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Life cycle variation and adaptation in jumping plant lice (Insecta: Hemiptera: Psylloidea): a global synthesis

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This paper integrates the scattered information on the life histories of the jumping plant lice or psyllids, examining those aspects of their biology that contribute to successful life cycle completion. Variation in life history parameters is reviewed across the world's psyllids and the relative importance of phylogeny and environment, including host-plant growth strategy, in determining life history strategies is assessed. Elements of life cycles considered include: development rate and voltinism, response to high temperature and drought, cold-hardiness and overwintering strategy, seasonal polymorphism, diapause, metabolism, host-plant selection and range, phenological and other adaptations to host plants, disease transmission and host amelioration, dispersal, reproduction and mate finding. Life history parameters are analyzed for 342 species. While a phylogenetic signal can be identified within the data, the main drivers for life history adaptation are environmental temperatures and water availability, acting directly on the psyllids or mediated through their host plants.

Keywords: psyllid; life-history; phylogeny; temperature; water

Introduction

Jumping plant lice, or psyllids (Psylloidea), comprise a group of around 3000 species of small plant-sap-feeding insects allied to the aphids and whiteflies. They occur throughout nearly all the world's major climatic regions where suitable host plants are found. This paper attempts to integrate the wealth of scattered information on the life histories of the psyllids and to examine those aspects of their biology that contribute to successful life cycle completion. A significant proportion of this information is contained in relatively old or obscure sources, or is to be found in current literature that escapes electronic abstracting and is thus in increasing danger of remaining unrecognized. The broad variations that occur within psyllid life cycles are documented and the modifications of biology and mechanisms by which psyllids adapt to exploit a diverse range of host plants growing under varying environmental conditions are examined. An attempt is made throughout to identify common themes and patterns. Table 1 draws together, in taxonomic sequence, the basic data and reference sources that are avilable for the life histories of the world's Psylloidea species and this forms the foundation for the subsequent analyses.

The great majority of psyllid species are narrowly host-specific and are predominantly associated with perennial dicotyledenous angiosperms (Klimaszewski 1973; Hodkinson and White 1981; Hodkinson 1983a, 1986a, 1988a; Gegechkori and Loginova 1990; Hollis 2004). A few species develop on monocots

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including *Livia* spp. on *Carex* and *Juncus*, *Bactericera tremblayi* (Wagner) and *B. kratochvili* (Vondracek) on *Allium* spp. (Alliaceae), and a few species on Palmaceae. These include an undescribed species on *Bactris gasipaes* in Colombia, five Hawaiian Megatrioza on *Pritchardia*, an undescribed Australian paurocephaline species on *Livistona* and an undescribed Indian "Psylla" species on *Areca catechu* (Klimaszewski 1973; Pava et al.1983; Uchida and Beardsley 1988; Hodkinson and Bird 2000; Mondal et al. 2003; Hollis 2004). Gymnosperms are similarly poorly exploited as host plants, with just two species of *Ehrendorferiana* Burckhardt breeding on *Austrocedrus* and *Fitzroya* (Cupressaceae) in Chile and *Trioza colorata* Ferris and Klyver and *T. dacrydii* Tuthill exploiting *Dacrydium* (Podocarpaceae) in New Zealand (Tuthill 1952; Burckhardt 2005a). Conifers, however, as discussed later, play a highly significant role as overwintering shelter plants for adults from a wide range of psyllid species.

The psyllid life cycle typically comprises of an egg stage, five larval instars and a sexually reproducing adult stage, with males and females usually showing only moderate deviation from a 1:1 sex ratio at emergence. Parthenogenetic reproduction, in which only females are found in the population, is rare but probably occurs in some populations of *Cacopsylla rara* (Tuthill), *Glycaspis operta* (Moore), *Glycaspis atkinsoni* Moore and *Cacopsylla myrtilli* (Wagner) (Hodkinson 1983b; Moore 1983; Hodkinson and Bird 2006a). The latter species appears as populations of parthenogenetic females throughout most of its circumboreal range but males become common at higher altitudes above tree line (Hodkinson and Bird 2006a).

