



Review

Diversity, biology, and management of the pear psyllids: a global look

Stefano Civolani^{1,*}, Victoria Soroker², W. Rodney Cooper³, David R. Horton³

¹Department of Chemical, Pharmaceutical and Agricultural Sciences, University of Ferrara, Ferrara, Italy, ²Department of Entomology, Agricultural Research Organization, The Volcani Center, Rishon LeZion, Israel, ³Temperate Tree Fruit and Vegetable Research, USDA-ARS, Wapato, WA 98951, USA *Corresponding author, mail: cvlsfn@unife.it

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The pear psyllids (*Cacopsylla* Ossiannilsson; Hemiptera: Psylloidea: Psyllidae) are a taxonomically difficult group of at least 24 species native to the Palaearctic region. One or more species occur in most pear-growing regions, in some cases as invasive introductions. Existing reviews of this group are primarily of taxonomic focus with limited overviews of biology. The earliest biological studies of the pear psyllids centered on a core group of a few western European species. In part, this focus arose because diversity of the pear psyllids was poorly understood. As taxonomic understanding has advanced over the last 3 decades, research has expanded taxonomically. Increasing difficulties in controlling the pear psyllids additionally has contributed to growth in research. Here, we review a now-extensive literature on diversity, biology, and management of the pear psyllids. Three broad observations emerged from this synthesis. First, large gaps in biological understanding of the pear psyllids persist for several geographic faunas, most notably for psyllids of the Eastern Palaearctic region. Second, taxonomic diversity is accompanied by biological diversity. Despite the commonality in host use among the pear psyllids, with each species being limited to development on *Pyrus*, striking differences exist among species in life cycles, wintering, and other biological traits. Third, many of the tools being used to manage pear psyllids today are in existence because of the long history of basic research which has targeted these pests. These tools include new insecticides of higher selectivity, various cultural and horticultural tactics, and practices that conserve natural enemies in orchards.

Key words: *Cacopsylla*, *Pyrus*, taxonomy, biology, biological control

The pear psyllids (Hemiptera: Psylloidea: *Cacopsylla*) comprise 24 known species of small sap-feeding insects limited in developmental hosts to pear (Rosaceae: *Pyrus*). The economic importance of the pear psyllids increased noticeably in the mid-1900s with the worldwide spread of intensive pear cultivation, arrival of synthetic insecticides in orchards, and the beginnings of insecticide resistance. Pear psyllids may cause any of several types of damage to commercial pear orchards, including russet and downgrading of fruit due to marking of the pear fruit by honeydew and sooty mold, premature leaf drop and tree decline, and vectoring of the pathogen that causes “pear decline”. Heavy infestations may produce honeydew in sufficient quantities to interfere with orchard practices such as summer pruning or harvest. Along with codling moth [Lepidoptera: Tortricidae: *Cydia pomonella* (L.)], the pear psyllids rank as the most damaging arthropod pests worldwide in commercial pear orchards. Of the more than 23 million tons of pears produced globally

in 2020, about 19 million tons are produced in the northern hemisphere, where China is the most important producer, followed by the United States, Italy, Turkey, and Spain (FAO 2020). In the southern hemisphere, Argentina, South Africa, Chile, Australia, and New Zealand are producers of pears (FAO 2020). One or more species of pear psyllid are found in all of these regions except for South Africa, Australia, and New Zealand (Cho et al. 2017, 2020).

This review provides an up-to-date introduction to the important literature worldwide on pear psyllid diversity, biology, and management. Previous reviews of the pear-feeding psyllids are limited to individual species or are primarily of taxonomic focus. The first extensive research on the biology, morphology, and anatomy of the pear psyllids was conducted by Slingerland (1892, 1896) in Eastern North America with the introduced *Cacopsylla pyricola* (Foerster), and by Bonnemaison and Missonnier (1955, 1956) with the West Palaearctic *Cacopsylla pyri* (L.). For several

decades following the studies of Bonnemaison and Missonnier, biological research mostly targeted a core group of a few West Palaearctic species. This narrow focus was due in part to their damaging presence in Western Europe and North America, but also because the limited taxonomic work with this group had not yet provided a true picture of its actual diversity. As our taxonomic understanding of this group has advanced in the last few decades, basic and applied biological research on this group has also expanded. We have made important progress in our understanding of pear psyllid feeding behavior, host preferences, acoustic communication, chemical ecology, dispersal and landscape ecology, biological control, and microbial interactions. One important product emerging in the current synthesis is the demonstration that taxonomic diversity is accompanied by biological diversity: species of pear psyllids often differ substantially from one another in biology. As also will become apparent, much of the research with this group has been prompted by their pest status. Advances in research are helping to prompt changes in psyllid control tactics. We are seeing important shifts in how pear psyllids are controlled in orchards, as broadly toxic insecticides are replaced with a combination of selective insecticides, biological control, and horticultural practices, often guided by degree-day models that predict psyllid phenology. This synthesis will review many of these topics for this important group of insects.

Taxonomy, Diversity, and Distribution of the Pear-feeding Psyllids

Order Hemiptera Linnaeus, 1758

Suborder Sternorrhyncha Duméril, 1806

Superfamily Psylloidea Latreille, 1807

Family Psyllidae Latreille, 1807

Genus *Cacopsylla* Ossiannilsson, 1970

The psyllids or jumping plant-lice (Hemiptera: Psylloidea) are small sap-feeding insects in the suborder that includes aphids, scale insects, and whiteflies (Sternorrhyncha). The known diversity of the Psylloidea exceeds 4000 described species worldwide, with possibly a similar number of undescribed species (Burckhardt et al. 2021). Psyllids are found in virtually all terrestrial habitats and inhabit all continents other than Antarctica (Burckhardt et al. 2021, Ouvrard 2022). Life stages consist of the egg, the immature (nymphal) phase, and the adult insect (Fig. 1). Traits of the adult that separate the Psylloidea from other homopterous Hemiptera include: filiform antennae generally of 10 segments; noticeably sclerotized exoskeleton; legs adapted for jumping; beak appearing to arise from between the forelegs; 2 pairs of membranous wings held cicada-like over the body, the forewing conspicuously veined and sometimes marked with darkened regions. The psyllid egg (Fig. 1D and E) is oval in shape, often has a slender filament at its distal end, and is

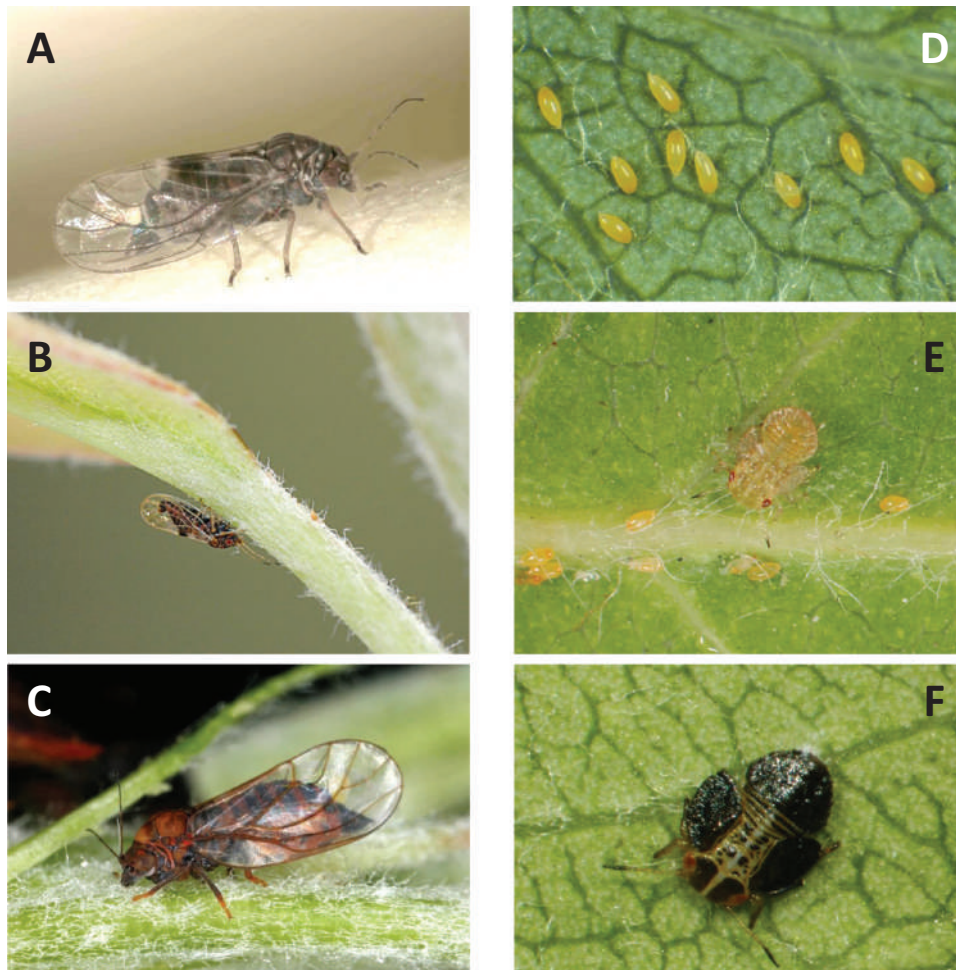


Fig. 1. (A) Female winterform and (B) male summerform of *Cacopsylla pyricola* (Foerster); (C) female *Cacopsylla pyrisuga* (Foerster); (D) eggs; (E) eggs and late-instar nymph; and (F) fifth-instar (hardshell) nymph of *C. pyricola*.

light yellow or cream-colored when deposited but darkens with age. A pedicel at the basal end of the egg inserts into the host tissue and is used to anchor the egg and to uptake water from the host (White 1968, Horton 1990). Length of the pedicel may exceed that of the body of the egg (Loginova 1979, Ossiannilsson 1992, Conci 2000). The immature (nymphal) psyllid develops through 5 instars; body oval and generally flattened dorso-ventrally; first instar nymph only slightly larger than the egg; last-instar stage much larger, often somewhat disk-like, and with conspicuous wing pads (Fig. 1F).

The pear psyllids (*Cacopsylla* spp.; Psyllidae) comprise a taxonomically difficult group of species distributed throughout the Palaearctic Region and (as introductions) in North and South America. Developmental hosts are limited to species of pears (*Pyrus*). *Pyrus* originated over 25 million years ago (Korotkova et al. 2018) in 3 areas: the Caucasus and Asia Minor area; the mountainous areas of Western China; and Western Asia in the region comprising Afghanistan, India, and the Asian republics of the former Soviet Union (Dondini and Sansavini 2012, Volk and Cornille 2019). This was followed ~6.6–3.3 million years ago by genetic differentiation into 2 main groups, a European/Central Asian group and an East Asia group (Volk and Cornille 2019). Speciation, hybridization, and spread has produced a widespread and diverse complex of wild and cultivated species distributed throughout the Palaearctic Region, from Western Europe to Eastern Asia and Russia, and into the Mediterranean Basin and North Africa (Silva et al. 2014, Volk and Cornille 2019). Domestication of pears in Asia began over 2,500 yr ago, primarily of the species *Pyrus pyrifolia* Nakai and *Pyrus ussuriensis* Maxim (Morgan 2015), while domestication in the Western Palaearctic (primarily of the European pear *Pyrus communis* L.) began possibly 2,300 yr ago (Dondini and Sansavini 2012). The widely cultivated *P. communis* is grown in 5 major regions: Europe, North America, South America, South Africa, and Oceania (Silva et al. 2014). Production of Asian pear, mostly *P. pyrifolia*, is concentrated in Asia (Silva et al. 2014). Pears arrived in Eastern North America with English and French settlers, and were introduced into South America by Spanish colonists (Morgan 2015).

The taxonomy of the pear psyllids is difficult. Seasonal dimorphism, subtle morphological differences between species, poor understanding of geographic ranges and host preferences, and uncritical use of species names has led to much historical confusion in the taxonomy and identification of pear psyllids (Hodkinson 1984, Burckhardt and Hodkinson 1986, Cho et al. 2017, 2020). Human-assisted spread of *Pyrus* followed by range expansion of psyllids makes it difficult to identify the native ranges of species. Geographical overlap of species leads to assemblages of different species co-occurring not just in the same growing region but often on the same individual trees (Overmeer 1961, Trapman and Blommers 1992, Lauterer 1999, Gajski and Pekár 2021). Taxonomic confusion is resolved through morphological work, geographical considerations, host information, and molecular genetics (Hodkinson 1984, Burckhardt and Hodkinson 1986, Luo et al. 2012, Cho et al. 2017, 2020, Chen et al. 2018). At the time of this review, 24 species of *Cacopsylla* are recognized as having *Pyrus* as a host plant (Cho et al. 2017). This total likely will increase as the less-studied psyllid faunas of the Middle East, India, Central Asia, and Far East Russia receive attention (Cho et al. 2017, 2020). Little is known about the biology of many species, particularly of the Asian psyllids.

The first taxonomic treatments of the pear psyllids were for the Western Palaearctic species. Morphological variation combined with data on geography and host associations identified a group of 7 species (Hodkinson 1984, Burckhardt and Hodkinson 1986). Geographic ranges of species in this assemblage extend as far west

as Britain and Western Europe, as shown by *Cacopsylla pyrisuga* (Foerster), *C. pyri*, and *C. pyricola*; eastwards into Uzbekistan, Turkey, and neighboring regions [*Cacopsylla fera* (Baeva) and *Cacopsylla bidens* (Šulc)]; and southwards into the Mediterranean Basin and Middle East, as shown again by *C. bidens* (Burckhardt and Hodkinson 1986, Cho et al. 2017, Akbar et al. 2018; see also Fig. 2). Descriptions and identification keys are available in Burckhardt and Hodkinson (1986). Most species in this group associate with the European pear (*P. communis*), although other *Pyrus* also are hosts, such as *Pyrus spinosa* Forsskål for *Cacopsylla notata* (Flor) and the wild pear *Pyrus korshinskyi* Litvinov hosting *C. fera* (Burckhardt and Hodkinson 1986, Cho et al. 2017). Sympatric species may separate ecologically through use of different *Pyrus* species (Burckhardt and Hodkinson 1986). Two species have colonized the New World (Fig. 2), likely by transport of infested pear host plants: *C. pyricola* into North America in the early 1800s (Slingerland 1892) and *C. bidens* into South America sometime before the mid-1900s (Valle et al. 2017).

Taxonomic work has begun to address the confusing group of pear psyllids in the Eastern Palaearctic Region, encompassing areas of eastern Russia, China, Taiwan, Japan, and Korea (Yang and Huang 2004, Luo et al. 2012, Cho et al. 2017, 2020, Chen et al. 2018). Species in the Eastern Palaearctic region commonly associate with the Asian pears *P. pyrifolia* and *P. ussuriensis* (Cho et al. 2017). Analysis of this fauna has relied on use of molecular genetics, morphology, geography, and host information. This approach has been used to untangle difficult complexes and to correct historical mistakes in species assignments (Luo et al. 2012, Cho et al. 2017, 2020, Chen et al. 2018). Cho et al. (2020) used DNA barcoding to separate species and to correct mistakes in the stated distributions of 2 Western Palaearctic species, *C. pyricola* and *C. pyrisuga*. These species at one time were thought to occur in East Asia but are now known to have been misidentifications of east Palaearctic species (Cho et al. 2017, 2020). There is no evidence for presence of any European pear psyllid in Eastern Asia (Cho et al. 2020). The synthesis of Cho et al. (2017) includes aspects of geography, life cycles, and host associations for the East Palaearctic pear psyllids, and provides keys to the Japanese and Korean species.

