2000; Spencer 1973).

MOVEMENT & DISPERSAL. No specific studies have been published but it is likely that the leafminer shows behaviour typical of leaf mining agromyzids; that is, naturally capable of short distance flights around and within a crop (Ridland 2009). Transport of cereals could facilitate dispersal (Ridland 2009).

MANAGEMENT. Early detection. A biosecurity plan for cereal leafminers (including *A. megalopsis*) has been prepared for the grains industry in Australia (Ridland 2009); this covers surveillance, basic biology and control measures to assist with preparedness should an incursion occur.

Control. Residues from crops should be removed and destroyed because leafminers can complete their life-cycle on cut plant material; deep ploughing is an alternative because adult emergence from puparia is reduced (Ridland 2009). In the Czech Republic, the use of the pyrethroid deltamethrin, together with liquid fertilizer on winter barley reduced leafminer populations (Kazda 1997). From a review of insecticide use, such as pyrethroids, carbomates and organophosphates, against agromyzids that attack cereals, Ridland (2009) also notes that these pests have not developed resistance in the same way that the polyphagous *Liriomyza* species have. However, the use of these chemicals may still have longer term negative effects; for example, by reducing parasitoid communities. Spencer (1973), summarizing earlier work, notes that high levels of parasitism from local hymenopterous parasitoids (chalcids and braconids) were reported from Germany in the 1960s. In Hungary, the parasitism rate of an overwintered population was 46%. The main parasitoid species was *Chorebus* Haliday sp. (Braconidae). Parasitized larvae remained in the leaf tissues (Darvas et al. 1984).

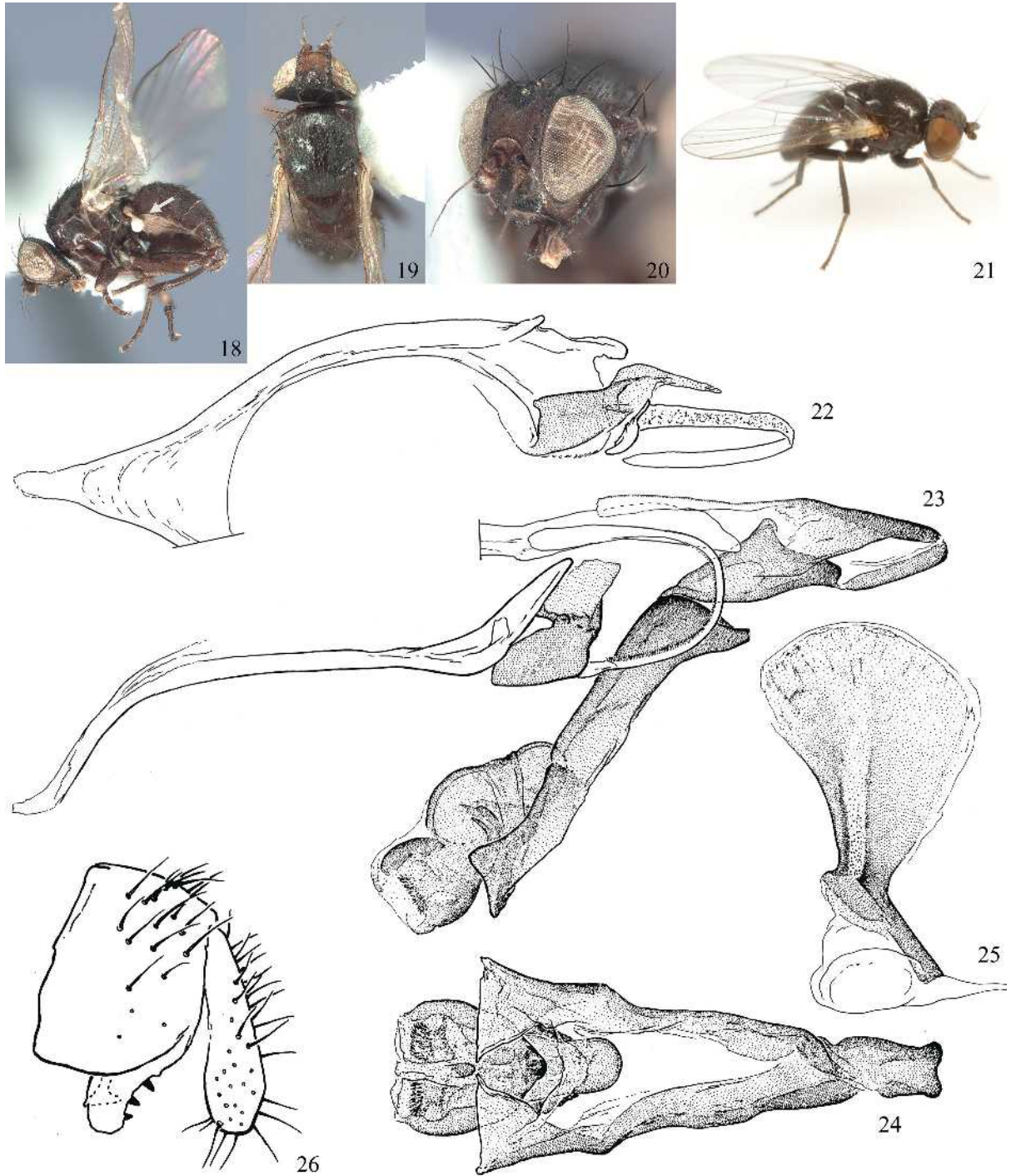
Agromyza parvicornis Loew

“Corn Blotch Leafminer”

(Figs 18–26)

IDENTIFICATION & DIAGNOSIS. Similar to all other *Agromyza*, *A. parvicornis* has one pair of prescutellar setae (Fig. 19) and a stridulatory file on the lateral margin of abdominal syntergite 1+2 (Fig. 18). Also similar to other grass-feeding species of *Agromyza*, it is mostly brown, has only the two posterior dorsocentrals well-developed (remaining setae strongly reduced and sometimes inconspicuous), a slightly enlarged and apically haired male first flagellomere (Fig. 20), a costa that extends to vein M_1 , and a characteristic phallus that has a capsule-like, sinuate mesophallus+distiphallus (Figs 23, 24). *Agromyza parvicornis* differs from the other grass-feeders in having the frons, at least the base of the first flagellomere and most of the gena orange-brown, the surstylus has over a dozen tubercle-like setae (Fig. 26), and the apical section of the distiphallus is laterally swollen and almost circular in appearance when viewed ventrally. Wing length is 2.5–3.2 mm. The posterior larval spiracles have 3 pores (Spencer 1973).

DISTRIBUTION. *Agromyza parvicornis* is widespread in the United States and presumed to be present in most states (Frick 1959). In Canada, it is known from Quebec (Zhu et al. 2004), British Columbia and Ontario (Spencer 1969). Martinez and Etienne (2002) note its presence in the Neotropics in Argentina, Cuba, Guadeloupe, Puerto Rico, the Dominican Republic and Saint Vincent. Reported feeding of *A. parvicornis* on corn in Egypt by Zeinab et al. (1991) is likely a misidentification and requires verification.



Figures 18–26. *Agromyza parvicornis* Loew, male. **18:** lateral; **19:** dorsal; **20:** head; **21:** live; **22:** hypandrium and pregonite, ventral; **23:** hypandrium, pregonite, epiphallus, base of phallopodeme and phallus, left lateral; **24:** phallus, ventral; **25:** ejaculatory apodeme; **26:** external genitalia, left lateral. Arrow indicates the stridulatory file, which is modified from the lateral margin of fused tergites 1 and 2 in both sexes of all *Agromyza*.

Hosts. *Agromyza parvicornis* is a leafminer known from three species of Poaceae: *Echinochloa crus-galli* (L.) P. Beauv., *Panicum miliaceum* L. (millet) and *Zea mays* (corn). The presence of this species on *Echinochloa* P. Beauv. was considered a misidentification by Spencer (1969), and while he later re-listed it as a host (Spencer 1973), this association should be verified by further rearing.

DAMAGE. In corn, larval feeding produces a broad blotch mine that may destroy a young leaf, but up to four larvae in a single developing leaf have been recorded (Spencer 1973) and many more can be found in a mature leaf. Feeding may consume all parenchyma, leaving only the epidermis behind, but in the tougher mature leaves only the lower parenchyma is touched (Spencer 1973; Wright 1998). The attacked leaf, depending on level of infestation, will dry and deform or shrivel, and sometimes die.

Spencer (1973) summarized some historical occurrences of outbreaks of *Agromyza parvicornis*, which are often small, isolated and produce moderate damage. However, instances of more considerable, severe destruction are known. Despite this, low to negligible loss of yield would be expected in corn, even given heavy feeding, unless combined with other biotic factors (Wright 1998) and poor growing conditions.

BIOLOGY. The following is taken from the summary of an earlier work by Spencer (1973), as no significant additional data have been published since that date. Oviposition occurs on the upper or lower surface of a young leaf, often apically, but eggs are laid anywhere on the leaf if mature. The development time of the larva is 10 or more days in the spring, but in the summer when temperatures increase, the time is only about four days. Pupation is external, just below the soil, and adult development takes about 14 days in summer months but several months in the winter.

In temperate regions, adults emerge by May and there are four generations per year. Further south, in Florida, adults emerge earlier (February) and some larval activity can continue through the winter.

MOVEMENT & DISPERSAL. No published information is available, but it is likely that this species shows behaviour typical of other leaf mining agromyzids, being capable of short distance flights. The transport of cereals and other hosts with leaves could facilitate dispersal.

MANAGEMENT. Early detection. General information about this species is provided in a fact sheet produced by the University of Florida, Cooperative Extension Service (Goyal and Nuessly 2008).

Control. Although no published information is available, experience with other cereal-feeding agromyzids suggests that the application of good sanitation methods (removal of crop residues, deep ploughing) in fields post-harvest is likely to reduce its incidence in subsequent seasons. A variation in susceptibility to attack has been shown in different maize cultivars in Egypt (Zeinab et al. 1991), although the target pest was likely misidentified. Goyal and Nuessly (2008) state that no chemicals are registered for the control of this leafminer in the USA. Spencer (1973) notes in a review of older literature that while this pest is expected to be problematic when it accumulates in large numbers, these numbers are generally kept in check by populations of local parasitoids. A review of North American species by Goyal and Nuessly (2008) includes eight species of hymenopterous parasitoids, seven eulophids and one braconid, but this does not include *Opius utabensis* Gahan (Hymenoptera: Braconidae), which was reared from the leafminer in Utah (Gahan 1913).

Amauromyza flavifrons (Meigen)

(Figs 27–34)

IDENTIFICATION & DIAGNOSIS. The setae, abdomen and thorax (lightly pruinose) of *Amauromyza flavifrons* are dark brown, contrasting the head, which is yellowish-orange except for the brown first flagellomere, back of head, palpus, face and clypeus (Fig. 27). The legs are also brown with the apex of the fore femur yellow. There are often 5–6 fronto-orbitals, but sometimes as few as 3 on one side, the postvertical and ocellar setae are strong, nearly equal in length to the fronto-orbitals, there are 4 dorsocentrals, no prescutellar setae and the acrostichal setulae are in four scattered rows. The surstylus is fused to the epandrium and without spines (Figs 28, 29), and the distiphallus is black, bifid and twisted with minute spinules apically on the surrounding membrane (Figs 33, 34). Like other *Amauromyza*, the hypandrium is stout and broadly rounded (Fig. 30) and

the ejaculatory apodeme has a broad, sclerotized “bowl”, although this bowl is pointed in *A. flavifrons* (Fig. 32). Wing length is 1.8–2.4 mm and the costa extends to vein M_1 . The posterior larval spiracle has 3 bulbs, one of which is elongate (Spencer 1973).

DISTRIBUTION. *Amauromyza flavifrons* occurs in the western Palaearctic Region (Spencer 1973; Martinez 2013), but it has been introduced into North America as early as 1964 in Ontario (Boucher 2012) and has spread throughout eastern North America to the west coast from Oregon to British Columbia, likely via accidental human-mediated transport on ornamentals.

•**Nearctic Region:** Canada (British Columbia, Ontario, Quebec), USA (widespread from New York to Minnesota and North Carolina; Oregon; Washington).

•**Palaearctic Region:** Albania, Belgium, Czech Republic, Denmark, Finland, France, Germany, Hungary, Italy, Kyrgyzstan, Lithuania, Netherlands, Norway, Poland, Romania, Russia, Spain, Sweden, Turkey, United Kingdom.

HOSTS. *Amauromyza flavifrons* is a leafminer that is primarily recorded from plants in the family Caryophyllaceae (the “pinks”). Hosts include plants in the genera *Agrostemma* L., *Cerastium* L., *Dianthus* L., *Gypsophila* L., *Moebria* L., *Saponaria* L., *Silene* L. [also records under the synonyms *Lychnis* L. and *Melandrium* Röhl.], *Stellaria* L. and *Vaccaria* Wolf (Benavent-Corai et al. 2005; Dempewolf 2004). Less frequent hosts include *Beta vulgaris* and *Spinacia oleracea* (Amaranthaceae). Laboratory experiments have shown that larval survival on *B. vulgaris* (beets) is lower than on caryophyll hosts (Scheffer 1999a). Genetic variation in larval survival on beets is lower than that of female oviposition choice, suggesting that populations of *A. flavifrons* in beet-growing regions may evolve to avoid oviposition on beets (Scheffer 1999b). Additional plants from which *A. flavifrons* has been reported include *Lepidium* L. (Brassicaceae), *Bidens* L. and *Catananche* L. (Asteraceae) (Gil-Ortiz et al. 2009; Lonsdale, unpublished data).

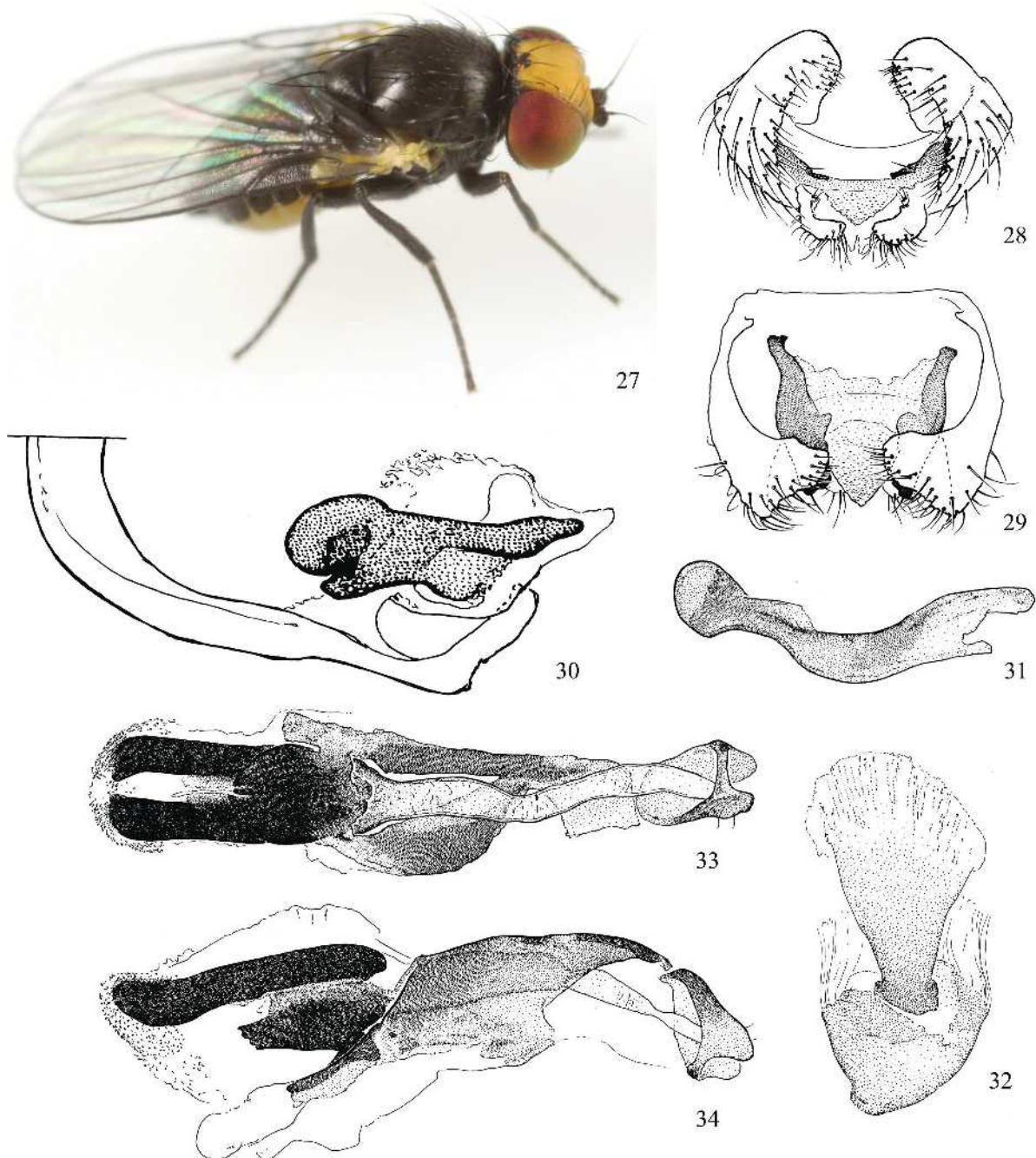
DAMAGE. The larva forms a leaf mine in the upper or lower layer that is initially linear, but then becomes a conspicuous blotch that may obscure the initial linear mine. Individual larvae may move between and feed on both upper and lower mesophyll of the leaf. Multiple mines on single leaves may remove essentially all of the mesophyll. As with most agromyzid leafminers of adult leaves, low levels of abundance appear to have little effect on host plants, but larval feeding associated with large populations can result in significant damage. In the case of the occasional host *Beta vulgaris*, larval survivorship on the plant has been shown to be low (Scheffer 1999b), and damage to this crop is negligible. Potential economic impacts of leafmining to *Dianthus* and other ornamentals may be more pronounced (Spencer 1973) Because the leaves of these hosts, as well as spinach, are integral to crop value and a relatively small number of leaf mines on these can reduce market value.

BIOLOGY. Adult *A. flavifrons* mate within 24 hours of emergence in association with a host plant. Females oviposit through either the upper or lower leaf surface, and this can vary depending on host species. Eggs can be seen directly using a dissecting microscope, making this species amenable to studies of oviposition preferences and behaviours (Scheffer 1999a, 1999b). Larvae exit the leaves in order to pupate in the soil. Generation time in the laboratory is approximately one month, and in the U.S.A., there are multiple generations a year.

MOVEMENT & DISPERSAL. Movement appears to consist of association with the relocation of host plants, which include many commercial and garden ornamentals. Within North America, regional dispersal from household gardens is also likely as several ornamental hosts have naturalized extensively, including *Saponaria officinalis* L., *Silene latifolia* Poir. ssp. *alba* (Mill.) Greuter & Burdet, and *Dianthus*. In the U.S., these naturalized populations commonly support large populations of *A. flavifrons*.

MANAGEMENT. Early detection. A fact sheet on this species is available (Agromyzids of the World 2021).

Control. No specific information is available. *Amauromyza flavifrons* is attacked by a number of parasitoid wasps in the families Braconidae, Eulophidae and Pteromalidae (Spencer 1973). Conservation of parasitoids is likely to be an important means of regulating *A. flavifrons* populations (Spencer 1973).



Figures 27–34. 27: *Amauromyza flavifrons* (Meigen), live female. 28–34: same, male genitalia: 28: external genitalia, ventral (subepandrial sclerite shaded); 29: same, anterior; 30: hypandrium and pregonite, ventral; 31: pregonite, left lateral; 32: ejaculatory apodeme; 33: phallus, ventral; 34: phallus, left lateral.

***Liriomyza brassicae* (Riley)**

“Cabbage Leafminer”

(Figs 35–42)

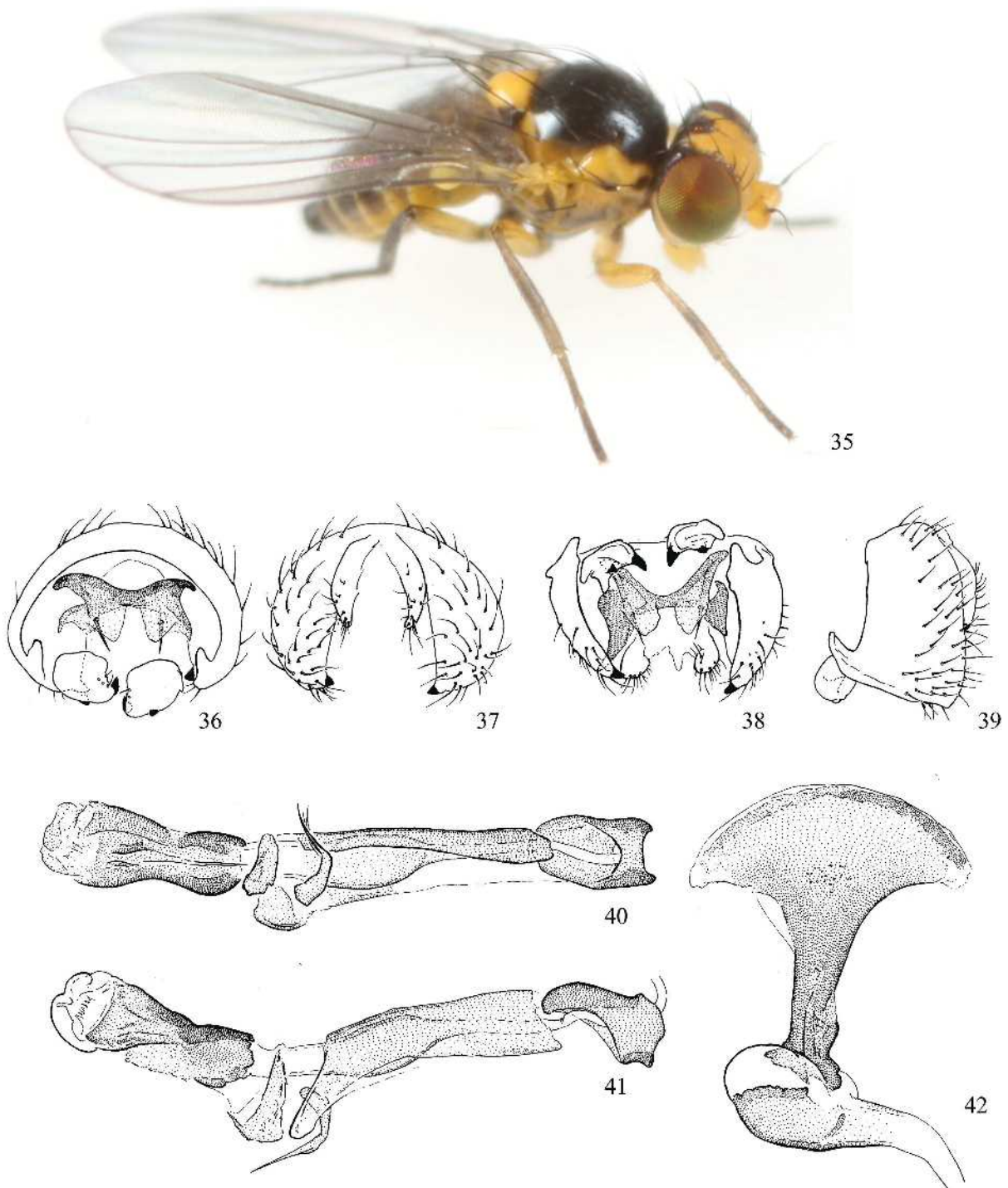
OTHER COMMON NAMES. Serpentine leafminer.

IDENTIFICATION & DIAGNOSIS. *Liriomyza brassicae* is similar to most other *Liriomyza* in having a black notum with the shoulders (postpronotum+notopleuron) and a medial stripe on the scutellum yellow (Fig. 35). Wing length is 1.2–1.8 mm. The phallus is most diagnostic and should be examined for confident morphological identification, with the distiphallus being dark and barrel-shaped (Figs 40, 41)). The lateral margin of the frons along the eye is sometimes very narrowly brown (as in the imaged specimen in Fig. 35), differentiating it from similar pest species. The shape of the phallus sometimes varies slightly, as does external morphology and behaviour, which may be indicative of the presence of cryptic species (Lonsdale 2011; Tavormina 1982).

DISTRIBUTION. *Liriomyza brassicae* has a nearly cosmopolitan distribution as a result of accidental human-facilitated transport. It is widespread in all biogeographic regions, but known distribution is patchy and it likely occurs in many more countries than those listed below (Deeming 2006; Etienne and Martinez 2003; Lonsdale 2011; Malipatil and Ridland 2008; Martinez 2013; Michalska 2003; Sasakawa 1977; Spencer 1977, 1989). It is likely widespread throughout much of the United States (Spencer 1973) and is frequently encountered in southern Quebec and Ontario, making it likely to occur across much of southern Canada. Within China, this species is known from Taiwan (Shiao et al. 1991) and from a female collected in Yunnan (Sasakawa 1986) to be considered suspect, but it is likely present throughout the country.

- Afrotropical Region:** Cape Verde Is., Ethiopia, Kenya, Mozambique, Oman, Senegal, Spain (Canary Islands), South Africa, Yemen, Zimbabwe.
- Australian Region:** Australia (widespread), Bonin Is., Fiji, French Polynesia (Austral Is, Gambier Is), Guam, New Caledonia, New Zealand, Northern Mariana Islands, Papua New Guinea, Solomon Islands, USA (Hawaii), Vanuatu.
- Nearctic Region:** Canada (Alberta, Manitoba, Ontario, Quebec, Saskatchewan), USA (California, Colorado, Florida, Iowa, Maryland, Minnesota, Missouri, Montana, New York, Virginia, West Virginia, Wisconsin).
- Neotropical Region:** Argentina, Brazil, Guadeloupe, Guyana, Martinique, Trinidad and Tobago, Saint Kitts and Nevis, Venezuela.
- Oriental Region:** Cambodia, China (Taiwan, Yunnan?), India (Bihar, Delhi, Maharashtra, Punjab, Rajasthan, Uttar Pradesh), Indonesia, Japan (Ryukus), Malaysia, Philippines, Singapore, Sri Lanka, Thailand.
- Palearctic Region:** Egypt, France, Germany, Malta, Poland, Spain, Iraq, Japan, Romania, Saudi Arabia, Turkey.

HOSTS. *Liriomyza brassicae* is a leafminer that is occurs frequently on Brassicaceae, especially on cabbage, cauliflower and broccoli (*Brassica oleracea*), but sometimes also Fabaceae (*Lathyrus* L., *Pisum* L.) and Tropaeolaceae (*Tropaeolum*) (Gil-Ortiz et al. 2009; Ipe and Sadaruddin 1984; Lonsdale 2011; Spencer 1973). Specimens have also been reared from Apiaceae (*Foeniculum* Mill.), Asteraceae (*Ambrosia* L., *Dablia* Cav.), Capparaceae (*Capparis* L., *Cleome* L. [also as *Gynandropsis* DC]), Caryophyllaceae (*Silene*), Ranunculaceae (*Aquilegia* L.), Resedaceae (*Reseda* L.), Verbenaceae (*Lantana* L.) and Zygophyllaceae (*Bulnesia* Gay). Mines of *L. brassicae* have been recorded on *Erysimum* L., *Lobularia* Desv. (Brassicaceae) and *Nicotiana* L. species (Solanaceae) (see Spencer (1976)), but these records require verification.



Figures 35–42. *Liriomyza brassicae* (Riley), live female. 36–42: same, male genitalia: 36: external genitalia, anterior (subepandrial sclerite shaded); 37: same, posterior; 38: same, ventral; 39: same, left lateral; 40: phallus, ventral; 41: phallus, left lateral. 42: ejaculatory apodeme.

The genera of Brassicaceae known to be attacked by this species are: *Arabis* L., *Barbarea* W.T. Aiton, *Brassica* L., *Cakile* Mill., *Cardamine* L., *Diplotaxis* DC, *Erysimum* L., *Hirschfeldia* Moench, *Isatis* L., *Lepidium*, *Matthiola* W.T. Aiton, *Moricandia* DC, *Nasturtium* W.T. Aiton, *Raphanus* L., *Rorippa* Scop., *Sinapis* L. and *Sisymbrium* L. (Frick 1959; Lonsdale 2011).

DAMAGE. Damage to hosts is usually negligible unless the larvae occur in large numbers; in the latter case when there are multiple larvae per leaf, they may sometimes feed across the entire leaf surface, severely damaging photosynthetic potential. Feeding can destroy younger plants, but mature plants usually fare better, with larvae affecting mostly the outer foliage that will dry and drop off while the plant apex continues to develop (Spencer 1973). Some brassicaceous host species appear to perform better against larvae, with some being “resistant” or “tolerant” (Abdel and Ismail 1999). Degree of damage varies within and across localities and crops, but *L. brassicae* has the potential to grow to pestiferous levels with severe impact. Populations are regularly pestiferous in some areas, such as India, where the species is the most significant pest of *Brassica rapa* L. (as “*Brassica campestris*”; Singh et al. 1991).

BIOLOGY. Adult female flies seem to prefer young, medium sized shaded leaves for oviposition (Ipe and Sadaruddin 1984). Females may show a tendency to oviposit in the host that the population developed on (Tavormina 1982). On *Tropaeolum majus* L. (garden nasturtium), eggs are laid on the lower surface of leaves, generally at the margins (Beri 1974).

Larvae typically form a narrow, mostly linear to irregular or serpentine mine on the lower or upper leaf surface (feeding in the palisade and spongy mesophyll); mature larvae exit the mine for pupation in the soil (Beri 1974; Dempewolf 2004; Spencer 1973). Average development times of the immature stages on *T. majus* at about 28°C are: egg, 7.3 days; larva, 6.6 days; pupa, 9.2 days. Emergence generally takes place in the later hours of the day (Beri 1974).

MOVEMENT & DISPERSAL. Spencer (1973) reported that *L. brassicae* was the “most truly cosmopolitan species known in the Agromyzidae”. It is likely that the distribution of *L. brassicae* was influenced by trade, as with other major *Liriomyza* species of economic importance. However, that the broad distribution of this species was observed well prior to that of even the most polyphagous invasive *Liriomyza* species, suggests that movement via trade cannot fully explain the broad distribution.

MANAGEMENT. Early detection. For field monitoring, some of the information given for *L. sativae* and other polyphagous leafminers (in this volume) may be of relevance for *L. brassicae*.

Control. General information on control is available on the Plantwise database (Plantwise 2015). Plant hosts of low leaf phenolic content are more susceptible to attack but leaves with rough texture may repel oviposition even in plants with low phenolic content (Ipe and Sadaruddin 1984). Abdel and Ismail (1999) found that levels of glucosinolates within various *Brassica* species influence successful leafminer mines. Applications of glucosinolates onto infested cabbage substantially reduced the number of living miners. Singh et al. (1991) report that in India, flooding decreases the incidence of the leafminer in *Brassica rapa* fields and thus may be used as an alternative to insecticides. Early work reported that systemic organophosphates (e.g. phorate) were effective for the control of *L. brassicae* on cotton (*Gossypium* species) in Texas, USA (Davis et al. 1966) but this pest may represent a misidentification of either *L. trifolii* or *L. sativae*. More recent work in India on cabbage and other crops suggests that phenthoate (organophosphate), carbaryl (carbamate) and entomopathogenic nematodes can individually give good control compared with no treatments (Nimbalkar and Borle 1970). However, in Hawaii, USA, the leafminer is resistant to most insecticides apart from the translaminar cyromazine (an insect growth regulator) and abamectin (a neurotoxin) (Crop Knowledge Master 2016). As with other major economically important *Liriomyza* species, *L. brassicae* is attacked by a diversity of local chalcidoid parasitoids. These parasitoid communities exert a good level of natural control: e.g. in early work in California, USA on cabbage (*Brassica oleracea*), average larval parasitism was 67.5% (Oatman and Platner 1969); and in Victoria, Australia, parasitism on Chinese cabbage (*Brassica rapa* var. *pekinensis* (Lour.)) reached 100% within six weeks of mines appearing (Bjorksten et al. 2005).

Liriomyza bryoniae (Kaltenbach)

“Tomato Leafminer”

(Figs 43–48)

IDENTIFICATION & DIAGNOSIS. Similar to most other *Liriomyza*, *L. bryoniae* has a black notum with the shoulders (postpronotum+notopleuron) and a central stripe on the scutellum yellow (Figs 43, 44). Wing length is 1.8–2.1 mm. The species belongs to a lineage of other polyphagous pests including *L. huidobrensis*, *L. langei* and *L. strigata*, diagnosed by a long membranous space between the pigmented section of the ejaculatory duct and the mesophallus, and a small distiphallus that is entirely divided medially, consisting of two short, pigmented tubules. The distiphallus of *L. bryoniae*, however, differs in having the apical tubules more broadly cup-shaped with a short, narrow base (Figs 47, 48) that in some illustrations appears very narrow and more abruptly constricted (e.g. Spencer 1973: figs 304, 305). Externally, this species is much paler than its relatives - the vertical setae are surrounded by yellow, the antenna is entirely yellow (Fig. 45; not including the arista; slightly pigmented in some Egyptian specimens (Spencer 1973)), the anepisternum is yellow with a small anteroventral spot, the brown spot on the katepisternum does not reach the base of the katepisternal seta (Fig. 43; an important character differentiating it from the related *L. strigata*, which has a brown marking behind the eye dorsum extend, or nearly extend to the base of the outer vertical seta (see Figs 50, 51)), and the femora are mostly yellow with sparse brown dorsal streaking.

The larval spiracles are shallowly semicircular with 7–12 pores (Spencer 1973: fig. 307). While adult males are relatively simple to diagnose morphologically, females and larvae are much more difficult, and published sequence data is recommended for comparison - e.g. Kox et al. (2005), Masetti et al. (2006) and Yang et al. (2013).

DISTRIBUTION. *Liriomyza bryoniae* is a widespread pest in the Palearctic Region from Europe to Japan, likely being present in most or all countries where favourable conditions permit development, and extends south into Oriental China, India and Vietnam (EPPO 2014). Wild populations are common in southern Europe and encountered with frequency in glasshouses further north (CABI & EPPO 2015a). Nearctic records have been proven invalid (EPPO 2014).