Within the equitable warm and wet conditions of lowland tropical evergreen rainforests psyllid life cycles tend to be continuous, with multiple generations per year. This probably typifies the environment under which psyllids originally radiated. This continuous multivoltine life cycle – appropriate to a climatically benign environment – has, however, subsequently undergone considerable modification. Psyllids have adapted to exploit a range of host plants that have themselves, over evolutionary time, diversified their physiognomy, physiology and phenology as they adapted to varying environmental conditions within widely different major climatic zones. Such evolution is driven by two overriding variables, temperature and precipitation, which vary in response to site latitude, altitude and continentality. Host plants have also undergone concomitant chemical evolution and adaptation during which their unique chemistry, in particular their complement of characteristic secondary compounds, has evolved. This unique chemistry is thought to form the basis for host selection and host fidelity in the psyllids.

In the only detailed study of psyllid plant coevolution, involving host-specific legume feeding psyllids on the Canary Islands, >60% of host associations resulted from phylogenetically conserved host switching among related legumes: strict cospeciation was only evident among more recent psyllid–host associations (Percy 2003a, 2003b; Percy et al. 2004). Thus, while precise evolutionary tracking of host plants may not always have occurred, related groups of psyllids tend usually to be typically associated with related host-plant taxa and individual psyllid species, with a few notable exceptions, display a high degree of host specificity (Hodkinson 1974, 1986b; van Klinken 2000). The exceptions are usually north temperate multivoltine pest species such as *Bactericera nigricornis*, *B. trigonica* Hodkinson and *B. cockerelli* feeding variously on a range of host-plant genera within the Solanaceae, Umbelliferae and Cruciferae (Pletsch 1947; Wallis 1955; Hodkinson 1981). Some

species that were initially thought to be polyphagous, such as the univoltine *Trioza rotundata* in Europe (on *Stellaria* (Caryophyllaceae), *Saxifraga* (Saxifragaceae) and *Cardamine* (Cruciferae), (Conci and Tamanini 1987, 1991)) have subsequently been shown to be complexes of species, each with a narrow host range (Burckhardt and Lauterer 2002).

Many psyllids form galls on their host plant. These may include simple irregular distortions of the leaf or shoot, through leaf pit galls or roll leaf galls to complex enclosed gall structures on leaves, shoots, flowers rootlets and stems. Detailed information on gall formation and the morphological adaptations for living in different types of galls is reviewed by Hodkinson (1984) and Burckhardt (2005b). This study avoids detailed description of gall formation and focuses, where appropriate, on the adaptive significance of galls within individual psyllid life cycles.

The paper initially considers the important constraints, adaptations and modifications of psyllid biology that have shaped their life cycles. It analyzes how these life cycle elements and adaptations have been assembled and combined to produce the wide range of life histories we observe among the world's psyllid fauna today. The relative significance of phylogeny and environment are assessed as predictors of psyllid life histories.

Important elements of psyllid life histories

Development rate and voltinism

Ambient temperature is a major determinant of egg and larval development rates in non-diapausing psyllids and, as such, governs the potential number of generations per annum (voltinism). The slowest development rate recorded is for *Strophingia ericae* on *Calluna* at high elevation, which, including two periods of winter diapause, takes 2 years to complete one generation, (Hodkinson 1973b). By contrast, multivoltine tropical/subtropical species such as *Heteropsylla cubana*, *Diaphorina citri*, *Trioza erytreae* and *Trioza magnicauda*, with free-running life cycles, may complete between 8 and 16 generations per annum (Table 1). Development rates and resultant generation times may, however, differ between seasons, depending on varying ambient temperatures as in *Phytolyma fusca* on *Milicia*, *Ctenarytaina spatulata* on *Eucalyptus* and *Diaphorina citri* on *Citrus* (Ledoux 1955; Bigornia and Obana 1974; Shahid and Khan 1976; Perez Otero et al. 2005). Many temperate species are univoltine, with a relatively short development period compressed within and synchronized with the early growing season of the host plant (Table 1). Arctic species, including many *Cacopsylla*, *Psylla* and *Bactericera* species, despite their adaptations to harsher climates, almost invariably show a similar trend to univoltinism (Table 1) (Hodkinson et al. 1979; Hodkinson and Bird in press). Among multivoltine temperate species such as *Trioza urticae* on *Urtica*, various *Cacopsylla* spp. on *Pyrus* and *Agonoscena cisti* on *Pistacia* the number of generations per annum rarely exceeds six, and is usually no more than than three to four (Onillon 1969; An et al. 1996; Lauterer 1998; Souliotis and Tsourgianni 2000). Some widely distributed species, such as *Trioza cinnamomi* on *Cinnamomum* are univoltine in the cooler parts of their range but become multivoltine elsewhere (Miyatake 1969; Rajapakse and Kulasekera 1982). *Strophingia ericae*, cited previously, becomes uni- rather than semivoltine at lower warmer altitudes (Hodkinson 1973b).