Biology

Seasonal Life Cycle

No single life cycle describes the seasonal biology of all pear psyllids. Species may differ in life stage that overwinters, generation numbers, dispersal tendencies, and use of winter shelter plants. Cho et al. (2017) classified the pear psyllids into 3 groups by morphology and life cycle (Table 1): the *Cacopsylla pyri*-group, *Cacopsylla pyrisuga*-group, and *Cacopsylla nigella*-group. Life cycle categories are based upon generation numbers, presence or absence of seasonal dimorphism, and overwintering stage (Table 1). Our understanding of the annual cycle is far more extensive for species in the *pyri*-group than the other 2 groups.

Cacopsylla pyri-type life cycle.

The *pyri*-group consists of 16 species from the Western or Eastern Palaearctic regions, and includes important pests such as *C. pyri*, *C. pyricola*, *C. bidens*, and *C. chinensis* (Table 1). Species in this group are multivoltine and overwinter in reproductive diapause as a seasonally distinctive form or morphotype (Table 1). Much of what is discussed here will focus on the well-studied *C. pyricola* whose life cycle is shown in Fig. 3A. Gray and blue fills depict presence of adult summer and winter seasonal forms, respectively. Important

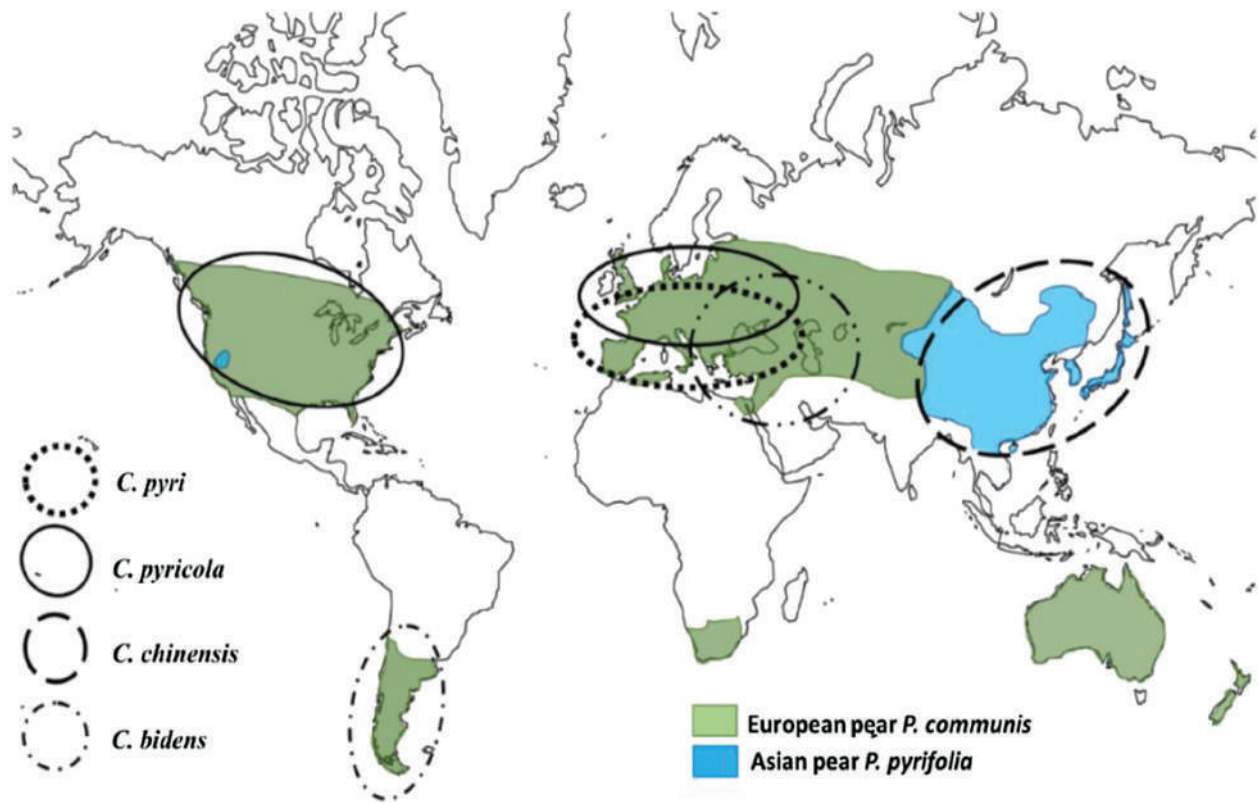


Fig. 2. Geographic distribution of the commercially important European; *Pyrus communis* and Asian; *Pyrus pyrifolia* cultivated pear species and approximate global distribution of 4 highly damaging pear psyllids (ovals).

Table 1. Classification of the pear psyllids into 3 groups by morphology and seasonal life histories (Cho et al. 2017); summaries of traits from literature (see text)

Trait	<i>C. pyri</i> -group	<i>C. pyrisuga</i> -group	<i>C. nigella</i> -group
Currently known species	<i>C. pyri</i> , <i>C. pyricola</i> , <i>C. bidens</i> , <i>C. chinensis</i> (+12 others ^a)	<i>C. pyrisuga</i> , <i>C.</i> <i>burckhardti</i> , <i>C. accincta</i>	<i>C. nigella</i> , <i>C. liaoli</i> (+3 others ^b)
Generations per year	Multiple	1: obligatory	2 (see text)
Diapause/wintering stage	Adult (winterform)	Adult	Second-instar im- mature (see text)
Seasonal dimorphism in size and color of adult	Yes	No	No
Dispersal of diapausing adult	Yes	Yes	—
Wintering site(s)	Pear host and nonhost shelter plants; leaf litter	Coniferous trees	Pear host
Diapause termination	Early winter	Likely early winter	Unknown
Timing and rate of postdiapause development	Controlled by temperature	Likely controlled by temperature	Likely controlled by temperature

^a*Cacopsylla betulaefoliae* (Yang & Li), *Cacopsylla donggangica* Li, *Cacopsylla fera* (Baeva), *Cacopsylla flavianthracina* Li, *Cacopsylla gyrogenma* Li, *Cacopsylla jukyungi* (Kwon), *Cacopsylla maculatili* Li, *Cacopsylla nervinigra* Li, *Cacopsylla notata* (Flor), *Cacopsylla permixta* Burckhardt & Hodkinson, *Cacopsylla xanthisma* (Yang & Li), *Cacopsylla yunli* (Li & Yang).

^b*Cacopsylla phaecarpae* (Yang & Li), *Cacopsylla sandolbaea* (Park & Lee), *Cacopsylla qianli* (Yang & Li).

time points in the life cycle include (Fig. 3A): phenology of the winter generation; onset and termination of diapause; autumn dispersal and winter return by the overwintering stage; timing of postdiapause development; and phenology of the summer generations. Psyllids of this group produce a large and dark overwintering adult known as the winterform that is distinct from the smaller and lighter summerform of the growing season (Fig. 3B). The dimorphism is

striking enough that morphotypes of some species were described originally as separate species (Hodkinson 1984, Burckhardt and Hodkinson 1986, Cho et al. 2017, 2020). Production of seasonal morphotypes is controlled by photoperiod (*C. pyricola*: Wong and Madsen 1967, McMullen and Jong 1976, Oldfield 1970; *C. pyri*: Bonnemaïson and Missonnier 1955; *C. bidens*: Soroker et al. 2013, Madar et al. 2017). Short days lead to production of the winterform

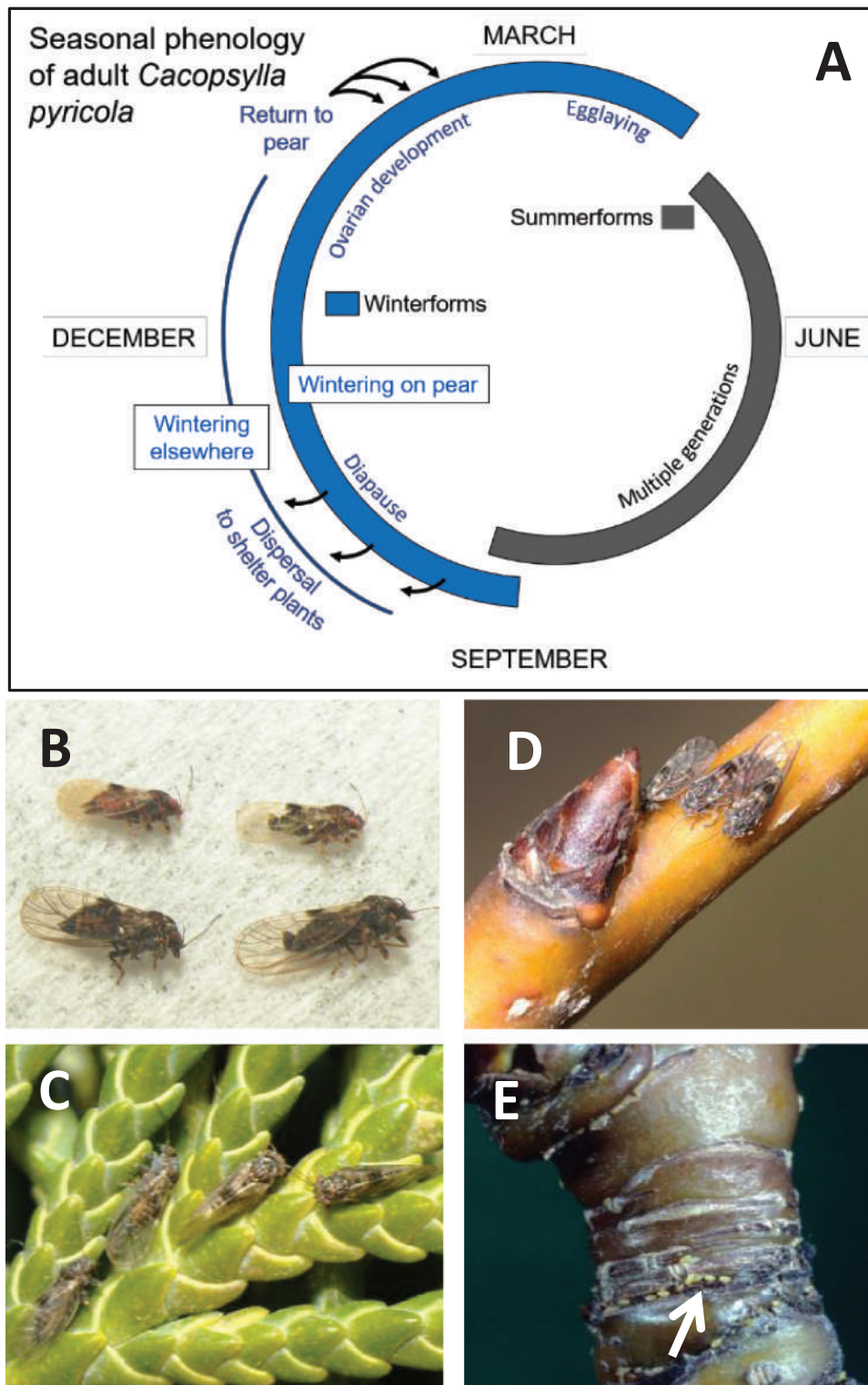


Fig. 3. (A) Life cycle of north temperate *C. pyricola*. Filled shapes depict intervals adults are present. Gray and blue colors show summerform and winterform generations, respectively; arrows show timing of autumn dispersal and winter orchard reentry. (B) Summerform (upper) and winterform (lower) specimens of *C. pyricola* (females on left). (C) Wintering *C. pyricola* on evergreen shelter plant, Washington State. (D) Postdiapause mating pair of winterform *C. pyricola* on dormant pear. (E) Eggs of *C. pyricola* (arrow) inserted into wood at base of spur.

adult, while long-day photoperiods produce the summerform adult. Morphometric analyses have quantitatively shown that size and shape of insects differ between morphotypes (*C. pyri*: Nguyen and Grassé 1985; *C. bidens*: Madar et al. 2017; and *C. pyricola*: Mustafa and Hodgson 1984).

The winterform morphotype overwinters in reproductive diapause characterized by postponed mating and delayed maturation of ovaries (Fig. 3A; *C. pyri*: Bonnemaïson and Missonnier 1955, Nguyen 1975; *C. pyricola*: Krysan and Higbee 1990, Krysan 1990, Horton et al. 1998, *C. bidens*: Swirski 1953, Madar et al. 2017).

Diapause may begin later and be of shorter duration in warmer regions than shown in Fig. 3A for north temperate *C. pyricola* (Swirski 1953, Nguyen 1975, Lyoussoufi et al. 1994, Soroker et al. 2003, Madar et al. 2017). Diapause terminates in winter (Fig. 3A; Krysan and Higbee 1990, Horton et al. 1998). Once diapause has ended maturation of ovaries is controlled by temperature (Krysan and Higbee 1990). Diapause is weaker in winterforms that emerge late in autumn than earlier. Thus, winterform *C. pyri* emerging in late summer required a longer time to begin egg laying when moved to long-day conditions than insects emerging in late autumn (Nguyen 1975). Winterform *C. pyricola* collected in December and moved to 20 °C required only ~6 days to begin egg laying, whereas those collected in early October required weeks before ovaries matured (Horton et al. 1998).

An important trait of at least some species in this group is dispersal by the winterform generation (Fig. 3A: arrows). This activity is most thoroughly described for North American populations of *C. pyricola*. A varying percentage of the winterform population moves out of orchards each autumn and winters on nonhost shelter plants. Dispersal leads to redistribution of psyllids among orchards as highly infested orchards in autumn lose insects through dispersal to less-infested orchards the following spring, making it difficult for pear growers to anticipate spring pest pressures (Fye 1983, Westigard and Hilton 1990, Horton et al. 1992). Dispersal is controlled by environmental conditions. Warm and dry conditions in autumn lead to larger numbers dispersing than cool and wet years, consequently the percentage of an orchard's population that disperses versus remains in the orchard varies year-to-year (Horton et al. 1992, 1994b). Dispersal peaks during leaf fall as psyllids are dislodged from trees and fall to the orchard floor (Horton et al. 1993). Densities of winterforms on the floor of severely infested orchards following leaf fall may exceed 250,000 psyllids ha⁻¹ (Fye 1983). Subsequent movement by dislodged insects leads to recolonization of the pear tree or exodus from the orchard (Fye 1983, Horton et al. 1993, 1994b).