•**Oriental Region:** China (Fujian, Guangdong, Guangxi, Taiwan, Yunnan, Zhejiang), India (Maharashtra), Vietnam.

•**Palearctic Region:** Albania, Austria (de Jong et al. 2020), Belarus (de Jong et al. 2020), Belgium, Bosnia and Herzegovina, Bulgaria, China (Anhui, Guizhou, Hainan, Hebei, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Sichuan), Croatia, Czech Republic, Denmark, Egypt, Estonia, Finland, France, Germany, Greece, Hungary, Iran (Hazini et al. 2013), Iraq (Saleh et al. 2013), Ireland, Israel, Italy, Japan, Latvia, Lithuania, Malta, Moldova, Montenegro (Radonjić and Hrnčić 2011), Morocco, Nepal, Netherlands, Norway, Poland, Portugal, Republic of Korea, Romania, Russia, Slovenia, Spain, Sweden, Turkey, Turkmenistan, Ukraine, United Kingdom, Yugoslavia (de Jong et al. 2020).

HOSTS. *Liriomyza bryoniae* is a leafminer that feeds on 112 host genera in 29 plant families (Benavent-Corai et al. 2005) including: Alismataceae, Amaranthaceae, Apiaceae, Araliaceae, Asteraceae, Basellaceae, Brassicaceae, Capparaceae, Caryophyllaceae, Chenopodiaceae, Crassulaceae, Cucurbitaceae, Dipsacaceae, Euphorbiaceae, Fabaceae, Gentianaceae, Hydrophyllaceae, Lamiaceae, Loasaceae, Malvaceae, Oxalidaceae, Pedaliaceae, Piperaceae, Polemoniaceae, Primulaceae, Scrophulariaceae, Solanaceae, Tropaeolaceae, Verbenaceae. Most host genera are Asteraceae, Brassicaceae, Cucurbitaceae, Fabaceae and Solanaceae. Populations are frequently pestiferous on cucurbits and tomatoes, but also on cabbage, lettuce and legumes.

DAMAGE. In Europe and the Mediterranean Region, the species is considered a major pest of Asteraceae, Brassicaceae, Cucurbitaceae and Solanaceae, including colder regions where crops are grown in glasshouses (EFSA Panel on Plant Health et al. 2020a). Larval feeding results in lower yield via reduction of photosynthetic

potential, leaf dwarfing, yellowing, drying, drooping and disfiguring, and sometimes fruit dropping and plant death; female oviposition and feeding punctures contribute to damage (Spencer 1973; Dempewolf 2004; CABI & EPPO 2015a). EFSA Panel on Plant Health et al. (2020a) noted that “in tomato, it was seen that yield losses can occur as a result of leafminer infestation but are not dependent on severity of damage alone; proximity to fruit at an early stage of development is very important”. Single larvae have been found to move through the stem via the petiole to multiple leaves if the young leaf / cotyledon is too small to support larval development, and multiple larvae are known to infest single larger mature leaves. Effects on younger plants, especially seedlings, are pronounced (Abul-Nasr and Assem 1961), and control measures in *Cucumis melo* whereby damage was delayed until later in plant development was successful in maintaining crop yield (Cheng 1994b). *Liriomyza bryoniae* is known to transmit the tobacco mosaic virus (Kalutskii 1992).

BIOLOGY. Eggs are laid mostly in the upper surface of cotyledons or young leaves, where larval mines predominate, but sometimes on the lower surface (FSA Panel on Plant Health et al. 2020). Mines are irregular to loose serpentine and not associated with the veins or midrib [see Dempewolf 2004; Spencer 1973 (figs 308–31)]. These mines are difficult to differentiate from those of other polyphagous species such as *L. sativae* and *L. huidobrensis*, although those of the latter more frequently occur along the midrib and lateral veins (Cannon et al. 2012; Spencer 1973). Spencer (1973) reports that larvae usually leave the mines and pupate in the soil, but studies by Saito (1988) on melon found that a higher percentage pupated on the leaves at higher temperatures.

Based on laboratory studies on tomato in the Netherlands, Minkenberg and Helderma (1990) found that the optimum temperature for reproduction and development within the range studied of 15–25°C, was at the upper value. The lower threshold for development was 8°C and that for oviposition, 11°C. The net reproductive rate (R_0) varied from 9 (female eggs per female) at 15°C to 54 at 25°C; and the generation time from 49 to 22 days at the same two temperatures. In Japan, Cheng (1994a) found from studies on musk melons that the respective temperature thresholds for development of egg, larval pupal and total development were 7.05, 7.08, 7.7 and 7.38°C; and that the development times for these stages were 4.7, 93.2, 187.8 and 322.2 day-degrees. No significant development occurred at temperatures above 30°C. The life span of females 3–12 days and the mean eggs laid per female, 171.2.

Linden (1993) found that while the mortality of *Liriomyza bryoniae* pupae during winter months in the Netherlands was high, some can survive a season with 30 frost days and a lowest minimum temperature of minus 11.5°C.

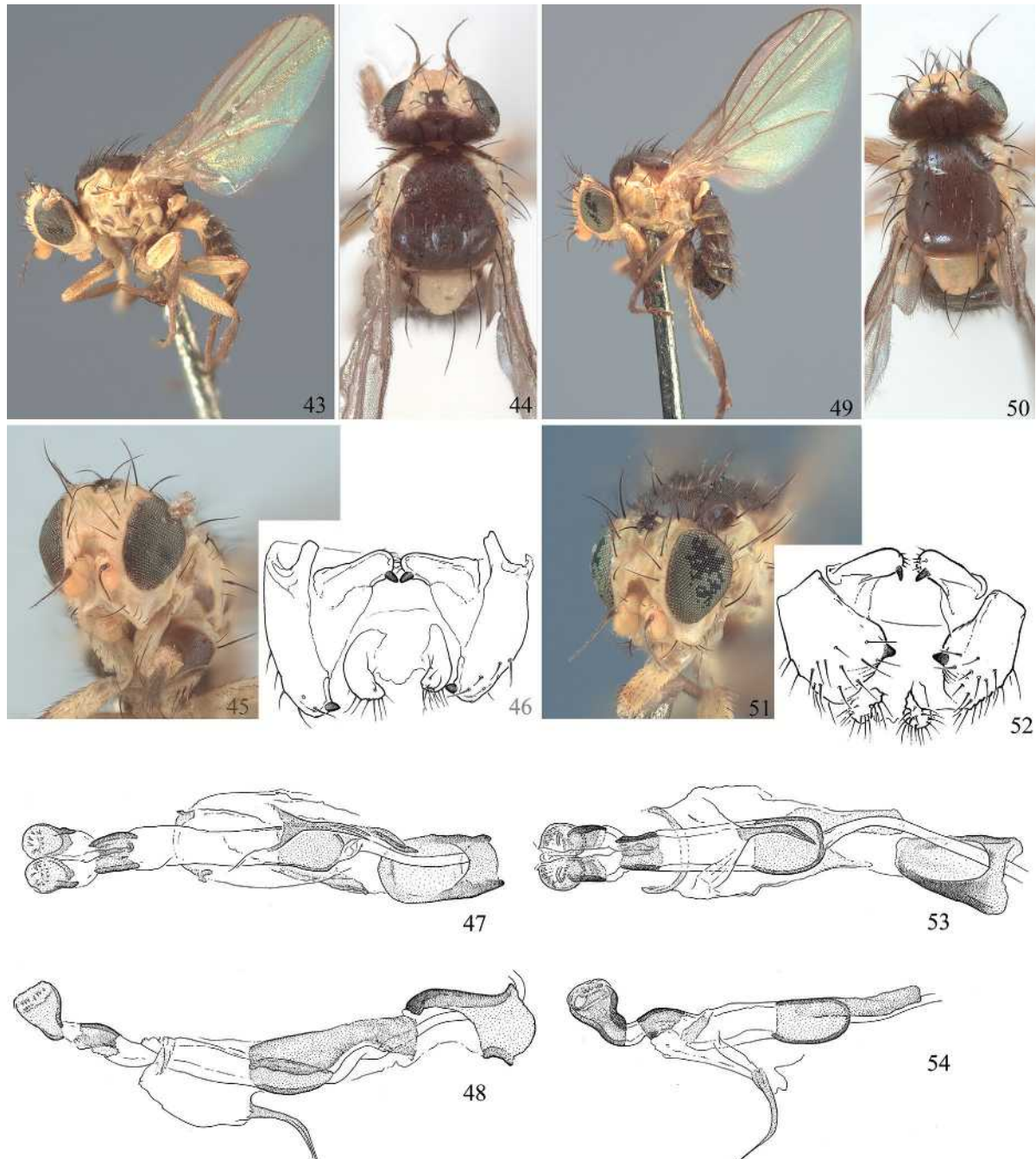
MOVEMENT & DISPERSAL. Cheng (1994a) reports that in Taiwan, adults can travel long distances, facilitated by prevailing winds. On muskmelon plants, adults are most active within the plant canopy. In Japan, flight is diurnal with peaks at 06.00–08.00 and 14.00–16.00 hours.

MANAGEMENT. Early detection. Methods for early detection and subsequent monitoring in Western Europe are reviewed by Bell et al. (2013); yellow stick traps are considered the most efficient means for detecting adults.

Control. Successful trials with trapping in commercial greenhouses in Lithuania using yellow traps with the addition of synthetic methyl salicylate (a known plant-produced volatile compound) have been reported by Būda & Radžiutė (2008). Likewise, in Lithuania, successful trials with the photosensitizer hematoporphyrin dimethyl ether (HPde) used as photopesticides have been undertaken; HPde applied in a feeding bait and then irradiated caused the rapid death of adults, with females dying quicker than males (Lukšienė et al. 2007). Traditional broad spectrum insecticides [e.g. organophosphates (chlorpyrifos); carbamates (oxamyl); pyrethroids (permethrin)] or products developed later from the 1970s (e.g. the growth regulator cyromazine and the neurotoxin, spinosad) have been researched and/or are in use in several countries in the Old World; in general, pyrethroids and carbamates have been effective against adult flies, and cyromazine, spinosad and organophosphates are effective against larvae (Natskova and Karadzova 1990; Tokumaru et al. 2005).

Reitz et al. (2013) summarized the history of resistance development of *Liriomyza* spp. against traditional broad-spectrum insecticides. In the European Union, the horticulture sector had to take steps to reduce insecticide use and develop integrated pest management (IPM) based on biological controls. This was because of the problem of insecticide resistance to broad spectrum products, and because of EU directives enacted in the 1990s relating to the phasing out of insecticides due to high human and environmental risk.

A diversity of hymenopterous parasitoids have been reported from the open field and/or glasshouses in several countries and/or regions; e.g. Western Europe (Nedstam 1983; Spencer 1973); Egypt (Neama et al.



Figures 43–54. 43–48: *Liriomyza bryoniae* (Kaltenbach), male: 43: lateral; 44: dorsal; 45: head; 46: external genitalia, ventral; 47: phallus, ventral; 48: phallus, left lateral. 49–51: *Liriomyza strigata* (Meigen), female: 49: lateral; 50: dorsal; 51: head. 52–54: same, male genitalia: 52: external genitalia, ventral; 53: phallus, ventral; 54: phallus, left lateral.

2014); China – Taiwan (Lee 1990); Japan (Saito et al. 1997). The species reported are mostly from the family Eulophidae (e.g. *Diglyphus* Walker spp.) although a few species are from the Braconidae (e.g. *Dacnusa* Haliday spp.). Much research has been done to underpin the conservation of species or their commercial use to protect glasshouse crops and this includes mass-rearing techniques; this work is reviewed by Liu et al. (2009). Good control has been achieved with *Diglyphus isaea* (Walker) in the Netherlands (Boot et al. 1992) and with a number of species in Russia (Ushchekov et al. 2002). *Diglyphus isaea* and *Dacnusa sibirica* Telenga are available commercially from biocontrol producers in Western Europe. The potential of entomopathogenic nematodes have been investigated in the UK (Williams and Macdonald 1995) and of bacteria in Kuwait (Al-Amad et al. 2001).

Liriomyza chinensis (Kato)

“Stone Leek Leafminer”

(Figs 55–61)

IDENTIFICATION & DIAGNOSIS. Like most *Liriomyza*, *L. chinensis* is black with yellow shoulders (postpronotum + notopleuron) (Figs 55, 56), but the scutum has a greyish pruinosity, the scutellum is entirely black (medially yellow in almost all other *Liriomyza*), the calypter margin and hairs are white, the first flagellomere is pointed anterodorsally and the parafacial and orbital plate are raised (Fig. 57). Wing length is 1.5–1.9 mm. The phallus (Figs 58, 59) is highly diagnostic and much larger than that of similar taxa, with one pair of long dark tubules mostly surrounded by a similarly dark, broad basal sheath with a short, narrow stem (=mesophallus). The surstylus is missing a spine, but this may be represented by the additional spine on the inner-ventral surface of the epandrium (Fig. 60). The larvae have 7–8 pores on the anterior spiracle and 8–10 on the posterior spiracle, similar to *L. cepae* (Hering).

Other *Allium* feeders include the continental European *L. cepae* and *L. nitzkei* Spencer, which are also dark in colouration with a white calypter and an angulate first flagellomere. The former also has an entirely black scutellum, but the margin of the head behind the eye is paler, the coxae and dorsum of the femora are brown, the sheath surrounding the tubules of the distiphallus is a short basal bowl, and the body is larger with a wing length of 2.0–2.5 mm. The latter has a scutellum narrowly to broadly yellow medially, the distiphallus is much smaller with a shallow basal bowl and the mesophallus is considerably longer. While sequence data for these two European species are not available, mitochondrial and nuclear gene sequences exist for *L. chinensis*, which can aid in differentiation from other major crop pests (Chiu et al. 2000; Kox et al. 2005; Scheffer et al. 2006), although external morphological data should be sufficient in these instances. Tokumaru et al. (2021) found two mitochondrial biotypes of *L. chinensis* that may be associated with two different mine types of *L. chinensis* on Welsh onion in Japan.

DISTRIBUTION. *Liriomyza chinensis* is known from the eastern Palaearctic Region and parts of the Oriental Region into southeast Asia, but also recently from France, Germany and Russia (Artokhin 2009; Chen et al. 2003; Dempewolf 2004; Scheffer et al. 2006; Malipatil and Ridland 2008; Pan and Jiang 2001; Santosh and Bhuiya 2014). Within China, there are few records in both the Palaearctic and Oriental Regions of that country, but the species is likely much more widespread. Mines from the Kirghiz Republic have been attributed to this species (Dovnar-Zapolski 1969), but could also belong to either *L. cepae* or *L. nitzkei* (Spencer 1973).

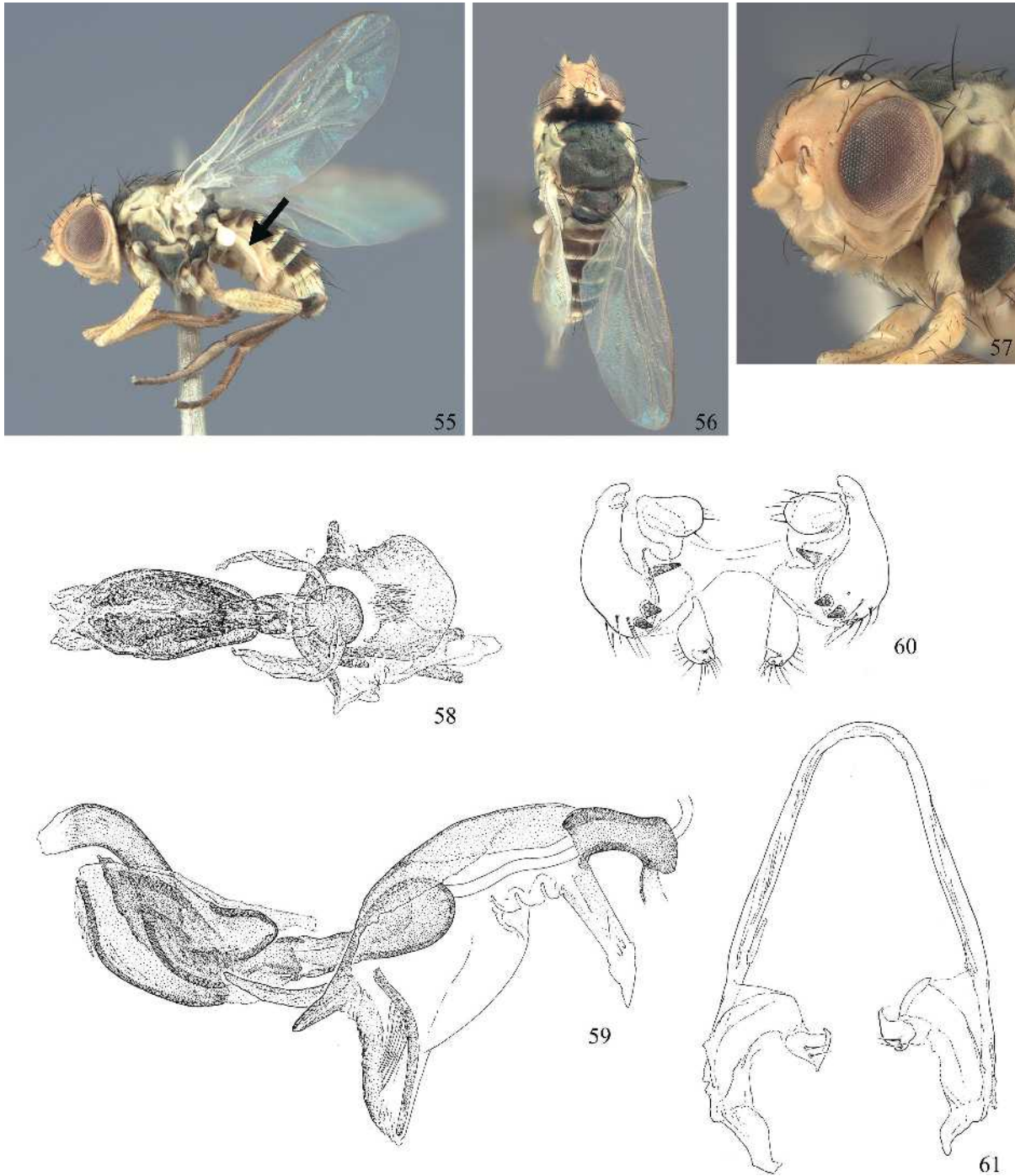
•**Oriental Region:** Bangladesh, China (Taiwan, Zhejiang), Indonesia, Malaysia, Philippines, Singapore, Thailand, Vietnam.

•**Palaearctic Region:** China (Beijing, Inner Mongolia, Shandong), France, Germany, Japan, Kirghiz Republic(?), Republic of Korea, Russia.

HOSTS. *Liriomyza chinensis* is a leafmining pest of *Allium* spp. (Alliaceae), known from *A. ampeloprasum* L., *A. cepa* L., *A. chinense* G. Don, *A. fistulosum* L., *A. odorum* L. (Martinez 1982) and possibly *A. sativum* L. (Dempewolf 2004).

DAMAGE. Larvae of this species lessen the health of plants by mining in and destroying leaves, and in some instances can be a primary crop pest (Ahn et al. 1991). While they can be considered severe pests, outbreaks are infrequent with only local occurrences (Dempewolf 2004).

BIOLOGY. General life cycle is similar to other polyphagous *Liriomyza* species (this volume). In laboratory studies in Japan at 25°C and 16L:8D photoperiod, *L. chinensis* females had an average life span of 9 days



Figures 55–61. *Liriomyza chinensis* (Kato), male: **55:** lateral; **56:** dorsal; **57:** head; **58:** phallus, ventral; **59:** phallus, left lateral; **60:** external genitalia, ventral; **61:** hypandrium, ventral. Arrow indicates the stridulatory file, which is modified from the abdominal membrane in some species of *Liriomyza*.

and laid an average of 108 eggs, and feeding and fecundity peaked at 5 days (Tran and Takagi 2005a); in the same study, development time from egg to adult in the laboratory was 22.6 days and it was found that the time for pupal development lasted slightly longer than the combined egg and larval stages. In further studies on the development time of immature stages (Tran et al. 2007a) it was found that development was inversely proportional to temperature from 15–30°C, ranging from 69.6 days at the former temperature to 17.1 days at the latter; development time began to increase at 32.5°C. The development time from egg to adult was 312.5 day-degrees above a threshold of 11.4°C. Tan and Takagi (2007) showed that cold hardiness of pupae rapidly decreases at low temperatures and extended exposure times: survival is zero below 5°C with 16 days of chilling but rises to 42.9% at 10°C. Using this information, these authors estimated that the species would be able to overwinter in the field in southern Japan, but not in the northern part of the country. The mines may appear continuous, but are sometimes also discontinuous, with the larva alternating between feeding below the epidermis and the inner cell layer along the hollow stem surface (Tokumaru et al. 2021, see Identification, above).

At 22.5°C the net reproductive rate (R_0) was 14.3 days and the generation time (GT) 27.1 days (Tran and Takagi 2005a).

MOVEMENT & DISPERSAL. The possibility for long-distance dispersal is significant if anecdotal evidence is correct in that puparia lodge in the skins of onion and are thus able to be transported internationally (Malipatil and Ridland 2008).

MANAGEMENT. Early detection. No published information is available but some of the information on field monitoring given for *L. sativae* and other polyphagous leafminers may be of relevance for *L. chinensis*.

Control. No published official guidance for control of the pest is available, but Tran and Takagi (2005b) and Tran et al. (2006) assessed conventional insecticide use by farmers for control of *L. chinensis* in Vietnam and Japan. Using field trails and the recommended field rates, cartap (a thiocarbamate), permethrin (a pyrethroid) and phenthoate (an organothiophosphate) were found to have little or no impact on larvae or adults. However, the translaminar insecticide cyromazine (an insect growth regulator) was effective for the control of larvae. Tran and Takagi (2006) reported that the endoparasitoid *Neochrysocharis okazakii* Kamijo (Eulophidae: Hymenoptera) is a dominant natural enemy of the leafminer in Vietnam and provided a report on its biology. In a study of hosts suitable for mass-rearing of this parasitoid for augmentative releases, Tran et al. (2007b) showed that *L. trifolii* is more suitable than *L. chinensis* because the intrinsic rate of increase (r_m) of the parasitoid is higher on the former.

Liriomyza congesta (Becker)

“European Pea Leafminer”

(Figs 62–68)

IDENTIFICATION & DIAGNOSIS. *Liriomyza congesta* is similar to other *Liriomyza* externally in having a black notum with the shoulders (postpronotum+notopleuron) and a wide medial stripe on the scutellum yellow (Figs 62, 63). Wing length is 1.3–1.7 mm. Similar to many other species, including other Fabaceae-feeders, it has a lightly grey pruinose scutum, two rows of acrostichal setulae (not four), and pale colouration including a wide yellow space on the head around the base of the vertical setae (not brown) (Fig. 64), a yellow anepisternum with a small brown anteroventral spot, a small brown spot on the katepisternum that does not reach the base of the katepisternal seta and yellow femora that are narrowly brown basally. Due to this external similarity to congeners, examination of the male genitalia is required for confident diagnosis: the phallus includes a dark stem-like mesophallus and a broad, bowl-shaped distiphallus enclosing one pair of short, wide tubules (Figs 65, 66). Typical of a species in the *L. bieracii* group, a dark bar with a terminal spine can be seen inside the ventral surface of the epandrium (Fig. 67). The posterior larval spiracle has 3 pores.

A similar phallus is seen in the Nearctic *Liriomyza fricki* Spencer (Lonsdale 2011: Figs 106, 107), which also feeds on a variety of Fabaceae, but the distiphallus of this species is much larger, bulging dorsally across the surface of the mesophallus, and the inner surface of the “bowl” is minutely textured (not smooth).

Liriomyza pisivora Hering also occurs on *Lathyrus* and *Pisum* in Europe, but the anterior two dorsocentrals are setula-like, the posterior larval spiracle has 7–8 pores (Spencer 1973) and the phallus is highly derived (see Dempewolf (2004) and Spencer (1973: figs 132–133)).

DISTRIBUTION. *Liriomyza congesta* is widespread across the Palaearctic Region, especially in Europe and North Africa, with most cases of crop damage occurring in Mediterranean countries; it has also been found in the southern Arabian Peninsula and India (Kashmir) (Dempewolf 2004; Deeming 2006; Černý 2013; Martínez 2013). Early records of this species in the New World are misidentifications of *L. trifolii* (Burgess) (Spencer 1973).

•**Afrotropical Region:** Oman, Yemen.

•**Oriental Region:** India (Kashmir).

•**Palaearctic Region:** Afghanistan (Spencer 1976), Albania, Andorra, Austria, Belgium, China (Ningxia) (Liu et al. 2005), Croatia, Czech Republic, Cyprus, Denmark, Egypt, Estonia, Finland, France, Germany, Greece, Hungary, Iran (Dousti 2010), Iraq (Saleh et al. 2013), Ireland, Israel, Italy, Japan, Republic of Korea, Latvia, Lithuania, Malta, Moldova, Netherlands, Norway, Poland, Portugal (mainland, Madeira), Romania, Russia, Slovakia, Spain (mainland, Canary Islands), Sweden, Switzerland, Turkey, United Kingdom and the former Yugoslavia.

HOSTS. *Liriomyza congesta* is a leafminer that feeds on 27 genera of Fabaceae (Benavent-Corai et al. 2005), including: *Anthyllis* L., *Astragalus* L., *Caragana* Fabr., *Cicer* L., *Colutea* L., *Coronilla* L., *Glycine*, *Glycycirrhiza* L., *Hippocrepis* L., *Hymenocarpus* Savi, *Lathyrus*, *Lens* Mill., *Lotus* L., *Lupinus*, *Medicago*, *Melilotus*, *Onobrychis* Mill., *Ononis* L., *Ornithopus* L., *Oxytropis* DC, *Phaseolus*, *Pisum*, *Robinia* L., *Scorpiurus* L., *Trifolium*, *Trigonella* L., *Vicia* L. *Lathyrus*, *Pisum* and *Vicia* are considered primary hosts (Spencer 1973, 1990). Specimens have also been reared from Spanish *Euphorbia* L. (Euphorbaceae) (Docavo et al. 1987).

DAMAGE. Populations uncommonly occur in numbers sufficient enough to cause more than minor damage (Spencer 1973), although outbreaks sometimes occur where the mines can cover most of the leaf surface and severely impede photosynthetic potential, weakening the plant and reducing fruit production. In Egypt, it has been considered one of the most important pests of *Vicia faba* L. (El-Khouly et al. 1997b).

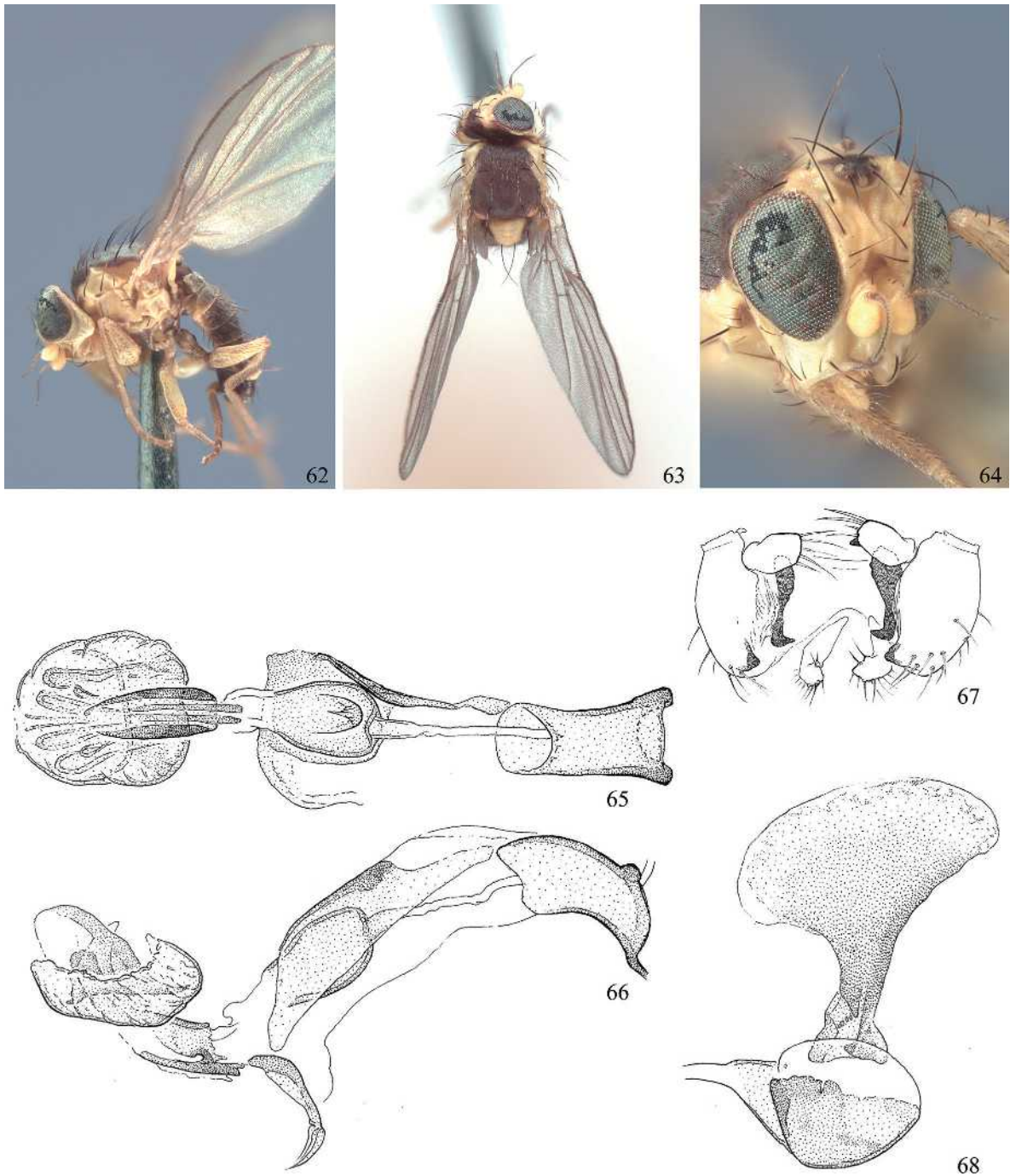
BIOLOGY. Dimetry (1971) published aspects of the life cycle and biology of this species on *Vicia faba* in Egypt. It was misidentified as *L. trifolii* even though Spencer (1965) had clarified that the pest species on this host in Egypt was *L. congesta*.

Mating takes place shortly after adult emergence: 8 hours in summer (May – June) and 1.6 days in winter (February). Eggs are typically located on the lower surface of primary and secondary leaves. The larvae create a linear to irregular mine on the upper surface of the leaf, usually with one larva per leaf. In the laboratory, duration of female oviposition period as well as fecundity are influenced by nutrition quality and temperature. Oviposition period primarily depends on temperature, ranging from 5–11 days in the summer and 7–23 days in the winter. Fecundity is greatly influenced by nutrition. Under laboratory conditions, maximum egg production was at 20°C and unfed females provided with only distilled water produced no eggs. Females fed with honey produced a mean of 135 eggs, those fed with sugar and yeast produced a mean of 79 eggs, and those fed with sugar solution produced a mean of 55 eggs. Overall, adults provided with a mixture of sugar and yeast lived longer (approximately 24 days females and 19 days males) than those without food.

Dimetry (1971) found that development times of immature stages in the laboratory were inversely proportional to increasing temperature from 20–35°C. At 20°C, the egg stage lasted a mean of 4.9 days, the larval stage

a mean of 10.4 days and the pupal stage a mean of 12.7 days. Pupation takes place outside the leaf and usually in the soil below the plant. Temperature and humidity both influence survival of the pupae with the optimum conditions for adult emergence being 20°C and 100% R.H. El-Khouly et al. (1997a) also reported that ambient temperature and RH account for changes in the population density of larvae on broad bean in the field.

MOVEMENT & DISPERSAL. No available published data, but horticultural trade involving peas may pose a risk of human aided dispersal.



Figures 62–68. 62–64: *Liriomyza congesta* (Becker), female: 62: lateral; 63: dorsal; 64: head. 65–68: same, male genitalia: 65: phallus, ventral; 66: phallus, left lateral; 67: external genitalia, ventral (internal process of epandrium shaded); 68: ejaculatory apodeme.

MANAGEMENT. Early detection. For field monitoring, some of the information given for *L. sativae* and other polyphagous leafminers may be of relevance for *L. congesta*.

Control. Several authors (Bastawisy et al. 1998; El-Khayat 1998; El-Khouly et al. 1997b) report variability in resistance between *Vicia faba* cultivars in Egypt with some cultivars showing reasonable degrees of resistance. Grill (1979) states that yellow sticky traps have been used successfully in France to control adults in glasshouse ornamentals production. Abbasi, Ghassemi-Kahrizeh and Hosseinzadeh (2021) investigated the effects of planting date and cultivar on yield in *Cicer arietinum* L. in Iran and found significant effect of both as well as their interaction. Several organophosphates have been trialed on *V. faba* in Egypt but the work is quite old and recent updates are not available. Among the more effective were fenthion and phosalone (contact insecticides) and formothion and methamidophos (contact and systemic action insecticides) (Assem et al. 1975; El-Kifl et al. 1974; Rizkalla et al. 1970). More recent trials of generally more effective insecticides were made against *Liriomyza trifolii*, including the neurotoxin abamectin (Saad et al. 2007) and may be effective for use against *L. congesta*. In Egypt, *L. congesta* on *V. faba* is attacked by several local chalcidoid (Hymenoptera) parasitoids (Hafez et al. 1974) including larval parasitoids (*Diglyphus* sp. and *Hemiptarsenus zilabisebessi* Erdős) and pupal parasitoids (*Opius* Wesmael sp. and *Halticoptera* Spinola sp.). *Diglyphus* sp. and *Opius* sp. were common throughout most of Egypt. Parasitism of the leafminer was recorded on beans plants not long after the first infestations of the leafminer were observed, reaching a rate of 75% towards the end of the growing season.

***Liriomyza huidobrensis* (Blanchard)**

“Pea Leafminer”

(Figs 69–73)

OTHER COMMON NAMES. Serpentine leafminer; South American leafminer; potato leafminer; minador de la hoja, minador pequeño, mosca minadora (Spanish).