Table 1. Life history characteristics of the world Psylloidea. The psyllid classification follows White and Hodkinson (1985) updated to include recent changes. Where subfamilies comprise of a single tribe the subfamily name is given. Note: abbreviations: **climatic zone**: TrM, tropical moist; TrD, tropical dry; TrS, tropical seasonal; M, Mediterranean; TeM, temperate moist; TeD, temperate dry; B, boreal; **plant functional type of Raunkiær, based on overwintering strategy**: P, *Phanaerophyte* (tall trees and shrubs, overwintering buds above soil surface); C, *Chamaephyte* (low growing or prostrate dwarf shrubs, overwintering buds <25 cm above soil surface); H, *Hemicryptophyte* (overwintering bud at soil surface); G, *Geophyte* (overwintering bud below soil surface); He, *Helophyte* (marsh plants); T, *Therophyte* (overwintering as seed); Par, parasitic on other plants; d, deciduous; e, evergreen; s, semideciduous; **overwintering stage**: E, egg; L, larva; A, adult; **overwintering site**: ***on the host plant***: T, trunk/stem; S, shoot; L, leaf; R, roots; B, buds; ***elsewhere***: C, conifers/evergreen shrubs; LL, leaf litter; **voltinism**: M, multiple generations per year, number not fully determined, otherwise number of generations per annum stated; **feeding site**: S, shoot apex; L, expanded leaf; F, flower; St, stem; R, roots; B, buds; **gall type**: D, general distortion of leaf and/or shoot; P, pit gall on leaf; R, roll leaf gall; Ro, root gall; Lf, leaf-fold gall; F, flower gall; El, enclosed leaf gall; Es, enclosed stem gall; Eb, enclosed bud gall; lerp formation indicated by (X).