Autumn movements by dislodged insects appear in part to be due to search for food resources, as suggested by attractiveness of foliar colors to winterforms during the dispersal period (Krysan and Horton 1991). Pear psyllids require water or a feeding source to survive winter (Swirski 1953, Kaloostian 1970, Horton et al. 1994a). Gut contents analyses show that an array of nonhost plants is fed upon by dispersing psyllids (Cooper et al. 2019). Wintering *C. pyricola* accumulate on a variety of plant taxa (e.g., Fig. 3C), including tree fruit species, later-defoliating deciduous plants, and evergreens (Ullman and McLean 1988a, Horton et al. 1994a, 1994b). Dispersing winterforms in fact may move from orchards to a deciduous species that retains its leaves later than pear, only to move again when leaf fall by that second species dislodges the insects (Cooper et al. 2019). Psyllids which winter in orchards or on other deciduous plants presumably feed through softer portions of the wood. European populations of *C. pyricola* or other pear psyllids may also winter outside of pear orchards. Wintering European *C. pyricola* occur in stone fruit and apple orchards, and on noncultivated tree species (Trapman and Blommers 1992, Lauterer 1999, Jarausch et al. 2009). While winter records for *C. pyri* and *C. bidens* outside of pear orchards are not as extensive as for *C. pyricola*, records show that both species can be collected from stone and pome fruit trees in winter (Swirski 1953, Trapman and Blommers 1992, Lauterer 1999, Burckhardt and Freuler 2000, Jarausch et al. 2009).

Reentry into orchards by overwintered psyllids begins in late-winter (Fig. 3A: return arrows). The first mature eggs appear in the ovaries of postdiapause *C. pyri* and *C. pyricola* by late-winter (Krysan and Higbee 1990, Trapman and Blommers 1992) or earlier

in populations at southern latitudes (Wong and Madsen 1967). Ovaries of females wintering on nonhost plants mature more slowly than ovaries of females wintering on the pear host (Horton et al. 1994a). Mating (Fig. 3D) and egg laying begin before bud development. The earliest eggs are deposited below unopened buds (Fig. 3E). As bud scales separate oviposition shifts to foliar and floral tissues. Offspring of the winterform generation emerge in late spring as the season's first summerform generation (Fig. 3A), followed by 1 or more additional generations per year depending upon latitude (Westigard and Zwick 1972).

Cacopsylla pyrisuga-type life cycle.

Pear psyllids of the *pyrisuga*-group have a substantially different life cycle (Table 1, Fig. 4). The *pyrisuga*-group consists of 1 Western Palearctic species and 2 Eastern Palearctic species (Table 1). The following details are for the Western Palearctic *C. pyrisuga* (Fig. 1C). *Cacopsylla pyrisuga* has a single generation per year and overwinters in diapause off of the host plant (Fig. 4). This life cycle leads to the unusual circumstance in which the pear host is free of the psyllid for most of the year, which caused a great deal of confusion in early biological accounts of this species (Brocher 1926). *Cacopsylla pyrisuga* winters almost exclusively on conifers, although there are scattered records from broad-leaf tree species (Lazarev 1975, Conci et al. 1993, Lauterer 1999). Ovarian maturation begins in overwintering sites, and insects collected from conifers in late-winter and moved to pear shoots will begin egg laying immediately (Lazarev 1975). Postdiapause *C. pyrisuga* migrate to pear trees from wintering sites in March and April (Conci et al. 1993, Burckhardt 1994, Lauterer 1999). The earliest eggs are deposited on new leaves or floral parts as buds begin to open (Burckhardt 1994, Lauterer 1999). The single generation of immatures is followed by new adults in May and June and dispersal onto shelter plants (Fig. 4; Lazarev 1975, Burckhardt 1994, Lauterer 1999). The population essentially will have disappeared from the pear host by June or July (Fig. 4; Overmeer 1961, Conci et al. 1993, Lauterer 1999). Dispersal to high-altitude conifers is assisted by up-slope summer winds (Lauterer 1999); return to the host plant in late-winter also is wind-aided (Lazarev 1975).

Cacopsylla nigella-type life cycle.

The *C. nigella*-group includes 5 species distributed in Eastern Russia, Korea, and temperate China (Table 1; Cho et al. 2017). Species in this group are defined by black or dark brown coloration and by patterns of spinules on the surface of the forewings (Luo et al. 2012, Cho et al. 2017). The life cycle assumed to apply to members of the *nigella*-group is from observations of *Cacopsylla liaoli* (Yang and Li). *Cacopsylla liaoli* is said to have 2 generations annually and to winter on the pear host as second instar immatures near buds or in the axils of branches (Pang and Pang 1990, Wang et al. 2012). This life history strategy appears to be unknown for any other *Cacopsylla* (Hodkinson 2009). Additional research with *C. liaoli* or new research with other members of the *nigella*-group to verify this life cycle would be useful.

Fecundity, Adult Longevity, and Development Time

Life history data are available for several West Palearctic species (*C. pyricola*, *C. bidens*, *C. pyri*, *C. pyrisuga*) and 1 Asian species (*C. chinensis*). Adult longevity differs among species depending upon life cycle. Longevity of the univoltine *C. pyrisuga* is 300–330 days with much of that time spent by the psyllid away from the pear host (Fig. 4; Lazarev 1975). Life span of the winterform morphotype of multivoltine psyllids may be ~6–7 mo, again with much of the interval spent in diapause (Fig. 3A). In contrast, longevity of summerform *C.*

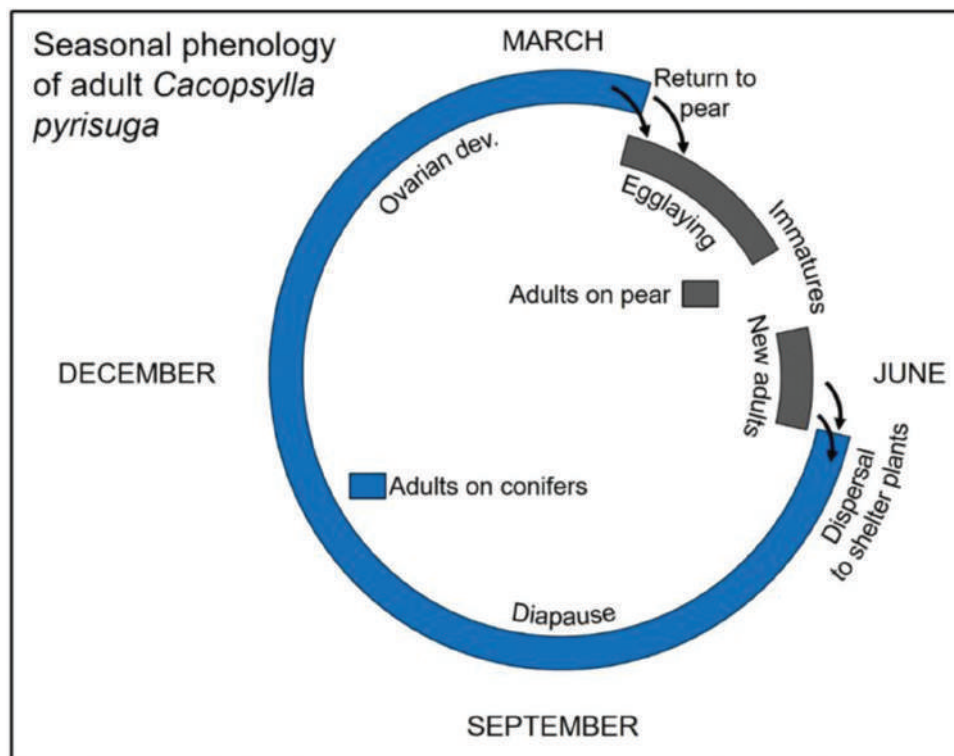


Fig. 4. Seasonal life cycle of *C. pyrisuga*.

pyricola reared under laboratory conditions is ~50–80 days at moderate temperatures (21–24 °C) or briefer at warmer temperatures (McMullen and Jong 1977). Life span in the field is even shorter, ranging between 16–32 days for *C. bidens* in Israel (Swirski 1953), 14–28 days for *C. pyri* in Greece (Kapatos and Stratopoulou 1996), and 18–26 days for *C. chinensis* in China (Wei et al. 2020).

Laboratory-based estimates of lifetime fecundity are impressively high for some species, exceeding 1,000 eggs per female by winterform *C. pyricola* (McMullen and Jong 1977, Horton and Lewis 1996) and the univoltine *C. pyrisuga* (Lazarev 1975). Weekly dissection and counting of mature eggs suggested that potential lifetime fecundity of winterform *C. pyri* exceeds 2,000 eggs (Lyousoufi et al. 1988). One winterform female *C. pyricola* in the assay of Horton and Lewis (1996) deposited over 2,700 eggs during an egg-laying period that exceeded 3 mo. Fecundity of *C. pyricola* in other laboratory studies is lower than these estimates, with averages of 300–490 eggs per winterform female and 140–660 eggs per summerform female (Burts and Fischer 1967, McMullen and Jong 1977). Fecundity drops at high temperatures (McMullen and Jong 1977). Field estimates of fecundity are noticeably lower than estimates from laboratory trials. Lifetime egg production under field conditions has been estimated for summerform *C. bidens* (50–170 eggs: Swirski 1953) and *C. pyricola* (70–190 eggs: Georgala 1956, McMullen and Jong 1972); and, winterform *C. pyricola* (200 eggs: Georgala 1956) and *C. pyri* (135–150 eggs: Kapatos and Stratopoulou 1996). Field data are available for 1 Asian species, *C. chinensis*, estimated at 25–70 eggs per summerform female (Wei et al. 2020).

Minimum temperatures allowing egg and nymphal development are 2–4 °C for *C. pyri* (Beránková and Kocourek 1994, Kapatos and Stratopoulou 1999, Schaub et al. 2005) and 6.5 °C for nymphs of *C. pyrisuga* (Lazarev 1975). Egg development times are about 1 wk at 22–24 °C but longer at cooler temperatures (Swirski 1953, Lazarev 1975, McMullen and Jong 1977, Kapatos and Stratopoulou 1999).

Total nymphal development times for *C. pyricola* at a constant 21 °C averaged about 24 days (McMullen and Jong 1977). Nymphal development times under orchard conditions have been reported at different intervals of the growing season for *C. bidens* (Swirski 1953), *C. pyri* (Kapatos and Stratopoulou 1999), and *C. pyricola* (Georgala 1956), and unsurprisingly changed with time of year due to temperature and changes in host quality. Phenological and demographic models have been developed from life history data for *C. pyri*, *C. pyricola*, and *C. chinensis*, and are now being used to guide pest control decisions (Schaub et al. 2005, Wei et al. 2020, Nottingham et al. 2022b).

Host Selection and Feeding Behavior

The term “host plant” as used for Psylloidea refers to plant species which allow egg-to-adult development (Burckhardt et al. 2014). Like other psyllid species, the pear psyllids regularly visit, probe, and ingest from plant species that do not allow development (Cooper et al. 2019). While the pear psyllids are limited in developmental hosts to species of *Pyrus*, psyllid species exhibit distinct differences in choice of *Pyrus* species (Hodkinson 1984, Burckhardt and Hodkinson 1986, Cho et al. 2017). Discriminating between host and nonhost species progresses through a series of behaviors which begin with locating a potentially suitable plant, settling upon and probing the plant, ingesting plant sap, and egg-laying. These behavioral components are governed by plant-associated cues that in turn are detected and evaluated by different types of sense organs or sensilla associated with different structures of the insect (Fig. 5). Many of these behavioral processes as well as the function of different sensilla are not well-understood.

The broadest grouping of behavioral components guiding host selection is feeding, which for sap-feeding insects includes all activities that lead to colonization of the host plant, decisions to insert the mouthparts into plant tissues, and ingestion of plant sap (Backus

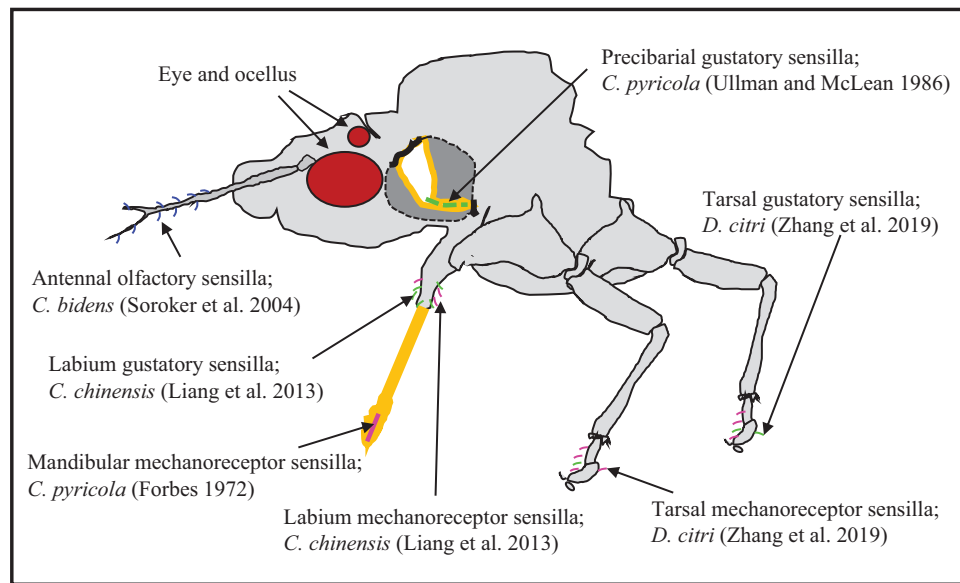


Fig. 5. Schematic of sensilla involved in feeding behavior of the pear psyllids.

2000). The initial component, locating the host from a distance, likely is governed by visual or olfactory cues detected by ocular organs and olfactory sensilla on the head and antennae (Fig. 5). The importance of visual cues is shown by the attractiveness of certain colors to pear psyllids (Adams et al. 1983, Krysan and Horton 1991). Reflectance peaks that mimic foliar colors (yellow or green hues) were more attractive to pear psyllids than blue, red, or black colors (Adams et al. 1983). In artificial feeding trials, reddish-orange hues are more effective at prompting *C. bidens* to probe than color-free or blue colors (V. Soroker unpubl.). The role of plant volatiles in host location by pear psyllids has received very little attention. Electroantennogram assays and olfactometer trials have shown that *C. bidens* responds to volatiles emitted from pear trees (Soroker et al. 2004). The compounds which elicited the responses are not known.

Colonization of a prospective host is followed by settling of the insect and probing activity (insertion of mouthparts into host tissues). These behaviors likely occur in response to chemical and physical cues on the plant surface, and apparently are detected by gustatory and mechanoreceptor sensilla on the mouthparts and tarsi (Fig. 5). *Cacopsylla pyricola* often scrapes the leaf surface with its tarsi prior to probing, presumably to confirm that the necessary chemical cues are present (Ullman and McLean 1988a, 1988b, Horton and Krysan 1990). This activity may indicate that chemoreceptors are present on the tarsi of pear psyllids (Fig. 5). Decisions to probe may be delayed following contact with leaves of nonhost species relative to the rapid probing decisions made when the pear host is colonized (Horton and Krysan 1991). The delay on nonhost species also suggests that cues on the leaf surface affect decisions to probe.