IDENTIFICATION & DIAGNOSIS. *Liriomyza huidobrensis* is a relatively dark species of *Liriomyza*, the species of which are usually characterized by a black notum with yellow shoulders (postpronotum+notopleuron) and a yellow medial stripe on the scutellum (Figs 69, 70) (as for the related *L. langei* – Figs 74, 75). In this species, described and illustrated in Lonsdale (2011), wing length is 1.9–2.7 mm, black pigment covers most of the pleuron (at least the dorsal 1/3 of anepisternum is yellow), all of the abdominal tergites, and most, if not all of the femora exclusive of the apices. The acrostichal setulae are also usually in 2–3 rows (less commonly 4), and the posterolateral corner of the frons is dark to at least the base of the outer vertical seta.

The genitalia are characterized by a phallus with a long, clear section of the ejaculatory duct in between its subapical pigmented section and the mesophallus, and the distiphallus is entirely split into two short, dark tubules (Figs 72, 73). A similar phallus occurs in other pestiferous species, including the predominantly Nearctic *L. langei* Frick (Figs 79, 80), which was once considered conspecific but was resurrected from synonymy and recharacterized by Scheffer (2000), Scheffer and Lewis (2001) and Lonsdale (2011). *Liriomyza langei* always has 4 rows of acrostichal setae (Fig. 74), there is a slight gap between the pigmented section of the ejaculatory duct and the hypophallus (Lonsdale (2011: figs 129–131)), and the orbital plate is usually darker. Morphological diagnosis is problematic, however, especially considering the degree of overlap between the two species, and molecular techniques for differentiation is recommended whenever possible. Recommended methodologies were presented in Scheffer et al. (2001), Nakamura et al. (2013) and Scheffer et al. (2014). The Nearctic *L. trifoliarum* Spencer, also an occasional pest on Fabaceae and *Solanum* L., is similarly dark and with a similar phallus, but the paraphalli are larger, triangular, divergent and wing-like (Lonsdale 2011).

Similar related polyphagous pests in the Old World include *Liriomyza bryoniae* (Fig. 43) and *L. strigata* (Fig. 49), which are paler and have an apically widened distiphallus.

Larvae are small and typically maggot-like. The posterior spiracle forms a crescent with six to nine raised pores (Spencer 1973: fig. 319).

DISTRIBUTION. *Liriomyza huidobrensis* is native to cooler highland areas in South America (Steck 1996), and maybe also Central America (Scheffer and Lewis 2001; Lonsdale 2011; but see Weintraub et al. (2017)). It is now widespread globally due to human-facilitated transport (Lonsdale 2011; EPPO 2014), at first likely via the flower trade, as discussed in Weintraub et al. (2017). Its recent appearance in Sydney (New South Wales Department of Primary Industries 2020) marks a new milestone in continental dispersal. It is competitive with other sympatric invasive leafminers in cooler climates or higher elevations (Tantowijoyo and Hoffmann 2010). Occurrences in North America are surprisingly few, although populations have been problematic in glasshouses in Canada, and there are several records from California (Lonsdale 2011). Subsequent surveying of Californian crops by Scheffer (et al. 2014), however, suggests that these Californian records are misidentifications, and that there is no evidence for the presence of the species in that state.

- Afrotropical Region:** Comoros, Kenya, Mauritius, Réunion, Seychelles, South Africa, Tanzania, Zambia, Zimbabwe.
- Australian Region:** Australia (NSW (New South Wales Department of Primary Industries 2020)), Easter Island, Guam.
- Nearctic Region:** Canada (possibly restricted to glasshouses in Alberta, British Columbia, Ontario, Nova Scotia).
- Neotropical Region:** Argentina, Belize, Brazil (Goiás, Minas Gerais, São Paulo), Chile (widespread, inc. Juan Fernandez Isl.), Colombia, Costa Rica, Dominican Republic, Ecuador, El Salvador, French Guiana, Guadeloupe (not established), Guatemala, Honduras, Mexico (Mexico State?), Nicaragua, Panama, Peru, Uruguay, Venezuela.
- Oriental Region:** Bangladesh, Cambodia (presence uncertain, intercepted on exports), China (Fujian, Guangdong, Yunnan), India (Uttar Pradesh), Indonesia (Java, Sulawesi, Sumatra), Malaysia, Philippines, Singapore, Sri Lanka, Taiwan, Thailand, Vietnam.
- Palearctic Region:** Arabian Peninsula, Austria, Belgium, Bulgaria, China (Gansu, Guizhou, Hebei, Hubei, Inner Mongolia, Shaanxi, Shandong, Sichuan, Xinjiang), Crete, Croatia, Cyprus, Czech Republic, Korea (Democratic People's Republic of), Finland, France, Germany, Greece, Hungary, Israel, Italy, Japan, Jordan, Korea (Maharjan et al. 2014), Lebanon, Malta, Montenegro, Morocco, Syria, Poland, Portugal, Serbia, Spain, Sweden (intercepted only), Switzerland, Turkey. Eradicated from Denmark, Ireland, Lithuania, Norway, United Kingdom.

Hosts. *Liriomyza huidobrensis* is a broadly polyphagous leafminer that feeds on many food and ornamental crops. It attacks at least 365 plant species in 49 families (Weintraub et al. 2017): Adoxaceae, Aizoaceae, Alstroemeriaceae, Alismataceae, Amaranthaceae, Amaryllidaceae, Apiaceae, Apocynaceae, Araceae, Araliaceae, Asparagaceae, Asphodelaceae, Asteraceae, Balsaminaceae, Basellaceae, Brassicaceae, Campanulaceae, Caryophyllaceae, Convolvulaceae, Cucurbitaceae, Euphorbiaceae, Fabaceae, Gentianaceae, Gesneriaceae, Hydrangeaceae, Iridaceae, Lamiaceae, Liliaceae, Linaceae, Malvaceae, Menispermaceae, Moraceae, Onagroideae, Oxalidaceae, Papaveraceae, Plantaginaceae, Plumbaginaceae, Poaceae, Polemoniaceae, Polygonaceae, Portulacaceae, Primulaceae, Ranunculaceae, Rosaceae, Scrophulariaceae, Solanaceae, Tropaeolaceae, Verbenaceae, Violaceae. Studies have reported preferences for some species of host plants, especially within Solanaceae (eg. Okoth et al. (2014)) and Fabaceae (eg. Baoping et al. (2006), Videla et al. (2006); but see Martin et al. (2005)), but females can oviposit in a variety of available hosts to produce robust offspring, although performance measures will vary to some degree (Martin et al. 2005).

Due to historical difficulties in differentiating *Liriomyza huidobrensis* from *L. langei*, published host records from the Nearctic are sometimes confused for the two taxa, but this issue was largely resolved by Lons-

dale (2011). Since *L. langei* is now known to have a restricted distribution (western USA, Hawaii, possibly Mexico), published records of these taxa from the Old World (excluding Hawaii) and eastern North America actually refer exclusively to *L. huidobrensis*.

DAMAGE. Damage to several vegetable crops (e.g. beans, peas, potato, tomato) and ornamental plant species have been reported largely from the open field in subtropical and tropical regions and from protected horticulture in temperate climates (CABI 2015b). Field potatoes have been particularly badly affected and the leafminer remains an issue on this and other crops in many countries and regions including Peru (ICIPE 2015; Mujica and Kroschel 2011), Argentina, Brazil, Costa Rica, Guatemala (Weintraub et al. 2017), Kenya (Foba et al. 2015; ICIPE 2015) and Indonesia (Rauf et al. 2000; Shepard et al. 1998). Severe outbreaks of the pest in Israel in the early 1990s (Weintraub and Horowitz 1995) subsided after very high temperatures in 1998 and it is now considered an occasional pest (Weintraub 2001a). Likewise, field grown *Pisum sativum* cultivars (sugar and snow peas) for export markets in Kenya are affected and this threatens the livelihoods of small holders who rely on horticultural cash crops for income (Gitonga et al. 2010).

In temperate Europe, *Liriomyza huidobrensis* became a pest from the late 1980s and early 1990s on protected horticulture but also on outcrops in the Mediterranean region (CABI 2015b). Crops affected include: *Chrysanthemum*, *Primula* L., *Verbena*, lettuces, beans, *Cucumis sativus* L., *Apium graveolens* and squashes/pumpkins (CABI 2015b).

Mining activity in the leaves of infested plants causes a reduction in photosynthetic activity (Parrella 1987). This can lead to a delay in the development of young plants, yield loss and leaf damage in ornamental plants (CABI 2015b; Parrella 1987). On *Solanum tuberosum* (potato), larval infestations start in the lower part of the plant, but damage is not as severe in growing plants as fully mature plants (Mujica and Cisneros 1997). There is a correlation between the presence of *Liriomyza huidobrensis* and the pathogenic fungus *Alternaria solani* Sorauer on potato (Soares et al. 2019).

BIOLOGY. The biology of this species has been recently reviewed by Weintraub et al. (2017). The life cycle is similar to other multivoltine agromyzids. Considerable research on the effects of temperature on oviposition, longevity, and larval growth and survival (Olivera et al. 1993; Chen and Le 2004). Host plant leaves are punctured by adult females for feeding and eggs are laid just below the leaf surface (Mujica and Cisneros 1997). Both feeding and oviposition are favoured by cooler temperatures (Olivera et al. 1993). The larvae of *L. huidobrensis* mine the chloroplast-containing spongy mesophyll layers, disrupting photosynthesis more than other leafminers that mine the palisade mesophyll layer (Parrella 1987). The larval mines are usually close to the leaf midrib and lateral veins (CABI 2015b). In Peru, females lived 3–28 days and males 2–6 days. Females laid an average of 117 eggs in winter and 161 in the spring. The egg stage lasts 3–4 days, the first instar larval stage 3–4 days, the second instar larval stage 2–3 days, the third instar larval stage 3–4 days, and the pupal stage 12–18 days (Mujica and Cisneros 1997). On lettuce as a host, the estimated minimum developmental temperature thresholds for the three larval stages and pupal stage were 5.4, 6.3, 6.2 and 5.7°C respectively; and the day-degree days for these stages were 84.3, 30.1, 58.9 and 143.7 respectively (Head et al. 2002). Mujica et al. (2017) investigated survival of all four life stages, female fecundity, and adult longevity across seven temperatures ranging from 10–35°C, and concluded that *L. huidobrensis* development requires a temperature between 12–28°C.

There have been a large number of studies on female oviposition preferences for different host plant species as well as for varieties within host species (Wei et al. 2000; Martin et al. 2005; Baoping et al. 2006; Videlia et al. 2006; Liying et al. 2008; Videlia et al. 2012; Maharjan and Jung 2016; Weintraub et al. 2017). In a laboratory study on *Pisum sativum*, *Solanum tuberosum*, *Lactuca sativa*, gai lan (*Brassica oleracea*), *Apium graveolens* (celery) and *Cucumis sativus* (cucumber), adults preferred *Cucumis* and gai lan for oviposition; but no difference was found in the proportion of adult emergence from the six crops (Martin et al. 2005). In Israel, adult flies are present in the field from the autumn through to the spring but not in summer (Weintraub and Horowitz 1996).

MOVEMENT & DISPERSAL. Studies using yellow sticky traps in potato crops in Israel showed that peak activity of the adults occurs in May and June. Adults are most active just after sunrise, with activity gradually decreasing during the day; activity in the morning was inversely correlated with temperature. Adults are less active at ground level, preferring to be at 0.2 m or more above the top of plants (Wientraub and Horowitz 1996).

As with other highly polyphagous *Liriomyza* species, long-distance dispersal of *Liriomyza huidobrensis* is human-facilitated and driven by the development of the global horticultural trade (Parrella and Keil 1984; Wientraub et al. 2017). Research in China has shown that the cold tolerance of *L. huidobrensis* pupae increases with latitude up to 35°N and that cold tolerance of populations was enhanced by pre-chilling pupae at 0°C, 5°C and 10°C. Beyond this latitude, the leafminer can only survive in protected habitats such as glasshouses (Chen and Kang 2004). A temperature-based phenological model Mujica et al. (2017) has been developed to allow prediction of life-stage parameters and population growth of *L. huidobrensis* in various climates.

MANAGEMENT. Early detection. *Liriomyza huidobrensis* is now widely distributed in the Old and New Worlds and is considered a major quarantine pest by many countries. There are many fact sheets on the leafminer available, including CABI (2015b) and Steck (2011). A plant health risk assessment for south Florida, USA, based on the temporal and spatial analysis of temperature data for the south and the day-degree development of the leafminer showed that the likelihood of breeding populations establishing was high (Milla and Reitz 2005). A broader assessment of the risks to plant health for the European Union concluded that the risk of establishment and spread was high because the leafminer is already present in many countries of the region and the pest can easily be moved with plant material. Overall impact was rated as minor for Mediterranean countries but in non-Mediterranean countries, impact was rated as moderate under protected crops and minor on outdoor crops (EFSA Panel on Plant Health 2012). For risk management, OEPP/EPPO (1990) recommended that plant propagating material of a defined list of vegetable crop and ornamental flower species from countries where the pest occurs must be inspected at least every month for three months and found to be pest free before transport. A phytosanitary certificate should also be issued for cut flowers and vegetable crops with leaves. EFSA Panel on Plant Health (2012) recommend ways in which risk management procedures could be tightened. For field monitoring, yellow sticky traps were used with effect by Wientraub (2001a) for the field monitoring of adult fly populations in Israel. Dankowska et al. (2000) also used these traps in Polish glasshouses but they laced the traps with 3-phenylpropionaldehyde to improve catch rate. Sampling plans for *L. huidobrensis* have been developed in several crops and locations, generally with the goal of facilitating decision making for IPM management. Alves et al. (2014) and Lopez et al. (2019) provide specific plans for estimating mines on potato and tomato crops, respectively, in Brazil.

Control. Management of vegetable waste, a source of new leafminer populations, was found to be effective for ornamental flower production in Italy (Bosio 1994). In Costa Rica, optimum sticky trap colour was found to be yellow (Wientraub et al. 2017); Civelek et al. (2004) found that mass trapping with yellow sticky traps and the use of exclusion nets were effective for cucumber production in glasshouses in Turkey. Intercropping for pepper (*Capsicum annuum* L.) production using sugar cane (*Saccharum officinarum* L.) increased local parasitism rates in China (Chen et al. 2011) and Valencia and Campos (1980) reported on the identification of some potato varieties showing some degree of resistance to attack. A range of insecticides are currently applied by farmers in tropical regions in attempts to control *L. huidobrensis*. Many products in use include conventional insecticides such as carbamates, pyrethroids and organophosphates (e.g., ICIPE 2015; Rauf 2000), and it is known that invasive highly polyphagous *Liriomyza* species rapidly develop resistance to these (Reitz et al. 2013) and resistance in *L. huidobrensis* was reported from the first outbreaks of the pest in South America in the early 1970s (Wientraub and Horowitz 1995). These products are also highly toxic to parasitoids (Reitz et al. 2013). Effective control of pea leafminer larvae has been achieved in trials with the translaminar insecticides cyromazine (an insect growth regulator), abamectin and spinosad (neurotoxins) in Israel (Wientraub and Horowitz 1998; Wientraub 2001b; Wientraub and Mujica 2006), the first two insecticides in Indonesia (Hidayani et al. 2005) and the first in European glass houses (CABI 2015b). Current research suggests that these insecticides are more

compatible with insect parasitoid biological control agents than conventional insecticides, but abamectin and spinosad are toxic to adult wasps, and are more toxic than cyromazine (Reitz et al. 2013; Weintraub and Horowitz 1998). Abamectin is also toxic to the entomopathogenic nematode *Steinernema feltiae* Filipjev but the organophosphates trichlofon and dimethoate are not (Head et al. 2000). In a global review of the biology and management of *L. huidobrensis* Weintraub et al. (2017) report that 106 parasitoid species have been reared from the leafminer. In the native range of the leafminer Salvo et al. (2005) using trap plants showed that parasitoid species diversity on this leafminer is high in Argentina and that overall parasitism is not lower in cultivated versus natural habitats; parasitism levels sometimes exceeding 50% in the former. Parasitoid diversity has been found to be relatively high in some parts of the adventive range, including Europe (EFSA 2012) and Indonesia (Rauf et al. 2000). Furthermore, a predatory fly, *Coenosia humilis* Meigen (Muscidae) has been reported as being common and important in control in Indonesia (Hidayani et al. 2005). In Kenya, an introduction of parasitoid species from Peru has been made to complement conservation measures of local parasitoids, and the species *Phaenobothris scabriventris* Nixon (Hymenoptera: Braconidae) has been released in the vegetable growing areas of the Central Highlands (ICIPE 2015). Several types of biological control agent have been researched/are being used for use in European glasshouses. The parasitoids *Dacnusa sibirica* (Braconidae) and *Diglyphus isaea* (Eulophidae) are produced commercially and used in combination for glasshouse crops early in the season but only *Diglyphus* is used later in the season when temperatures rise (van der Linden 2004). Numerous studies in Europe have also demonstrated significant parasitism levels from native parasitoid species that move into glasshouses naturally (EFSA 2012). Research has shown the potential of using entomopathogenic nematodes, particularly *Steinernema feltiae*, in foliar applications on glasshouse crops against the leafminer larval stages (William and Waters 2000). Further work has shown that this nematode causes high mortality of parasitoid larvae (Head et al. 2003).

***Liriomyza langei* Frick**

“California Pea Leafminer”

(Figs 74–80)

OTHER COMMON NAMES. *Liriomyza langei* has been referred to in the past as the “pea leafminer”. This is no longer recommended as it may cause confusion with *L. huidobrensis*, a widespread global invasive species and former senior synonym.

IDENTIFICATION & DIAGNOSIS. *Liriomyza langei* is a relatively dark species of *Liriomyza*, most species of which have a black notum with yellow shoulders (postpronotum+notopleuron) and a yellow medial stripe on the scutellum (Figs 74, 75). This species is highly similar to the globally distributed *L. huidobrensis*, with which it was once considered conspecific, but later resurrected by Scheffer and Lewis (2001). The diagnostic phallus of *L. langei* (Figs 79, 80) is very similar to that of *L. huidobrensis* (Figs 72, 73), composed of one pair of short, dark and entirely divided tubules. *Liriomyza langei*, however, has a restricted, non-overlapping distribution, there are always 4 rows of acrostichal setulae (often 2–3, but sometimes 4 in *L. huidobrensis*), wing length is slightly smaller (1.6–2.3 mm), the orbital plate is usually darker and there is no gap between the pigmented section of the ejaculatory duct and the hypophallus. Considering the difficulties involved in diagnosing these species, molecular techniques are recommended following initial morphological screening, as outlined in Scheffer et al. (2001), Nakamura et al. (2013) and Scheffer et al. (2014).

DISTRIBUTION. *Liriomyza langei* is widespread in California, but also extends to Oregon, Washington, Texas and Mississippi, and has been introduced into Hawaii (Scheffer et al. 2001). Populations reported from Florida, Utah and Virginia did not establish (Steck 1996). It is suspected that Mexico, at least in regions adjoining California, also hosts populations of the species, reinforced by the presence of these flies in intercepted shipments originating in an unknown location within Mexico (Takano et al. 2005).

HOSTS. *Liriomyza langei* is a leafminer recorded from seventeen families: Amaranthaceae, Apiaceae, Asteraceae, Brassicaceae, Caryophyllaceae, Chenopodiaceae, Convolvulaceae, Cucurbitaceae, Fabaceae, Gentianeae, Liliaceae, Liliaceae, Primulaceae, Solanaceae, Turneraceae, Valerianaceae, Violaceae. An updated catalogue of host plant genera for *Liriomyza langei* was provided by Lonsdale (2011).

DAMAGE. *Liriomyza langei* was reported causing economic damage to peas (*Pisum sativum*) but also to celery (*Apium graveolens*), spinach (*Spinacea oleracea*), sugar beet (*Beta vulgaris*) and asters in California in the late 1940s (Frick 1951). Since this time further outbreaks have been reported from California and other areas in the USA: in California, Elmore and Ranney (1954) reported damage to seedling chili pepper plants (*Capsicum*), causing considerable yield losses, but more mature plants were not affected; also in California, Lange et al. (1957) reported serious damage to autumn *Spinacia oleracea*; in Mississippi, Davis et al. (1969) reported damage to snap beans (*Phaseolus vulgaris*) and peas (*Pisum sativum*); in Texas, Chow and Heinz (2005) inferred that the leafminer was a problem on *Chrysanthemum* in semi-protected field production systems; and in Florida, Poe and Montz (1981) reported an outbreak (as '*L. huidobrensis*') in a field of *Gypsophila* that was assumed to originate from transported nursery stock from an infested area in California.

Since these reports, in California at least, the leafminer varies in pest status from 'a sporadic fall (= autumn) pest, relatively easily controlled, to a pest throughout most of the vegetable growing season that is essentially not able to be controlled in many crops' (Steck and Dixon 2006). Lettuce is the most highly affected crop (Steck and Dixon 2006). Damage to crops is primarily caused by the mining of leaves by the larvae but Steck and Dixon (2006) report that feeding punctures can kill seedlings and reduce photosynthesis. Costa et al. (1958) and Bennett and Costa (1961) showed from studies in California that the leafminer can transmit (via plant sap) sowbane mosaic virus to sowbane (*Chenopodium murale* (L.) S. Fuentes, Uotila & Borsch) and tobacco mosaic virus from various sources to sowbane and petunias, but not to tomato.

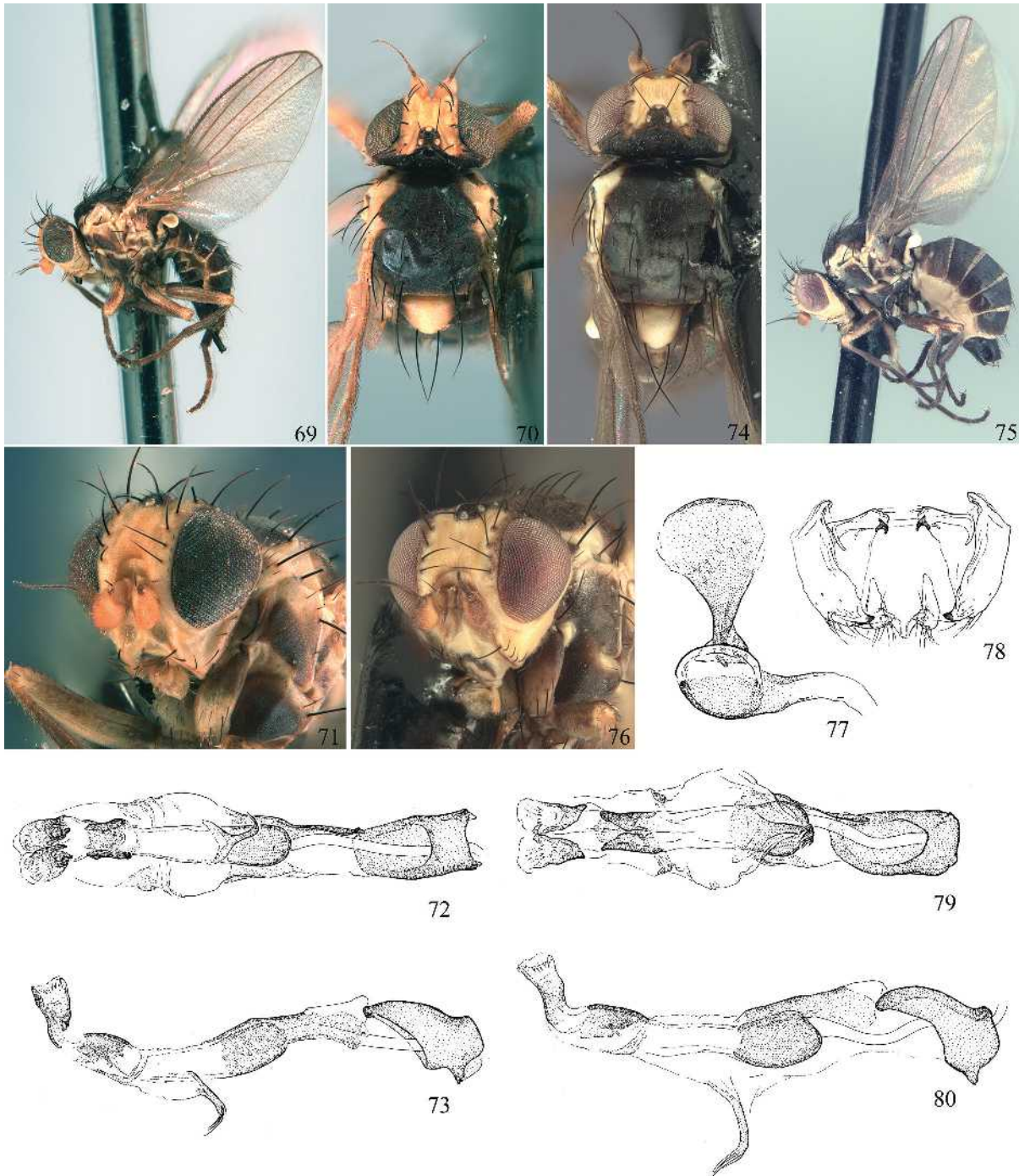
BIOLOGY. As *Liriomyza langei* was synonymized with *L. huidobrensis* until relatively recently, and the latter has become of global significance, little direct work on the biology on the former has been reported. Given prior confusion over the status of *L. langei* and *L. huidobrensis*, however, studies conducted in the USA on *L. huidobrensis* were likely made on *L. langei*.

While no assumptions can be made about specific aspects of the leafminer from the information available to date, the general life cycle biology of *L. langei* is similar to the biology of the major polyphagous *Liriomyza* species. Female leafminers feed on plant sap by making punctures in the leaves with their ovipositor; they also lay eggs in leaves via punctures made in the same way. The eggs hatch after 2–4 days and larvae mines in the spongy mesophyll of the lower leaf surface; the serpentine mines are usually associated with the midrib and lateral veins. Frick (1951) states that the larval mine is quite wide in this species, being almost twice the larval width for most of the length of the mine. The larvae emerge from the mines and pupate on the leaf surface, or more commonly, in cracks in the soil. The leafminer completes many generations each year and the entire life cycle can be completed in less than three weeks when conditions are warm (Steck and Dixon 2006).

Parrella and Bethke (1984), working in California on the leafminer (as "*L. huidobrensis*"), found that larval development time was shorter on *Pisum sativum* than on *Chrysanthemum* or aster. No differences were found in the duration of the egg or pupal stages or on adult longevity on the three hosts. The largest number of pupae per female and the highest survival rate of pupae were those reared on pea. In addition, Reitz and Trumble (2002) found that Californian populations to have higher reproductive success on pea compared with other hosts.

MOVEMENT & DISPERSAL. There is no readily published information on dispersal, but as the general biology of species is very similar to that of other polyphagous *Liriomyza* species, dispersal mechanisms are likely to be similar: natural dispersal by flight over limited distances that may be facilitated by wind and broader human facilitated travel via horticulture and ornamental flower trades.

MANAGEMENT. Early detection. Given the pest status of *Liriomyza langei* in California and its possible movement within the USA via the horticultural trade, a pest alert has been produced for Florida by the Florida Department of Agriculture and Consumer Services (Steck and Dixon 2006). Heinz and Chaney (1995) provided a sequential sampling plan for the estimation of larval populations of this species (as Californian "*L. huidobrensis*") and mining damage on celery.



Figures 69–80. 69–71: *L. huidobrensis* (Blanchard), female: 69: lateral; 70: dorsal; 71: head. 72–73: *L. huidobrensis*, male genitalia: 72: phallus, ventral; 73: phallus, left lateral. 74–76: *L. langei* Frick, female: 74: dorsal; 75: lateral; 76: head. 77–80: *L. langei*, male genitalia: 77: ejaculatory apodeme; 78: external genitalia, ventral; 79: phallus, ventral 80: phallus, left lateral.

Control. The effects of vacuum and controlled atmosphere treatments on *L. langei* mortality for lettuce production are summarized by Liu (2003). On host plant resistance, Mou and Ryder (2003) report on experimental work in California where several lines of lettuce and spinach resistant to attack by *L. langei* were identified. Although no line was completely immune, the trait for ‘resistance’ proved stable and thus provided the potential for crop improvement. Further work is described by Mou and Ryder (2010) on a green lettuce line resistant to leafminer and lettuce mosaic virus that was adapted to major lettuce production areas of the central coast of California. Shi and Mou (2016) evaluated 300 USDA spinach lines for resistance to *L. langei* and identified five molecular markers potentially of use by plant breeders. Early attempts at control on asters, *Lactuca sativa*, *Spinacea oleracea* and *Beta vulgaris* in the 1950s and 1960s included the insecticide parathion (Jefferson and Eads 1952; Wilcox and Howland 1955), and for *B. vulgaris*, phorate (Duffus and McCalley 1964). The organophosphate, methamidophos, was reported as being effective for control (Parrella and Keil 1985). *Liriomyza langei*, however, may have developed strong resistance to a broad range of insecticides (for example, see Steck and Dixon 2006) that mirrors the situation with other polyphagous *Liriomyza* species (Parrella and Keil 1984) but this remains to be shown experimentally. There is no published work known by the authors on the efficacy of modern products such as insect growth regulators, which are suggested as being effective by Reitz et al. (2013) for other *Liriomyza* species in general. In Hawaii, attempts to control the leafminer on onions by planting bean borders to boost local parasitoid populations were not successful (Johnson and Mau 1986). Chow and Heinz (2005, 2006) reported on experimental studies using *L. langei* as a model system, and on improved rearing techniques to avoid male-biased sex ratios for the hymenopterous parasitoid *Diglyphus isaea* (Eulophidae) in semi-protected field production of *Chrysanthemum* in Texas; *D. isaea* is one of the few parasitoids produced commercially for leafminer control (Chow and Heinz 2004). Likewise, Bader et al. (2006) used a similar system in Texas to study the feasibility of producing a marketable crop using parasitoid species alone or in combination, specifically, *D. isaea* and *D. sibirica* (Braconidae). Interspecific competition between the species was undetectable at leafminer densities typical of field grown *Chrysanthemum*, and release of both parasitoids simultaneously produced no positive benefits.

***Liriomyza sativae* Blanchard**

“Vegetable Leafminer”

(Figs 81–86)

OTHER COMMON NAMES. Serpentine vegetable leafminer, cabbage leafminer, tomato leafminer (CABI & EPPO 2015c).

IDENTIFICATION & DIAGNOSIS. *Liriomyza sativae* is highly variable in adult morphology and superficially similar to many other species, making male dissection necessary for confident identification. Comparison to published molecular sequence data might be required, especially for larvae or females – see Amin et al. (2014) and Nakamura et al. (2013) as examples. The variation in adult morphology may be due, in part, to the presence of deeply divergent mitochondrial lineages, suggestive of the possibility of cryptic species (Scheffer and Lewis 2005), but much remains to be resolved.

Like almost all other *Liriomyza*, adult *L. sativae* has the thorax mostly black dorsally with the shoulders (notopleuron + postpronotum) and centre of the scutellum yellow (Fig. 81). Furthermore, wing length is 1.3–1.8 mm, the pleuron and femora are variably light to dark, the surface of the thorax is very lightly dusted with pruinosity, and the posterolateral corners of the frons around the base of the vertical setae are usually brown to black; while these states are also seen in other *Liriomyza*, these differentiate it from the common plant pest *L. trifolii* (Fig. 87), which is similar in size (1.2–1.9 mm), but has an almost entirely yellow pleuron, entirely yellow femora, a denser grey dusting of pruinosity and an entirely yellow frons with only the ocellar tubercle brown.

The male genitalia of *Liriomyza sativae* are most diagnostic: the surstylus has only one spine (Fig. 83); the mesophallus is slender and separate from the distiphallus; the distiphallus is small, slender and cup-shaped, and in profile, a weak C-shape is apparent due to deeper sclerotization of the apical, basal and ventral surfaces (Figs 85, 86). Although quite similar to the distiphallus of *L. trifolli* (Figs 90, 91), a related species, the phallus of *L. sativae* differs in being more rounded and robust, the distiphallus and mesophallus are separate, and the distiphallus venter is thicker and darker (best seen laterally).

Larvae are typically maggot-shaped, and the posterior spiracles are on subconical projections with three bulbs, two of which are elongate (Spencer 1973: fig. 325).

DISTRIBUTION. Described from Argentina in the 1930s, populations were also found in California at about the same time, suggesting an original widespread distribution spanning the American continents. *Liriomyza sativae* has been found throughout the New World as far north as California, Colorado and Maryland in the United States. Specimens have also been found in greenhouses north to Maryland, Ohio and Pennsylvania and Ontario (CABI & EPPO 2015c; Lonsdale 2011). This species is often common in growing regions within its range. In tropical and sub-tropical regions, the leafminer mostly occurs in lowland areas (Andersen et al. 2002).

Additional invasive populations occur in the Afrotropical, Australian, Oriental and Palaearctic Regions (CABI 2014; CABI & EPPO 2015c; EPPO 2014; Dempewolf 2004; Lonsdale 2011; Scheffer and Lewis 2005):

- **Afrotropical Region:** Cameroon, Kenya, Nigeria, Oman, Sudan, Yemen, Zimbabwe. Likely not present in Democratic Republic of Congo, Ethiopia, South Africa or Tanzania.
- **Australian Region:** Australia (Torres Strait) (Blacket et al. 2015), Cook Islands, French Polynesia, Guam, Micronesia, New Caledonia, Northern Mariana Islands, Papua New Guinea (Blacket et al. 2015), Samoa, Tahiti, Vanuatu, USA (American Samoa, Hawaii). Eradicated from Australia (Queensland).
- **Nearctic Region:** Canada (Ontario – greenhouse), Mexico, USA (Texas to California, Colorado and South Carolina; in glasshouses in Ohio, Maryland and Pennsylvania).
- **Neotropical Region:** Antigua and Barbuda, Argentina, Bahamas, Barbados, Brazil (Ceará, Paraná, Pernambuco, Rio de Janeiro), Chile, Colombia, Costa Rica, Cuba, Dominica, Dominican Republic, French Guiana, Guadeloupe, Jamaica, Martinique, Montserrat, Netherlands Antilles, Nicaragua, Panama, Peru, Puerto Rico, St. Kitts and Nevis, St. Lucia, St. Vincent and Grenadines, Trinidad and Tobago, Venezuela. Likely absent from Suriname.
- **Oriental Region:** Bangladesh, China (Fujian, Guangdong, Yunnan), India (Uttar Pradesh), Indonesia (Java), Japan (Ryukus), Malaysia (Peninsular Malaysia), Philippines, Sri Lanka, Thailand, Vietnam. Likely absent from Cambodia, Laos, Pakistan.
- **Palaearctic Region:** Arabian Peninsula, China (Anhui, Beijing, Hainan, Hebei, Henan, Hunan, Shandong, Shanghai, Shanxi, Sichuan, Xinjiang, Zhejiang), Egypt, Greece (Deeming 2006), Israel, Japan, Jordan, Russia, Turkmenistan, Uzbekistan. Likely absent from Europe, with restricted populations in Turkey.