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Psyllidae												
Strophingiinae	*Strophingia ericae* (Curtis)	TeM	Pe/C	L	S		1 or 0.5	S			*Calluna*	Hodkinson (1973a, 1973b), Parkinson and Whittaker (1975), Lauterer (1976), Whittaker (1985), Miles et al. (1997, 1998), Hodkinson et al. (1999), Butterfield et al. (2001)
	S. cinereae Hodkinson	TeM/M	Pe/C	L	S		1	S			*Erica*	Rapisarda (1990a), Hodkinson et al. (1999)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Liviinae	*Livia crefeldensis* Mink	TeM	H	A	S		1	S	D		*Carex*	Ossiannilsson (1992)
	L. junci (Schrank)	TeM	H	A	S		1+	S	D		*Juncus*	Verrier (1929), Heslop-Harrison (1949b), Schmidt (1966), Gegechkori (1984)
	L. maculipennis (Fitch)	TeM	H	A		C	1?	S	D		*Juncus*	McAtee (1915), Weiss and West (1922), Heslop-Harrison (1949b)
	L. mediterranea Loginova	M/TeD	H	A		C	1	S			*Juncus*	Gegechkori (1984)
Aphalarinae												
Phytolymini	*Phytolyma fusca* Alibert	TrS	Ps	ELA	S		M	S/L	El		*Milicia*	Vosseler (1906), White (1966, 1967), Ledoux (1955)
	P. lata (Walker)	TrS	Ps	ELA	S		M	S/L	El		*Milicia*	White (1966, 1967), Cobbinah (1986)
Gyropsyllini	*Gyropsylla ilicis* (Ashmead)	TrS	Pe	A	S		1	L	R		*Ilex*	Mead (1983)
	G. spegazziniana (Lizer)	TeM	Pe	E	S		1	L	R		*Ilex*	Brèthes (1921), Leite and Zanol (2001)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Aphalarini	*Aphalara affinis* (Zetterstedt)	TeM	H	A		C	1?	L			*Stellaria*	Ossiannilsson (1992)
	A. avicularis Ossiannilsson	TeM	H	A		C/L	2+	L	P		*Polygonum*	Lauterer (1991), Ossiannilsson (1992)
	A. borealis Heslop-Harrison	TeM	H	A		C	1				*Polygonum*	Lauterer (1979), Conci et al. (1993)
	A. calthae (L.)	TeM	He	A		C	1	S/L/F			*Caltha*	Ossiannilsson (1992)
	A. crispicola Ossiannilsson	TeM	H	A		C	?	L	P		*Rumex*	Lauterer (1982)
	A. exilis (Weber and Mohr)	TeM	H	A		C/L	1	S			*Rumex*	Lauterer (1976), Gegechkori (1984), Ossiannilsson (1992)
	A. freji Burckhardt and Lauterer	TeM	H	A		C	1–2	S			*Polygonum*	Gegechkori (1984), Lauterer (1991), Ossiannilsson (1992), Conci et al. (1993) (all as *A. polygoni*), Burckhardt and Lauterer (1997)
	A. longicaudata Schaefer	TeM	H	A		C/L	1	S			*Polygonum*	Lauterer (1976)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Aphalarini	*A. maculipennis* Löw	TeM	H	A		C	1	L			*Polygonum*	Gegechkori (1984), Conci et al. (1993)
	A. nigrimaculosa Gegechkori	TeD	H	A		?	1	?			*Rumex*	Gegechkori (1984)
	A. polygoni Foerster	TeM	H	A		C	2	L			*Rumex*	Lauterer (1982), Gegechkori (1984), Ossiannilsson (1992) (all as *A. rumicicola*) Burckhardt and Lauterer (1997)
	Craspedolepta bulgarica (Klimaszewski)	TeM	H	L	R?		1	S			*Achillea*	Conci et al. (1993)
	C. campestris Lauterer and Burckhardt	TeM	H	L	S		1	S			*Senecio*	Lauterer and Burckhardt (2004)
	C. conspersa (Löw)	TeM	H	L	R?		1	S			*Artemisia*	Conci et al. (1993)
	C. crispata Lauterer and Burckhardt	TeM	H	L	S		1	S			*Senecio*	Lauterer and Burckhardt (2004)
	C. eas (McAtee)	TeD	H	L	S		1	St			*Phlox*	Wheeler (1994)
	C. flavipennis (Foerster)	TeM	H	L	S		1	S			*Leontodon*	Lauterer and Burckhardt (2004)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Aphalarini	*C. malachitica* (Dahlbom)	TeM	H	L	R?		1	S			*Artemisia*	Conci et al. (1993), Hodkinson (unpublished)
	C. nebulosa (Zetterstedt)	TeM/B	H	L	R		1	S			*Chamerion*	Lal (1934), Sampo (1975), Lauterer (1993a), Bird and Hodkinson (1999, 2005), Hodkinson and Bird (2006b)
	C. nervosa (Foerster)	TeM	H	L	R		1	L			*Achillea*	Lauterer (1991), Hodkinson (unpublished)
	C. omissa Wagner	TeM	H	L	R		1?	S			*Artemisia*	Lauterer (1991)