Probing consists of all activities that occur while the mouthparts (stylets) are embedded in host tissues, and includes manipulation of stylets through plant tissues, salivation, tasting, and ingestion. These activities are governed by gustatory and mechanoreceptor sensilla associated with the mouthparts and alimentary canal (Fig. 5). Because stylet-activities occur within plant tissues and cannot be directly observed, electropenetration graph technology (EPG) has been used to examine the probing behavior of pear psyllids (*C. pyricola*: Ullman and McLean 1988a, 1988b; *C. pyri*: Civolani et al. 2011, 2013). Probing begins with pathway activities as the stylets penetrate parenchyma tissues to reach the vascular tissues (Fig. 6A and B). A salivary

sheath is deposited during this activity and is thought to protect the stylets and to suppress plant defenses (Fig. 6B). Stylets penetrate the tissues intracellularly (Ullman and McLean 1988a, 1988b, Civolani et al. 2011). Pathway activities typically are followed by xylem ingestion (Fig. 6C) or by phloem activities (Fig. 6D). Phloem activities include alternating bouts of salivary discharge and ingestion of phloem sap. Nymphs of *C. pyri* reach the vascular tissues more quickly than adults and exhibit longer durations of phloem-feeding (Civolani et al. 2011). Winterform *C. pyri* spend less time in phloem and more time in xylem than summerforms (Civolani et al. 2011).

The final component of host selection is egg laying. Decisions to deposit eggs apparently are governed in part by cues perceived by the female while probing. Female *C. pyricola* rarely initiate egg laying immediately upon contact with the host plant but first engage in bouts of probing, suggesting that cues at the plant surface alone are not enough to prompt egg laying (Horton and Krysan 1990, 1991). Mechanical cues appear to have a role in egg placement. Eggs deposited by overwintered psyllids often are placed in grooves below fruit spurs (Fig. 3E) possibly in response to physical cues. Summerforms of *C. pyricola* preferentially insert eggs along leaf midvein, in leaf deformations, or next to debris on the leaf surface (Horton 1990). Psyllids in search of oviposition sites drag the tip of the abdomen across the plant surface presumably in search of appropriate physical cues (Horton and Krysan 1990). This behavior may indicate that mechanoreceptors are present at the tip of the psyllid abdomen. Female *C. pyricola* can be “tricked” to insert eggs into smooth and less preferred regions of the leaf by attaching a physical cue such as a small piece of adhesive tape to the leaf blade (Horton 1990).

Nutritional Ecology

To compensate for the poor nutritional quality of phloem sap, the pear psyllids consume large volumes of the sap and egest the undigested end-products in a sugary honeydew. Le Goff et al. (2019) identified the components of phloem sap used by *C. pyri* by comparing sugar and amino acid composition of phloem to that of egested honeydew. Sugars in the phloem of *Pyrus* consist of sorbitol and sucrose. Concentration of sucrose in honeydew was lower than in phloem, indicating that sucrose was ingested and assimilated by *C. pyri*, likely as an energy source (Le Goff

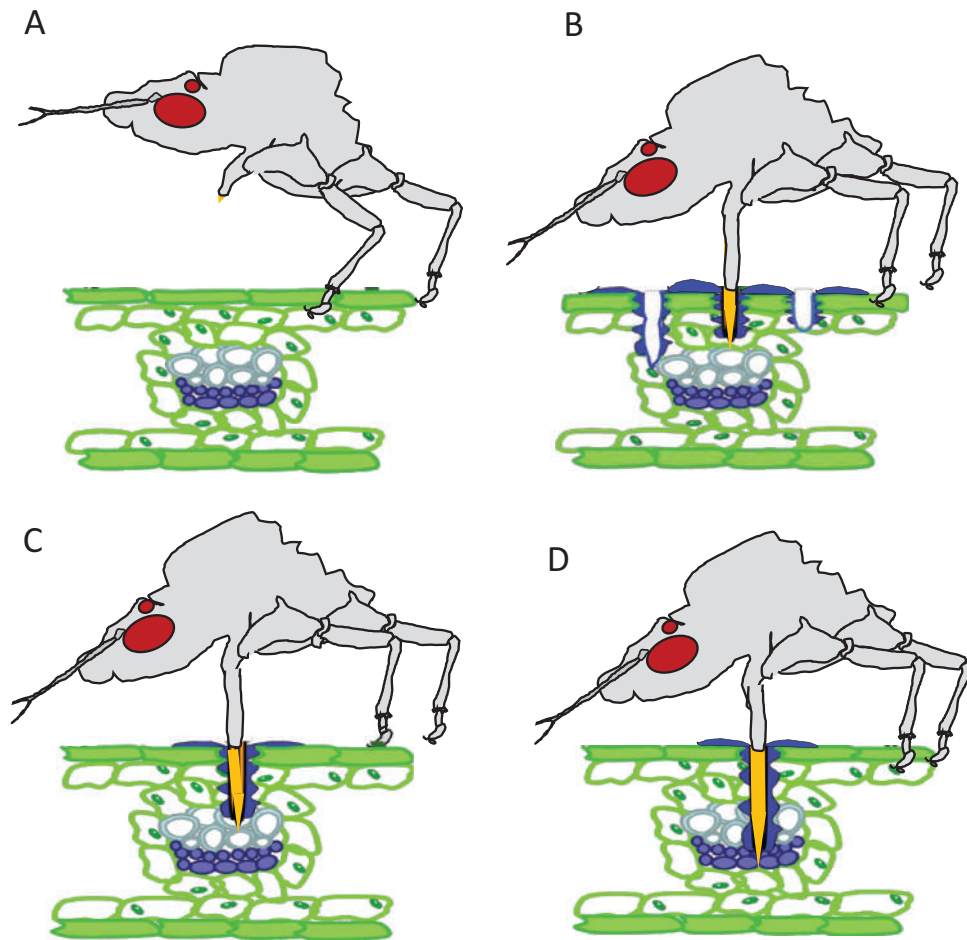


Fig. 6. Probing sequences for *C. pyri* leading to ingestion from the host plant (Civolani et al. 2011, 2013). (A) Nonprobing phase; (B) penetration of parenchyma tissues by stylets and deposition of the salivary sheath; (C) penetration of the xylem by stylets and ingestion of xylem contents; (D) penetration of phloem sieve elements by stylets, and subsequent bouts of salivary discharge and ingestion of phloem contents.

et al. 2019). Sorbitol appears not to be assimilated in quantity. Quantities of different amino acids in phloem versus honeydew suggested that 7 amino acids (serine, histidine, arginine, alanine, phenylalanine, leucine, and lysine) were assimilated by *C. pyri* in large amounts (Le Goff et al. 2019). Four other amino acids (methionine, tryptophan, asparagine, and glutamine) were either not detected in phloem or were egested in larger amounts than expected (Le Goff et al. 2019). The authors suggested that these 4 amino acids probably are synthesized by bacterial endosymbionts harbored by the psyllid (discussed below in Microbial Interactions).

Mating Behavior

Studies of mate-locating behavior, cues used in locating mates, courtship, and events leading to insemination are limited to 4 species: *C. pyri*, *C. bidens*, *C. pyricola*, and *C. chinensis*. Research with the Psylloidea indicates that 3 codependent modalities (acoustic, olfactory, visual) combine to bring the sexes together for mating (Lubanga et al. 2014). The male psyllid must first locate the female, approach and successfully court her, engage in copulation, and then transfer sperm. The precise roles of acoustic, olfactory, and visual cues in mediating this sequence of events are not fully understood despite significant progress in the last 3 decades (reviews in Lubanga et al. 2014, Mankin and Rohde 2020, Liao et al. 2022).

Acoustic communication.

Vibrational communication between male and female psyllids occurs in at least 6 families of Psylloidea and in more than 100 psyllid species in 47 genera (Liao et al. 2022). The vibrations are sent through the plant substrate and are quite different from the airborne acoustic signals of other insects in operating at a much shorter range (Lubanga et al. 2014, Liao et al. 2022). Ossiannilsson (1950) was first to describe vibrational sounds of psyllids after detecting a faint buzzing noise emanating from a psyllid-filled glass tube. More than 30 yr later, the first recording (oscillogram) of waveforms produced by psyllids was described from the vibrations of Liviidae psyllids (Liao et al. 2022). Signaling is in the form of duets, in which male and female insects exchange sex-specific vibrations (Liao et al. 2022). The duet is initiated by the male, with the female responding to the male's call (Lubanga et al. 2014, Liao et al. 2022). The back-and-forth exchange of signals brings the sexes together for mating (Lubanga et al. 2014, Liao et al. 2022). Signals appear to be produced by rapid vibration of wings and rubbing of the axillary sclerites and anal vein or anal region of the forewings against ridges on the psyllid thorax (Fig. 7A). Taylor (1985) suggested that hind wings may also be involved, but this remains uncertain (Liao et al. 2019, Avosani et al. 2022).

Eben et al. (2015) were first to describe the male and female acoustic signals for a pear psyllid (*C. pyri*). The vibrational sequence of male *C. pyri* consists of 4–11 (Eben et al. 2015) or 6–18

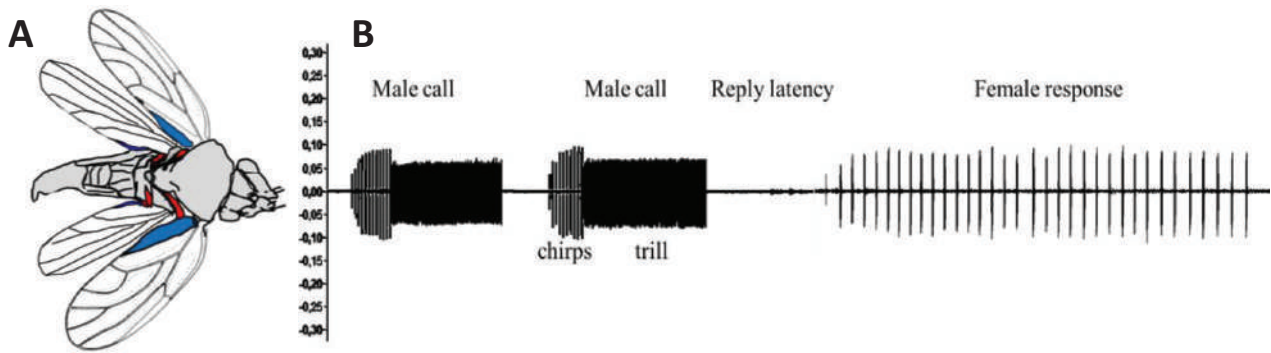


Fig. 7. (A) Schematic of psyllid in dorsal view showing anal region of wings (blue shading) and regions of thoracic ridges (red shading) thought to be involved in producing vibratory signals (Taylor 1985, Eben et al. 2015, Liao et al. 2019, Avosani et al. 2022). (B) Oscillogram of the *C. pyri* male–female duet (S. Civolani, unpublished data; see also Eben et al. 2015).

(S. Civolani unpubl.) short-pulsed “chirps” followed by a drawn-out interval of 300 or more rapid pulses collectively referred to as a “trill” (Fig. 7B). The female signal is a series of short pulses, or “chirps”, which may extend for several seconds (Fig. 7B; Eben et al. 2015). Females call only in the presence of calling males (Eben et al. 2015). A short and variable delay (“reply latency”) occurs between the end of the male signal and initiation of female response (Fig. 7B; Eben et al. 2015, S. Civolani unpubl.). The vibrational signals of a second pear psyllid, *C. pyricola*, have also been described (Jocson 2020). Waveforms of summerform *C. pyricola* are somewhat similar to those of *C. pyri*. The male song again begins with a series of pulses which transition into a trill or “whine” (Jocson 2020). Following a reply latency of several seconds, the female responds with a series of short chirps (Jocson 2020). The song of the winterform morphotype appears to be of lower pitch than that of the summerform (Jocson 2020). Additional research almost certainly will show that pear psyllids other than *C. pyri* and *C. pyricola* also engage in acoustic duets. *Cacopsylla bidens*, for example, exhibits a wing-vibrating behavior during courtship (V. Soroker unpubl.), which likely is evidence for vibrational signaling.

Chemical communication.

Chemical communication via pheromones has a significant role in mate location behavior of many insects. Electroantennogram trials with *C. bidens* showed that male antennae are sensitive to female-produced volatiles, while olfactometer trials showed that male psyllids are attracted to volatiles from females (Soroker et al. 2004). This study is the first evidence for any psyllid species that mate selection involves female-produced chemical cues. Subsequently, males of 3 other pear psyllids, *C. pyricola*, *C. pyri*, and *C. chinensis*, were shown in olfactometer trials to be attracted to females or to surface washes of females (Horton et al. 2008, Guédot et al. 2009a, 2011, Wan et al. 2013, Ganassi et al. 2018). Efforts to identify the attractants have focused on cuticular hydrocarbons (CHCs). The epicuticle of pear psyllids harbors long chain hydrocarbons consisting largely of straight chain and branched alkanes. Most of the compounds are found in both sexes (Guédot et al. 2009b, Soroker et al. 2010, Wan et al. 2013, Ganassi et al. 2018). However, the sexes do differ in relative quantities of chemicals. Compounds at higher quantities in females than males include 13-methylheptacosane (13-Me C27) in *C. pyricola*, *C. bidens*, *C. pyri*, and *C. chinensis* (Guédot et al. 2009b, Soroker et al. 2010, Wan et al. 2013, Ganassi et al. 2018); 11,15-dimethylheptacosane, 2-Me C27, and 3-MeC27 in *C. pyri* (Ganassi et al. 2018); and 7-Me C27 and 11, 15-dimethylheptacosane in *C. bidens* (Soroker et al. 2010). In olfactometer trials, males of

C. pyricola were attracted to 13-Me C27 (Guédot et al. 2009b) while males of *C. bidens* were attracted to 7-Me C27 (Soroker et al. 2010).

The similarity in chemical profiles across species of pear psyllids suggests that the methyl-branch heptacosanes are important in sexual communication within this taxon, while the slight differences among species probably evolved as species isolation mechanisms. The low volatility of the compounds means that they likely act only at close range. Males of *C. pyricola* antennate females upon contact (Krysan 1990) likely in response to these compounds. During the initial postcontact stages of sexual behavior the hydrocarbons may function in mate recognition and in evaluating reproductive status. Attraction to these chemicals is not strong and fluctuates seasonally (Guédot et al. 2009b, Soroker et al. 2010), thus it is possible that the CHCs are not the only chemical signals operating in sexual communication by the pear psyllids. Molecules of higher volatility produced by adult psyllids, their secretions, or psyllid-infested host plants could be present and contribute to longer-range sexual attraction (Lubanga et al. 2014).

Courtship, mating, and sperm transfer.