HOSTS. *Liriomyza sativae* is a highly polyphagous leafminer recorded from 32 families, including many agricultural crops (Lonsdale 2011): Amaranthaceae, Apiaceae, Asteraceae, Bigoniaceae, Boraginaceae, Brassicaceae, Capparaceae, Caryophyllaceae, Chenopodiaceae, Cucurbitaceae, Datisceae, Dioscoreaceae, Euphorbiaceae, Fabaceae, Lamiaceae, Liliaceae, Malvaceae, Moringaceae, Oleaceae, Onagraceae, Passifloraceae, Plantaginaceae, Poaceae, Polemoniaceae, Polygonaceae, Ranunculaceae, Sapindaceae, Scrophulariaceae, Solanaceae, Tropaeolaceae, Verbenaceae, Zygophyllaceae. Fabaceae, Cucurbitaceae and Solanaceae appear to be most preferred (Spencer 1973).

DAMAGE. *Liriomyza sativae* is one of the world's most damaging agromyzid pests, being both highly polyphagous and highly invasive. With heavy leafmining there may be serious damage to numerous important vegetable crops and ornamental plants, principally those in preferred plant families (see above), including

tomato (*Solanum lycopersicum*), beans, melons, cucumber (*Cucumis sativus*), *Pisum sativum* and *Chrysanthemum* (CABI 2015c; Hofsvang et al. 2005; Waterhouse and Norris 1987; Xie et al. 1997).

Damage is caused in several ways (Parrella 1987): destroying young seedlings, reduction in crop yields, leaf damage of ornamental plants and vectoring disease (for the last see Zitter et al. 1977). Tomato plants can tolerate a reasonable amount of mining damage without affecting yield (Levins et al. 1975; Parrella 1987) but young plants are highly susceptible (Hofsvang et al. 2005). Most damage is caused by the developing larvae feeding within mines, but feeding punctures on leaves made by females have been shown to cause a reduction in the vigour of plants; e.g. a reduction of photosynthesis rate in tomato (Johnson et al. 1983).

BIOLOGY. Mating usually occurs in daylight hours and within one day of emergence. The female ovipositor is used to puncture the dorsal surface of leaves, producing sap that is used for feeding; eggs may also be deposited within some of these punctures. Egg-laying starts about a day after emergence, peaks after one week and then continues at a lesser rate for a couple of weeks. Several eggs may be laid per leaf, the actual number depending on the type of host plant. Larvae feed within the mesophyll layer, producing a mine shape that is variable, but often broadly linear to serpentine. The third-instar larva exits the mine by cutting an opening at the end of the mine, subsequently pupating on any surrounding foliage or by dropping to the ground and pupating in the upper surface of the soil (Parkman et al. 1989; Pettitt and Wietlisbach 1994; Spencer 1989; Waterhouse and Norris 1987).

Duration of the developmental stages depends on host plant and temperature: in general, the egg stage lasts 2–5 days and larvae last 4–7 days above a mean temperature of 24°C. The entire life cycle (egg to adult) takes from less than 3 weeks to more than nine weeks (CABI & EPPO 2015c; Pettitt et al. 1991); or 250 day-degrees (DD) above a threshold of 10.2°C (Haghani et al. 2007). The mortality rate of immature stages rises significantly above 30°C. On cucumber, the highest intrinsic rate of natural increase (r_m) and net reproductive rate (R_0) were obtained at 25°C (Haghani et al. 2006). In the tropical mountain region of central Java, Indonesia, temperature was found to play an overriding influence on the distribution of *L. sativae* and a competing species, *L. huidobrensis*; the former was not found above 1200 m where the average temperature was 20.7°C (Tantowijoyo and Hoffmann 2010).

MOVEMENT & DISPERSAL. The adult is capable of natural dispersal by flight but this is likely only effective over limited distances (EPPO 2015; Parrella 1987). For polyphagous *Liriomyza* species in general, Parrella (1987) notes that prevailing winds influence the rate and direction of dispersal but in a study with yellow sticky traps, Tryon et al. (1980) noted that catches of *L. sativae* declined when wind gusts exceeded 20 mph. A study also using yellow sticky traps showed that adult flies were more active in the middle height of tomato plants (Zehnder and Trumble 1984).

The main factor known to influence long distance dispersal has been human activity through the development of an extensive global trade in horticultural and ornamental plants, especially flowers (Parrella and Keil 1984). The presence of extensive greenhouse networks in northern China, which allows the overwintering of pupae, is facilitating the spread of this species further north (Chen and Kang 2005).

MANAGEMENT. Early detection. Information on the global distribution is available via the CABI Invasive Species Compendium (CABI 2015c) and several fact sheets are available on the internet such as CABI & EPPO (2015c). *Liriomyza sativae* is listed as a major quarantine pest in many regions of the globe. For example, EPPO recommends that propagation material (except seeds) of a defined list of vegetable and ornamental plants from countries where *L. sativae* is known to occur be inspected at least monthly for three months and shown to be pest free. In addition, a phytosanitary certificate should be required for cut flowers and for harvested and transported vegetables with leaves (OEPP/EPPO 1990).

Sticky traps have been used in the field to monitor adult fly activity and numbers, with yellow traps being more effective than those of other colours (CABI 2015c; Chandler 1981; Tryon et al. 1980). Johnson et al. (1980c) recommended the collection and counting of puparia in trays placed beneath tomato plants to monitor popula-

tions of *L. sativae*. Zehnder and Trumble (1985) developed sequential sampling plans for tomato crops using yellow sticky traps for adult flies and trays for pupal populations; for the former, the authors provided the minimum number of traps that must be counted to estimate various mean densities of adult flies with given levels of precision.

Control. Maintaining general hygiene within horticulture and ornamental flower farms by clearing debris and treating soil to destroy pupae has been suggested by Velez et al. 1980. Some success has been obtained by placing yellow sticky traps close above plants for trapping males as it is suggested that this reduces the number of sexually active males (CABI 2015c). Some authors have reported varietal resistance in tomatoes but this technology has not been adopted commercially. *Liriomyza sativae*, like other polyphagous *Liriomyza*, are classic secondary pests (Parrella and Keil 1984; Reitz et al. 2013). The indiscriminate use of insecticides from the 1950s against other pests generated the first outbreaks of *Liriomyza* leaf miners in the USA, and the situation was exacerbated by the direct use of insecticides against *Liriomyza*. The effects were twofold: the development of resistance within fly populations and the reduction of natural enemy populations due to greater susceptibility (Waterhouse and Norris 1987). Nonetheless, insecticides are necessary where biological and other controls cannot keep leaf miners below economic thresholds, and much research has focused on new groups of insecticides and their compatibility with parasitoids. Cyromazine (an insect growth regulator) is currently considered to be one of the most effective available products, along with neurotoxins such as abamectin, spinosad and other spinosyns (Reitz et al. 2013), but it is likely that these only remain effective where there is no excessive spraying or concentration of other insecticides (Mason et al. 1989). These products are more compatible with parasitoids than carbamates, organophosphates or pyrethroids (Reitz et al. 2013), but abamectin and spinosad have been shown to be more toxic to parasitoids than cyromazine (Hossain and Poehling 2006). *Liriomyza* species vary in their susceptibility to different insecticides; e.g. *L. sativae* is more susceptible to cyromazine than *L. trifolii* in China (Gao et al. 2012). Research continues on potential biological control agents with most studies and practices to date focusing on hymenopterous parasitoids (Liu et al. 2009). Parasitoid communities are diverse, both in North America (e.g. Schuster et al. 1991; Schuster and Wharton 1993) and in countries where the pest has been introduced; a summary is provided by Murphy and LaSalle (1999). Observations suggest that parasitoids tend to be habitat/host plant specific rather than leaf miner specific. While Johnson et al. (1980b) showed in a study on pole tomato in California that parasitoids can control *L. sativae* in the absence of insecticides, few other practical biocontrol programmes have been conducted on field vegetable crops. One of the most notable is the programme of parasitoid introductions into Hawaii and other Pacific Islands in the 1970s, where successful control was achieved by *Ganaspidium utilis* Beardsley (Eucilidae) and *Neochrysocharis diastatae* (Howard) (Eulophidae) (Johnson et al. 1993). Early efforts were made at control in glasshouses by using inoculative releases of *Diglyphus* species (Eulophidae).

***Liriomyza strigata* (Meigen)**

(Figs 49–54)

IDENTIFICATION & DIAGNOSIS. Like other *Liriomyza*, *L. strigata* has a black notum with the shoulders (postpronotum+notopleuron) and a medial stripe on the scutellum yellow (Figs 49, 50). Wing length is 1.8–2.2 mm. The phallus is similar to that of the related pests *L. huidobrensis* and *L. bryoniae*, where there is a long membranous space between the pigmented section of the ejaculatory duct and the mesophallus, and the distiphallus is small and entirely divided medially, consisting of two short, pigmented tubules. The cup-like tubules of the distiphallus in *L. strigata* (Figs 53, 54) are broader, however, similar to those of *L. bryoniae* (compare to Figs 47, 48), but the segment is slightly longer with a longer, wider base, and it is somewhat better sclerotized. Externally, it differs from relatives in having the brown stripe behind the eye reach, or nearly reach, the base of the outer vertical seta (Fig. 51; stripe usually wider in *L. huidobrensis* and nearly absent in *L. bryoniae*), the first flagellomere is yellow (infuscated in *L. huidobrensis*), the anepisternum has a small to well-developed ventral spot/stripe (smaller in *L. bryoniae*, larger in *L. huidobrensis*), the katepisternum has a small ventral spot not reaching the base of

the katepisternal seta (reaching seta in *L. huidobrensis*), the femora are yellow with light dorsal streaking (more extensive in *L. huidobrensis*) and there are 4 rows of acrostichal setulae (usually less in the other species).

The larval posterior spiracle has 10–12 pores across a wide, shallow, semicircular lobe. While morphological identification of males is possible following dissection, differences are slight, and female and immature stages are character poor. As such, molecular methods of differentiation are recommended (see Kox et al. (2005)) when possible following initial morphological screening of adult males, as is the comparison of leaf mines.

DISTRIBUTION. The distribution of this species is relatively well known in Europe and central Asia (Spencer 1976; Deeming 2006; Martinez 2013), but its presence from eastern Europe to the eastern Palaearctic requires further study, as it is possibly quite widespread. Dempewolf (2004) mentions specimens identified as *L. strigata* from the Oriental and possibly eastern Palaearctic Regions in India, Malaysia, Singapore and China that require verification. It appears to be absent from Japan, which is relatively well-sampled for Agromyzidae.

•**Palaearctic Region:** Albania, Belarus, Belgium, Bosnia and Herzegovina (Jovanovic and Dimic 1980), Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Iraq, Ireland, Italy, Kazakhstan, Kyrgyz Republic, Lithuania, Netherlands, Portugal (Madeira Isl.), Norway, Poland, Romania, Russia, Slovakia, Spain, Sweden, Switzerland, Turkey, Ukraine, United Kingdom, Uzbekistan.

HOSTS. *Liriomyza strigata* is a highly polyphagous leafminer that has been recorded from more than 200 genera of host plants in 35 families (Benavent-Corai et al. 2005), with the addition of *Polemonium* L. by Edmunds (2008) and *Cistus* by Ostrauskas et al. (2003): Acanthaceae, Alliaceae, Amaranthaceae, Apiaceae, Araliaceae, Asteraceae, Boraginaceae, Brassicaceae, Campanulaceae, Cannabaceae, Capparaceae, Caryophyllaceae, Celastraceae, Chenopodiaceae, Cistaceae, Convolvulaceae, Cucurbitaceae, Dipsacaceae, Euphorbiaceae, Fabaceae, Hydrophyllaceae, Lamiaceae, Linaceae, Loasaceae, Malvaceae, Papaveraceae, Plantaginaceae, Polemoniaceae, Primulaceae, Resedaceae, Scrophulariaceae, Solanaceae, Tropaeolaceae, Valerianaceae, Verbenaceae, Violaceae. Most hosts belong to the families Asteraceae (76 genera) and Brassicaceae (32 genera). Species of Asteraceae, Campanulaceae and Lamiaceae are preferred (Spencer 1976).

DAMAGE. *Liriomyza strigata* is a widespread species often encountered on food crops, and while it usually causes little appreciable damage, its potential to develop to pestiferous levels make it significant (Spencer 1973). The species also occurs on a number of ornamentals, where the conspicuous mines could reduce economic value. Its overlap in host preference and morphology with other highly injurious taxa such as *L. huidobrensis* and *L. bryoniae* will likely confuse identification and subsequent control measures, and care must be taken during diagnosis.

BIOLOGY. Spencer (1973) mentions that ‘surprisingly no detailed studies have been made of the life history of this species’ and this still seems to be the case. According to very early work summarized in Spencer (1973), an adult female lays an egg near the margin of the leaf where the young larva then mines the lower surface until it reaches the midrib, at which point it switches to mining the upper surface. Here the main mines are formed, which are short, straight or irregular offshoots laterally along the veins (Spencer 1973: figs 502, 514; Dempewolf 2004). This is similar to some *L. huidobrensis*, but in contrast to the irregular serpentine mines formed by *L. bryoniae*, which can be much more difficult to differentiate as an adult. Pupation is external.

MOVEMENT & DISPERSAL. Published data are not available.. The horticultural trade in host flowers and vegetables will likely aid in this species’ dispersal but this has not been confirmed.

MANAGEMENT. Early detection. Populations of the leafminer are monitored in glasshouses in France by the use of yellow pans (Villevielle 1987). Some of the information given for *L. sativae* and other polyphagous leafminers may be of relevance for *L. strigata*.

Control. In glasshouses in Lithuania, trials with the neurotoxin abamectin have been shown to be effective for control of larvae, but similar trials with the neem-based insect growth regulator azadirachtin were not (Duchovskienė & Survilienė, 2009). A wide range of local species of parasitoids (Hymenoptera: Chalcidoidea) have been recorded from Western Europe, as reviewed in (Spencer 1973). More recent records include those from several *Liriomyza* species in greenhouses in southern Spain, where *Neochrysocharis formosa* (Westwood) (Eulophidae) was found to be most common, causing parasitism levels of 51% on tomatoes, 31.4% on eggplants, and 31.2% on green beans (*Phaseolus vulgaris*) (Cabello et al. 1994). Similar local parasitoid diversity has been recorded from the field in Turkey (Uygun et al. 1995; Gençer, 2009); *Diglyphus isaea* (Eulophidae) was found to be the most common by Uygun et al. (1995).

***Liriomyza trifolii* (Burgess)**

“American Serpentine Leafminer”

(Figs 87–91)

OTHER COMMON NAMES. Chrysanthemum leafminer; Serpentine leafminer; minador pequeño del frijol (Spanish); mineuse du gerbera (French) (CABI 2015d).

IDENTIFICATION & DIAGNOSIS. Relatively small, pale species 1.2–1.9 mm (wing length) (Fig. 87). Similar in appearance to many *Liriomyza*, *L. trifolii* has a black notum with the shoulders (postpronotum+notopleuron) and the medial stripe on the scutellum yellow, but the scutum is covered with a greyish pruinosity and there are usually only two rows of acrostichal setulae (but sometimes up to four). The femora are yellow, but sometimes with very limited brown spots, the abdomen is broadly yellow laterally and the pleuron is relatively pale with a spot on the katepisternum and very limited brown mottling on the anepisternum. The head is especially diagnostic among pestiferous *Liriomyza* in that the frons is entirely yellow, including the posterolateral region around the base of the vertical setae, but the ocellar tubercle remains brown; the antenna (excluding arista) is entirely yellow with the first flagellomere sometimes slightly pointed anterodorsally.

The male genitalia are characterized by a pale, slender phallus with a small cup-like distiphallus fused to a very narrow mesophallus (Figs 90, 91), and the surstylus has only a single spine (Fig. 88).

Minor variations across specimens of *Liriomyza trifolii* may be indicative of the presence of cryptic sister species exhibiting restricted host preference, as suggested by analyses of mitochondrial sequence data (Scheffer and Lewis 2006; Pérez-Alquicira et al. 2019).

Larvae are typically maggot-shaped and indistinguishable from those of *Liriomyza sativae* (Spencer 1973).

DISTRIBUTION. *Liriomyza trifolii* is native to the New World, possibly with origins in the Neotropics, although the phylogeography of this species is yet to be confidently resolved. The ability of this species to disperse and colonise following human-mediated transport is considerable (Minkenberg 1988a). Interceptions via trade are frequent, especially on *Chrysanthemum*, resulting today in a wide global distribution (Lonsdale 2011; Černý and Tschirnhaus 2014; EPPO 2014; CABI & EPPO 2015d). Aside from known occurrences, this species is likely present but undetected in many additional localities, including the lower 48 states in the USA and all Mediterranean countries (CABI 2015d). Additional focused sampling in Africa, Oceania and central, east and southeast Asia is required for better global estimates.

Populations appear to be less common in northern Canada, Europe and Asia where they are unable to overwinter, but may be sustained in glasshouses. South temperate countries and Australia may be similarly restricted or less ideal for development.

•**Afrotropical Region:** Angola, Benin, Cameroon (Duclaire et al. 2014), Cote d’Ivoire, Ethiopia, France (Mayotte), Guinea, Kenya, Madagascar, Mauritius, Mayotte, Nigeria, Oman, Réunion, Senegal, South Africa, Sudan, Tanzania, Yemen, Zambia, Zimbabwe.

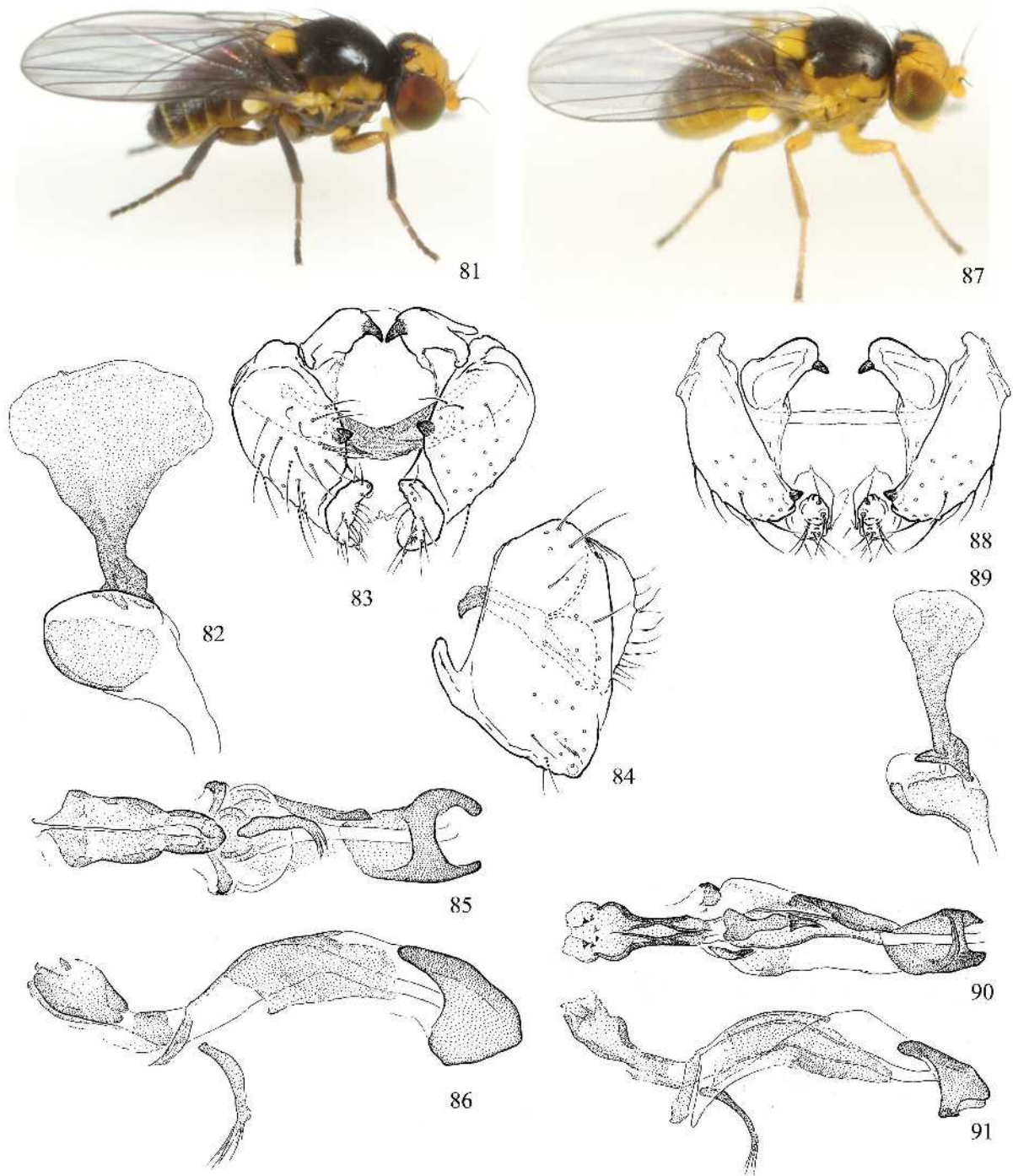
- Australian Region:** Australia (northern WA, northern QLD (IPPC 2017)), Guam, Micronesia, Northern Mariana Islands, Samoa, Tonga, USA (American Samoa, Hawaii).
- Nearctic Region:** Canada (Alberta, Nova Scotia, Ontario, Prince Edward Island, Quebec), USA (Arizona, California, Delaware, District of Columbia, Florida, Indiana, Iowa, Maryland, Massachusetts, Michigan, New Jersey, New Mexico, New York, Ohio, Oregon, Pennsylvania, South Carolina, Texas, Utah, Washington, Wisconsin).
- Neotropical Region:** Argentina, Bahamas, Barbados, Bermuda, Brazil (Minas Gerais, Pernambuco, São Paulo), Chile (Juan Fernandez Islands), Colombia, Costa Rica, Cuba, Dominican Republic, Ecuador, French Guiana, Guadeloupe, Guatemala, Guyana, Martinique, Mexico (states unknown – Mexican specimens recovered in exported plant products), Netherlands Antilles, Peru, Puerto Rico, St. Kitts-Nevis, Trinidad & Tobago, Venezuela, Virgin Islands (British, US).
- Oriental Region:** China (Fujian, Guangdong), India (Andhra Pradesh, Delhi, Gujarat, Haryana, Karnataka, Kerala, Madhya Pradesh, Maharashtra, Orissa, Punjab, Tamil Nadu, Uttar Pradesh, West Bengal), Philippines, Taiwan, Vietnam. Likely absent in Cambodia, Malaysia and Thailand.
- Palearctic Region:** Austria, Belgium, Bosnia & Herzegovina, China (Hainan, Jiangsu), Croatia, Cyprus, Egypt, Finland (occasional glasshouse occurrences), France, Greece, Iran, Israel, Italy, Japan, Jordan, Korean Republic, Lebanon, Malta, Netherlands, Portugal, Romania, Russia, Saudi Arabia, Serbia, Slovenia, Spain, Switzerland, Tunisia, Turkey, United Arab Emirates. Considered eradicated from Bulgaria, Czech Republic, Denmark, Estonia, Germany, Hungary, Ireland, Norway, Poland, Slovakia, Sweden, and United Kingdom.

Hosts. *Liriomyza trifolii* is a highly polyphagous leafminer that has been recorded from many host plant species in 41 families (Benavent-Corai et al. 2005), including: Acanthaceae, Amaranthaceae, Anacardiaceae, Apiaceae, Asclepiadaceae, Asteraceae, Basellaceae, Brassicaceae, Campanulaceae, Capparaceae, Caryophyllaceae, Chenopodiaceae, Convolvulaceae, Cucurbitaceae, Euphorbiaceae, Fabaceae, Goodeniaceae, Iridaceae, Lamiaceae, Liliaceae, Malvaceae, Onagraceae, Passifloraceae, Piperaceae, Plantaginaceae, Poaceae, Polemoniaceae, Polygonaceae, Portulacaceae, Primulaceae, Ranunculaceae, Rosaceae, Sapindaceae, Scrophulariaceae, Solanaceae, Tropaeolaceae, Turneraceae, Typhaceae, Valerianaceae, Verbenaceae, Zygophyllaceae.

Major hosts are found among the 50 genera of Asteraceae known to be attacked (see Lonsdale (2011)), including *Helianthus* L. and *Lactuca* L., as well as numerous ornamentals including *Aster* L., *Bidens*, *Dahlia*, *Gerbera* L., *Tagetes* L. and especially the commercially important *Chrysanthemum*. Affected crops in other families include beets (*Beta vulgaris*), carrot (*Daucus carota sativus* (Hoffm.) Schübl. & G.Martens), celery (*Apium graveolens*), peppers (*Capsicum*), cotton (*Gossypium*), onions (*Allium cepa* L.), leek (*A. ampeloprasum*), garlic (*A. sativum*), oat (*Avena sativa* L.), barley (*Hordeum*), melons, okra (*Abelmoschus esculentus*), potato (*Solanum tuberosum*), spinach (*Spinacia oleracea*), tomato (*Solanum lycopersicum*), *Senecio* L., *Gypsophila*, *Brassica*, and many Fabaceae including clover, soy and many beans and peas (Lonsdale 2011; CABI 2015d).

Mitochondrial sequence data has found that *L. trifolii* feeding on *Capsicum* sp., *Physalis philadelphica* Lam. and possibly *Apium graveolens* together form a clade that is distinct from *L. trifolii* feeding on other sampled hosts, suggesting the presence of a cryptic species with a relatively restricted host range (Scheffer and Lewis 2006; Pérez-Alquicira et al. 2019). This is consistent with previous findings of a pepper-adapted population in central California (Morgan et al. 2000; Reitz and Trumble 2003). Considerably more sampling of *L. trifolii* from additional hosts and locations, for both molecular and morphological analysis will be necessary to better understand host-use and population structure in *L. trifolii*.

DAMAGE. This leafminer is an important pest of many vegetable crops and ornamental flowers (CABI 2015d). Damage manifests in several ways - feeding punctures cause 'stippling' and a reduction in the quality of crops and ornamentals; leafmining larvae delay development or destroy young seedlings; older plants exhibit leaf drop and/or yield loss; plants are exposed to infection by pathogenic fungi; transmission of plant viruses



Figures 81–91. 81–86: *Liriomyza sativae* Blanchard, male: 81: live specimen; 82: ejaculatory apodeme; 83: epandrium, ventral; 84: epandrium, left lateral; 85: phallus, ventral; 86: phallus, left lateral. 87–91: *Liriomyza trifolii* (Burgess), male: 87: live specimen; 88: epandrium, ventral; 89: ejaculatory apodeme; 90: phallus, ventral; 91: phallus, left lateral.

(CABI 2015d; PaDIL 2016; Parrella 1987). On bell pepper (*Capsicum annuum*) in Texas, USA, the number of mines per plant was not a good indicator of the total damage to the plant (Chandler and Gilstrap 1987).

Economic losses have been considerable. In California, the species caused a loss of US\$93m to the *Chrysanthemum* industry over five years in the early 1980s (Parrella 1987) and losses to celery of US\$9m in Florida in 1980 (Foster and Sanchez 1988).

BIOLOGY. Adult flies mostly emerge before midday and mating usually takes place within 24 hours (CABI 2015d). Females puncture leaves for both feeding and egg laying, with approximately 15% of punctures containing eggs (Parrella et al. 1981). The larval feeding produces a linear upper-surface mine; the larva exits the mine from the upper epidermis to pupate in the soil (Eiseman and Lonsdale 2018). The particular biological characteristics (e.g. feeding punctures, viable eggs) of *L. trifolii* vary according host plant species, with Parrella et al. (1983) finding that the ratio of fertility to feeding punctures per female was greatest on *Chrysanthemum*, followed by celery and then tomato. Many studies of the life history of *L. trifolii* have been conducted on tomato as host; using yellow sticky traps Chandler (1985) and Zehnder and Trumble (1984b) showed that adult flies are more active in the lower part of tomato plants.

The development times of each life stage have been reported by several authors; Minkenberg (1988b) studied development at a number of constant and fluctuating temperatures on tomato. At 15 and 25°C, the duration in days of the immature stages was, respectively: egg 6.6 and 2.7; first star larva 3.3 and 1.4; second instar larva 3.7 and 1.4; third instar larva 3.7 and 1.8; and pupa 26.8 and 9.3; total development time at the two temperatures were 44.0 and 16.6 days, respectively. At these temperatures, the intrinsic rates of increase (r_m) were -0.0023 viable female eggs per female per day to 0.1254 eggs per female per day. The development threshold is 9.7°C and development in degree-days (egg to adult) is 564.7 (UC IPM 2015). Leibe (1984) found that the maximum oviposition rate of 38.67 eggs per female per day and fecundity of 405.67 eggs per female were at 30°C.

In the southern USA, breeding is likely to be throughout the year (CABI 2015d). In the UK, pupae remain viable outdoors for several months and can tolerate freezing temperatures (Millar and Isgar 1985).

MOVEMENT & DISPERSAL. Natural dispersal by flight is probably only over limited distances (Parrella 1987) and in horticultural crops, adult flies remain close to the crops (Zehnder and Trumble 1984a). In *Chrysanthemum* greenhouses, Jones and Parrella (1986) found that on average, females fly further than males and that density decreased (from the release point) more rapidly for the latter than the former. Parrella (1987) notes that prevailing winds influence the rate and direction of dispersal of *Liriomyza* species, and it has been suggested that agromyzids can travel long distances aided by wind (PaDIL 2016). However, of more importance in long distance dispersal of *L. trifolii* is the global development of the extensive horticulture and ornamental flower trades (Parrella and Keil 1984).

MANAGEMENT. Early detection. Up-to-date information on global distribution is available via the CABI Invasive Species Compendium (CABI 2015d). Risk assessments covering key features of the biology of the leafminer, pathways of movement and methods of identification have been produced for Europe (EFSA Panel on Plant Health 2012) and Australia (PaDIL 2016). Adult flies can be monitored in the field using sticky traps, with yellow traps performing better than other colours (CABI 2015d; Chandler 1981). A sequential sampling plan using yellow traps has been developed to estimate adult populations in *Chrysanthemum* greenhouses, but the technique has limited value in predicting immature stages (Parrella and Jones 1985). Sequential sampling plans have also been developed for tomato crops, using yellow sticky traps and trays to estimate populations from adult and pupal stages, respectively (Zehnder and Trumble 1985). Yellow sticky traps have also been used to monitor insecticide resistance in *Liriomyza trifolii* populations (Sanderson et al. 1989).

Control. Sanitation methods, including the removal of crop plant residues and the deep burying of old weeds, are recommended as these can still be infested with the leafminer. Sticky traps have been effective in controlling adults in onion crops in the Philippines, with yellow traps performing better than other colours (Arida et al. 2013). *Chrysanthemum* cuttings should be maintained in glasshouses for 3–4 days after lifting to allow all eggs to hatch, followed by storage at 0°C for 1 to 2 weeks to kill larvae (CABI 2015d). Kapsey and Parrella (2006) also suggested the release of sterile male flies to improve biological control in glasshouses. Several studies have detected an effect of oviposition deterrence in extracts from mature leaves of *Capsicum annuum* (Kashiwagi et al. 2005; Dekebo et al. 2007; Tebayashi et al. 2007). *Liriomyza trifolii* became a major problem on crops and ornamentals because

of overuse of insecticides in the second half of the 20th century (Parrella and Keil 1984; Reitz et al. 2013), mainly through the development of resistance, but also by indirect effects on local natural enemies. In the USA in Florida, the average life of effectiveness of an insecticide was roughly between two to four years (Reitz et al. 2013). Reitz et al.'s (2013) review of insecticides stated that the insect growth regulator cyromazine is currently one of the most effective products for control, but abamectin and spinosyns such as spinosad, which act as neurotoxins, are also effective. However, these will only remain effective where there is no excessive frequency of spraying (Mason et al. 1989) and where different insecticides are rotated on a regular basis (CABI 2015d). Much work has been done on the natural enemies and biological control of *L. trifolii*, with good reviews provided by CABI (2015), Liu et al. (2009) and Waterhouse and Norris (1987). The leafminer is attacked by a range of natural enemies such as insect predators and entomopathogenic nematodes, fungi and bacteria, but insect parasitoids have been the most exploited agents to date because species are quite common and diverse (Liu et al. 2009). Commonly used parasitoid species include: *Diglyphus* and *Chrysocharis* Förster (Eulophidae); *Dacnusa* and *Opius* (Braconidae) and *Ganaspidium* (Cynipidae). Introduction biological control using parasitoids was successful in Hawaii in the late 1970s on watermelon and possibly celery using *Ganaspidium utilis*. Effective control of the leafminer in Tonga was also achieved using this agent on a range of vegetable crops in the late 1980s, together with *Chrysocharis oscinidis* Ashmead (Johnson 1993). For the control of the leafminer in glasshouses, inundative releases of *Diglyphus isaea* and *Dacnusa sibirica* have been used successfully in Europe and Japan (Liu et al. 2009). For ornamentals, *Diglyphus begini* (Ashmead) has been used to control the leafminer on marigolds (Heinz et al. 1988). Studies on the more suitable insecticides have shown that abamectin and spinosad are more toxic to parasitoids than cyromazine (Hossain and Poehling 2006).