Once duetting or other behaviors have brought the male and female psyllid together, activities that lead to copulation begin. These behaviors are initiated by the male (Cook 1963, Krysan 1990). Approach of the female by the male psyllid seems to be governed in part by visual cues, as sexually active male psyllids readily approach other males, aphids, or even psyllid-sized bits of debris that have been dislodged onto beating sheets during sampling (D. Horton unpubl.). Male *C. pyricola* in small plastic arenas detected females from distances of 3 cm or more (Krysan 1990), presumably through use of visual and possibly chemical cues. The male psyllid directly approaches the female (Cook 1963, Krysan 1990). Contact is followed by antennation of the female by the male (Krysan 1990). The male then rotates his body to be aligned parallel with that of the female and curves the tip of his abdomen toward the tip of the female’s abdomen for coupling (Cook 1963, Krysan 1990). A female may resist copulation by raising the tip of her abdomen away from the male (Krysan 1990). Positioning of genitalic structures during copulation is described for *C. pyricola* by Slingerland (1892) and Cook (1963). Sperm are transferred to the female in packets (spermatophores), with a single spermatophore being transferred per copulation (Krysan 1990). Copulation duration for *C. pyricola* averages between 10 and 30 min although couplings exceeding 3 hrs have been reported (Burts and Fischer 1967, Krysan 1990). Both sexes mate repeatedly (Krysan 1990), and in fact repeated mating is needed to attain maximum fecundity and egg fertility (Burts and Fischer 1967).

A single male *C. pyricola* may transfer over 9 spermatophores to a female within a 24-h period (Krysan 1990).

Microbial Interactions

The pear psyllids harbor bacterial endosymbionts having any number of effects, including roles in host nutrition, feeding behavior, and vector competency. “*Ca. Carsonella rudii*” is a maternally-inherited, obligate endosymbiont found in all psyllid species, including in the pear psyllids (Thao et al. 2000b, Cooper et al. 2015, Schuler et al. 2022). This bacterium lacks genes for basic metabolic function and relies upon the psyllid host to provide metabolic needs (Nakabachi et al. 2006). *Carsonella* provides the psyllid with essential amino acids lacking in the phloem diet (Nakabachi et al. 2006). In other phloem-feeding insects, elimination of obligate endosymbionts having a nutritional role results in death of the host (Rupawate et al. 2023). *Carsonella* bacteria reside within specialized insect cells called bacteriocytes contained in an orange bacteriome (Fig. 8A and B; Chang and Musgrave 1969, Cooper and Horton 2014). This endosymbiont often is accompanied in the bacteriome by either “*Ca. Arsenophonus*” or “*Ca. Sodalis*” (Fig. 8C). Both endosymbionts likely assist with psyllid nutrition (Sloan and Moran 2012, Hall et al. 2016, Morrow et al. 2017). *Arsenophonus* has been detected in *C. pyrisuga*, *C. pyri*, and *C. pyricola* (Cooper et al. 2017, Štarhová Šerbina et al. 2022b). In addition to effects on psyllid nutrition, *Arsenophonus* also may affect susceptibility to insecticides, parasitism, disease, or host plant defenses, as shown in other psyllids (Thao et al. 2000a, Spaulding and von Dohlen 2001, Hansen et al. 2007). *Sodalis* is present in psyllids from multiple families (Thao et al. 2000a, 2000b, Sloan and Moran 2012, Hall et al. 2016, Cooper et al. 2022); its detection in the pear psyllids at this time is limited to the eastern Palaearctic *C. burckhardtii* (Nakabachi et al. 2022).

Other bacteria harbored by the pear psyllids include taxa which occur also in the *Pyrus* host plant. “*Ca. Liberibacter*” are insect-transmitted bacterial plant pathogens associated with globally important crop diseases such as citrus greening and potato zebra chip (Jagoueix et al. 1994, Hansen et al. 2008, Liefing et al. 2008). The first *Liberibacter* to be found in a pear psyllid, “*Ca. Liberibacter europaeus*”, was discovered in populations of *C. pyri* in Italy (Raddadi et al. 2011). A broader survey revealed that 2 other pear psyllids, *C. pyricola* and *C. pyrisuga*, also harbor the pathogen (Camerota et al. 2012). The bacterium has not been detected in North American populations of *C. pyricola* (Cooper et al. 2017). *Liberibacter europaeus* does not appear to cause disease symptoms in pear or other fruit trees (Raddadi et al. 2011, Camerota et al. 2012) but may cause mild symptoms in scotch broom (*Cytisus scoparius*) following transmission of the pathogen by a broom psyllid, *Arytainilla spartiophila* (Foerster) (Thompson et al. 2013, Tannières et al. 2020). *Liberibacter*s alter the biology and behavior of some psyllid species (Davis et al. 2012, Mann et al. 2012a, Nachappa et al. 2012, Mas et al. 2014), but it is not known whether *Liberibacter europaeus* affects biology of pear psyllids, nor is it clear how the bacterium is maintained in psyllid populations.

“*Ca. Phytoplasma pyri*” is the pathogen that causes decline disease in pears, shown by yellowing of leaves, decreased tree vigor, and death of the tree. Known vectors of *Phytoplasma pyri* are *C. pyricola*, *C. pyri*, and *C. pyrisuga* (Jensen et al. 1964, Lemoine 1991, Riedle-Bauer et al. 2022). The pathogen is found in pear-growing regions of North America, Europe, Africa, and Asia (Eleftheriou and Tamoutseli 1985, Jarausch and Dosba 1995, Lee et al. 1995, Davies and Adams 2000, Ben Khalifa et al. 2007, Liu et al. 2011). Although resistant rootstock now protects trees from long-term infection, 20–30% of pear psyllids in North America and Europe still harbor

the pathogen, with the highest incidence of infection in overwintered psyllids (Camerota et al. 2012, Cooper et al. 2017, Riedle-Bauer et al. 2022). Overwintered psyllids likely re-infect trees each spring. *Phytoplasma* is acquired by psyllids when they feed upon the phloem of infected plants. The pathogen passes through the midgut wall of the psyllid (Fig. 8D), multiplies in the salivary glands, and is transmitted when the insect discharges saliva into phloem of the pear host (Sugio and Hogenhout 2012, Cruz et al. 2018). Some phytoplasmas may manipulate the feeding or host-seeking behavior of insect hosts, possibly by altering attractiveness of the host, or by affecting biology of the insect vector (Sugio and Hogenhout 2012). The behavioral changes may improve vector competency. Little is known of whether *Phytoplasma pyri* affects behavior of the pear psyllids, although Cruz et al. (2018) showed that phytoplasma-infected *C. pyricola* were less likely than uninfected psyllids to disperse from the pear host and become captured on yellow traps. The possible effects of this behavioral change on spread of the pathogen are unknown.

Pest Management

Types of Damage

The pear psyllids cause several types of damage. The primary damage is “pear russet”, or marking of fruit by psyllid honeydew and an associated sooty mold. Immature psyllids excrete large quantities of a syrupy honeydew (Fig. 9A) which causes blotches or streaks as it drips onto the surface of the pear fruit (Fig. 9B), leading to downgrading of the harvested pear (Burts 1970). Heavily infested orchards also become very sticky, which interferes with harvesting or other labor activities. Damage known as “psylla shock” also is caused by nymphs. High densities of nymphs lead to defoliation, reduced fruit size, and premature fruit drop (Burts 1970). The damage apparently is caused by a toxin in the saliva of nymphs (Beers et al. 1993). Symptoms may carry over between consecutive years (Beers et al. 1993). Lastly, “pear decline”, caused by a phytoplasma vectored by adult pear psyllids (see previous section), leads to decline in health of infected pear trees. The disease in North America was initially detected during the 1940s in western Canada (McLarty 1948). It possibly was present earlier than this in Europe (Ogawa and English 1991). Pear decline was extraordinarily damaging in Western North America during the 1960s, with the loss of almost 1 million pear trees in Washington, Oregon, and California (Ogawa and English 1991). The disease is managed by planting on rootstock that prevents overwintering of the pathogen in roots (Westwood and Lombard 1966, Çağlayan et al. 2022).

Monitoring

Several sampling methods have been developed to monitor the pear psyllids. These tools deliver information on generational phenology, timing of autumn dispersal and spring reentry, and onset of egg laying in spring (reviewed in Horton 1999). Monitoring is also a critical part of making control decisions, particularly when it can be combined with information on levels of economic damage expected from a given psyllid density (Westgard et al. 1981, Burts 1988, Nottingham et al. 2022b). Each monitoring tool has its own strengths and weaknesses in ease of use and in what the count data mean with respect to actual densities of psyllids and damage potential.

The typical method for sampling the adult psyllid is by jar-ring the insects from tree limbs onto a cloth-covered tray (Burts and Retan 1973, Nottingham et al. 2022b). Samples are taken by holding the tray beneath a limb and sharply rapping the limb with a section of stiff rubber hose. Dislodged insects cling to the cloth

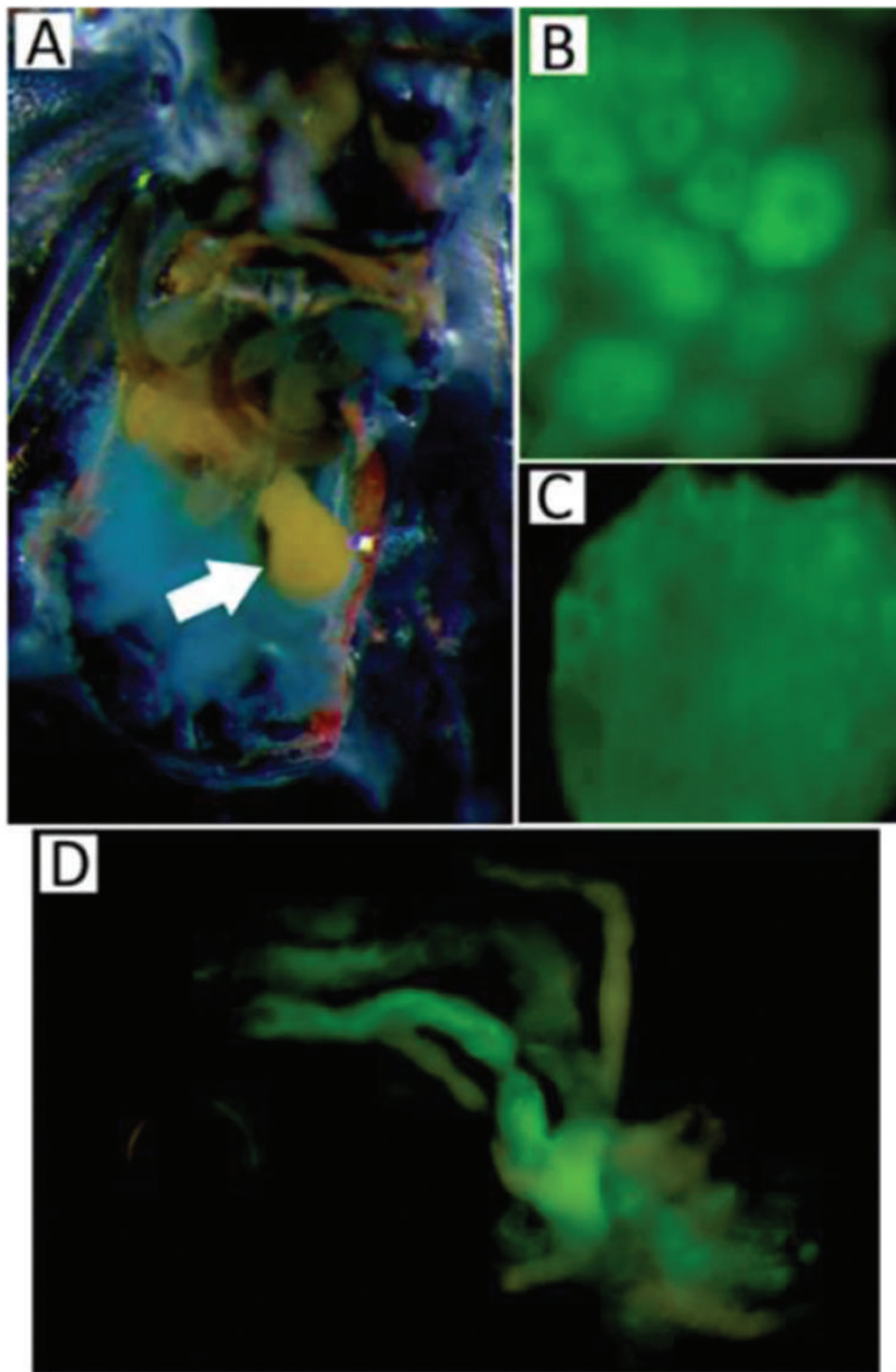


Fig. 8. (A) Orange-colored bacteriome of *C. pyricola* indicated by the white arrow houses beneficial bacteria. (B) The obligate endosymbiont, *Carsonella rudii*, fluorescing green to show its location within bacteriocytes of *C. pyricola*; note the shadows showing the nucleus of the bacteriocyte. (C) The secondary endosymbiont, *Arsenophonus*, fluorescing green to show its location within the syncytium tissues of the bacteriome; note the shadows showing location of bacteriocytes without *Arsenophonus*. (D) Phytoplasma fluorescing green to show its location in the alimentary canal of *C. pyricola* collected from phytoplasma-infected pear trees.

and are counted. The threshold counts of psyllids on trays which indicate that treatment is necessary to manage russet are discussed in Nottingham et al. (2022b) and DuPont et al. (2023). A second method for monitoring the adult psyllid is with use of sticky cards. This tool is less useful for guiding management decisions than trays

because trap catch includes components of psyllid behavior that act independently of psyllid density. Trap counts suffer from the confounding effects of psyllid flight activity making it difficult at times to interpret what a given trap catch indicates (Horton 1993, 1994, 1999). Trap captures are almost invariably male-biased (Fig. 10),

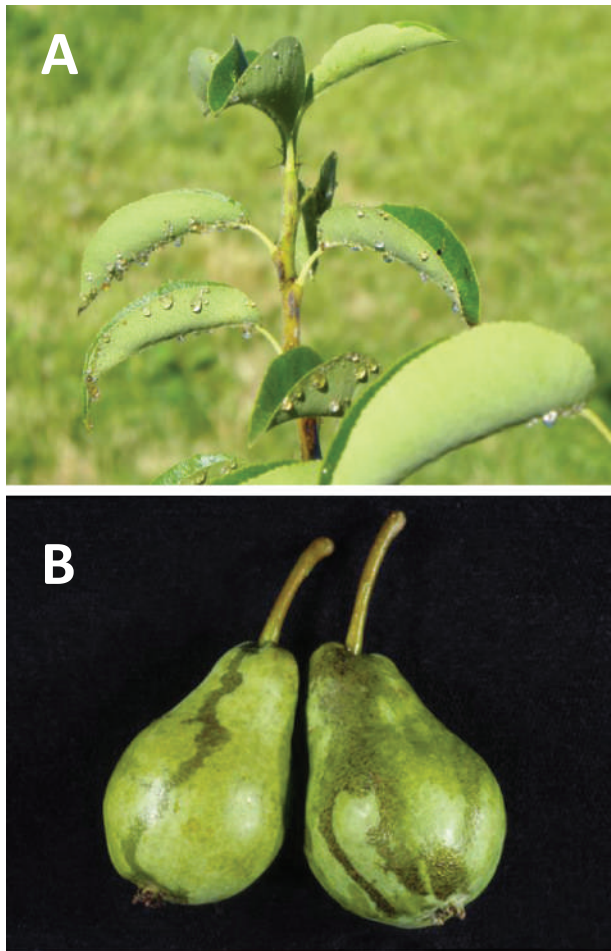


Fig. 9. (A) Glistening honeydew in orchard heavily infested with *C. pyricola*; (B) marking of fruit by honeydew and sooty mold.

even at times when male and female counts on beating trays are close to equal or are female-biased, apparently due to search by males for females. This can lead to relatively poor correlation between trays and traps in estimates of psyllid pressure in pear orchards (Horton and Lewis 1997).