***Melanagromyza sojae* (Zehntner)**

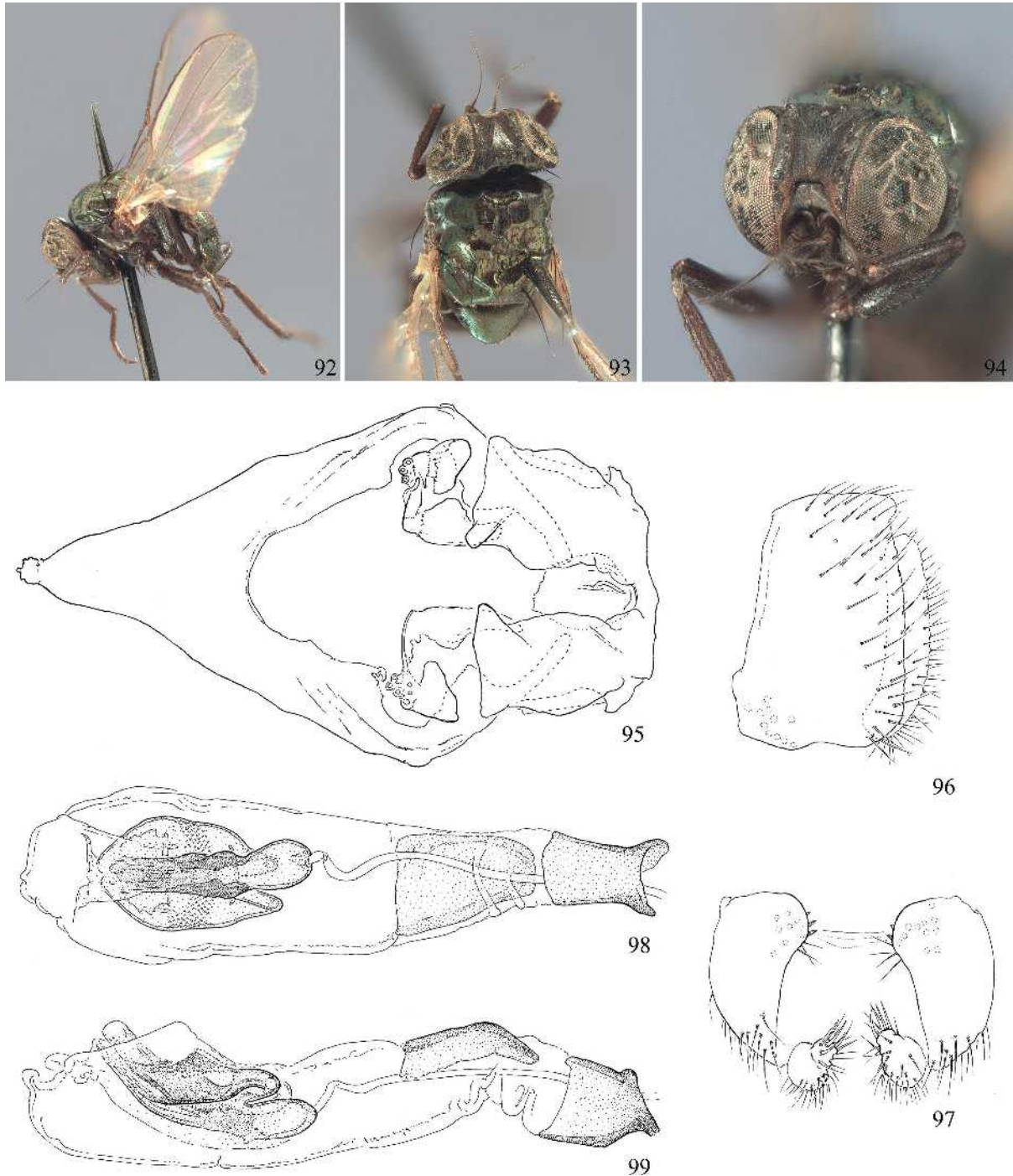
“Soybean Stem Miner”

(Figs 92–99)

OTHER COMMON NAMES. Asparagus miner; bean stem miner; soy miner; soybean fly; soybean stem borer; soybean fly; soybean stem borer; agromyze des tiges du soja (French) (CABI 2020).

IDENTIFICATION & DIAGNOSIS. *Melanagromyza sojae* males should be dissected for confident diagnosis. Like many other *Melanagromyza* externally, it is relatively small with a wing length of 1.7–2.1 mm, there are two dorsocentral setae with the anterior seta slightly smaller, there are four fronto-orbital setae, there are about eight rows of acrostichal setulae, and the calypter margin and hairs are white (Figs 92–94). The body is dark brown to blackish; a minimal greenish or bluish shine is sometimes evident on the notum, and the abdomen is distinctly metallic green. The head of the species is relatively distinct in that the eyes of both sexes are bare (in most *Melanagromyza*, the dorsal surface of the eye has at least some minute hairs that can be dense and bushy in males of many species), the orbital plate is narrow with only a single irregular row of reclinate setulae, the ocellar triangle is almost shining and long (nearly reaching the anterior margin of the frons), and the gena is highest near the anterior margin. The phallus (Figs 98, 99) has a basiphallus that is as long as, and is adjacent to the phallophorus, and the basiphallus is separated from the distiphallus by approximately its own length. The dorsal chamber of the distiphallus is relatively small, not strongly pointed or extended apically, and is minimally spinulose internally; the ventrolateral tubules emerging from the base of the chamber are quite thick and prominent, looping far basally. The mesophallus is inserted into the dorsal chamber ventromedially near the base of the segment, and extends basally past the chamber, including the ventrolateral tubules. Almost all *Melanagromyza* have a single spine in the inner posteroventral margin of the epandrium, but it is missing in this species (Figs 96, 97). To differentiate the immatures from other bean flies, the posterior spiracles have a central horn that is highly atrophied (see Spencer (1973: figs 44–46)).

DISTRIBUTION. Most of the known distribution of this species was summarized by CABI (2020). Since the immature stages occur in the host stem, and the seed and pods are traded internationally, the probability



Figures 92–99. *Melanagromyza sojae* (Zehntner), male: **92:** lateral; **93:** dorsal; **94:** head; **95:** hypandrium and epiphallus; **96:** epandrium, right lateral; **97:** epandrium, ventral; **98:** phallus, ventral; **99:** phallus, left lateral.

of accidental introduction into other regions is relatively low (CABI 2020). Screening of whole plants for international trade and breeding, however, should be done with care.

- Afrotropical Region:** South Africa, Sudan (Abdel-Banat et al. 2017).

- Australian Region:** Australia, Solomon Islands.

- Neotropical Region:** Argentina (Vera et al. 2020), Bolivia, Brazil (Goiás, Rio Grande do Sul, Santa Catarina (Arnemann et al. 2015)), Paraguay (Guedes et al. 2017).

•**Oriental Region:** Bangladesh, China (Fujian), India (Bihar (Singh and Ipe 1973), Delhi, Karnataka, Madhya Pradesh, Maharashtra, Nagaland (Longchar et al. 2019), Rajasthan, Uttar Pradesh, Uttarakhand), Indonesia (Java, Sumatra), Laos, Malaysia (Peninsular), Philippines, Taiwan, Thailand, Vietnam.

•**Palaeartic Region:** China (Heilongjiang (Yang et al. 1994), Jiangsu, Shandong), Egypt, Israel, Japan, Nepal(?), Saudi Arabia, South Korea, Turkey, Spain. Deeming (2006) additionally recorded Bahrain, Saudi Arabia, Oman and Yemen.

Thapa (2012) identified specimens from India and Nepal, but illustrated specimens representing inter-specific variability clearly belong to multiple taxa; the phallus of one illustrated male (plate 2) mostly agrees with known morphology.

Hosts. *Melanagromyza sojae* feeds primarily as a stem miner and is oligophagous, with favored hosts primarily in the Phaseoleae (Spencer 1990). Soybean (*Glycine max*) is recorded as the most strongly favoured host by CABI (2020). Additional food crops include Chinese clover (*Astragalus sinicus* L.), pigeon pea (*Cajanus cajan*), sunn hemp (*Crotalaria juncea* L.), alfalfa (*Medicago sativa* L.), common bean (*Phaseolus vulgaris*), pea (*Pisum sativum*), adzuki bean (*Vigna angularis* (Willd.) Ohwi & H. Ohashi), black gram (*V. mungo*), mung bean (*V. radiata*), asparagus bean (*V. sinensis sesquipedalis* (L.) Van Eselt.) and cowpea (*Vigna unguiculata*) (Spencer 1973; CABI 2020). The species also attacks *Indigofera suffruticosa* Mill. and *I. tinctoria* L. (true indigo), which are used as dyes, and wild hosts include *Aeschynomene indica* L., *Flemingia* Roxb. ex W. T. Aiton sp. and *Swainsona galegifolia* (Andrews) R.Br. (see Spencer (1973)). It has recently been reported from *Cicer arietinum* (Vera et al. 2021).

DAMAGE. *Melanagromyza sojae* mostly affects soybean but can be a problem on mung bean and black gram. The insect tends to be more of a problem in dry seasons than wet seasons (CABI 2020). Estimates of yield loss vary according to the study and location but in general, on soybean, yield loss decreases in relation to plant age; thus, yield loss is highest in young seedlings at the unifoliate or trifoliate stages but the insect rarely results in plant mortality. In Taiwan, yield loss was estimated at 31% from an assessment of attack on 163 soybean varieties (CABI 2020). In Indonesia, despite high levels of infestation, yield loss was found to be minimal under either early or late stage of plant attack by the fly (van den Berg et al. 1998). However, in Egypt, Alfy et al. (2019) mention yield losses of nearly 100%. Pozebon et al. (2021) did not quantify damage incurred from the species in South America crops where populations are rapidly spreading, but mentioned that in Rio Grande do Sul, Brazil, 95–100% of plants in all second season soybean crops surveyed incurred damage along the length of the plant stem.

BIOLOGY. The following is summarized from CABI (2020) and Spencer (1973) with additional information added where relevant. Adults mostly emerge in the early hours of the day. Females puncture the upper surface of leaves of a host plant for feeding; in Taiwan, the adults live 6–19 days (Wang 1979). The eggs are laid in the undersides of leaves, usually near the leaf base. Normally, only one or two eggs are laid per leaf but more may be laid at high adult population densities. After hatching, the young larvae enter the nearest leaf vein and then tunnel through the petiole to the stem pith and then downwards to the top part of the taproot. If not fully developed, the larvae move back up the stem until ready to pupate. They pupate deep within the stem but before doing so, they create a tunnel to the epidermis to allow the subsequent adult to escape.

In Taiwan, the eggs take from 2–7 days to hatch with a peak at 3 days (Wang 1979). There are three larval instars and the total development time at 32±2°C and 70% RH was seven days. The natural mortality of the larvae is quite high with 62% in the first instar, and 24 and 20% in the second and third (Wang 1979). The pupal stage lasts about eight days at 30±2°C and 70% RH. In lowland Indonesia, the total development time from egg to adult is 16–26 days.

MOVEMENT & DISPERSAL. The adults are weak fliers and thus movement is influenced by local weather conditions (CABI 2020).

MANAGEMENT. Early detection. CABI (2020) data sheet provides up to date information on the current global distribution and on likely pathways of spread. The current advice for field monitoring is the same as for *Ophiomyia phaseoli* (Plantwise 2020).

Control. In many regions in the Old World, *Melanagromyza sojae* affects the same legumes as another agromyzid, *Ophiomyia phaseoli*, a species that can be a more serious pest. Given the similar life histories of the two species, the general advice on management of *M. sojae* is to follow that of *O. phaseoli* (CABI 2019). However, specific information from studies is as follows. Searches for soybean accessions that are resistant to attack by *M. sojae* have been made in Asia and Africa. For example, Chiang and Talekar (1980) report on accessions of ‘wild soybean’ (*Glycine soja* Siebold & Zucc.) that are resistant to the insect. However, breeding these into cultivated soybean (*Glycine max*) was not successful because wild soybean has thin stems which, when expressed in crosses, results in plants that cannot support high pod production. Talekar (1989) suggests that late-maturing soybean cultivars may be less susceptible than early ones. In Egypt, Alfy (2017) found that yellow and white sticky traps suppressed populations in soybean fields. Insecticides are the mostly widely used control method by farmers. Preventative and curative insecticides are recommended although the former is likely to have more impact as most yield loss is at the seedling stage (CABI 2020). In India, the use of a systemic seed dressing (thiamethoxam) along with foliar sprays was found to suppress *M. sojae* populations in field soybeans (Gotyal and Prasad 2013). Talekar (1990) provides an overview of chemical controls. Studies in several countries in the Old World (India, Indonesia and Taiwan) have shown that *M. sojae* is attacked by a variety of hymenopterous parasitoids (Beche et al. 2018; CABI 2020). In Maharashtra, India, for example, the pest is attacked by ten parasitoids with peak parasitism reaching 50%. *Eurytoma* Illiger sp. (Eurytomitidae) and *Gronotoma* Förster sp. (Figitidae) were most prevalent throughout the crop season but *Sphégigaster* Spinola sp. (Pteromalidae), a pupal parasitoid, was the most common mid-season (Fand et al. 2018). A *Sphégigaster* sp. has been recorded from Egypt where the maximum parasitism recorded was 38.7% (Alfy et al. 2019). *Syntomopus parisii* De Santis (Pteromalidae) has been recorded as a major parasitoid of the larva and pupa in South America (Beche et al. 2018). In Sumatra, Indonesia, average parasitism reached 60% at the end of crop seasons (van den Berg et al. 1995). In some of these studies the authors suggest that efforts should be made to develop conservation strategies to enhance the impacts of these parasitoids. However, in general, parasitism tends to come late in the crop season and after the pest has done most damage, so such strategies may have little impact on reducing crop losses (CABI 2020).

Ophiomyia phaseoli (Tryon)

“Bean Fly”

(Figs 100–105)

OTHER COMMON NAMES. Bean stem maggot. Note that the common name “Bean Fly” is also used to refer to *O. spencerella* and *O. centrosematis*.

IDENTIFICATION & DIAGNOSIS. *Ophiomyia phaseoli* is a small, completely black species with a wing length of 1.7–2.2 mm (Figs 100, 101). The frons is most diagnostic, being relatively narrow with a finely textured frontal vitta that strongly contrasts a narrow shining orbital plate and a highly polished ocellar triangle; the triangle itself is narrow, sharply delimited and nearly attains the anterior margin of the frons (Fig. 102). Like all *Ophiomyia*, the anterior margin of the clypeus is truncated, but unlike many congeners it is more broadly U-shaped, and neither it nor the buccal cavity are narrowed (as in *O. simplex* – see Fig. 109). Also contrasting most other *Ophiomyia*, the narrow gena is not projecting anteriorly, and the facial carina is very shallow and almost indistinct. Other external diagnostic characters include two reclinate posterior fronto-orbitals and two shorter inclinate anterior fronto-orbitals (only anterior seta strongly incurved); two strong dorsocentrals; a costa that extends to vein M₁; a brown to dark brown calypter margin and hairs; and no posterolateral seta on the mid tibia. The male genitalia are also diagnostic, characterized by a H-shaped basiphallus

that lies under the ejaculatory duct, and a short, lobate mesophallus that is positioned ventrobasally to a longer, narrow distiphallus that is darker and swollen basally (Figs 103, 104).

DISTRIBUTION. This species likely occurs throughout the Old World tropics in sub-Saharan Africa, and south and Southeast Asia. Collection records extend north into Oriental China and Japan, and the southern Palearctic, including northern Africa, Israel, Turkey and Iran. It is additionally known from Australia, Hawaii (widespread – see Hardy and Delfinado (1980)) and Oceania (CABI 2019; EPPO 2019). It is not known from the continental United States (USDA 1984).

•**Afrotropical Region:** Burundi, Cape Verde Islands (Černý and Tschirnhaus 2014), Congo, Ethiopia, Kenya, Libya, Madagascar, Malawi, Mali, Mauritius, Mozambique (Davies 1998), Nigeria, Oman (Deeming 2006), Réunion, Rwanda, Senegal, South Africa, Sudan, Tanzania, Uganda, Zambia, Zimbabwe.

•**Australian Region:** Australia (New South Wales, Northern Territory, Queensland, Western Australia), Caroline Island (Waterhouse 1998), Fiji, Guam, Northern Mariana Islands, Palau, Papua New Guinea, Samoa, Solomon Islands, USA (Hawaii [introduced]).

•**Oriental Region:** Bangladesh, Brunei (Waterhouse 1998), China (Fujian (Shi et al. 2015), Guangdong, Guangxi, Hong Kong), Christmas Island, India (Andhra Pradesh, Andaman and Nicobar Islands (Mitra et al. 2010), Assam, Bihar, Gujarat, Karnataka, Meghalaya, Odisha, Punjab, Rajasthan, Tamil Nadu, Uttar Pradesh, Uttarakhand), Indonesia (Irian Jaya, Java, Sumatra), Japan (Ryukus), Laos, Malaysia (Sabah, Sarawak, Malaya), Myanmar, Pakistan, Philippines, Singapore, Sri Lanka, Taiwan, Thailand, Vietnam.

•**Palearctic Region:** Egypt, Iran, Iraq (Deeming 2006), Israel, Jordan, Nepal, Saudi Arabia. Reports of *Ophiomyia phaseoli* in northern China (Shandong) in Anonymous (1978) are attributable to *Melanagromyza sojae* (Zehntner).

Hosts. *Ophiomyia phaseoli* attacks a wide range of leguminous plants (Fabaceae), but is especially damaging to the commonly cultivated bean (*Phaseolus vulgaris*). Other host species can be highly affected regionally, including soybean (*Glycine max*) (Bhattacharjee 1980; Arunin 1978), black gram (*Vigna mungo*) (see Prodhan et al. (2000)), mung bean (*V. radiata*) (Thapa and Timsina 1990) and pea (*Pisum sativum*) (Yadav et al. 2019a; Kooner et al. 1977).

Minor hosts include *Cajanus cajan*, *Crotalaria juncea*, *C. pallida* Aiton, *Cyamopsis tetragonoloba* (L.) Taub., *Lablab purpureus*, *Macroptilium lathyroides* (L.) Urb. var. *lathyroides*, *Macrotyloma uniflorum* (Lam.) Verdc., *Medicago sativa*, *Mucuna pruriens* (L.) DC, *Phaseolus coccineus* L., *P. lunatus*, *Psophocarpus tetragonolobus* (L.) DC, *Vigna aconitifolia* (Jacq.) Marechal, *V. angularis*, *V. sinensis sesquipedalis* and *V. unguiculata* (Plantwise 2023). Other hosts for which this species has been reared include: *Crotalaria laburnifolia* L. (Abate 1991), *Canavalia ensiformis* (L.) DC, *Macroptilium atropurpureum* (Moc. & Sessé ex DC.) Urb., *M. panduratum* (Mart. ex Benth.) Maréchal & Baudet, *P. acutifolius* A. Gray (USDA 1984), *P. aurea* (Roxb.) Maekawa (Mazumdar and Bhuiya 2014) and *V. umbellata* (Spencer 1973). Reported occurrence of the bean fly on okra (*Abelmoschus esculentus*, Malvaceae) in Rai et al. (2014) is in error.

DAMAGE. *Ophiomyia phaseoli* has proved to be a major constraint on the production of common bean, one of the world's most import legume crops (Achiri et al. 2021). Oviposition occurs in leaves, stems, and cotyledons, typically of young seedlings (Plantwise 2023; Achiri et al. 2021). Punctures made by females can damage the leaves such that photosynthetic rates are reduced with defoliation possible when many punctures are present. The mining of leaf material by young larvae can cause leaves to wilt but the most serious damage is done by later stage larvae that have tunneled downwards through the plant stem and into the top part of the tap root. This can interfere with the transport of water and nutrients and can cause the plant to wilt, weaken and become stunted, sometimes resulting in plant death. Aggregation of puparia within the stem base can also cause it to swell and split (USDA 1984). Damaged plants are likely to have poor pod and seed formation (Nderitu et al. 1990a) and

are also likely to break at the soil surface under windy conditions (Greathead 1969). Some plants may respond to attack by developing adventitious roots and, after recovery, are able to withstand further attack (Greathead 1969).

Other host legume species, as well as different cultivars of common bean can show different levels of susceptibility (Ojwang et al. 2010; Tengecho et al. 1988).

In Kenya on common bean, numbers of leaf punctures and eggs peaked at 5–6 weeks after plant emergence, and later plantings in any season had higher infestation levels of bean fly than early plantings (Nderitu et al. 1990a; Songa and Ampofo 1999). The latter was also reported for plantings in Tanzania (Sarah and Makundi 2007). Damage among crops is higher during dry seasons (Abate 1991; Manohar and Balasubramanian 1980; Nderitu et al. 1990b; Plantwise 2023), especially in areas with low soil fertility (Ojwang et al. 2011a). In East Africa, the damage caused to common bean may be exacerbated because of the overlap in distribution with another major damaging similar agromyzid, *O. spencerella* (Greathead 1969).

There is a long history of extensive larval damage to common bean in multiple geographic regions. Crop or plant loss can be total, with examples of 100% seedling loss of late-planted beans in Egypt (Hammad 1978) and 100% crop loss in Western Australia (Morgan 1940). Other reported damage has included 100% plant infestation with 80% seedling mortality in Indonesia (van der Goot 1930), and 100% seedling infestation in Tanzania (Swaine 1968), sometimes with 30–50% yield loss (Wallace 1939). Cultivars of *P. vulgaris* show differing degrees of resistance to the species (Ssekandi et al. 2016; Tengecho et al. 1988; Rogers 1980), and genetic modification supplementing inherent cultivar resistance in these beans is being investigated (eg. Ojwang et al. 2011b).

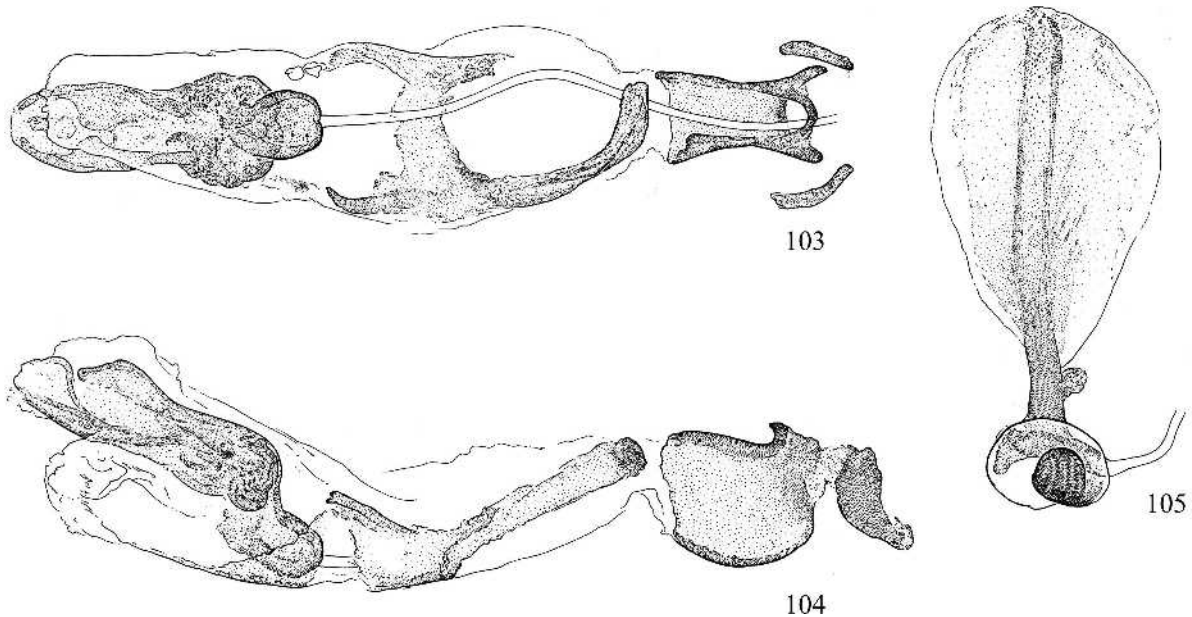
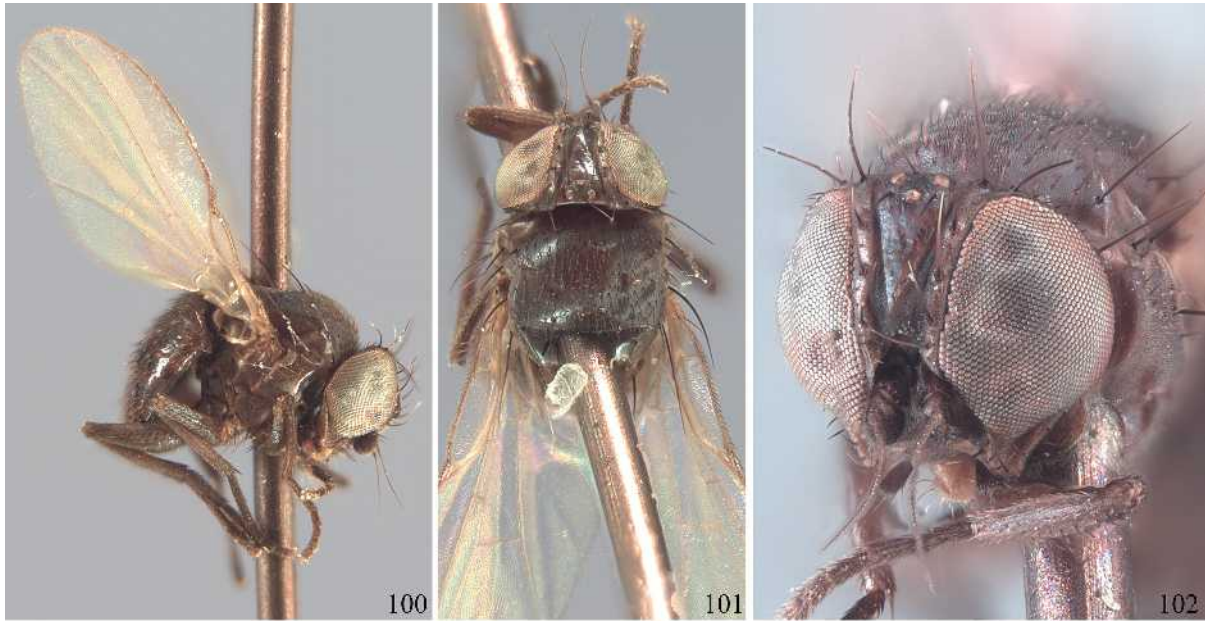
In other hosts, Arunin (1978) reported 90% seedling loss in soybean, and Kooner et al. (1977) reported up to 40% mortality and approximately 50% yield loss in pea.

It has been suggested the bean fly further contributes to crop damage via the introduction of root rot at ground level, which can rapidly contribute to yield loss; *Athelia rolfsii* (Curzi) C.C. Tu & Kimbr., *Rhizoctonia solani* J.G. Kühn and *Fusarium solani* (Mart.) Sacc. were all identified in infested plants in Mozambique (Davies 1998).

BIOLOGY. Several reviews of the literature are available; the following, where common bean is the host, is summarized from the CABI (2019) and Waterhouse (1998), with additional information added where relevant. Female *Ophiomyia phaseoli* begin oviposition 3–4 days after emergence and are most active on warm clear days. On bean, they primarily puncture the upper, but sometimes the lower epidermis of leaves or cotyledons with their ovipositors for feeding on plant sap and oviposition. However, only 10–15% of punctures receive an egg. A study on pigeon pea in India found that eggs are always laid on the underside of young leaves and the larvae pupate in the stem (Savde et al. 2018; Yadav et al. 2019). Oviposition can continue for a couple weeks over which 100 to 300 eggs may be laid. The incubation period lasts 2–4 days depending on temperature.

Ophiomyia phaseoli is unusual among miners as the larvae are able to move between tissue types within the plant. The first instar mines along leaf veins towards the mid-rib and in seedlings, the hatched larva forms a narrow, curved mine that is more visible on the underside of the leaf. The second instar feeds mainly in the mid-rib before entering the petiole where it moults into the third instar. This final instar mines down the main stem mostly beneath the epidermis usually to the level of the soil. The fully-grown larva creates a semi-circular hole in the stem epidermis to allow the adult to emerge following pupation. Larvae from eggs laid in leaves in older plants pupate in the main stem below a petiole (Greathead 1969). The total development time on bean depends on temperature: Greathead (1969) found that egg to adult took 27–31 days at about 21°C with a preoviposition of about 2 days.

Fly density in individual bean plants have been reported to be as high as 25 larvae in Egyptian crops, with seedlings beginning to succumb at densities of 10–15 larvae (Hassan 1947). Ethylene production associated with plant stress in the presence of larvae contributes to the production of adventitious roots, as well as the thickening of roots below ground (see Tengecho et al. (1988)); the success of adventitious root development is dependent on moisture availability (Abate 1993).



Figures 100–105. *Ophiomyia phaseoli* (Tryon), male: 100: lateral; 101: dorsal; 102: head; 103: phallus, ventral; 104: phallus, left lateral; 105: ejaculatory apodeme.

MOVEMENT & DISPERSAL. The adults are active fliers and most active on warm days (CABI 2019). There is no available information on natural dispersal but CABI (2019) lists the plant parts that are liable to carry the pest in trade and transport.

MANAGEMENT. Early detection. The CABI (2019) data sheet provides up to date information on the current global distribution and on likely pathways of spread. Should the species be accidentally transported to the New World, the threat to bean crops would be severe, although the risk of introduction is lessened by the fact that affected parts of the plant are usually not packaged for export, with the beans themselves being

untouched by direct larval damage. Advice includes searching bean crops for small black flies sitting on young leaves and/or evidence of leaf punctures (CABI 2019).

Control. The potential for several generations a year (Avidov and Harpaz 1969), compounded by the ability to accumulate population numbers in a relatively broad spectrum of alternate leguminous hosts, make this species potentially difficult to control. As the bean fly will attack its host crops from the early seedling stage, it is important to act within the first 4–5 weeks after crop emergence. This is particularly important in regions where legume crops such as soybean and mungbean are grown in a dry season following a wet season. Furthermore, as the main damage is hidden within the stem, it is necessary to know the seasonality of the pest in order to judge the timings of interventions (Plantwise 2023). Summaries of management practices are given by Yadav et al. (2019b), Achiri et al. (2021 and in the Plantwise database (Plantwise 2023)). Specific information from studies on control are as follows. Cultural controls have been reviewed by Achiri et al. (2021). Ridging crops 2–3 weeks after emergence is suggested to help cover adventitious roots that are sometimes produced by attacked plants. In East Africa, other variously successful practices to avoid severe attacks on common bean include early planting and sanitation (Ssekandi et al. 2016). Effects of planting density and special arrangement, including intercropping, on attack by *O. phaseoli* have been explored with good results (Peter et al. 2009; Achiri et al. 2001); pest populations are lower in mixed cropping systems than in a mono-cropping system (Abate and Ampofo 1996). Cultivars of *P. vulgaris* show differing degrees of resistance to the species (Ssekandi et al. 2016; Tengecho et al. 1988; Rogers 1980), and genetic modification supplementing inherent cultivar resistance in these beans is being investigated (eg. Ojwang et al. 2011b). Effort has been made by some international research centres and others to develop resistant cultivars (e.g. Ojwang et al. 2010), but in general, research is still ongoing (Nkhata et al. 2021). It is worth noting that in East Africa, there are local preferences by small landholders to grow mixtures of traditional and modern cultivars which they believe provide some resistance to pests and diseases, including the bean fly (Letoureau 1994; Ssekandi et al. 2016), but the effectiveness of this is not known. Insecticides are the mostly widely used control methods in cases where farmers can afford the expense. Given that larvae are hidden in stems, systemics are recommended. Some current recommended advice does not specify specific chemical insecticides because of variable regulations around insecticides from country to country (Plantwise 2023). Studies of natural enemies from several countries indicates that the bean fly is mostly attacked by hymenopterous pupal parasitoids (see Waterhouse 1998). Over 50 species have now been recorded. The most important species are in the family Braconidae and superfamily Chalcidoidea. In general, the recorded parasitism levels have been quite low but exceptions include that from the braconid *Opius phaseoli* Fischer in East Africa, and this species plus the Eurytomid *Eurytoma* sp. in India, where in both cases, parasitism levels of 90% or more were observed. Only introduction biological control has been used against the bean fly and an extensive review is provided by Waterhouse (1998). The parasitoids *Opius phaseoli* and *O. importatus* Fischer were introduced into Hawaii from Uganda in 1969; and the former species from Hawaii into Taiwan in 1974–75. In Hawaii, the parasitoids did produce acceptable control in most months for several years but their subsequent effectiveness became reduced possibly due to increased use of insecticides. The outcome of the introductions in Taiwan are unknown. Fungal inoculation of bean plants by various endophytes reduces feeding and oviposition by the “bean fly”, a common name encompassing *O. phaseoli*, *O. spencerella* and *O. centrosematis*, thus raising the possibility of fungal endophytes as management tools for these species (Mutune et al. 2016).

Ophiomyia simplex (Loew)

“Asparagus Miner”

(Figs 106–115)

IDENTIFICATION & DIAGNOSIS. Like most *Ophiomyia*, *O. simplex* is small (wing length 2.1–2.5 mm) and entirely black (Figs 106–108) with the anterior margin of the clypeus straight (Fig. 109), but it is otherwise quite distinct. Unlike most congeners, neither the buccal cavity nor the clypeus are narrowed, the facial keel is very

shallow and without a medial bulb, the gena is not projecting, and the male vibrissa is not multiplied to form a “horn”. Also unusual for *Ophiomyia* is a costa that only extends to vein R_{4+5} , and the orbital plate and parafacial are shining, relatively thick and easily viewed laterally. With regards to the male genitalia, the basiphallus is composed on one pair of narrow twisting bands, and the distiphallus is small and bell-shaped (Figs 111, 112).

DISTRIBUTION. *Ophiomyia simplex* is known from north temperate regions and Hawaii in association with cultivated asparagus.

- Australian Region:** United States (Hawaii) (Hardy and Delfinado 1980).
- Nearctic Region:** Widespread in asparagus growing regions of North America, including California, New York (Spencer and Steyskal 1986), Ontario and Quebec (Spencer 1969).
- Palearctic Region:** Albania, Austria, British Isles, Denmark, France, Germany, Greece, Hungary, Italy, Poland, Turkey (see Papp and Černý (2015), Ukraine (Guglya 2011).

HOSTS. *Ophiomyia simplex* is a stem feeding pest of asparagus (*Asparagus officinalis* - Asparagaceae).

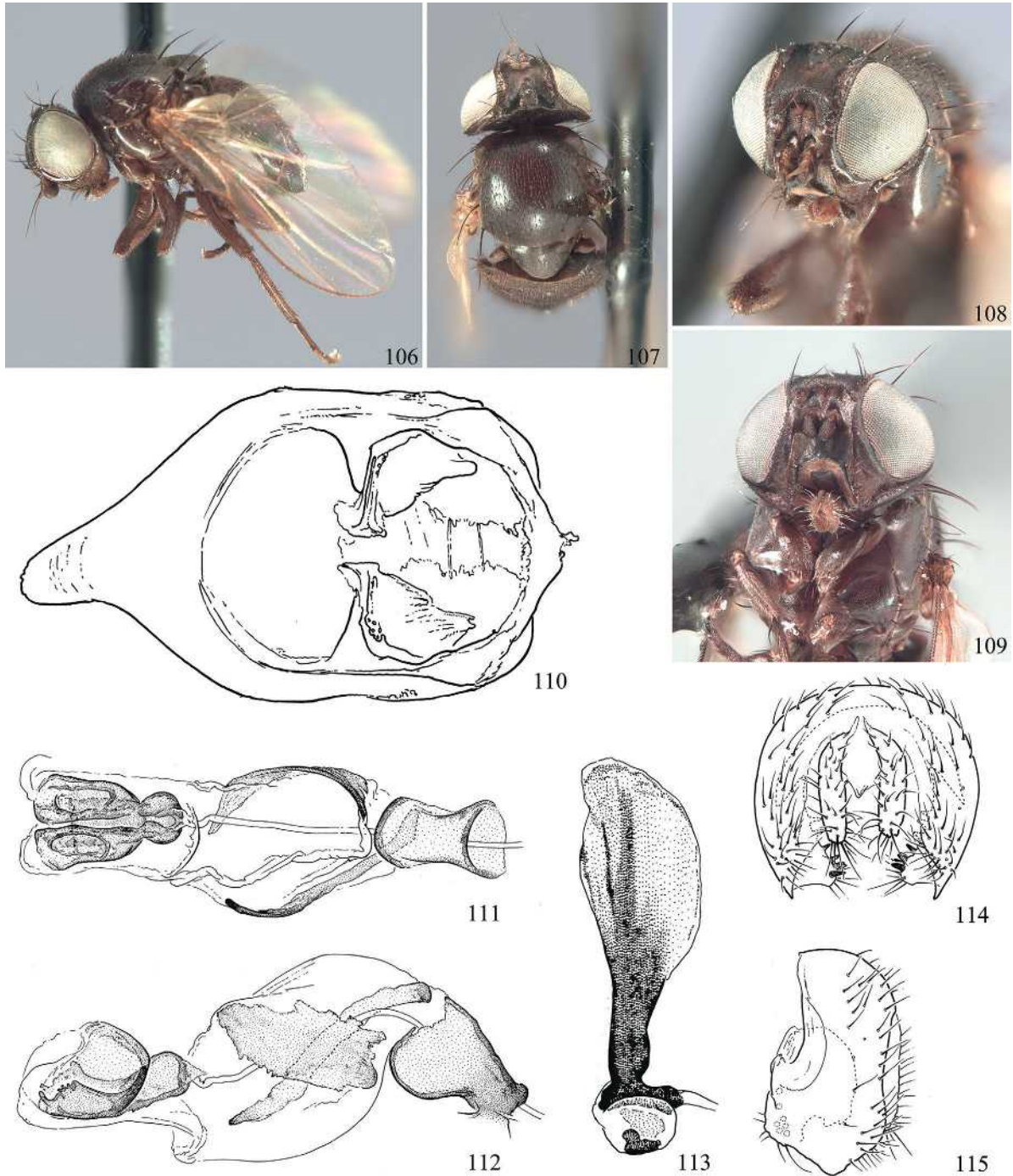
DAMAGE. This species is of substantial economic concern in the asparagus production industry. Mining by the larvae in the cortex at the base of the stem can cause cosmetic injury and thus affects yield and marketing (Michigan State University Extension 2011). However larval feeding activity may cause more direct damage by cracking and splitting the epidermis, and/or girdling the plant, resulting in yellowing and sometimes plant death. Heavy infestation may result in rot, structurally weakening the plant to the point where wind or rain may break the stem. As a portion of photosynthesis occurs in the green asparagus stem (Downton and Törökfalvy 1975), larval damage reduces productivity.

Ophiomyia simplex has been additionally implicated with “early decline” syndrome in asparagus, where-in *Fusarium* Link species contribute to crown and root rot, reducing yield to the point where it may not be profitable to harvest (Morrison et al. 2011). The species is suspected of vectoring the fungus, with pathogenic *Fusarium* found on the larva, pupa, adult, larval mine and frass (Ferro and Gilbertson 1982; Gilbertson et al. 1985; Tuell and Hausbeck 2008). The species has been positively shown to be an exacerbating factor in the rot, with rot damage proportionate to mine number (Damicone et al. 1987). Infected plants, visibly symptomatic by midsummer, are characterized by “wilting, dwarfing, chlorosis, browning of vascular tissue, death to the growing point, and damping off in seedlings”, and current-day crops in Michigan are productive for only half of the time they were in the 1950’s (Morrison et al. 2011).

BIOLOGY. In Western Europe and in North America, adults emerge in the late spring; there are two generations per year, with the second overwintering as pupae (Ferro and Gilbertson 1982; Spencer 1973).

After mating, adult females are attracted to young plants in fern. On the plant, they feed at the base of un-opened flowers but oviposit near the base of the stems; this can be either just above or below the soil surface (Ferro and Gilbertson 1982). On hatching, the larvae first tunnel up the stem for up to 30 cm and then reverse, and tunnel downwards, sometimes entering into the tap root. As many as nine larvae have been reported per inch of stem. The mature larvae pupate close to the epidermis and this mostly occurs at or about 3 cm below the soil early in the season, whereas the later overwintering pupae are usually found around 5–7 cm down (Lampert et al. 1984). However, if they mature before they reach this level, they pupate in the root or up the main stem (Barnes 1937); in some cases, pupae have been recovered over 17 cm below ground. The total life cycle (egg to adult) takes between 1500 and 2000 degree-days (Morrison III et al. 2014a).

MOVEMENT & DISPERSAL. The adults are strong fliers and most active above temperatures of 16°C. In asparagus crops in Massachusetts, USA, during hot spells with temperatures in excess of 30°C, the adults disperse to weedy areas around crops (Ferro and Gilbertson 1982).



Figures 106–115. 106–109: *Ophiomyia simplex* (Loew), female: **106:** lateral; **107:** dorsal; **108:** head; **109:** head, ventral aspect, showing straight anterior margin of clypeus that is definitive of the genus *Ophiomyia*. **110–115:** same, male genitalia: **110:** hypandrium and epiphallus, ventral; **111:** phallus, ventral; **112:** phallus, left lateral; **113:** ejaculatory apodeme; **114:** external genitalia, posterior; **115:** external genitalia, left lateral.

MANAGEMENT. Early detection. In Massachusetts, USA, yellow sticky stakes have been effective in monitoring adult populations in asparagus crops (Ferro and Suchak 1980). At local levels, a degree-day model that predicts timing of events in the phenology of the miner has been produced; this provides farmers advanced warning of the times to make management interventions to prevent population outbreaks (Morrison III et al. 2014a).

Control. Recommendations in the USA include the clearing of all wild or old stalks of asparagus from fields before the growing season and to use *Fusarium*-resistant cultivars (University of Massachusetts Exten-

sion 2015). Broad spectrum insecticides are mostly used by growers in the USA (Michigan State University Extension 2011). Studies in the UK and the USA have shown that in both regions, the miner is attacked by several species of hymenopterous parasitoids, mostly in the families Braconidae, Eulophidae, and Pteromalidae. In the USA, species of Pteromalidae were the most common (Barnes 1937; Michigan State University Extension 2011; Morrison III et al. 2014b). Conclusions of this research are that efforts should be made to conserve these parasitoids in asparagus fields (Morrison III et al. 2014b).

***Ophiomyia spencerella* (Greathead)**

“Bean Fly”

(Figs 116–124)

OTHER COMMON NAMES. Note that the common name “Bean Fly” is also used to refer to *O. phaseoli* and *O. centrosematis*.

IDENTIFICATION & DIAGNOSIS. Highly similar in appearance to *Ophiomyia phaseoli* (Fig. 100), being small and black (Figs 116–117) with a minutely textured frons with a shining orbital plate and a long, narrow, highly polished ocellar triangle that nearly attains the anterior margin of the frons (Fig. 118). It differs subtly from *O. phaseoli* externally, however, in having a wing length of 1.8–2.0 mm (not 1.7–2.2 mm), the surface of the ocellar triangle is sometimes very uneven laterally, and there is sometimes a single posteromedial seta on the mid tibia. The phallus of *O. spencerella* should be examined for confident diagnosis (Figs 122, 123): it is much higher and wider than that of *O. phaseoli* (Figs 103, 104). The less diagnostic female egg guide is wider, blunter and with serrations that are shallower and triangular (Greathead 1969: fig. 6). The puparium is blacker in *O. spencerella* and whiteish in *O. phaseoli* (Spencer 1990).

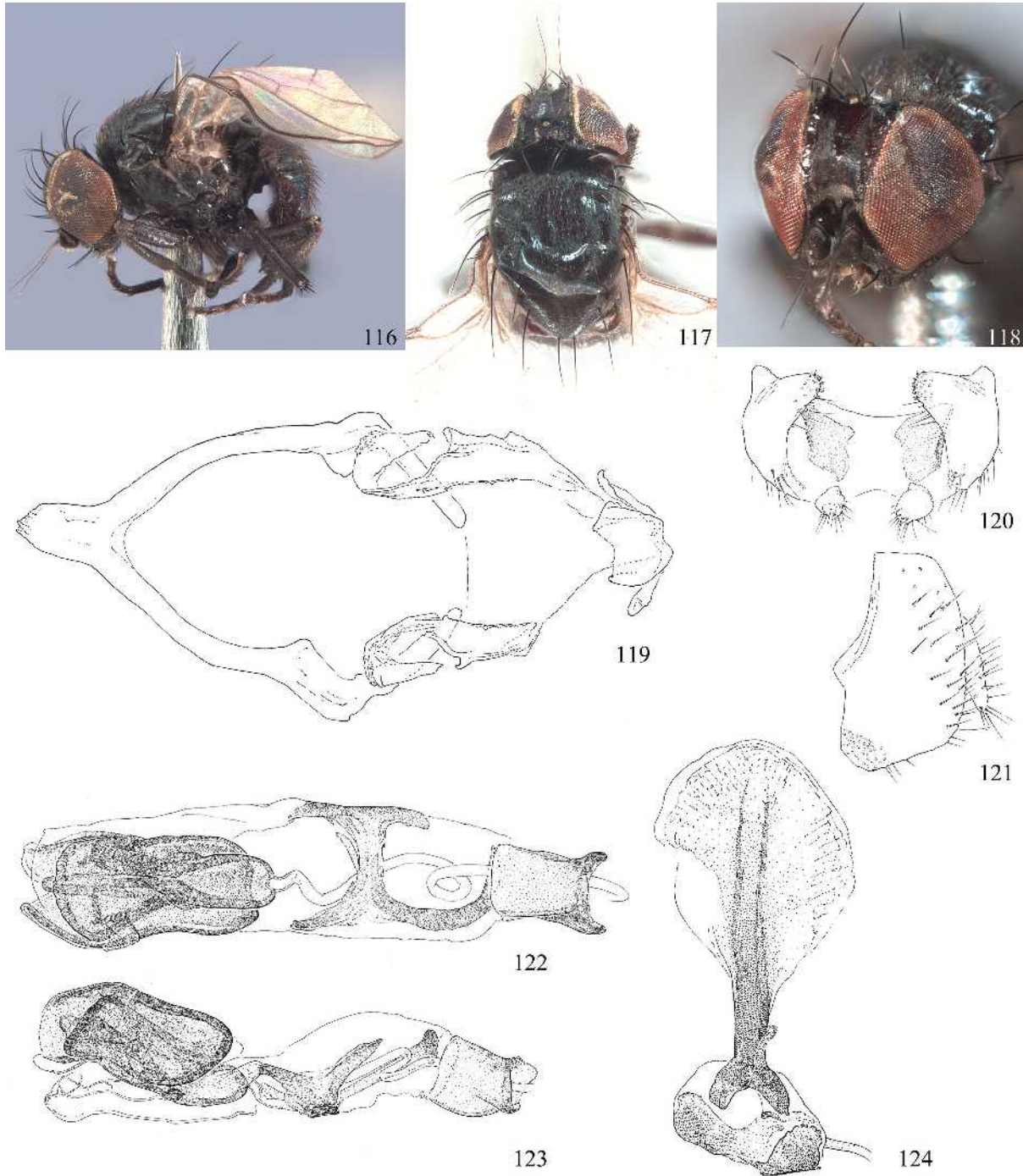
DISTRIBUTION.

•**Afrotropical Region:** Burundi (Autrique 1991), Democratic Republic of Congo (Mushambanyi 2002), Ethiopia (Getu et al. 2018), Kenya (Spencer 1973), Malawi (Letourneau 1994), Mozambique (Davies 1998), Nigeria (Spencer 1973), Rwanda (Trutmann et al. 1992), Tanzania (Spencer 1973), Uganda (Greathead 1969), Zambia (Greenberg et al. 1984).

HOSTS. *Ophiomyia spencerella* is primarily a stem feeding pest of legumes (Fabaceae). Its primary host is common bean (*Phaseolus vulgaris*), but it also attacks lima bean (*P. lunatus*), *Lablab p. purpureus*, black gram (*Vigna mungo*), rice bean (*V. umbellata*) and cowpea (*V. unguiculata*) (Spencer 1973).

DAMAGE. The damage caused to host plants by *Ophiomyia spencerella* is very similar to that by *O. phaseoli* except reports on damage to leaves differ: Greathead (1969) states that *O. spencerella* mostly only scarify leaves and lay few eggs there, with most eggs being laid in the hypocotyl and/or lower stem (see ‘Biology’ below); whereas Nderitu et al. (1990b) state that the adults normally oviposit in leaf punctures. Oviposition in the plant stem is considered more serious to the health of the plant, as this structure more is susceptible to harm and results in more immediate damage and mortality (Nderitu et al. 1990a). As seen in plants attacked by *O. phaseoli*, where damage causes physiological damage and structural instability, damage can be mitigated if the plant is able to generate adventitious roots above any stem damage (Greathead 1969). Additional subsequent damage from fungal root rot caused by the activities of *O. spencerella* also appears to be serious (Trutmann et al. 1992).

Different cultivars of bean species are known to show different levels of susceptibility (Tengecho et al. 1988). The build-up of *Ophiomyia spencerella* populations on later bean plantings in main crop seasons in Kenya and Tanzania increases in same way as with *O. phaseoli* (Sarah and Makundi 2007; Songa and Ampofo 1999).



Figures 116–124. *Ophiomyia spencerella* (Greathead), male: **116:** lateral; **117:** dorsal; **118:** head; **119:** hypandrium and epiphallus, ventral; **120:** external genitalia, ventral; **121:** external genitalia, left lateral; **122:** phallus, ventral; **123:** phallus, left lateral; **124:** ejaculatory apodeme.

BIOLOGY. The life cycle of this species is very similar to that of *O. phaseoli* so only the differences with that species are mentioned here. According to Greathead (1969), females puncture leaves (presumably for feeding on sap) but only a few eggs are deposited in these. Instead it was observed that most oviposition occurs in the hypocotyl at the ground level after plant emergence, but some eggs are also laid in the stem above the cotyledons. However, Nderitu et al. (1990b) state that this species normally lays eggs in the leaves but also in the main stem. These observations may reflect that oviposition behaviour may vary among females or populations of *Ophiomyia spencerella*.

Greathead (1969) notes that the larvae that develop from eggs in the leaves follow the same feeding pattern as *Ophiomyia phaseoli* whereas those that develop from the eggs in the hypocotyl mine down into the tap root. The last instar then returns to the ground level where it pupates in the same way as *O. phaseoli*. The total development time on bean depends on temperature: Greathead (1969) found that egg to adult took 28–35 days at about 21°C and with a preoviposition period of about 2 days.

Ophiomyia spencerella emerges as the dominant bean fly pest in East Africa at higher elevations where it is cooler and wetter, and it appears to be more prevalent in later-sown crops than *O. phaseoli* (Davies 1998; Songa and Ampofo 1999; Songa 1999; Abate et al. 2000). In some subregions it supercedes *O. phaseoli* as the most serious annual pest (eg. northern Tanzania – see Sariah et al. (2007)). Letourneau (1994) additionally found soil nitrogen levels to be positively correlated with dominance of *O. spencerella* populations over *O. phaseoli*, and later found that fertilization of crops increased the density of both pest species while not increasing bean yield (Letourneau 1995).

MOVEMENT & DISPERSAL. There is no specific information published for this species but given the similarity of the biology of this species to *Ophiomyia phaseoli* see the section on that species.

MANAGEMENT. Little specific information on this species has been published but a few papers on some aspects of management covering this species and *Ophiomyia phaseoli* are available; see *O. phaseoli* for further information. Key points are highlighted below.

Early detection. No published information is available but see the section on *O. phaseoli*.

Control. In East Africa, practices to avoid attacks on common bean include early planting, ridging, sanitation and bean variety mixtures (Letourneau 1994; Ssekandi et al. 2016). In relation to the last mentioned, research station studies on different cultivars of bean species do show different levels of susceptibility (Ojwang et al. 2010; Tengecho et al. 1988). However, as with *O. phaseoli*, insecticides are the mostly widely used control method. Few studies on natural enemies have been undertaken but in East Africa hymenopterous parasitoids have been reported (Davis 1988; Greathead 1969). In Kenya and Uganda, rates of parasitism were generally low and with only one main species, the pupal parasitoid *Gronotoma* sp. (Cynipidae). Although some of the main pupal parasitoids of *O. phaseoli*, such as *Opius* spp., will attack *O. spencerella*, they were never found to be common (Greathead 1969).

Phytobia cambii (Hendel)

“European Cambium Miner”

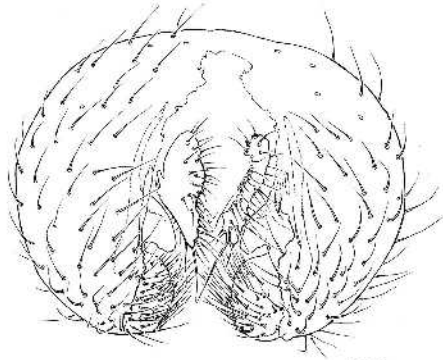
(Figs 125–128)

IDENTIFICATION & DIAGNOSIS. Characteristic of *Phytobia* species, *P. cambii* has the wing apex situated between veins R_{4+5} and M_1 , there is usually one pair of prescutellar acrostichal setae, the orbital setulae are upright to reclinate and the lunule is semicircular and silvery (Fig. 125). Among the other 11 west Palaearctic species of *Phytobia*, which were reviewed by Zlobin (2008), *P. cambii* can be diagnosed by a relatively large wing length of 3.7–4.1 mm, a projecting parafacial and orbital plate that form a ring around the eye, at least 6 fronto-orbital setae with the anterior two inclinate, 4 dorsocentrals, a costa that extends to vein M_1 , and a black pruinose frons, antenna and thorax. The phallus is also diagnostic, with a dark stem-like mesophallus fused to a much wider apical, chambered distiphallus (Figs 127, 128). Slight variation in phallic morphology was previously used to differentiate *P. cambii* from *P. betulae* (Kangas), but after comparison of a number of males across host plants, Tschirnhaus (1992) decided to synonymize the two. The larva is narrow and long, sometimes reaching 15–20 mm in length; the mandible has two teeth, sometimes interspersed with two smaller teeth and the posterior spiracle has three pores (Spencer 1973: figs 482–483).

DISTRIBUTION. *Phytomyza cambii* is known from Austria, Czech Republic, Denmark, Finland, France, Germany, Japan, Latvia, Lithuania, Netherlands, Poland, Russia, Sweden and the United Kingdom

(Zlobin 2008). It is likely much more widespread in the Palearctic Region although it appears to be absent from the extreme north (Tschirnhaus 1992).

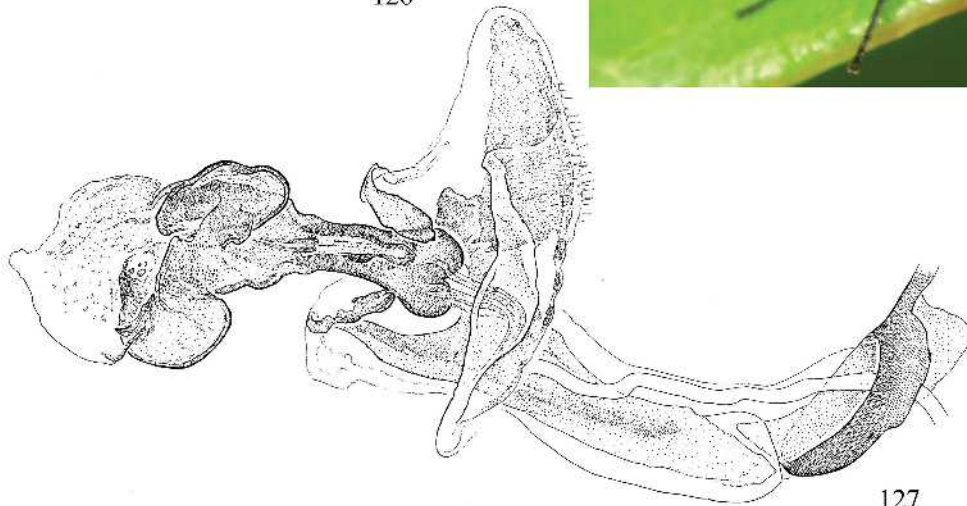
Hosts. *Phytobia cambii* feeds under the bark of woody trees and shrubs. It is known from the families Betulaceae (*Alnus* Mill., *Betula* L., *Carpinus* L., *Corylus* L.) and Salicaceae (*Populus* L., *Salix* L.) (Benavent-Corai et al. 2004; Tschirnhaus 1992).



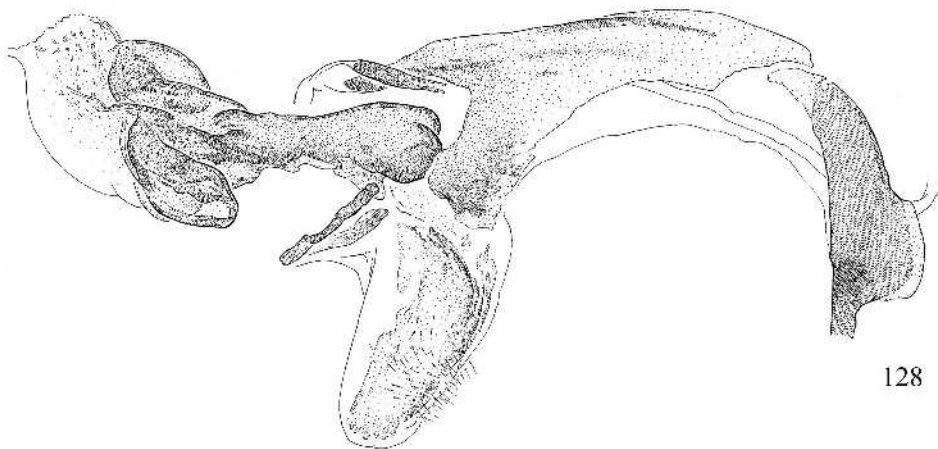
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127



128

Figures 125–128. 125: *Phytobia cambii* (Hendel), live. 126–128: same, male genitalia: 126: external genitalia, posterior; 127: phallus, ventral; 128: phallus, left lateral.

DAMAGE. *Phytobia* species feed within the young xylem of tree trunks, twigs and roots, tissue incorrectly referred to in the literature as cambium (Spencer and Steyskal 1986; Ylioja et al. 1998). As a result of feeding, thinner branches used for weaving or other activities become weakened, and wood becomes lined with discoloured “pith flecks”, which are remnants of larval traces up and down the plant along the annual rings where the plant filled the mines with darker tissue. This damage introduces imperfections and reduces wood strength, quality, appearance and market value (Greene 1914; Spencer 1973; Ylioja et al. 2000). Various species of bacteria have been isolated from the discoloured mines left by larvae (Ridé and Prunier 1963), but these bacteria and larval activity have not been linked to the presence of either necroses or cancers in wood (Kam 1986; Moraal and Grijpma 1987). As such, infestations can cause considerable economic damage to nurseries that may go unnoticed under the bark for years, and impact the furniture, veneer, flooring and construction industries, among others.

BIOLOGY. Eggs of *P. cambii* are laid within fresh shoots, with females favouring strong-growing shoots in the canopy (Ylioja et al. 2000). Spencer (1973) noted that from earlier work that the eggs take 7–14 days to hatch. The hatched larva works its way downwards into the plant where it continues the remainder of its development, with subsequent up-and-down movement in the trunk and roots, resulting in multiple mines per larva in a section of wood (Ylioja et al. 2000). The mature larvae cut exit slits from the mines and fall to the ground where they overwinter as pupae (Spencer 1973). There is one generation per year.

MOVEMENT & DISPERSAL. No published information is available.

MANAGEMENT. Early detection. No published information is available.

Control. Trials with insecticides in the 1980s with preventative application of carbofluran (a carbamate pesticide) to young poplars in the Netherlands were found to reduce larval galleries (Moraal 1989; Moraal and Grijpma 1987); this chemical is no longer in use in Europe because of its high toxicity. Trials using deltamethrin (a pyrethroid) that were reported by the same authors were inconclusive. Studies on natural enemies in the Netherlands by Moraal (1987) showed parasitism by two braconid parasitoids, *Symphya ringens* (Haliday) and *S. hians* (Nees), and one ichneumonid parasitoid, *Cremnodes atricapillus* (Gravenhorst).

***Phytomyza gymnostoma* Loew**

“Allium Leafminer”

(Figs 129–137)

IDENTIFICATION & DIAGNOSIS. Like other *Phytomyza*, *P. gymnostoma* has proclinate fronto-orbital setulae (Fig. 131), a costa that extends only to vein R_{4+5} and vein dm-cu is missing (Fig. 129). It can be further characterized by a relatively large wing length (2.8–3.5 mm), 5 fronto-orbitals, reduction of the vibrissae, 4 rows of acrostichal setulae (Fig. 130), a large epistoma and a strongly projecting parafacial and orbital plate that forms a ring around much of the eye (Zlobin 1994; Dempewolf 2004). The head is also yellowish with a stripe along the posterior margin of the eye to about the midpoint of the orbital plate, the palpus and first flagellomere are black, the notum is matt greyish-black and the legs are dark with the femora yellow apically (Spencer 1976). The posterior larval spiracles are irregular with 18–20 bulbs (Zlobin 1994). The male genitalia (Figs 132–137) are especially diagnostic - the surstylus is free (Fig. 133; not fused to the epandrium) and the phallus is atrophied apically, with the meso/distiphallus reduced to an apical membranous lobe with one pair of small curved sclerites (Figs 135, 136). Additional study of the morphology and genetic variability of this species is required as it may encompass additional cryptic species (Dempewolf 2004) that could vary with regards to host usage and pest status.

All other Agromyzidae on *Allium* are either *Liriomyza* species, which have a black notum with the shoulders and a medial stripe on the scutellum yellow, or the polyphagous *P. horticola* (Goureau) (Fig. 138).

The latter is slender, the notum is grey pruinose and virtually without acrostichal setulae, and the phallus (Figs 141–143) is drastically different.

DISTRIBUTION. *Phytomyza gymnostoma* is widespread in continental Europe (Martinez 2013; EPPO 2014) and has been found in Russia (Zlobin and Drugova 2002) and Turkmenistan (Zlobin 1994). This pest is presently known from Austria, Croatia, Czech Republic, Denmark, Finland, France, Germany, Greece (Simoglou et al. 2008), Hungary, Italy, Lithuania, Netherlands, Poland, Romania (Coman and Roşca 2011a), Russia (Zlobin and Drugova 2002), Serbia, Slovakia, Slovenia, Spain, Sweden, Turkey (Civelek et al. 2000), Turkey, Turkmenistan, Ukraine, United Kingdom (Collins and Lole 2005; Sumption 2012). Invasive Nearctic populations of the pest have also been recorded from the USA 2015, and while it is presently only known from Pennsylvania, New York and New Jersey (Barringer et al. 2018), it is almost certain to spread more widely in Canada and the United States.

Considering the rate at which the pest appears to be spreading, it will likely be uncovered in additional European and central Asian countries, and the risk of introduction into other parts of Asia or other biogeographic regions should be considered high.

HOSTS. *Phytomyza gymnostoma* is a leafminer on onion (*Allium cepa*), leek (*A. porrum*), garlic (*A. sativum*) and chives (*A. schoenoprasum*) (Coman and Cean 2009), but Barringer et al. 2018 also report giant onion (*A. giganteum* Regel), wild garlic (*A. vineale* L.), garlic chives (*A. tuberosum* Rottler ex Spreng. not Roxb.), wild onion (*A. canadense* L.) and nodding onion (*A. cernuum* Roth). The pest likely occurs on other *Allium* species as well (Dempewolf 2004). Leek and chives appear to be the most severely impacted crops.

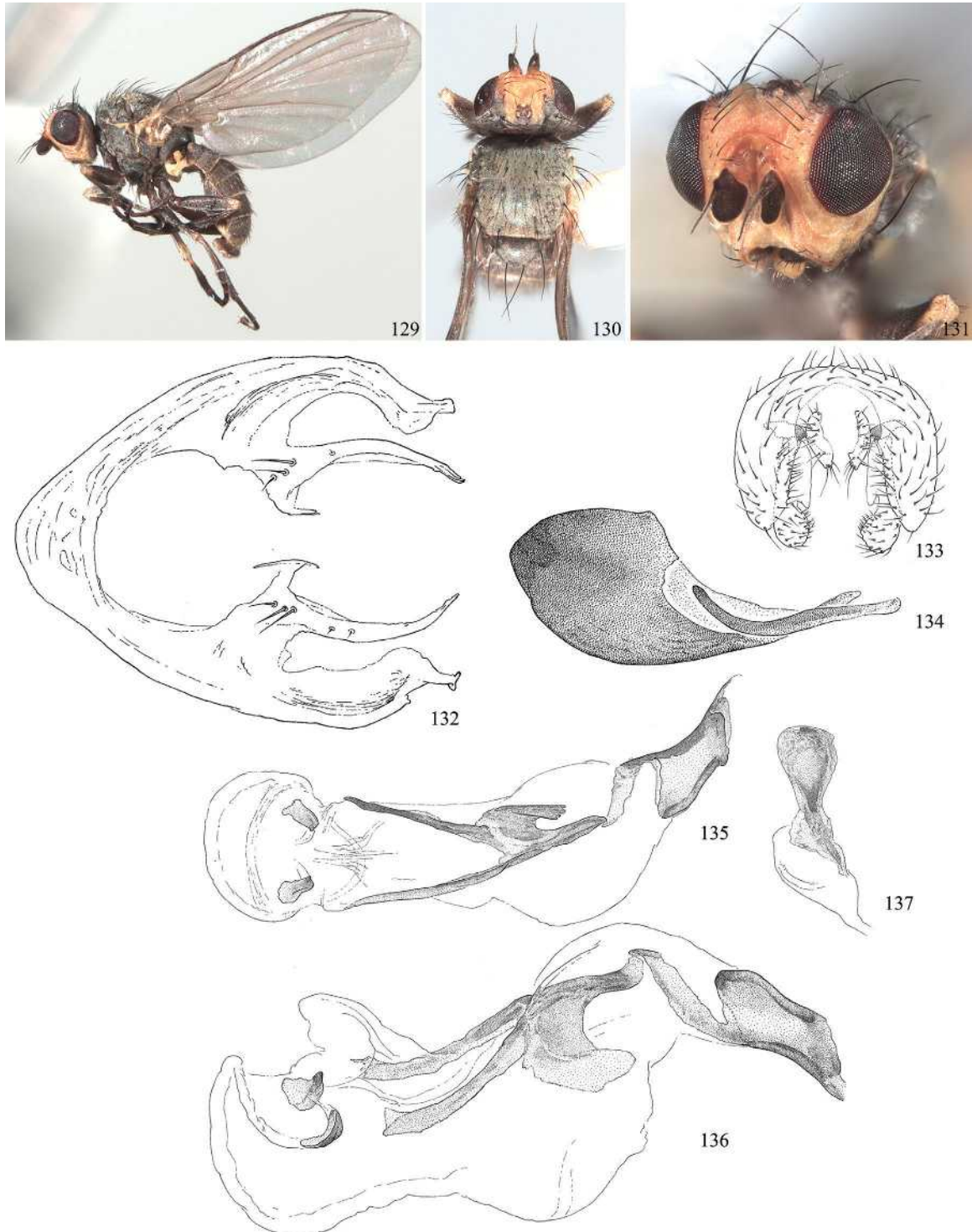
DAMAGE. Reports of crop damage due to this emergent pest are relatively recent, but studies of life history and host usage are rapidly accumulating, reflecting the widening distribution, impact and economic significance of the species (Dempewolf 2004).

Feeding damage through leaf mining and possible entry into the bulb weakens, softens and kills the plant when numerous larvae are present, but even minor traces or female feeding punctures can destroy crops by rendering the plant unsellable (Dempewolf 2004, and see Coman and Roşca (2011a)). Subsequent infections from bacteria or fungi, including the white rot *Sclerotium cepivorum* Berk., can also be severe (Simoglou et al. 2008). In central and eastern Europe, reports are revealing some infestations to result 80–100% of plants hosting larvae (Darvas et al. 1988; Burghause 1998; Billen 1999; Coman and Roşca 2011a).

BIOLOGY. Female flies make feeding punctures on leaves (Kahrer 1999). Oviposition is in the leaf, where the larva hatches and mines towards or into the bulb; pupation is internal (Zlobin 1994) and usually near the soil line (Dempewolf 2004). In Austria, the lower threshold for development is in the range, 3.2–5.1°C and egg to adult development at 20°C took: 73 days under a light: dark regime, L 6–10: D 18–14; 112 days with L14: D10; and 120 days with L18– D6. Pupation takes place at the end of the mines. Post-diapause development is triggered by temperature changes and not changes in the light: dark cycle (Kahrer 1999). The leafminer has been reported as being bivoltine in several countries (Austria – Kahrer 1999; Croatia – Mešić et al. 2009; Romania – Coman and Roşca 2011b; USA – Barringer et al. 2018) with generations in the spring and autumn but no activity between these seasons.