Spur and leaf samples are used to monitor densities of eggs and nymphs (Burts and Retan 1973, Westigard et al. 1979, Burts 1988). Before bud swell in late-winter most eggs are found at the base of fruiting spurs (Fig. 3E; Westigard et al. 1979). Once flowers within a single cluster have separated, the leaves associated with fruiting spurs are monitored (Burts and Retan 1973, Westigard et al. 1979). For summer generations leaf samples are taken (Burts and Retan 1973, Westigard et al. 1979). Treatment thresholds for russet using spur and leaf samples are provided by Nottingham et al. (2022b) for *C. pyricola* and Sanchez et al. (2022) for *C. pyri*. Complications in sampling are caused primarily by seasonal changes in the spatial distribution of eggs and nymphs (Burts 1988, Stratopoulou and Kapatos 1992, Sanchez and Ortín-Angulo 2011).

Chemical Control and Insecticide Resistance

Synthetic insecticides have been the cornerstone of pear psyllid control since the arrival of the organophosphates in the 1940s. Difficulties in controlling the pear psyllids is due to several biological traits, including high fecundity, overlapping generations, and insecticide resistance. Resistance substantially affected the

progression of insecticides arriving both in Europe (Atger 1979) and North America (Harries and Burts 1965), characterized by the arrival and then replacement of individual insecticides or of entire classes of insecticides. Resistance largely was responsible for the beginnings of integrated control in which selective insecticides are used in combination with biological control and cultural practices (Burts 1981). Quantities and types of insecticides often are quite variable across pear-growing regions. In Washington and Oregon, integrated programs for *C. pyricola* may consist of 6–8 applications of insecticides annually (DuPont and Strohm 2020, DuPont et al. 2021). In contrast, programs for *C. pyri* in Northeast Italy rely on 2 or 3 applications of insecticides annually (S. Civolani unpubl.); in Spain 3–4 applications (D. Bosch-Serra pers. comm.); and in southern France often only prebloom applications of kaolin clay and a summer application of an insecticide (G. Sévérac pers. comm.). In southwestern Turkey, 8–10 applications of insecticides annually may be used against *C. pyri* (Oz and Erler 2021). Six applications may be used to control *C. bidens* in Israel (V. Soroker unpubl.), while in Chile – where *C. bidens* is introduced – the insect apparently is not targeted with insecticides (S. Civolani unpubl.).

Chemical control of the pear psyllids focuses on 2 seasonal time periods divided by tree growth stage (Fig. 11): dormant/delayed dormant (prebloom); and, the postbloom period. The life stages of psyllids targeted by insecticides change through time and between pre- and postbloom time periods (Fig. 11). Prebloom insecticides were first used against a pear psyllid in the early-1900s against North American populations of *C. pyricola*. The overwintered psyllid was targeted with applications of petroleum oil to kill eggs and to deter egg-laying (Strickland 1925, Ross 1926). Oil combined with an insecticide was used against newly hatched nymphs beginning in the early 1900s with mixtures of oil and lime sulphur (Hartzell 1925, Strickland 1925). At mid-century, insecticides such as dinitro-ortho-cresol (Hamilton 1948, Madsen and Marshall 1961) or the organophosphates were used in oil during the prebloom period, but were abandoned with arrival of pyrethroids in the 1980s (Buès et al. 2003). As it became apparent that prebloom insecticides interfered with season-long control of psyllids due to disruption of biological control (e.g., Westigard 1973a, Burts 1981), classes of products having lesser effects on natural enemies began to appear (Fig. 11): kaolin clay; juvenile hormone (JH) mimics; inhibitors of chitin biosynthesis; mitochondrial electron transport inhibitors (METI); oil of cinnamon (Cinnerate); chitin synthesis inhibitors (CSI); and the neonicotinoids. These products all appear to have lesser effects on natural enemies than the earliest synthetic insecticides and today are important components of prebloom programs (Nottingham et al. 2022b).

Postbloom sprays target eggs, nymphs, and adults of the summer generations (Fig. 11). Between the late-1940s and 1970s, nonselective insecticides such as the organophosphates, carbamates, and pyrethroids arrived for summer use (Westigard and Zwick 1972, Westigard et al. 1979). The time course in arrival, use, and replacement of a product was driven by loss of efficacy due to resistance, especially in US populations of *C. pyricola* (Harries and Burts 1965, Westigard and Zwick 1972). Resistance of *C. pyricola* to the organophosphate parathion began within 10 yr of the chemical's arrival in the late-1940s (Burts 1964, Harries and Burts 1965). The loss of parathion was only the first in a long series of such events, in which a new psyllicide would arrive, be used for a few years, and then would be lost to resistance (Burts 1964, Harries and Burts 1965, Westigard and Zwick 1972). Cross-resistance was common, in that resistance to 1 insecticide was accompanied by resistance to other insecticides within the same class (Burts 1964). The loss of parathion

and other organophosphates was followed by arrival and then loss of the cyclodienes, chlorinated hydrocarbons, and pyrethroids (Burts 1964, Harries and Burts 1965, Follett et al. 1985, Croft et al. 1989). Resistance of *C. pyri* has been less dramatic than seen for *C. pyricola*, but nonetheless is a problem. Selection assays produced significant levels of resistance to organophosphates in French populations of *C. pyri* within ~30 generations (Berrada et al. 1995, Buès et al. 2000). Buès et al. (2003) documented increases in resistance by *C. pyri* to the pyrethroid deltamethrin that ranged from 31-fold to 135-fold.

Beginning in the 1970s, postbloom control of psyllids began shifting to insecticides of higher selectivity (Burts 1981). This shift included the arrival of new classes of chemicals such as amitraz,

an octopamine receptor agonist with activity against nymphs but with lesser effects on natural enemies (Souliotis and Moschos 2008). Its efficacy in Europe against *C. pyri* weakened by the early 2000s (Schaub et al. 2001). A substitute was the chitin synthesis inhibitor diflubenzuron (Westgard 1979, Souliotis and Moschos 2008). Product efficacy again declined (Schaub et al. 1996), and the chemical largely has been abandoned in Europe but is being used in the US (Fig. 11). The macrocyclic lactone abamectin arrived in the 1980s (Burts 1985, Berrada et al. 1996) and continues to be used in psyllid programs (Fig. 11). A slight drop in efficacy has been seen in Spanish and Italian populations of *C. pyri* (Civolani et al. 2007, 2010, 2015, Miarnau et al. 2010). A more substantial drop was

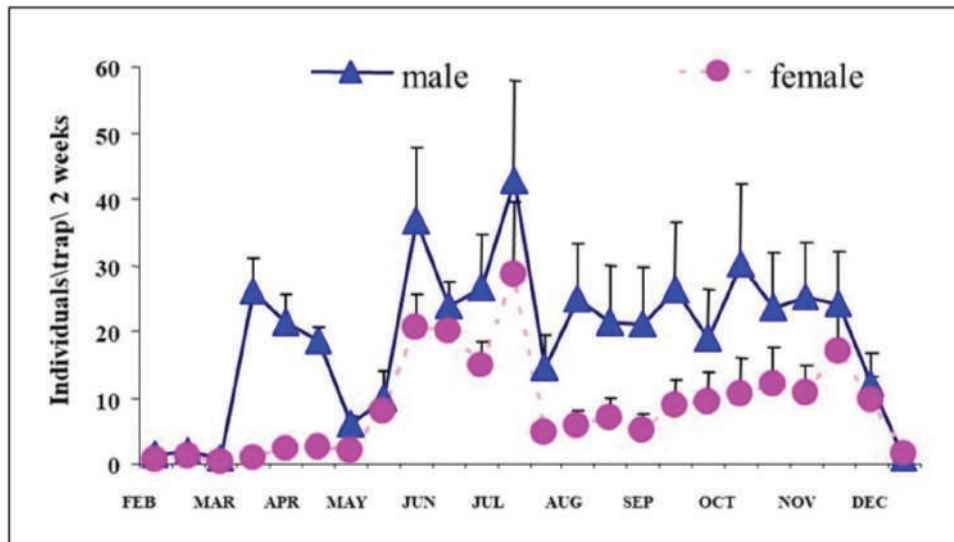


Fig. 10. Two-week captures of male and female *C. bidens* on yellow sticky cards showing male-biased trap catch (V. Soroker, unpublished data); Israel.

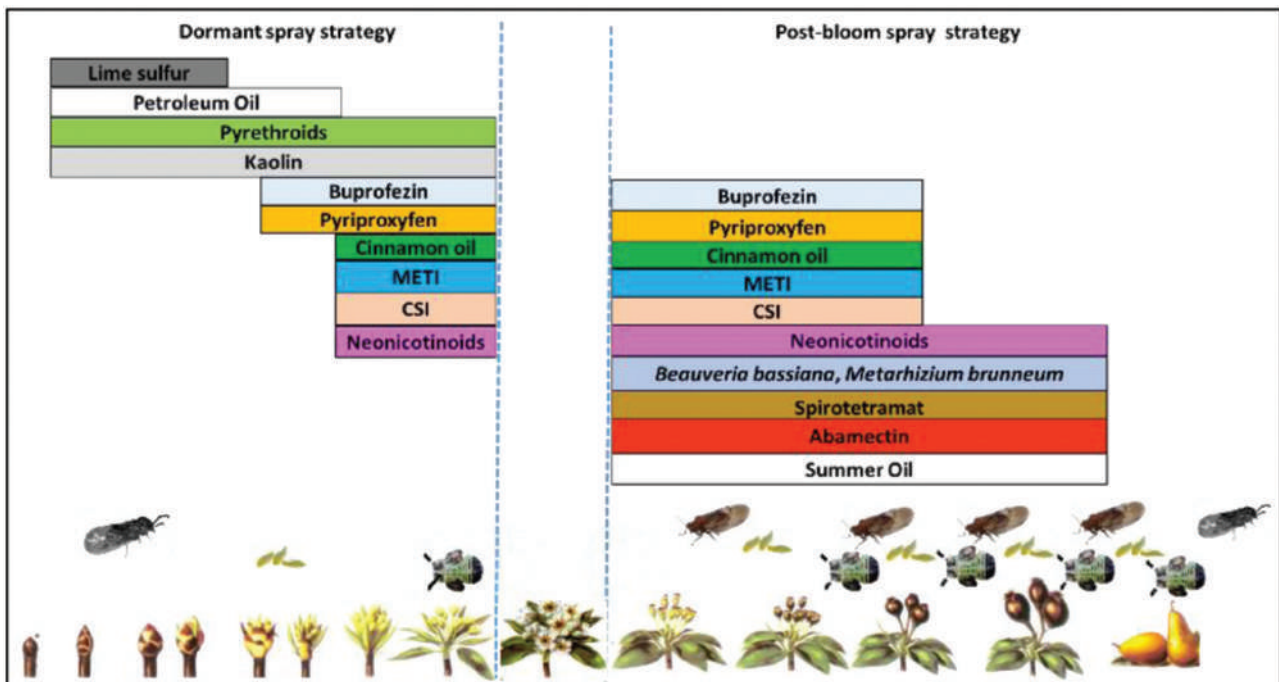


Fig. 11. Important pre- and postbloom insecticides used to manage the pear psyllids. Use of the different products varies regionally and with species of psyllid. Frequency of spray applications (typical number of applications per season) also differs substantially among regions (see text).

observed in Turkey leading to the abandonment of the insecticide (E. Erler, pers. comm.). Spirotetramat, an alternative to abamectin, arrived in the early 2000s and continues to be used (Fig. 11). The compound should be rotated with other classes of chemicals to reduce chances of resistance (Civolani et al. 2015, Esmaily et al. 2022). Both abamectin and spirotetramat are components of psyllid control programs in several growing regions but are in the process of being phased out in Europe and will need effective replacements (Civolani et al. 2023).

Decades of starts and stops in arrival and replacement of insecticides have led to a wide-ranging choice of insecticides for managing the pear psyllids (Fig. 11). Importantly, the newer products consist of compounds differing in modes of action, which lowers chances that psyllids will develop resistance. The insecticides also are of lower-toxicity to natural enemies, which allows for biological control. Some products are available for both prebloom and postbloom intervals, such as pryiproxyfen, the neonicotinoids, cinnamon oil, and the CSI or METI (Fig. 11). Dormant oil has been replaced in some programs by kaolin clay, which has effects on psyllids like those caused by oil (Glenn et al. 1999, Pasqualini et al. 2003, Erler and Cetin 2007) but with longer residual life. In some climates, fungal pathogens (*Beauveria*, *Metarhizium*) can be useful (Puterka 1999, Erler et al. 2014). Finally, years of advances in oil distillation have led to the manufacture of highly refined horticultural oils that can be applied during summer with low risk of phytotoxicity (Fig. 11). These oils provide growers with a postbloom treatment having relatively high selectivity.

Biological Control

The pear psyllids have been referred to as “induced” pests in that outbreaks may often be caused by grower practices, especially by insecticidal destruction of natural enemies (Westigard 1973a, Burts 1981, 1983, Solomon et al. 1989). A large community of predators and parasitoids attack pear psyllids both within their native Old World range and in regions where the psyllids have been introduced. Taxa show a gradation in how generalized or specialized they are ranging from opportunistic generalists such as spiders and earwigs, to true bug species that associate primarily with homopterous or psyllid prey, and culminating with the psyllid-specific activities of some parasitoids. This bewildering diversity of natural enemies has led to a very large literature that touches on numerous aspects of psyllid biological control. Research has helped identify taxa of importance in pear orchards, while also providing basic biological data critical in designing integrated control programs for the pear psyllids.

Natural enemies of the pear psyllids.