MOVEMENT & DISPERSAL. No specific studies have been published but it is likely that leafminer shows typical behaviour of leaf mining agromyzids: thus, naturally capable of short distance flights. International pathways could be through trade in *Allium* crops (EPPO 2014).

MANAGEMENT. Early detection. As *Phytomyza gymnostoma* has been spreading in Europe since the 1990s, the European Plant Protection Organisation (EPPO) added the species to their alert list in 2005 but it



Figures 129–137. *Phytomyza gymnostoma* Loew, male: **129:** lateral; **130:** dorsal; **131:** head; **132:** hypandium; **133:** external genitalia, posterior; **134:** pregonite, left lateral; **135:** phallus, ventral; **136:** phallus, left lateral; **137:** ejaculatory apodeme.

was taken off in 2006 because it was considered that sufficient warning had been given (EPPO 2006). Also, the UK Central Science Laboratory (now part of the UK Food and Environment Research Agency) produced a Pest Risk Analysis in 1997; this has been updated several times since (CSL 2016). In the USA, alerts have been disseminated by several states; e.g. Maryland (University of Maryland Extension 2016). For field monitoring,

the use of yellow stick traps or yellow plastic bowls containing soapy water are recommended by Maryland state (University of Maryland Extension 2016).

Control. In Poland, research indicates that late planting of leeks reduces damage from the spring generation of the leafminer (Sionek 1999). In Romania, growers are advised to cover autumn grown leeks with nets as soon as flies emerge and to bury infested plants deep in soil (Coman and Roşca 2011a). Experiments in Slovenia on the use of intercrops (*Origanum vulgare* L., *Salvia rosmarinus* Spenn. and *Lavandula angustifolia* Mill.) to reduce damage to onion crops showed no effects (Lazik et al. 2012). In France, Picault et al. (2016) emphasized the need to develop alternative controls methods such as physical controls or repellents, because of the limited number of insecticides available for use in Europe as a result of regulation of the latter by the EU in the early 1990s. Early work in Austria with insecticides showed that organophosphates were effective for controlling larvae (Kahrer 1999). Within the EU, trials have focused on insecticides that meet EU regulations; in Italy, cyromazine (which acts as an insect growth regulator), the neurotoxin, spinosad and the organophosphate, fenitrothion were the most effective for control of larvae (Talotti et al. 2004a, b). In Croatia, dipping onion bulbs or spraying crops with dimethoate (an organophosphate) and imidacloprid (a systemic neonicotinoid) were also effective (Mešić et al. 2008). Studies on natural enemies by Sionek and Wiech (2004) revealed several hymenopterous parasitoids; these were reared from pupae collected from leek and included species from the families, Ichneumonidae, Braconidae and Figitidae.

Phytomyza horticola Goureau

“Garden-Loving Leafminer”

(Figs 138–145)

OTHER COMMON NAMES. Cruciferous leafminer, pea leafminer; mustard leafminer.

IDENTIFICATION & DIAGNOSIS. *Phytomyza horticola* is similar to most *Phytomyza* in having proclinate orbital setulae (Fig. 140), a costa that extends only to vein R_{4+5} and an absence of crossvein dm-cu (Figs 138, 139).

The status of this species was historically confused with that of the similarly pestiferous *Phytomyza syngenesiae* (Hardy) (Figs 146, 147) under the name *P. atricornis* Meigen until Griffiths (1967) clarified its status. Both species are dark brown with yellow knees and a dense greyish pruinosity on the thorax, wing length is 2.2–2.6 mm (up to 2.7 mm in *P. horticola*), and the head is light yellow with the antenna brown; there are only three fronto-orbital setae, the eye is very sparsely short pubescent, and the acrostichal setulae are absent, although the odd setula(e) is sometimes present in two rows. The terminal components of the male genitalia are used to differentiate the two species – while both have a single small, pigmented, medially bent tubule centrally, it is shorter and more gracile in *P. horticola*, dorsally extending into one pair of faintly to strongly sclerotized leaf-like processes, and it is ventrally flanked by one pair similar, inwardly curved sclerites (Figs 141–143); in *P. syngenesiae*, the ventral sclerites are absent, and the dorsal sclerite is narrow, apically split and accompanied by one pair of sclerotized distolateral points (Fig. 146).

DISTRIBUTION. *Phytomyza horticola* is a nearly cosmopolitan species, present throughout much of Africa, Europe and Asia, being absent only in the Australian Region and the New World (Griffiths 1967; Spencer 1973; Sasakawa 1977, 2006; Cogan 1980; Deeming 2006; Martinez 2013; Černý and Tschirnhaus 2014; CABI 2016d), where the risk of introduction should be considered extremely high.

•**Afrotropical Region:** Cameroon, Cape Verde, Central African Republic, Congo, Eritrea, Ethiopia, Gabon, Kenya, Madagascar, Malawi, Rwanda, Senegal, South Africa, Uganda, Yemen, Zimbabwe.

•**Oriental Region:** China (widespread), India (widespread), Indonesia, Japan (Ryukus), Malaysia, Philippines, Thailand, Vietnam.

•**Palearctic Region:** Austria, Belgium, Bulgaria, China (widespread), Croatia, Czech Republic, Denmark, Egypt, Eritrea, Finland, France, Germany, Hungary, Iran (Hazini et al. 2013), Iraq, Ireland, Isra-

el, Italy, Japan, Democratic People's Republic of Korea, Republic of Korea, Kuwait, Libya, Lithuania, Macedonia, Malta, Republic of Moldova, Mongolia, Montenegro, Morocco, Nepal, Netherlands, Norway, Pakistan, Poland, Portugal (Azores, mainland), Romania, Russia, Saudi Arabia, Serbia, Slovakia, Spain (Canary Is., mainland), Sweden, Switzerland, Thailand, Turkey, Ukraine, United Kingdom.

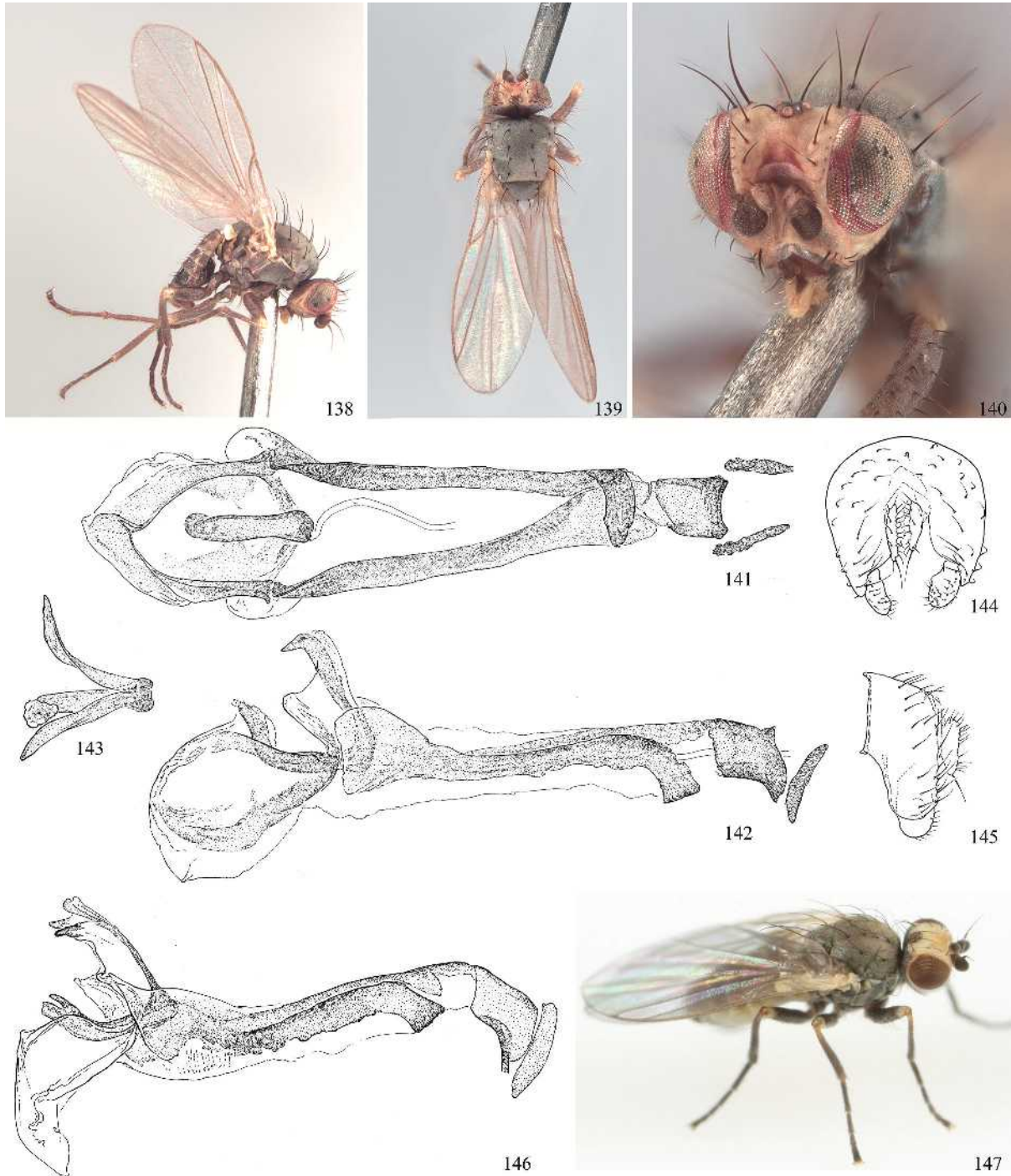
Hosts. *Phytomyza horticola* is a highly polyphagous leafmining pest of at least 237 host genera in 42 plant families (although 268 genera are listed in CABI (2016)). Host genera are documented in Benavent-Corai et al. (2005) and Ortiz (2009), although other records are in need of verification, and it is almost certain that numerous additional previously undocumented host genera exist. Affected families are: Acanthaceae, Alliaceae, Amaranthaceae, Anacardiaceae, Apiaceae, Asteraceae, Balsaminaceae, Boraginaceae, Brassicaceae, Campanulaceae, Cannabaceae, Caprifoliaceae, Caryophyllaceae, Cleomaceae, Convolvulaceae, Cucurbitaceae, Euphorbiaceae, Fabaceae, Gentianaceae, Lamiaceae, Linaceae, Loasaceae, Malvaceae, Onagraceae, Orobanchaceae, Papaveraceae, Phrymaceae, Plantaginaceae, Plumbaginaceae, Poaceae, Polemoniaceae, Polygonaceae, Primulaceae, Ranunculaceae, Resedaceae, Rutaceae, Scrophulariaceae, Solanaceae, Tropaeolaceae, Urticaceae, Verbenaceae, Violaceae. Hosts primarily belong to the families Apiaceae (16 genera), Asteraceae (49 genera), Boraginaceae (17 genera), Brassicaceae (36 genera), Fabaceae (18 genera) and Lamiaceae (21 genera). Main host crops are listed in CABI (2016) include: *Allium*, Apiaceae, Asteraceae, *Chrysanthemum*, lettuce (*Lactuca sativa*), radish (*Raphanus raphanistrum sativus* (L.) Domin), Cucurbitaceae, beans, peas, tomato (*Solanum lycopersicum*), *Cicer*, *Mentha*, *Brassica* and other cruciferous crops.

DAMAGE. *Phytomyza horticola* is considered a serious pest wherever it occurs, primarily attacking a number of vegetable and fruit crops, but also economically important ornamentals such as *Chrysanthemum*, sweet pea (*Lathyrus odoratus* L.), *Phlox* L., *Nicotiana* and marigolds (*Calendula*) (Spencer 1973; CABI 2016d). Although single leaf mines are often negligible in their damage, populations can readily reach outbreak levels, likely in no small part due to the high fecundity of females (Dempewolf 2004). Feeding within the leaf by larvae severely weakens the plant by affecting photosynthetic potential, withering and prematurely dropping leaves, thereby reducing yield (Spencer 1973; Dempewolf 2004). Effects on seedlings are especially serious as they are much more susceptible to damage, leading to reduced growth and possibly death (CABI 2016d). Female feeding punctures also cause some damage (Spencer 1973).

Field crops are affected in warm and temperate growing areas, but populations in glasshouses can also be severe, including northern European glasshouse crops of tomato and lettuce (Harris 1976; Paikal'nishkis 1984).

BIOLOGY. A female fly mainly feeds and oviposits on the tip and lateral margins of leaf; with more eggs laid on lower surface than on the upper surface of the leaf (Wang and Yan 1986; Yoshida and Sasakawa 1975). Up to 150 feeding punctures per leaf have been recorded for pea but only a few eggs were laid in the leaves (Hill 1986). Oviposition begins 1–3 days after adult emergence (Wang and Yan 1986). A female may produce 100 to 500 eggs each, laying a maximum of 50 a day (Dempewolf 2004). The latter observation compared with that of Hill (1986) – see above – may be due differences in the host plants under study. The larval mines are irregularly linear (Spencer 1973) and pupation takes place at the end of the mine (Hill 1986).

Older literature from Italy and India on development times have been reviewed by Spencer (1973) and include: egg 2–4 days; larva 5.2 days (at 23–28°C); and pupa 7–15 days, although this may be several months in areas where there is an overwintering period. More precise data are provided from work on sweet peas in Taiwan by Wang and Yang (1986) conducted at 21°C, 70–80% RH and with a LD cycle 12:12: egg 1–3 days; first, second and third instar larvae 2.50, 1.69, and 1.75 days respectively; and pupa 7.53 days. The survival rate of the egg stage was 96.68%, whilst that of the first instar larva was 34.97%; no mortality occurred in the remaining two instars. The survival rate of the pupal stage was 82.75%.



Figures 138–147. 138–145: *Phytomyza horticola* Goureau, male: **138:** lateral; **139:** dorsal; **140:** head; **141:** phallus, ventral; **142:** phallus, left lateral; **143:** detail of supporting sclerite, ventral; **144:** external genitalia, posterior; **145:** external genitalia, left lateral. **146, 147:** *Phytomyza syngenesiae* (Hardy): **146:** phallus, left lateral; **147:** live male.

Spencer (1973) notes that there are three to four generations in temperate Europe while in India the leafminer is active during the cooler drier months (January to April).

MOVEMENT & DISPERSAL. The leafminer will be naturally capable of short distance flights, but Iwasaiki et al. (2008) documented this species migrating in the spring from southern to northern Japan on low-level

el jet streams – a distance of over several hundred km - representing the first documented case of an agromyzid migrating over long distances. As the leafminer feeds on many important horticultural crops, there is a risk of movement via international trade pathways.

MANAGEMENT. Early detection. A factsheet on this leafminer is available on the internet (Lucid keys 2016).

Control. In Uttar Pradesh, India, sowing peas later in a growing season (early December rather than late October) reduced the incidence of leafminer populations (Srivastava et al. 1974). Earlier work in India recommended the use of insecticides such the organophosphates, phorate and disulfoton (Vyas and Saxena 1982) but these compounds are classed as highly toxic (World Health Organisation 2009). Other work in India identifies other, less hazardous insecticides as being effective when applied in ultra-low-sprays: the organophosphates malathion, dimethoate and fenitrothion (Singh et al. 1975). Also, in India, Singh et al. (1986) compared a range of 10 organophosphates, 4 carbamates, 4 synthetic pyrethroids and one cyclodiene insecticides and recommended the carbamates thiodicarb and carbaryl, as these are effective and do not leave toxic residues compared with the other products tested. In Japan, several products were identified as being effective in laboratory assays, but notably the translaminar insecticides cyromazine (an insect growth regulator) and the neurotoxin spinosad (Saito 2004), which are also recommended for control of *Liriomyza* spp. (Reitz et al. 2013). Saito (2004) speculated that outbreaks of the leafminer on pea crops in the early 2000s was due to the overuse of insecticides, resulting in reduced susceptibility of the leafminer and high mortality of native hymenopterous parasitoids. Studies on natural enemies have revealed diverse native hymenopterous parasitoid complexes from: Japan (Takada and Kamijo 1979); Korea (Paik 1979); China (Sheng et al. 1989); India (Bhat and Bhagat 2009); and Iraq (Mekhlif and Abdul-Rassoul 2002). Chalcid and braconid species predominate in records, especially *Chrysocharis* and *Diglyphus* spp. (Eulophidae), and *Dacnusa* and *Opius* spp. (Braconidae). Takada and Kamijo (1979) note that the leafminer is rarely a problem in Japan because of the high mortality caused by parasitoids.

***Phytomyza ilicicola* Loew**

“American Holly Leafminer”

(Figs 153–155)

IDENTIFICATION & DIAGNOSIS. Like most *Phytomyza*, *P. ilicicola* has proclinate fronto-orbital setulae, a costa that extends only to vein R_{4+5} and vein dm-cu is missing (Fig. 153). Wing length is 1.7–2.1 mm. There are 4 dorsocentral setae, 4–6 rows of acrostichal setulae, four fronto-orbitals (anterior seta smaller), the head is greyish, the antenna is dark brown to black, the thorax is dark brown with a slightly iridescent grey pruinosity, the legs are brown, becoming paler apically, and the mesophallus is dark and rod-like and the distiphallus is entirely divided into two dark tubules. Like other eastern Nearctic holly leafminers, the epandrium also has a bulging subconical process above the anus, the posterior ocelli are widely spaced, and the ocellar tubercle is subrectangular and close to the vertex.

This species can only be confidently diagnosed morphologically from other eastern holly leafminers using subtle characters of the male genitalia: the distiphallus is curved dorsally and slightly shorter than the distiphallus, and the sclerotized paired plates of the hypophallus are relatively long and curved (Figs 155, 156). Mitochondrial DNA sequence data are available for all known holly leafminer species (Scheffer and Wiegmann 2000; Scheffer et al. 2021). When possible, molecular data should be used to corroborate morphological identifications.

DISTRIBUTION. *Phytomyza ilicicola* is the most commonly encountered holly leafminer in eastern North America, known from Ontario, Delaware, the District of Columbia, Florida, Kentucky, Massachusetts, Maryland, North Carolina, New York, Ohio, Pennsylvania and South Carolina (Lonsdale and Scheffer 2011). Leaf mines possibly representing this species are also known from Connecticut, Tennessee and Virginia (Lonsdale and Scheffer 2011).

HOSTS. This species forms a linear-blotch mine, primarily on the evergreen holly *Ilex opaca* Aiton (Kulp 1968; Lonsdale and Scheffer 2011), including the subspecies *I. opaca arenicola* (Ashe) Ashe. It may also occur on *I. ×attenuata* Ashe [*cassine* × *opaca*] and other hybrids involving *I. opaca* in horticultural settings. It has been known to rarely occur on *I. aquifolium* L.

DAMAGE. Damage from *P. ilicicola* can be extensive, resulting from both the presence of the leaf mines as well as the oviposition and feeding punctures. The mines are conspicuous and during heavy infestations may cover entire leaf surfaces. Trees often abscise mined leaves, potentially resulting in significant leaf loss in heavy infestations. Adult flies are able to emerge from mines in abscised leaves that have fallen to the ground (Kahn and Cornell 1989). Feeding and oviposition punctures made on newly emerging leaves in the spring cause leaves to become deformed and unsightly. Because the ornamental use of hollies depends on attractiveness of its foliage, both leaf mine and puncture damage can reduce market value. On *I. opaca* in its native understory habitat, *P. ilicicola* populations rarely reach levels of infestation observed in sunny, horticultural settings (Potter 1985).

BIOLOGY. Males and females emerge and mate on the leaf surfaces in the early spring, coincident with the emergence of new spring leaves. Feeding and oviposition punctures can be easily observed on the young leaves, which may become curled when numerous punctures have been made. *Phytomyza ilicicola* has a single generation a year with a life cycle considered unusual for an agromyzid. Following oviposition in April/May, and egg hatch in June, larval feeding and development times are considerably extended, with the third instar larvae present from December to March. Pupation takes place within the mine with the anterior spiracles emerging from the upper leaf surface. Adults emerge in April and May, with some variation due to latitude. Leaves of *I. opaca* growing in the sun are mined more heavily than those in the shade.

Phytomyza ilicicola has been the subject of numerous ecological studies on host-plant relations and parasitism (Potter 1985, 1992; Potter and Gordon 1985; Potter and Kimmerer 1986, 1989; Kimmerer and Potter 1987; Marino and Cornell 1992, 1993; Scheffer et al. 2021).

MOVEMENT & DISPERSAL. Regional dispersal of *P. ilicicola* has undoubtedly taken place in association with the extensive movement of American hollies and hybrids within the ornamental trade.

MANAGEMENT. Early detection. Feeding and oviposition punctures are the first signs of a new *P. ilicicola* population. These will typically be followed by the presence of leafmines.

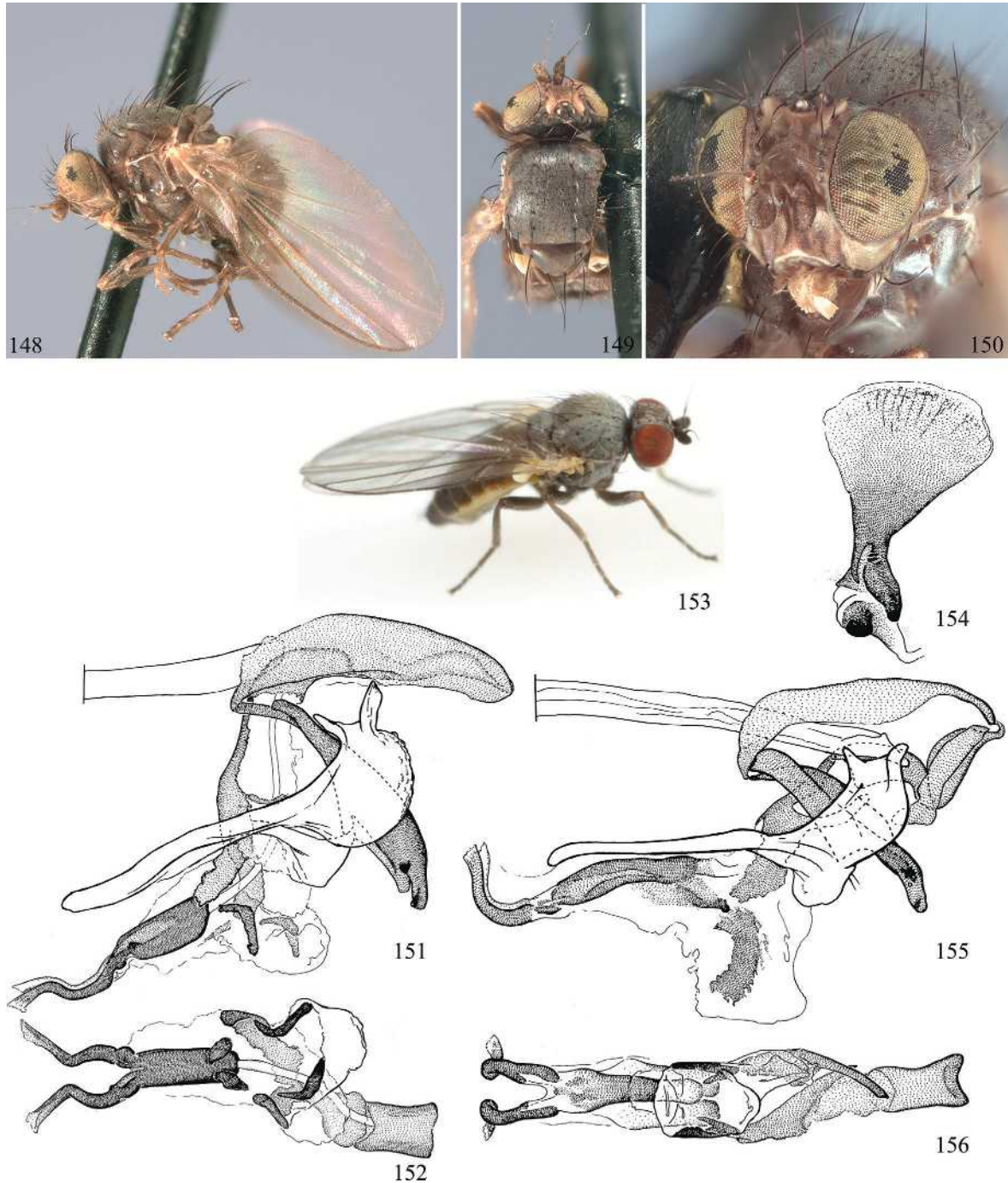
Control. With infestations of nursery plants and other small trees, it may be possible to manually remove and destroy leaves prior to adult emergence (North Carolina State Extension 2023). Plants grown in shade conditions are less likely to be mined than those grown in the sun. Insecticide use with leafminers is notoriously difficult as the eggs and larvae are protected within the leaves but systematic insecticides may also provide control of larvae (North Carolina State Extension 2023). *Phytomyza ilicicola* is attacked by a number of parasitoid wasps in the families Braconidae, Eulophidae and Pteromalidae. Overall rates of parasitism may commonly reach 50–80% (Braman and Pendley 1993). Conservation of parasitoids is likely to be an important means of regulating *P. ilicicola* populations. Insecticides should be used with care to avoid parasitoid mortality.

Phytomyza ilicis Curtis

“European Holly Leafminer”

(Figs 148–152)

IDENTIFICATION & DIAGNOSIS. Like most *Phytomyza*, *P. ilicis* has proclinate fronto-orbital setulae (Fig. 150), a costa that extends only to vein R_{4+5} and vein dm-cu is missing (Fig. 148). Wing length is 2.8–3.7 mm, making it the largest of the holly leafminers. There are 4 dorsocentral setae, 6 scattered rows of acrosti-



Figures 148–156. 148–152: *Phytomyza ilicis* Curtis, male: 148: lateral; 149: dorsal; 150: head; 151: hypandrium, pregonite, epiphallus, base of phallapodeme and phallus, left lateral; 152: phallus, ventral. 153: *Phytomyza ilicicola* Loew, female. 154–156: same, male genitalia: 154: ejaculatory apodeme; 155: hypandrium, pregonite, epiphallus, base of phallapodeme and phallus, left lateral; 156: phallus, ventral.

chal setulae, four fronto-orbitals (anterior seta smaller), the head is greyish, the antenna is mostly dark brown to black, the thorax is dark brown with the notopleuron sometimes yellowish, the legs are brown with yellow knees and the tibiae and tarsi paler, and the mesophallus is dark and rod-like and the distiphallus is entirely divided into two dark tubules (Figs 151, 152).

Unlike other holly leafminers, *Phytomyza ilicis* is much larger, the basicosta is white with a brown spot, the epandrium is evenly rounded, the ocellar tubercle is widely separated from the vertex (Fig. 149) and the

hypophallus has a narrow L-shaped sclerite. It is the only holly leafminer in the western Nearctic Region, although *P. vomitoriae* Kulp occurs in California.

DISTRIBUTION. Native to the Palearctic Region, this species is known from Belgium, Denmark, France, Germany, Ireland, Italy, the Netherlands, Norway, Sweden, Switzerland and the United Kingdom (Lonsdale and Scheffer 2011; Martinez 2013). It has been introduced to the western Nearctic Region, likely multiple times independently on its host, and has established in Oregon, Washington and British Columbia (Lonsdale and Scheffer 2011).

HOSTS. This species is only known to occur on the evergreen holly *Ilex aquifolium* L. (Aquifoliaceae) (Kulp 1968; Lonsdale and Scheffer 2011).

DAMAGE. *Phytomyza ilicis* produces irregularly circular blotch mines typically associated with the leaf midrib. The mines are conspicuous on the upper leaf surface and are often generally white to yellowish in colour with patches of red or purple. There are usually only one or a few mines on a leaf. Mines are unsightly and reduce market value of ornamental products.

BIOLOGY. Adult *P. ilicis* emerge in the spring coincident with the annual flush of new leaves on its host. Females oviposit in the midrib or petiole of the leaf. Following hatching, the larva feeds along the leaf midrib and after the first moult, it begins to form a blotch in the center of the leaf. As with *Phytomyza ilicicola*, the larval feeding stage is unusually long, with feeding extending well into winter. Pupation occurs within the leaf with the anterior spiracles emerging from the mine surface. Adult emergence occurs near the end of April. There is a single generation each year.

Phytomyza ilicis in Europe has been the subject of numerous ecological studies on population dynamics, determinants of geographic range and parasitism (Heads and Lawton 1983; Valldares and Lawton 1991; McGeoch and Gaston 2000; Eber 2001, 2004; Brewer and Gaston 2002, 2003; Klok et al. 2003; Gaston et al. 2004).

MOVEMENT & DISPERSAL. Regional movement undoubtedly occurs in association with commercial movement of its host plant.

MANAGEMENT. Early detection. Feeding and oviposition punctures are the first signs of a new *P. ilicis* population.

Control. With small trees, it may be possible to manually remove and destroy mined leaves prior to adult emergence, including leaves both under and remaining on the trees. The host *Ilex aquifolium* is naturalized within the Pacific Northwest, however, and likely serves as a reservoir for local pest populations. Recommendations for use of insecticides is the same as for *P. ilicicola* (see above). With respect to biological control, *P. ilicis* within its native range is rarely considered to reach pest status (Eber et al. 2001). However, within the Pacific Northwest, where it had been introduced by the early 1900s, damage from this species prompted biological control efforts focused on the importation of natural enemies from its native range (Cameron 1939).

Phytomyza nigra Meigen

“Corn-Linear Leafminer”

(Figs 157–164)

IDENTIFICATION & DIAGNOSIS. Like most *Phytomyza*, *P. nigra* has proclinate fronto-orbital setulae (Fig. 159), a costa that extends only to vein R_{4+5} and vein dm-cu is missing (Fig. 157). Furthermore, the first

flagellomere is relatively short, the frons is yellow but sometimes brownish, there are 3–4 fronto-orbital setae, the acrostichal setulae are in only two rows (Fig. 158) and wing length is 1.9–3.0 mm.

The apex of the phallus (Fig. 157, 163) is highly derived and the best way by which to diagnose this species – the distiphallus is a simple pigmented tube, flanked dorsally and laterally by three pairs of long, narrow sclerites. A similar phallus is seen in two East African species - *P. nigrissima* (Spencer) and *P. subnigra* (Spencer) (Spencer 1985) - and their relationship to *P. nigra* should be re-evaluated. Externally, the eyes are densely covered with minute hairs in both sexes; a similar state is seen in *P. fuscula* (Zetterstedt), which is also a pest on grasses, but the eye pubescence on *P. fuscula* is much sparser and the phallus is simpler, with a clear tubular distiphallus flanked by a small, thin, filamentous sclerites (see Griffiths (1980: figs 51–52)). The larval anterior spiracles are characterized by long stalks with up to 18 bulbs used to project through the host epidermis; the posterior spiracles are short and have 10–13 bulbs (Spencer 1976).

Phytomyza nigra after the mid 1970's was treated as part of the genus *Chromatomyia* until that genus was found to be an artificial assemblage and synonymized into *Phytomyza* (Winkler et al. 2009; Lonsdale and Eiseman 2021). The species itself is suspected to be a complex of multiple taxa, but until more detailed study is conducted, it is recommended that the single entity of *P. nigra s.l.* be recognized (Griffiths 1980).

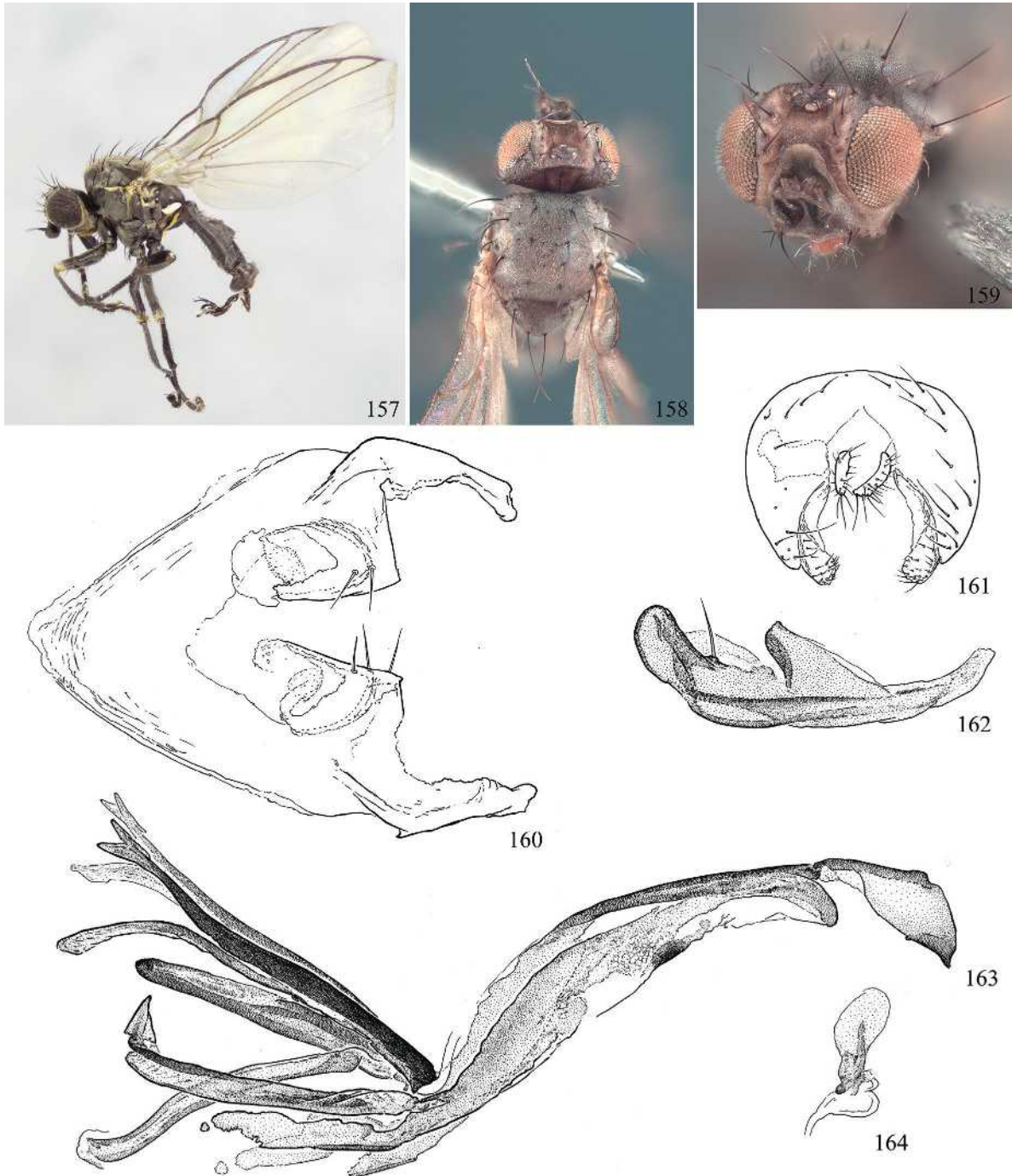
DISTRIBUTION. *Phytomyza nigra* is widespread in the western Palaearctic, but it also occurs in eastern Russia, India, Japan, Taiwan and western North America (Griffiths 1980; Spencer and Steyskal 1986; Martinez 2013). Griffiths (1980) treated the species as a 6-form “superspecies”, that following additional study, will likely be split into distinct species with more restricted distributions and diet.