Overviews of predatory taxa in pear orchards are available for several regions including France (Nguyen et al. 1984, Herard 1985, 1986), Italy (Civolani and Pasqualini 2003), Greece (Santas 1987), Spain (Artigues et al. 1996), Israel (Shaltiel and Coll 2004), Turkey (Erler 2004), Northern and Central Europe (Solomon et al. 2000, Gajski and Pekár 2021), and North America (Westigard and Zwick 1972, Horton et al. 2002, DuPont and Strohm 2020). Important predators include especially the true bugs led by the minute pirate bugs (Anthocoridae) and zoophytophagous plant bugs (Miridae) (Fig. 12). Several true bug taxa seem to prefer homopterous Hemiptera and often are found in association with psyllid prey, such as shown by some *Anthocoris* species (Scutareanu et al. 1999, Horton et al. 2004). Taxa less closely associated with psyllids include Coccinellidae and Neuroptera, which attack aphids in fruit orchards

but also feed on pear psyllids. Generalist predators that feed opportunistically on pear psyllids are spiders (Araneae) and earwigs (Dermaptera). Both groups include effective but underappreciated predators of the pear psyllids (van der Blom et al. 1985, Solomon et al. 2000, Miliczky and Calkins 2001, Orpet et al. 2019).

Biological research with these taxa in pear orchards is extensive. Studies of phenology, including descriptions of wintering, have been conducted in several regions (Herard 1985, Artigues et al. 1996, Scutareanu et al. 1999, Horton et al. 2002, Civolani and Pasqualini 2003, Horton 2004, Shaltiel and Coll 2004, DuPont and Strohm 2020). Phenology data for natural enemies have now made their way into psyllid control programs (Nottingham et al. 2022b). Laboratory assays have quantified rates at which predators consume pear psyllids (Westigard 1973b, Brunner and Burts 1975, Sigsgaard 2010, Petrakova et al. 2016, Ge et al. 2019), while molecular tools have identified predators which feed on psyllids under field conditions (Unruh et al. 2008, Valle et al. 2022). Monitoring tools include nonselective devices such as beating trays, tree bands, or sticky traps (Horton et al. 2002, Jones et al. 2016, Mills et al. 2016b, DuPont and Strohm 2020), as well as tools of higher selectivity such as cardboard refuges for earwigs (Orpet et al. 2019). Multiple studies have examined the effects of insecticides on natural enemies (Westigard 1973a, 1973b, Trapman and Blommers 1992, Sauphanor et al. 1993, Berrada et al. 1996). Today's assays often examine both acute and sublethal effects of toxicants (Amarasekare and Shearer 2013, Amarasekare et al. 2016, Mills et al. 2016a). These studies help guide insecticide recommendations in integrated programs (Beers et al. 2016, Nottingham et al. 2022b).

Lists of parasitoids emerging from pear psyllids are available for both Old World and New World regions (Jensen 1957, McMullen 1966, 1971, Rieux et al. 1990, Cross et al. 1999, Jerinić-Prodanović et al. 2019). Three species of Encyrtidae (Hymenoptera) are most important: *Trechmites insidiosus* (Crawford), *Prionomitus mitratus* (Dalman), and *Prionomitus tiliaris* (Dalman) (Fig. 13). All 3 are parasites of nymphal Psylloidea. The adult parasite emerges from the mummified late-instar of the nymph (Fig. 13). Pear psyllids that are reported as hosts for 1 or more of these parasitoids include *C. pyri*, *C. pyrisuga*, *C. pyricola*, and *C. bidens* (Jensen 1957, Herard 1986, Guerrieri and Noyes 2009, Jerinić-Prodanović et al. 2019, Noyes 2019, Tougeron et al. 2021). All 3 parasitoids are widespread in the Palaearctic Region (Guerrieri and Noyes 2009, Noyes 2019). Each is present in North America as an introduction or because the species is naturally Holarctic. Observations on host use, behavior, hyperparasitoids, and life histories are available in several publications (Gutierrez 1966, Nguyen and Delvare 1982, Delvare 1984, Le Goff et al. 2021, Tougeron et al. 2021). *Trechmites insidiosus* largely is restricted to pear psyllid hosts but may occasionally parasitize other *Cacopsylla* (Herard 1986, Jerinić-Prodanović et al. 2019). It is a valuable source of biocontrol in European and North American orchards (Nguyen et al. 1984, Rieux et al. 1990, Armand et al. 1991, Unruh et al. 1995, Olszak and Jaworska 2003, Tougeron et al. 2021). While parasitism of pear psyllids by *Prionomitus* spp. is at a lower rate than that by *T. insidiosus* (Armand et al. 1991, Olszak and Jaworska 2003), biologically significant rates have been reported (Nguyen et al. 1984, Herard 1985). Both *Prionomitus* are more generalized than *T. insidiosus* and regularly parasitize psyllids other than pear psyllids (Jensen 1957, Nguyen et al. 1984, Zuparko 2015, Jerinić-Prodanović et al. 2019, Noyes 2019). Neither *Prionomitus* is common in North American *C. pyricola* (Unruh et al. 1995), instead preferring other psyllid taxa (Jensen 1957, McMullen 1971, Zuparko 2015).

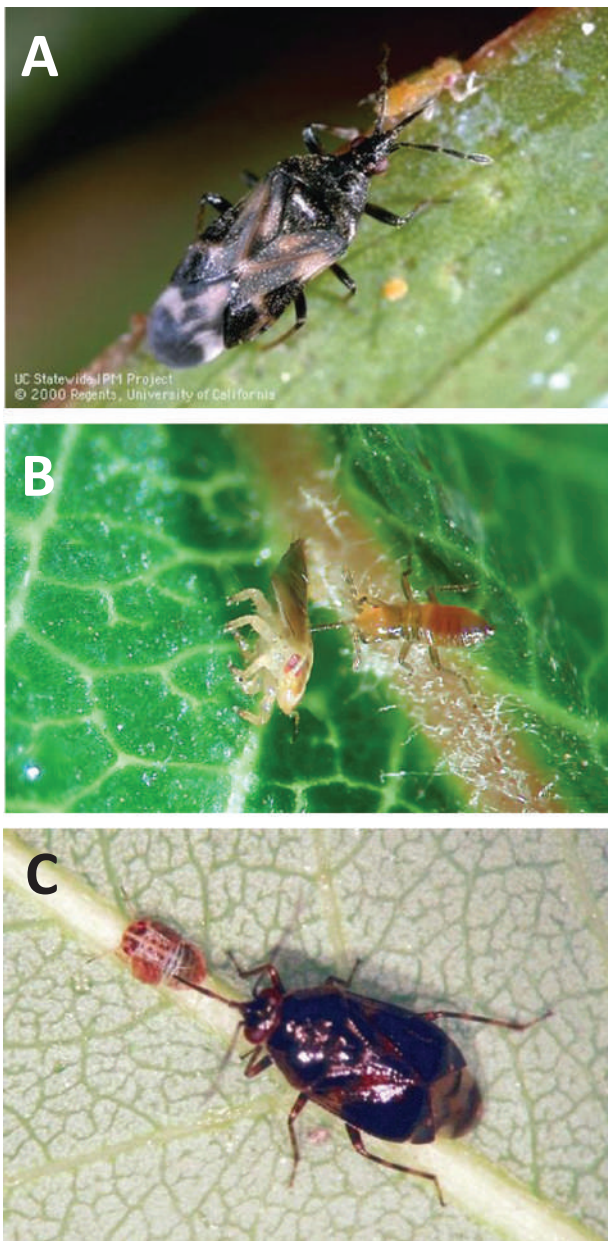


Fig. 12. Important true bug predators of pear psyllids. (A) Adult and (B) immature of *Anthocoris*; (C) adult *Deraeocoris brevis* feeding on immature *C. pyricola*.

Conservation and augmentation of natural enemies.

Approaches to conserve or augment natural enemies in orchards include releases of predators or parasitoids into regions where they are absent, mass-release of native predators, use of trees or hedges as reservoirs of natural enemies, and replacement of broadly toxic insecticides with less harmful chemicals. Releases of natural enemies into North America for control of *C. pyricola* include both parasitoids and predators. The parasitoids *T. insidiosus* and *P. mitratus* were released into western North America on several occasions beginning in the 1960s. The parasites were collected from pear psyllids in several parts of the Palaearctic region (Unruh et al. 1995). Both parasitoids in fact were present in North America earlier than the releases. Indeed, *T. insidiosus* was described from specimens collected in the eastern US (Crawford 1910), likely having arrived in the US on psyllid-infested pear trees from Europe. Records for *P. mitratus* in North America extend as far back as the 1940s (Jensen 1957).

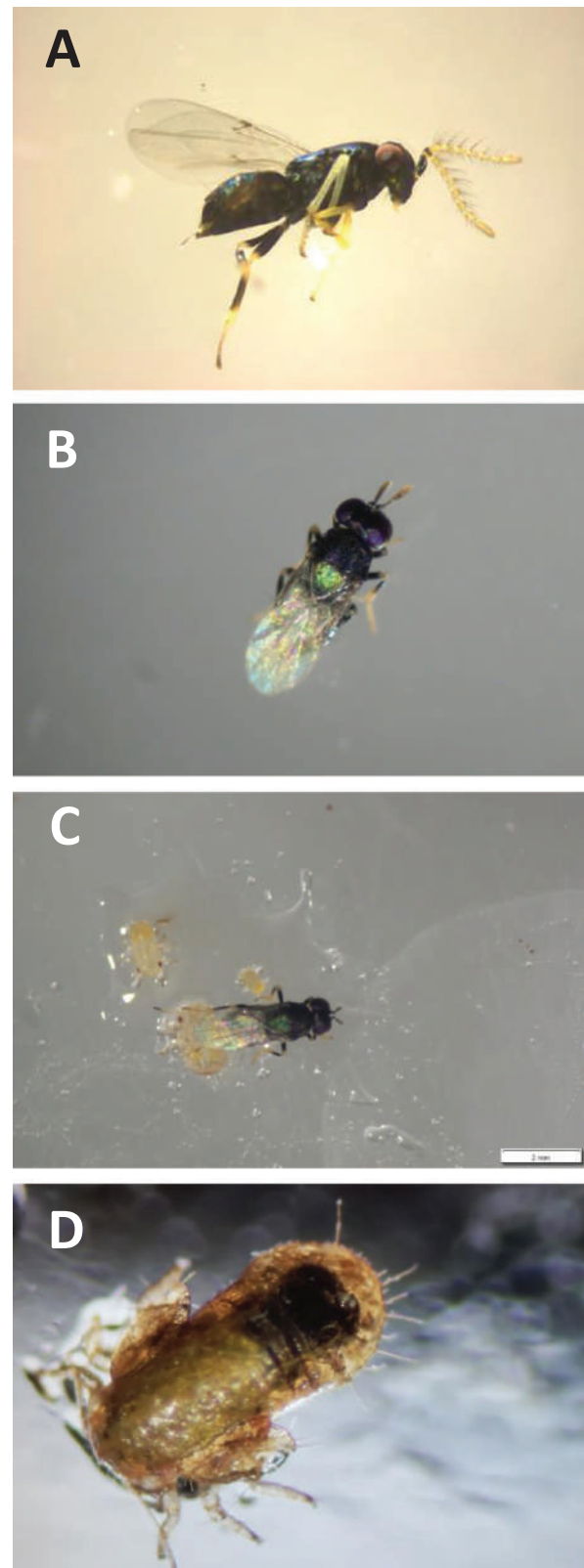


Fig. 13. Two parasitoids (Encyrtidae) of the pear psyllids. (A) *Prionomitus* sp.; (B) adult *Trechnites insidiosus*; (C) *T. insidiosus* depositing egg into nymph of *C. pyricola*; (D) developing *T. insidiosus* in "mummy" of *C. pyricola* host.

This generalized parasite of psyllids probably is naturally Holarctic (Zuparko 2015). The Old World predator *Anthocoris nemoralis* (Fabricius) was released into orchards of British Columbia and Washington in the 1960s and 1970s (McMullen 1971, Unruh et al.

1995). The predator since has been recovered from several regions between British Columbia and southern California (Hagen and Dreistadt 1990, Horton et al. 2004, Horton and Lewis 2009). The impact of the predator on North American *C. pyricola* is not known. Releases of mass-produced *A. nemoralis* in Denmark orchards led to reductions in densities of *C. pyri* by 30–40% (Sigsgaard et al. 2006).

Several approaches have been used to examine whether habitats near pear orchards are reservoirs of natural enemies. Regional lists show that predators and parasitoids of pear psyllids regularly occur on trees, shrubs, and hedgerow plants that host nonpest psyllids (Jensen 1957, Nguyen et al. 1984, Horton and Lewis 2000, Miliczky and Horton 2007). A shortcoming of these lists is that they are not proof that natural enemies disperse from these habitats into orchards at biologically relevant rates. A study with the parasitoid *P. mitratus* and the pear psyllid *C. pyri* evaluated whether presence of *P. mitratus* in pear orchards depended upon *Cacopsylla* species other than *C. pyri* (Nguyen and Delvare 1982). Overwintered wasps in spring parasitize nymphs of a univoltine hawthorn psyllid on *Crataegus* (Rosaceae) and the univoltine pear psyllid *C. pyrisuga* on pear due to the unavailability of *C. pyri* nymphs (Fig. 14). Parasitism shifts to a second univoltine hawthorn psyllid and to *C. pyri* in later generations (G1 and G2) of the parasitoid as the initial hosts disappear (Fig. 14). The univoltine hosts preceding the switch to *C. pyri* are referred to as “relay hosts” by Nguyen and Delvare (1982). Movement by predators from nonorchard habitats into orchards has been assessed indirectly by monitoring seasonal fluctuations in predator numbers in hedgerows and in nearby orchards. Scutareanu et al. (1999) analyzed predator (*Anthocoris*) and psyllid numbers in orchards and hedgerows to show that predator counts in orchards increased just when densities of immature pear psyllids began to peak, presumably due to movement by *Anthocoris* from hedgerows. Populations of *A. nemoralis* in Israel build to high densities on psyllid-infested hedges of buckthorn (*Rhamnus*) in March before arriving in *C. bidens*-infested orchards in May (Shaltiel and Coll 2004). Psyllid numbers were found to be lower on pear trees near hedges than on trees at a distance from hedges.

Conservation of natural enemies in orchards by use of less toxic insecticides began decades ago in both Europe and North America (Westigard 1973a, Burts 1981, 1983, van der Blom et al. 1985, Solomon et al. 1989, Trapman and Blommers 1992). Laboratory assays have become more and more sophisticated, to the extent that assay data are suitable for use in estimating projected rates of field increase or decrease in densities of predators (Amarasekare et al. 2016, Mills et al. 2016a). This information in turn is helping to develop integrated pest management programs that control psyllids with minimal disruption of the natural enemy community (Beers et al. 2016, Shearer et al. 2016, Amarasekare and Shearer 2017, Nottingham et al. 2022b). Comparisons of psyllid control programs across commercial orchards in both Europe and North America have shown that substituting selective insecticides and biological control for conventional insecticides leads to conservation of natural enemies and to psyllid control (DuPont and Strohm 2020, DuPont et al. 2021, Sanchez et al. 2022).

Host Plant Resistance and Breeding Programs

Pyrus resistance traits.

All commercially important cultivars of the European pear, *P. communis*, are susceptible to the European pear psyllids *C. pyri* and *C. pyricola* (Chang 1977, Bell and Stuart 1990, Dondini and Sansavini 2012), while Asian species such as *P. betulifolia* Bunge,

P. calleryana Decne., and *P. ussuriensis* Maxim. are resistant (Westigard et al. 1970, Quamme 1984, Bell 1991). In contrast, the Asian pear psyllid *C. chinensis* develops poorly on *P. communis* (Wei et al. 2020). Resistance is divided into 2 mechanisms, antixenosis and antibiosis (Painter 1951). One or both mechanisms may be present in a given resistant cultivar of *Pyrus* (Bell and Puterka 2004, Shaltiel-Harpaz et al. 2014). Antixenosis interferes with host acceptance, feeding, and egg-laying, while antibiosis causes mortality of nymphs and delays in development. Mechanisms of antixenosis may include differences in tree volatiles of susceptible and resistant cultivars (Miller et al. 1989, Yahyaa et al. 2019) and physical traits of leaves which interfere with feeding (Xu et al. 2019). Antibiosis effects likely are a product of secondary plant compounds carried in the phloem of resistant *Pyrus* (Bell 1984, Butt et al. 1988, 1989, Civolani et al. 2013). For example, Asian cultivars resistant to European pear psyllids produce flavone glycosides that are absent in the susceptible *P. communis* (Challice and Williams 1968). Higher concentrations of phenolics have been found to predict resistance of pear cultivars to *C. pyri* (Fotirić Akšić et al. 2015).

Breeding programs.

The earliest efforts to breed psyllid resistance into commercial pear cultivars began in the 1920s at government laboratories in North America where hybrids of Asian and European species were evaluated for resistance to *C. pyricola* (Nin et al. 2012). East Asian pear species are resistant to the European pear psyllids, but small fruit size and gritty or coarse texture of the fruit limits their use in breeding programs. Thus, while interspecific hybrids of *P. communis* with Asian cultivars are resistant to *C. pyricola* and *C. pyri* (Westigard et al. 1970, Harris 1973, Quamme 1984, Robert and Raimbault 2005), the hybrids do not produce marketable fruit. Developing pear cultivars with psyllid resistance using these traditional breeding methods is laborious and time consuming, partly due to the limited understanding of the genetic basis of *Pyrus* resistance. Resistance to psyllids is thought to be quantitatively inherited (Harris and Lamb 1973), yet resistance often does not transmit well from resistant hybrid lines to progeny (Lespinasse et al. 2008, Bell 2013). Resistance traits may result from the combined results of several small-effect resistance genes or from combined dominance and epistatic effects (Pasqualini et al. 2006).

The use of DNA markers in breeding programs greatly increases the efficiency of breeding compared to conventional methods. This method identifies DNA markers that are linked to genes or to Quantitative Trait Loci (QTL) of interest. The markers are then used prior to field tests to identify plants carrying the desired genes (De Franceschi and Dondini 2019). The first QTL identified for a pear psyllid was linked to nymphal antibiosis. This QTL was mapped in progeny of a European cultivar crossed with a resistant selection, and was validated in subsequent selections or progeny (Dondini et al. 2015). QTLs were also mapped to resistance traits of the Asian pear *P. bretschneideri* in crosses with susceptible *P. communis* (Montanari et al. 2013). Complete genomes are also now available for *P. communis* (Chagné et al. 2014) and *P. bretschneideri* (Wu et al. 2013). Availability of DNA markers and knowledge of *Pyrus* genomes will allow pear breeding programs to develop new pear cultivars with desirable agronomic traits and resistance. Advances in biotechnology may also allow resistance genes to be inserted into the genomes of commercial cultivars. For example, “Bartlett” pear was transformed with the antimicrobial gene D5C1, which confers resistance to fire blight. Survival of *C. pyricola* was reduced on transgenic trees (Puterka et al. 2002).

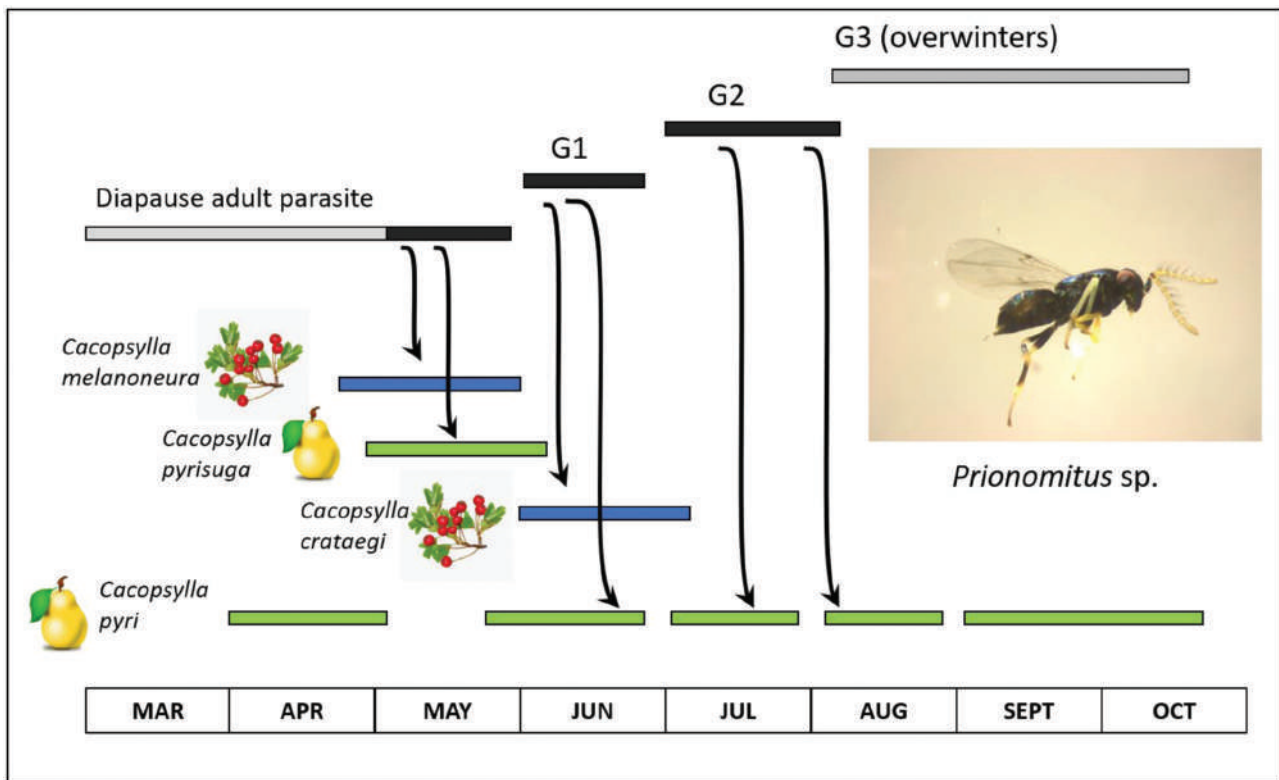


Fig. 14. "Relay" sequence of *Cacopsylla* hosts used by the parasitoid *Prionomitus mitratus* in hawthorn (*Crataegus*) and pear orchards during succeeding generations of the parasitoid (southern France); "G" indicates generation number of the parasitoid. Modified from Fig. 2 in Nguyen and Delvare (1982).

A final method for breeding pear cultivars with resistance to pear psyllids that also produces marketable fruit is with the use of resistant interstock grafted between rootstocks and fruit-bearing cultivars. This possibility was investigated in Israel as an approach to manage *C. bidens*. Resistant selections "760" and "701" were tested as interstock with the commercial cultivar ("Spadona") as the scion. These interstock grafts produce and export metabolites to the tree canopy that appear to confer resistance to *C. bidens* nymphs (Shaltiel-Harpaz et al. 2018).

Acquired resistance.

Acquired resistance in plants is activated upon initial attack by arthropod or microbial pests and confers a general defensive mechanism which protects plants from subsequent attack. Acquired resistance can be activated artificially by applying chemical defense elicitors. Foliar applications of elicitors such as harpins, chitosans, and acibenzolar-S-methyl (ASM) have been tested for control of *C. pyricola* (Cooper and Horton 2015, 2017, Orpet et al. 2021) and *C. pyri* (Civolani et al. 2022). Applications of ASM were shown to alter probing behavior of psyllid nymphs (Civolani et al. 2022) and to reduce nymphal survival and adult oviposition (Cooper and Horton, 2015, 2017). The protective effects are modest, and the compounds are unlikely to be a stand-alone tool for psyllid control. However, elicitors such as ASM are used to manage fire blight in pear orchards, and the products may secondarily lower psyllid densities.

Cultural Tactics

Other tools not yet mentioned which fit into integrated control programs for the pear psyllids include cultural practices that prevent fruit damage or that disrupt psyllid behavior. One of the earliest cultural practices to be used against the pear psyllids is management of

tree vigour (Burts 1981). This tactic remains an important part of today's control programs (Nottingham et al. 2022b). Availability of lush pear foliage encourages population growth of psyllids. Fertilizer management is used to control tree vigour, while summer pruning is used to remove excess vegetative growth (Burts 1981, Nottingham et al. 2022b). Summer pruning also opens the tree canopy and allows penetration of insecticide sprays (Nottingham et al. 2022b). Another decades-old tactic still in place today is "tree washing" to remove psyllid honeydew and prevent fruit marking (Brunner and Burts 1981, Nottingham et al. 2022b). High volumes of water sometimes combined with detergents are applied with sprayers or overhead sprinklers to remove buildup of honeydew in trees (Nottingham et al. 2022b). Finally, under-tree mulches used to assist with weed control or photosynthesis of the pear tree may also repel psyllids. A reflective plastic mulch beneath pear trees leads to lower densities of *C. pyricola* by disrupting colonization of trees by egg-laying winterforms (Nottingham and Beers 2020, Nottingham et al. 2022a).

Conclusions

Three general conclusions are prompted by this synthesis. First, while the most recent taxonomic overviews of the pear psyllids list 24 known species, much of what we know about the biology of the group is concentrated on a much smaller set of species consisting primarily of species having a west Palearctic origin. Moreover, much of the research has focused on 2 European species, *C. pyri* and *C. pyricola* – the latter now a permanent and damaging component of North American pear orchards – and 1 species (*C. bidens*) found in a region encompassing areas of the Mediterranean basin, Eastern Europe, Western Asia, and South America. Other than taxonomic study, much less is known of the remaining psyllid fauna, with the

possible exception of the East Asia *C. chinensis*. Consequently, while our synthesis is stated to encompass a global overview of the pear psyllids, many species within the collection of 24 species have seen little or no biological research and consequently have received little attention in this review.

Second, taxonomic diversity of the pear psyllids is accompanied by biological diversity. Even while developing on a single shared genus of plants, species in this assemblage diverge extensively in biological traits. Interspecific variation is seen in life cycle, host preferences, fecundity, endosymbionts, features of the acoustic mating signal, and chemical composition of pheromones. Perhaps the most striking difference among species is the seasonal cycle. Three distinct types of life cycle can be described: multivoltine species which winter in the adult stage as a seasonally distinct form; univoltine species; and multivoltine species which winter as an early instar nymph. Some of the earliest biological research to be done on any pear psyllid in fact was aimed at untangling the confusing multivoltine life cycle and seasonal dimorphism of *C. pyricola*. This study led to the realization that *C. pyricola* was a single, seasonally dimorphic species and not (as then thought) 2 separate species (Slingerland 1896). The life cycle of *C. pyricola* stands in sharp contrast to the univoltine cycle of *C. pyrisuga*, in which a single reproductive generation in spring is followed by disappearance from the pear host until the following spring. *Cacopsylla pyrisuga* may spend a full 7–8 months of the year on plant species other than the *Pyrus* host. The evolutionary pressures which have led to interspecific divergence in life cycles – or in many of the other biological traits mentioned in this review – remain to be discovered.

The final general conclusion to be produced by this review is that many of the control tools being used against the pear psyllids exist because of basic research with these pests. Control programs for the pear psyllids in some regions have become truly integrated. A good example is the program for *C. pyricola* developed by Washington State University, which combines use of monitoring, phenology models, economic thresholds, selective insecticides, cultural and horticultural tactics, and biological control to manage the pest (Nottingham et al. 2022b). Decades of biological research underpin these tactics. Studies of psyllid life cycles, seasonal phenology, and developmental thresholds helped produce degree-day based models now being used to guide timing of insecticide applications. Phenology and biological data for natural enemies are included in the same guide, thus allowing growers to manage *C. pyricola* while also conserving natural enemies. Broadly toxic chemicals have been replaced by lower-toxicity insecticides such as growth regulators or by behavior-modifying chemicals such as kaolin clay. Commercialization of these products and incorporation into the psyllid control package was possible only after extensive research. Cultural and horticultural practices to manage the pear psyllids, such as the use of tree washes to reduce marking of fruit by honeydew or management of tree vigor to slow psyllid population growth, were studied multiple decades ago but continue to be part of integrated programs in many regions.

The assemblage of *Cacopsylla* species on *Pyrus* likely has been the target of more biological research than any other group of Psylloidea with the possible exception of the citrus psyllids. This research should continue, both to address shortcomings in our knowledge of poorly studied species, but also to search for additional understanding of well-studied species leading to new biological information and possibly to new and novel management tactics. Deficiencies in research are best shown in the relatively poor understanding we have of the complex of Asian species, although new deficiencies will be added as previously unknown species of pear psyllids are discovered in poorly sampled regions of Eurasia or the

Middle East. Finally, new avenues of research with the pear psyllids may unlock new approaches for management. For example, use of synthesized acoustic cues to disrupt mating of pests is now being examined in crop systems (Mazzoni et al. 2019, Avosani et al. 2022), while research on the endosymbionts of phloem-feeding insects may one day allow us to manipulate these communities and cause death of targeted pests (Rupawate et al. 2023). This synthesis has shown that the basic research needed to eventually implement either control strategy for the pear psyllids is well underway.

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Photo Credits

Photographs in Figs. 1B, D–F, 3D–E, and 9A–B were provided by Elizabeth Beers, Washington State University. The photograph of *Cacopsylla pyrisuga* in Fig. 1C was taken by Vladimír Motyčka (<https://www.biolib.cz/en/image/id183554/>) and is used with permission. The photograph of *Anthocoris* in Fig. 12A was taken by Jack Kelly Clark, University of California. Photographs of *Trechnites* and psyllid mummy in Fig. 13B–D were taken by Rebecca Schmidt-Jeffris, USDA-ARS, and are used with permission. All other photographs were taken by authors.

Author Contributions

Stefano Civolani (Conceptualization [Lead], Data curation [Equal], Supervision [Equal], Writing – original draft [Equal], Writing – review & editing [Equal]), Victoria Soroker (Writing – original draft [Equal], Writing – review & editing [Equal]), William Cooper (Writing – original draft [Equal], Writing – review & editing [Equal]), and David Horton (Supervision [Equal], Writing – original draft [Equal], Writing – review & editing [Equal])

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