- Nearctic Region:** Canada (British Columbia), United States (California, Oregon, Washington (Spencer 1973)).
- Oriental Region:** India (Sandhu and Deol 1975), Taiwan.
- Palaearctic Region:** Austria, Belarus, Belgium, Czech Republic, Denmark, Estonia, Finland, France, Germany, Hungary, Iceland, Iran (Shahreki et al. 2012), Ireland, Italy, Republic of Korea (Ku 1969), Japan, Latvia, Lithuania, Montenegro, Netherlands, Norway (Andersen and Jonassen 1994), Poland, Portugal (Madeira), Russia, Serbia (Spasic 1991), Slovakia, Sweden, Switzerland, United Kingdom.

HOSTS. This species mines the leaves of many Poaceae, and is so far known from 46 host genera (Griffiths 1980; Benavent-Corai et al. 2005): *Aegilops* L., *Agropyron* Gaertn., *Agrostis* L., *Alopecurus* L., *Ammophila* Host, *Anthoxanthum* L., *Apera* Adans., *Arrhenatherum* P. Beauv., *Avena* L., *Brachypodium* P. Beauv., *Briza* L., *Bromus* Scop., *Calamagrostis* Adans., *Catapodium* Link., *Chaetopogon* Janch., *Cynosurus* L., *Dactylis* L., *Deschampsia* P. Beauv., *Desmazeria* Dumort., *Eleusine* Gaertn., *Festuca* L., *Gaudinia* P. Beauv., *Helictotrichon* Besser, *Hierochloa* R. Br., *Holcus* L., *Hordeum*, *Lagurus* L., *Lamarkia* Moench, *Lepturus* R. Br., *Lolium* L., *Melica* L., *Milium* L., *Molinia* Schrank, *Nardus* L., *Phalaris* L., *Phleum* L., *Pholiurus* Host ex Trin., *Poa* L., *Polypogon* Desf., *Secale* L., *Sesleria* Scop., *Setaria* P. Beauv., *Triticum*, *Trisetum* Pers., *Vulpia* C.C. Gmel., *Zea* L.

DAMAGE. *Phytomyza nigra*, along with *P. fuscula*, are regular pests on cereal crops including corn (*Zea mays*), barley (*Hordeum*), rye (*Secale cereale*) and wheat (*Triticum*) (Spencer 1973), and is sometimes quite locally abundant (Roik and Walczak 2012); for example, Darvas et al. (1981) reported damage to winter wheat leaves in Hungary. *Phytomyza nigra* is usually of minor significance outside of Japan, where it can be very destructive (Sasakawa 1953). More eggs are found to be laid on early-maturing varieties of barley and wheat (Sasakawa 1954).

BIOLOGY. The life cycle is that of a typical leaf mining agromyzid (see Spencer 1973). Larvae produce linear leaf mines in the upper or lower layers of grass blades that sometimes appear blotchy when channels are adjacent (Griffiths 1980). Pupation is internal. Temperature has been shown to be a significant factor



Figures 157–164. *Phytomyza nigra* Meigen, male: **157:** lateral; **158:** dorsal; **159:** head; **160:** hypandium; **161:** external genitalia, posterior; **162:** pregonite, left lateral; **163:** phallus, left lateral; **164:** ejaculatory apodeme.

influencing reproduction, with cool temperatures (15°C) and short days (LD 10:14) favouring reproduction compared with warmer temperatures and longer days (Kamm 1977).

MOVEMENT & DISPERSAL. No available published information.

MANAGEMENT. Early detection. In Poland, yellow sticky traps are used for early warning and dates for application of insecticides (Walczak 1998).

Control. In Japan, egg laying by females was positively correlated with the time of early maturation in different varieties of wheat and barley. Larval mortality was inversely correlated with the crude protein content of the leaves of different varieties (Sasakawa 1954). Applications in France of the insecticide deltamethrin (a pyrethroid), dimethoate and phosalone (organophosphates) for control of the wheat aphid, *Sitobion avenae*, negatively affected populations of the leafminer within years, but not between years (Fischer and Chambon 1987). Records of natural enemies include hymenopterous parasitoids (Spencer 1973). Parasitism of field populations in the USA was less than 15% in the autumn and winter but increased to 77% in April (Kamm 1977). In North America, natural parasitism by parasitoids cause leafminer populations to crash and the use of chemicals is not recommended (Pacific North West Insect Management Handbook 2023). Lu et al. (2010) reported significant parasitism by the braconid *Ephedrus plagiator* (Nees) in China.

***Phytomyza rufipes* Meigen**

“Cabbage Leafminer”

(Figs 165–171)

IDENTIFICATION & DIAGNOSIS. As for most *Phytomyza*, *P. rufipes* has proclinate orbital setulae, a costa that extends only to vein R_{4+5} , and crossvein dm-cu is absent. Externally, it differs from congeners as follows: the head is yellow although the antenna is deeper yellow to orange with the outer surface of the first flagellomere sometimes brownish (segment apparently sometimes entirely dark (Spencer 1976)), the frons between the orbital plates is sometimes orange to slightly brownish, and a brown stripe reaches the posterior margin of the eye (Fig. 165). The thorax is dark brown with a thick grey pruinosity, with the shoulders (notopleuron + postpronotum), the dorsal 1/3 of the anepisternum and the dorsal margin of the katepisternum (encompassing the base of the katepisternal seta) are yellow. The femora are yellow with a dorsal brown stripe of variable size. Wing length is 2.1–3.5 mm, there are 4–5 fronto-orbitals, the parafacial and orbital plate are raised and continue below eye as a distinct “cheek”, the epistoma is broad, and the acrostichal setulae are absent or limited to a few setulae anteriorly.

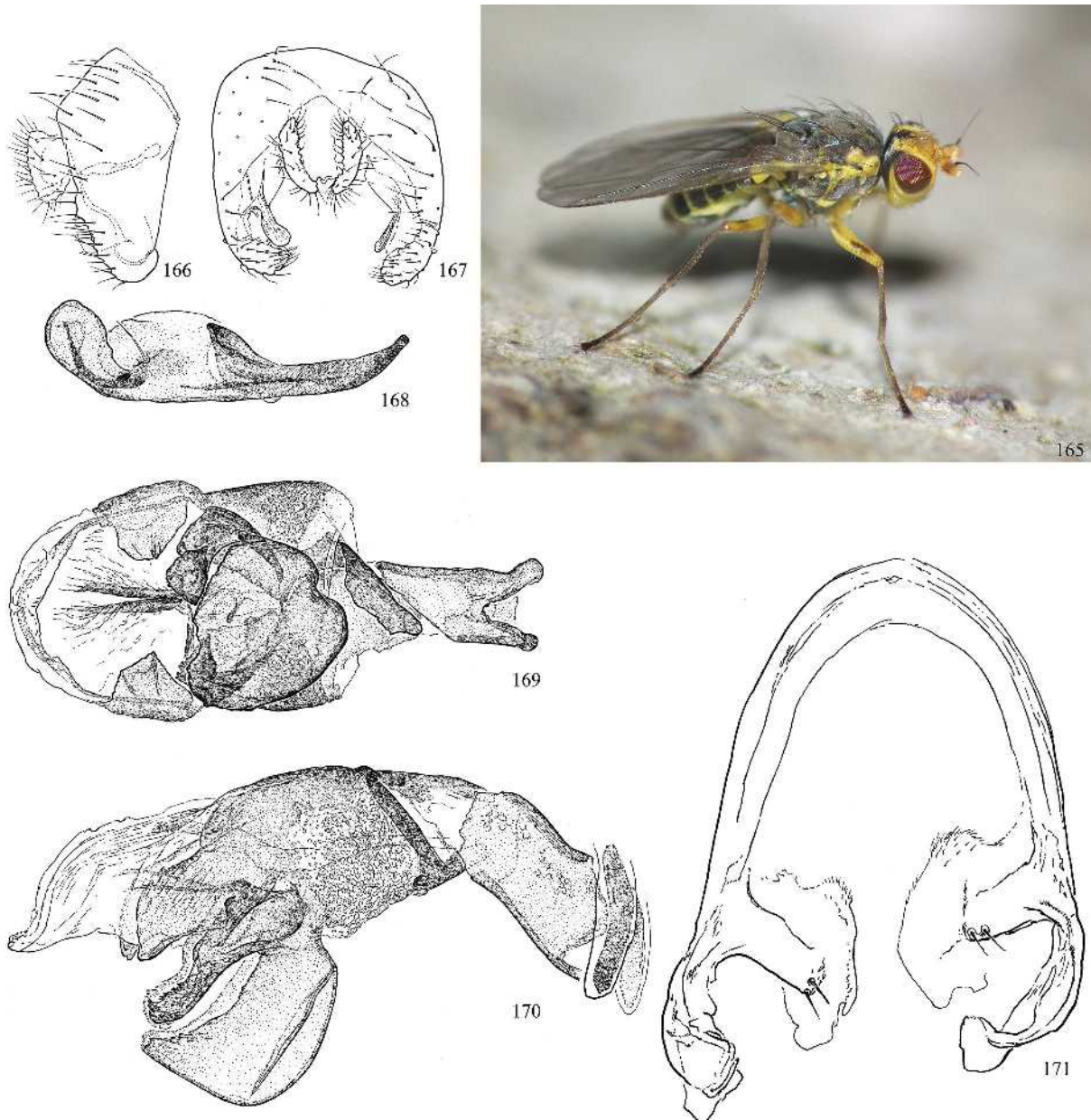
The phallus is unique, being broad and cylindrical basally, there is a broad distoventral “cup”, and an apical chamber is enclosed by several processes and a weakly sclerotized dome (Figs 169, 170).

DISTRIBUTION. This species occurs throughout much of Europe into Russia (Martinez 2013; Spencer 1973) and Iraq (Al-Saffar 2014). It has also been found in parts of North and South America, where it is considered to be introduced (Scheffer and Winkler 2008).

- Nearctic Region:** Canada (New Brunswick, Newfoundland) (Spencer 1969), USA (California – all records previous to Scheffer and Winkler (2008) are considered misidentifications).
- Neotropical Region:** Argentina (Valladares et al. 1999), Colombia (Spencer 1984).
- Palaeartic Region:** Czech Republic, Denmark, Egypt, Estonia, Finland, France, Germany, Iceland, Iraq, Ireland, Italy, Lithuania, Netherlands, Norway, Poland, Portugal (Madeira), Russia, Slovakia, Spain (mainland, Canary Islands), Sweden, Switzerland, Turkey (Civelek 2002), United Kingdom, former Yugoslavia.

HOSTS. *Phytomyza rufipes* can feed in the leaf, midrib, petiole and stem, often moving between these plant tissues. It feeds on a number of Brassicaceae – *Alliaria* Heist. ex Fabr., *Armoracia* G.Gaertn., B.Mey. & Scherb., *Brassica*, *Coringia* J.Presl & C.Presl, *Diplotaxis*, *Moricandia*, *Peltaria* Jacq., *Raphanus*, *Rorippa*, *Sinapis*, *Sisymbrium* (Spencer 1973; Benavent-Corai et al. 2005). It is commonly found on agriculturally important *Brassica* species.

DAMAGE. Economically significant damage is known only from Europe where it is a common pest of cabbage and cauliflower, but other *Brassica* species including kale, broccoli, turnip, leaf mustard and rape serve as hosts and experience limited damage (Dempewolf 2004). Larval damage changes seasonally and with crop



Figures 165–171. *Phytomyza rufipes* Meigen, male: **165:** live specimen; **166:** external genitalia, left lateral; **167:** external genitalia, posterior; **168:** pregonite, left lateral; **169:** phallus, ventral; **170:** phallus, left lateral; **171:** hypandium.

type, but it is regularly severe when the flies occur in large numbers, sometimes with up to 10 larvae per stalk and 25 larvae per plant (Hochapfel 1937). Spencer (1973) noted instances where up to 50,000–1,650,000 puparia were found per acre of field in England, and there was an occurrence of up to 70% of host leaves being destroyed in Finland. Zuran'ska (1985) reported severe damage to winter rape in the 1970s in Poland.

Older plants are less susceptible to economic damage, with larvae feeding in the outer leaves that can be shed or removed, and usually do not remain in the processed portion of the plant intended for consumption. Younger plants, however, are very susceptible and can be stunted, weakened or killed unless growing conditions are favourable. If growth continues to maturity, leaves may still crack, yellow, brown and wither following harvest (Spencer 1973). Feeding punctures from the females also cause injury including leaf distortion in seedlings and stem damage followed by root rot (Spencer 1973).

Despite the historical and potential damage represented by this pest, Dempewolf (2004) has noted that there have been few recent instances of serious impact on crop yield, either because pest populations normally exist below an economic threshold, or because crop loss was not properly attributed to the pest.

BIOLOGY. *Phytomyza rufipes* has a life cycle of typical other leafmining agromyzids. Information about the biology of this particular leafminer is largely summarized by Carden (1962) and Spencer (1973), with very little new information published since that time. Females tend to create feeding punctures near leaf margins; eggs are subsequently laid at the rate of about 5 per day near a vein close to the leaf margin. The hatched larva mines to the nearest vein and burrows towards the midrib and petiole, where the majority of feeding begins. It may return to back along the petiole if feeding is incomplete, or it may enter the stem if the plant is young, but the larva will rarely burrow out of the petiole to enter another leaf. The average time of development of the egg, larval (all stages) and pupal stage are 3.7, 11.9 and 18.7 days, respectively (study temperatures not reported).

In England, 3–4 generations per year may occur starting from May, with larvae still active in November.

MOVEMENT & DISPERSAL. The confirmed presence of *Phytomyza rufipes* in the USA (Scheffer and Winkler 2008) and South America (e.g. Valladares et al. 1999) suggests that the species can be introduced to other countries globally through the horticultural trade (Scheffer and Winkler 2008).

MANAGEMENT. Early detection. Web-based factsheet information on *Phytomyza rufipes* is provided by Dempewolf (2004).

Control. There is evidence from Poland that a hybrid brassica (*Brassica campestris* × *B. chinensis*) can serve as a potential trap plant for the leafminer when used at the edges of winter rape fields (Palosz and Sien'kowski 1992). For insecticides, previous guidance in the UK was for the use of weekly applications of organophosphate insecticides such as dimethoate (Coaker 1973), but these are no longer available because of tighter regulations on insecticide use. Current recommendations are not to use insecticides as the leafminer is no longer considered to be economically damaging in the UK (AHDB 2015). Studies on natural enemies in Europe have shown a range of hymenopterous parasitoids including species in the families Braconidae, Eulophidae and Pteromalidae (Spencer 1973). Carden (1962) reported a parasitism level of 27%.

***Phytomyza syngenesiae* (Hardy)**

“Chrysanthemum Leafminer”

(Figs 146, 147)

OTHER COMMON NAMES. Cineraria leafminer.

IDENTIFICATION & DIAGNOSIS. *Phytomyza syngenesiae* is similar to most *Phytomyza* in having proclinate orbital setulae, a costa that extends only to vein R_{4+5} and an absence of crossvein dm-cu (Fig. 147). Within the genus, Griffiths (1967) allied it with a number of other species in the *P. syngenesiae* group, including *P. horticola* Goureau, a pest that was often confused with *P. syngenesiae* in the literature prior to his treatment. This group is characterized by three (not four) fronto-orbitals with the anterior seta inclinate, a brown antenna with the first flagellomere black, rounded and relatively small, very sparse short pubescence on the eye, a mostly yellow frons and face, a dark brown thorax with thick grey pruinosity, reduced acrostichal setulae, dark femora with yellow apices and at least some basal pruinosity on the ov scape.

Phytomyza syngenesiae can be differentiated from related species in part by having a wing length of 2.2–2.6 mm, either no acrostichal setulae or one to four isolated setulae anteriorly (usually entirely absent in *P. horticola*) and partially brown fore coxae, but the phallus is critical for diagnosis. The supporting sclerite of the distiphallus (Fig. 146) is only split on the distal half (split to base in *P. horticola* – see Figs 141–143), the

basiphallus is well-defined apically (not faded and diffuse) and the hypophallus is entirely membranous. The larva has 8–10 pores on the posterior spiracles.

DISTRIBUTION. *Phytomyza syngenesiae* is considered to be native to Europe with subsequent human-mediated dispersal to other parts of the globe (Griffiths 1967, 1972; CABI 1987b; Martinez 2013). Spencer (1984) attributed leaf mines on several Asteraceae in Colombia to this species, but verification is required.

- Afrotropical Region:** Kenya (Černý and Tschirnhaus 2014).
- Australian Region:** Australia, New Zealand.
- Nearctic Region:** Canada (Alberta, British Columbia), USA (California, Massachusetts, Oregon, Rhode Island, Washington; records from Connecticut, Illinois, Montana, New Hampshire, New York, Pennsylvania and Wisconsin require verification) (Eiseman and Lonsdale 2018).
- Neotropical Region:** Colombia(?).
- Oriental Region:** India (Tamil Nadu) (Murugasridevi et al. 2021), Sri Lanka (Wijesekara 2002).
- Palearctic Region:** Austria, Belgium, Czech Republic, Denmark, Finland, France, Germany, Ireland, Italy, Japan, Netherlands, Norway, Portugal, Russia (Zlobin and Drugova 2002), Saudi Arabi (Deeming 2006), Spain (mainland, Balearic Is., Canary Is.), Sweden, Switzerland, United Kingdom, former Yugoslavia.

HOSTS. *Phytomyza syngenesiae* is a polyphagous leafminer known almost exclusively from Asteraceae, with single records confirmed for Apiaceae (*Daucus* L.) and Fabaceae (*Pisum*) (Eiseman 2019). This species is sometimes noted as being present on Lamiaceae (*Mentha*, *Stachys* L.), Malvaceae (*Malva* L.), Plantaginaceae (*Plantago* L.) and other Fabaceae (*Melilotus*), but these are now considered misidentifications of the similar *P. horticola* (Spencer 1990; Benavent-corai et al. 2005).

Known asteraceous host genera are as follows (Griffiths 1967; Eiseman 2019, 2021): *Ambrosia*, *Antennaria* Gaertn., *Anthemis* L. (Griffiths 1967; species unknown), *Arctium* L., *Arctotheca* Vaill., *Argyranthemum* Webb ex Sch.Bip., *Arnoseris* Gaertn., *Artemisia* L., *Aster*, *Bellis* L., *Bidens*, *Callistephus* Cass., *Carduus* L., *Cichorium* L. (Dempewolf 2004), *Chrysanthemum*, *Cineraria* L., *Coreopsis* L., *Crepis* L., *Cynara* L., *Dahlia*, *Delairea* Lem., *Erechtites* Raf., *Erigeron* L., *Eupatorium* L., *Gaillardia* Foug., *Galinsoga* Ruiz & Pav., *Glebionis* Cass., *Gazania* Gaertn., *Gerbera*, *Helianthus*, *Helichrysum* Mill., *Helminthotheca* Vaill. ex Zinn, *Jacobaea* Mill., *Lactuca*, *Leontodon* L., *Leucanthemum* Mill., *Limbarda* Adans., *Matricaria* L., *Packera* Á. Löve & D. Löve, *Parthenium* L., *Pericallis* D. Don, *Petasites* Mill., *Picris* L., *Senecio*, *Serratula* L., *Silybum* Adans., *Smallanthus* Mack., *Solidago* L., *Sonchus* L., *Tanacetum* L., *Taraxacum* F.H. Wigg., *Tephrosia* (Rchb.) Rchb., *Xeranthemum* L. and *Zinnia* L.

DAMAGE. Lettuce (*Lactuca sativa*) is a favoured host in England, but *Chrysanthemum* and *Cineraria* are especially susceptible and readily colonized, often experiencing severe damage in any areas the species is present, otherwise sustaining itself at low levels on other local Asteraceae (Spencer 1973). Introductions into glasshouses can be particularly problematic (Dempewolf 2004). Up to 90% of *Chrysanthemum* plants in a crop have been reported to be attacked, with up to 20–30 larvae per leaf, and in one instance in England, every leaf of every plant hosted larvae (Spencer 1973). Damage type and level varies among *Chrysanthemum* species and varieties, but mined leaves usually shrivel and die if attacked, weakening the plant and reducing flowering (Spencer 1973).

BIOLOGY. Female flies tend to select plants or leaves in the shade for oviposition, where eggs are laid on the bottom or upper surface of the leaf, but the latter is usually preferred (Gurney 1960; Spencer 1973). The young larva mines the spongy mesophyll for a few millimetres and then penetrates the palisade layer. The mine is long and irregular, and pupation takes place in the mine (Ibrahim and Madge 1977; Spencer 1973). The egg, the three larval instars (separately) and pupal stages lasted on average 4, 3.5, 2, 4 and 11 days at 20°C and at 16:8 L:D cycle (Ibrahim and Madge 1977a; Cheah 1987). In day degrees, females need 207.0 above 12.9°C and males 211.0 above 11.6°C. Frick (1972) noted that the average pre-oviposition period of unmated females was longer than that of mated females.

MOVEMENT & DISPERSAL. As with other economically important agromyzids, *P. syngenesiae* has undoubtedly moved around the globe through the ornamental plant and horticultural industries.

MANAGEMENT. Early detection. No specific risk assessments are available, but a number of leaflets summarizing symptoms of damage, life history and recommended controls were produced in past decades by the UK (then) Ministry of Agriculture, Fisheries and Food (Gratwick 1992). More recently, the UK Department of Environment, Food and Rural Affairs, has published a general leaflet for growers and others covering symptoms of damage (DEFRA 2007). Yellow sticky traps are recommended for monitoring adults in floriculture and nurseries in California (Dreistadt 2001).

Control. A study in the UK showed that some *Chrysanthemum* cultivars are less susceptible to attack than others, and that feeding puncture : egg ratio was not found to be a reliable indicator of susceptibility (Ibrahim and Madge 1977b). The glasshouse industries in Europe and the USA largely depended on broad spectrum products (organophosphates and carbamates etc) from the 1960s (e.g. Bragg 1974; Gurney and Hussey 1974). Many of these products were phased out under changes in policy that came into force in countries from about the 1990s because of concerns about health and environmental risks, the development of resistance within pest populations and/or the impacts on natural enemies. Early trials on the organic systemic fungicide, pyrazophos showed that it was also effective for the control of *P. syngenesiae* (Ledieu and Helyer 1983). Current recommendations for glasshouses are to use biological control. Studies in the UK (Ibrahim and Madge 1979; Cornelius and Godfrey 1984), Italy (Mineo et al. 2003) and the USA (Lange et al. 1980) show that *P. syngenesiae* is parasitized by a variety of hymenopterous parasitoids. In Europe, important species attacking the larval stage are *Diglyphus isaea* and *Cirrospilus vittatus* Walker (Eulophidae); the pupal stage is attacked by *Chrysocharis* spp. (Eulophidae) and *Halticoptera* spp (Pteromalidae). Collectively, the larval parasitoids can cause up to 80% mortality of larvae in the field (Ibrahim and Madge 1979). Most biological control in glasshouses in Europe either involves the conservation of naturally occurring *Diglyphus isaea* (Burgess 1974) or inoculative releases of this species obtained from commercial suppliers.

***Tropicomyia theae* (Cotes)**

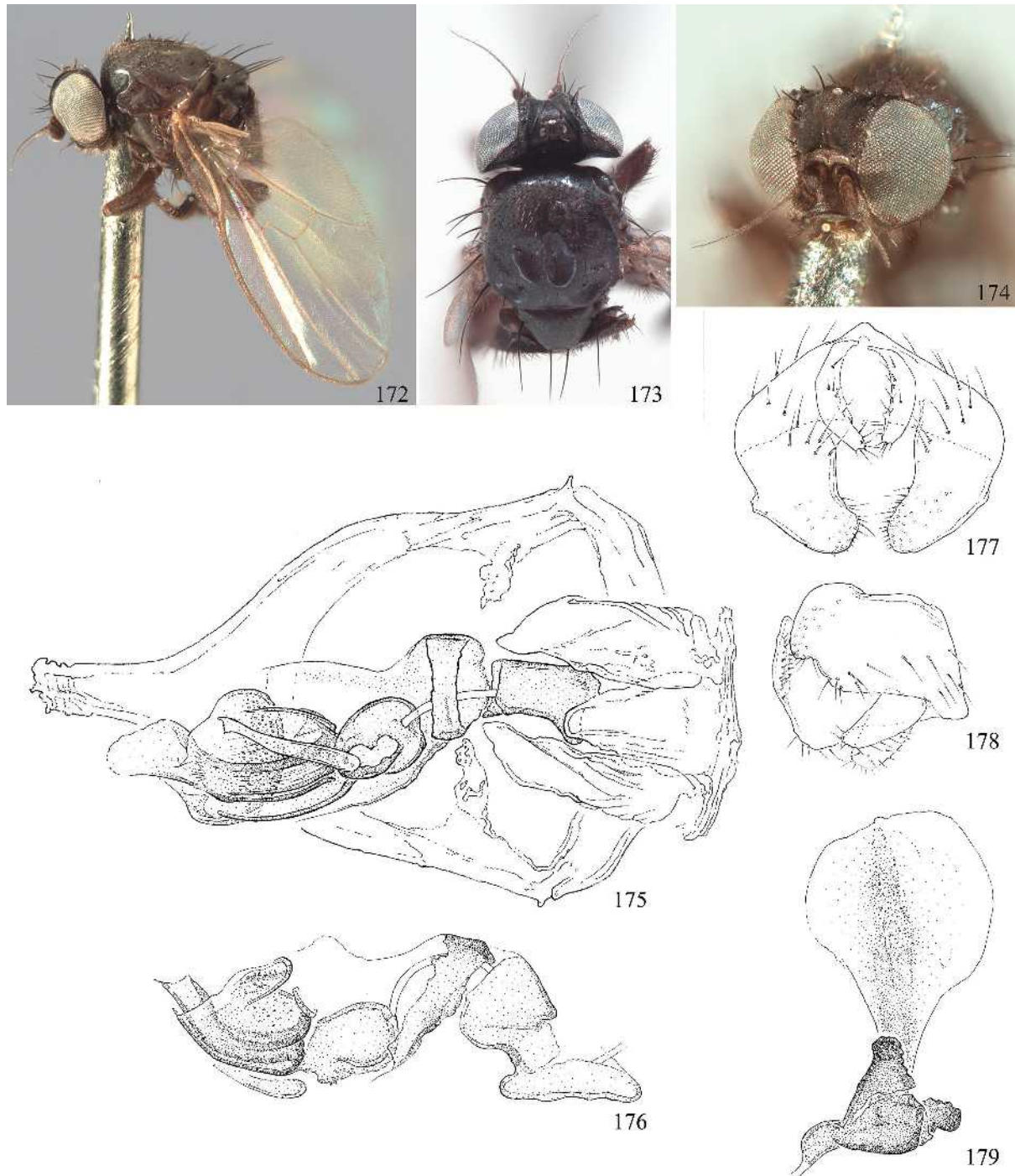
“Tea Leafminer”

(Figs 172–179)

IDENTIFICATION & DIAGNOSIS. *Tropicomyia theae* is one of a number of polyphagous or oligophagous *Tropicomyia* species that can be difficult to differentiate. Species in this genus are brown, non-metallic and usually small, they have four fronto-orbitals, only two well-developed dorsocentrals, 0–1 medial seta on the mid tibia and minutely toothed or “serrated” larval mandibles (Spencer 1973). *Tropicomyia theae* (Figs 172–174) differs in having a slightly raised parafacial and orbital plate, a larger wing length (2.0 mm) and a costa that only extends to vein R_{4+5} . The genitalia are most diagnostic, however: the mesophallus is relatively small and ovate, and the distiphallus is cup-like, higher than wide, with a dorsal subapical fold and an apical opening that is broad, angled dorsally and with a longer central medial tubule (Figs 175, 176).

Besides tea, *Tropicomyia theae* also occurs on coffee (*Coffea*). A related species, *T. flacourtae* (Séguy) also occurs on coffee but since this species is restricted to Africa, a diagnosis can be made based on host association and geography, but the male terminalia also differ and should be consulted for confident determination (see illustrations of *T. flacourtae* in Lonsdale (2014: figs 87–94)). Another *Tropicomyia* reported to attack coffee is *T. coffeae* (Koningsberger), but Spencer (1990) found this to be a junior synonym of *T. theae*.

DISTRIBUTION. *Tropicomyia theae* is known from Indonesia, Papua New Guinea, Sri Lanka (Spencer 1990), India (Singh and Beri 1971) and Taiwan (Shiao and Wu 1999), but is likely more widespread in the Orient and Pacific.



Figures 172–179. *Tropicomyia theae* (Cotes), male: **172:** lateral; **173:** dorsal; **174:** head; **175:** hypandrium, epiphallus and phallus, ventral; **176:** phallus, left lateral; **177:** external genitalia, posterior; **178:** external genitalia, oblique lateral; **179:** ejaculatory apodeme.

Some authors have listed this species in Seychelles (Dempewolf 2004) and Madagascar (Černý 2011). While it would not be unusual for this species to extend into, or be accidentally introduced elsewhere in the Old World tropics, its presence in the Afrotropics should be verified to ensure that it has not been confused with other *Tropicomyia* such as *T. flacourtae*, with which it has had a complicated nomenclatural history. Revision of the genus is required to confidently reassess species boundaries and distributions.

HOSTS. *Tropicomyia theae* is a polyphagous leafminer known from four host genera in four plant families (Spencer 1990): Apocynaceae (*Allamanda* L.), Convolvulaceae (*Ipomoea* L.), Rubiaceae (*Coffea*) and Theaceae (*Camellia* L.). Spencer (1990) also lists Asclepiadaceae (*Hoya* R. Br.), Dioscoreaceae (*Dioscorea* L.) and Moraceae (*Cudrania* Trécul) as possible hosts, attributing leaf mines to this species, but these require verification.

Other species of *Tropicomyia* such as the Afrotropical *T. flacourti* (21 genera in 14 families), the Australian *T. polyphyta* (27 genera in 19 families) and the Oriental *T. polyphaga* (Spencer) (16 genera in 10 families) are more broadly polyphagous and also pose risks, but *T. theae* is discussed here due to its occurrence on both tea and coffee, and its potential for accidental spread among other growing areas through the transport of live plants.

DAMAGE. Although mines on tea (*Camellia sinensis*) crops may be frequently observed, damage is often limited and the species has never been considered a major pest (Spencer 1973), although one report of a heavier attack on coffee (*Coffea*) required chemical control (Chacko and Ramanarayana 1976). Mined leaves may distort as they mature and become prone to fungal infection.

BIOLOGY. The following is largely from Spencer (1973), who summarized information known at that time, as little new work has been published since. Females prefer the second and third leaves from the bud but older leaves will be used occasionally; young leaves seem to be avoided. Oviposition is on the upper leaf surface, and while usually 2 larvae occur per leaf, as many as 5 larvae have been observed. In a study in India, 88% of sampled leaves had one larva (Banerjee 1988).

The larva makes an irregular silvery epidermal mine; pupation is at the end of the mine. The approximate development times of larvae and pupae are 11 and 15 days, respectively.

MOVEMENT & DISPERSAL. International dispersal may be possible via the commercial transport of infested leaves of tea.

MANAGEMENT. Early detection. No published information is available.

Control. In India, the pyrethroids deltamethrin and cypermethrin, and the organophosphate, ethion, are used in tea estates for general control of insect pests, including *T. theae* (Sharma and Kashyap 2002). Early studies on natural enemies in Sri Lanka indicate that the leafminer is controlled by parasitoids, with parasitism levels as high as 70% (Spencer 1973). Later work in India reported a parasitism level of 78.5% in leaves with two larvae and 73% in those with only one larva; the main parasitoids were *Closterocerus insignis* Waterston (Eulophidae) and *Trigonogastra* Ashmead sp. (Pteromalidae) (Banerjee 1988).

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Damage from species of leafminer flies (Agromyzidae: Diptera) on their plant host(s) is caused mostly by internal larval feeding, but also from female oviposition and feeding punctures, which results in structural damage, the vectoring of viruses and pathogenic fungi, and the exposure of tissue to secondary infection. Many plants of agricultural and ornamental importance are attacked in the field and in glasshouses, and while fly populations are normally kept in check by hymenopterous parasitoids, they sometimes occur in large enough numbers to affect yield and may destroy entire crops. Species affecting crops may be specialists on one host or a larger number of related hosts, but only 16 species of *Liriomyza*, *Phytomyza* and *Tropicomyia* are truly polyphagous. The threat of these flies is compounded by increasing insecticide resistance and the ease by which polyphagous species can multiply on weeds around growing areas or on alternate crops. All species are also readily spread through trade on their host plant or in soil, causing some species to become globally invasive, with some being of quarantine concern. An overview of agromyzid biology, ecology and agricultural importance is provided, and detailed consideration is given for 26 major pests of special concern. For each of these species, an overview of contemporary knowledge is provided for identification and diagnosis, global distribution, hosts plant(s), host damage, biology, and means of dispersal. To aid in their control, early warning systems, and means of field monitoring and management are provided.



Agromyzidae (Diptera) Plant Pests

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Species depicted: *Liriomyza sativae* Blanchard, male.