	C. sonchi (Foerster)	TeM	H	L	S		1?	S			*Leontodon*	Lauterer and Burckhardt (2004)
	C. schwarzi (Ashmead)	B	H	L	R?		1	S			*Chamerion*	Hodkinson and Bird (1998, unpublished)
	C subpunctata (Foerster)	TeM	H	L	R		1	R/S	Ro		*Chamerion*	Lauterer and Baudys (1968), Bird and Hodkinson (1999, 2005), Hodkinson and Bird (2006b)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Aphalarini	*C. veaziei* (Patch)	TeM/TeD	H	L	S		1	S			*Solidago*	Journet (1984), Hodkinson (unpublished)
	Rhodochlanis bicolor (Scott)	M	Th	EL	S		1	S			*Salicornia, Suaeda Salsola, Petrosimonia*	Conci et al. (1993)
	R. salsolae (Lethierry)	M	Pe	EL	S		1	S			*Suaeda*	Conci et al. (1993)
Rhinocolinae Rhinocolini	*Agonoscena cisti* (Puton)	M	Pe	A		L	5–6	L			*Pistacia*	Lauterer et al. (1998), Souliotis and Tsourgianni (2000)
	A. pistaceae Burckhardt and Lauterer	TeD	Pe	A	T		2–5	L			*Pistacia*	Tokmakoglu (1973), Mohammed and Sheet (1989) (as *targionii*), Souliotis and Tsourgianni (2000), Mehrnejad (2002), Mehrnejad and Copland (2005, 2006a, 2006b)
	A. succincta (De Geer)	M	Pe	L	L		3	L			*Ruta*	Heeger (1856), Douglas (1878), Boselli (1930), Ramirez Gomez (1960)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Rhinocolini	*A. targionii* Lichtenstein	M	Pe	A	S		M	S			*Pistacia*	Davatchi (1958), Conci et al. (1993)
	Rhinocola aceris (Foerster)	TeM	Pd	E	S		1	S			*Acer*	Löw (1880), Gegechkori (1984), Lauterer (1991), Rapisarda and Belcari (1999)
	R. fusca Burckhardt	M	Pd	EN	S		1	S			*Acer*	Conci et al. (1993)
Pachypsy-lloidini	*Acaerus calligoni* (Baeva)	TeD	Pe	L	S		1	S			*Calligonum*	Loginova (1970, 1976)
	A. deminutus (Loginova)	TeD	Pe	L	S		1	S			*Calligonum*	Loginova (1970, 1976)
	A. luridus (Loginova)	TeD	Pe	L	S		1	S			*Calligonum*	Loginova (1970, 1976)
	A. memoratus (Loginova)	TeD	Pe	L	S		1	S			*Calligonum*	Loginova (1970, 1976)
	A. tumidulus (Loginova)	TeD	Pe	L	S		1	S			*Calligonum*	Loginova (1970, 1976)
	A. turkistanika (Löw)	TeD	Pe	L	S		1	S			*Calligonum*	Loginova (1970, 1976)
	Pachypsylloides aemulus Loginova	TeD	Pe	L	S		>1	S	Es		*Calligonum*	Loginova (1970)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Pachypsy-lloidini	*P. argutus* Loginova	TeD	Pe	L	S		>1	S	Es		*Calligonum*	Loginova (1970)
	P. errator Loginova	TeD	Pe	L	S		>1	S	Es		*Calligonum*	Loginova (1970)
	P. patulus Loginova	TeD	Pe	L	S		>1	S	Es		*Calligonum*	Loginova (1970)
	P. pompatus Loginova	TeD	Pe	L	S		>1	S	Es		*Calligonum*	Loginova (1970)
	P. reverendus Loginova	TeD	Pe	L	S		>1	S	Es		*Calligonum*	Loginova (1970)
Paurocephalinae	*Camarotoscena speciosa* (Flor)	M/TeD	Pd	A		C	2?	L	R		*Populus*	Loginova and Parfentiev (1958), Gegechkori (1984), Lauterer (1993b), Conci et al. (1993)
	Paurocephala psylloptera Crawford	TrM	Pe	ELA	L		C	S/L	T		*Morus*	Hsieh and Chen (1977)
	P. russellae Mathur	TrM	Pe	L	L		7	L	P		*Kydia*	Mathur (1935, 1975)
Togepsyllinae	*Togepsylla matsumurana* Kuwayama	TeM	Pe	A		C	1	L	P		*Lindera*	Miyatake (1970)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Euphyllurinae												
Diclidophlebiini	*Diclidophlebia eastopi* Vondracek	TrM	Ps	ELA	S		C	S			*Triplochiton*	Kudler (1968), Osisanya (1974a, 1974b)
	D. harrisoni Ossisanya	TrM	Ps	ELA	S		C	S			*Triplochiton*	Osisanya (1974a, 1974b)
	D. longitarsata (Brown and Hodkinson)	TrM	Pe	ELA	S		C	S			*Miconia*	Brown and Hodkinson (1988, unpublished)
	D. lucens (Burckhardt et al.)	TrM	Pe	ELA	S		C	S			*Miconia*	Burckhardt et al. (2005)
	D. nebulosa (Brown and Hodkinson)	TrM	Pe	ELA	L		C	L			*Luehea*	Brown and Hodkinson (1988, unpublished)
	D. tuxtlaensis (Conconi)	TrM	Pe	ELA	S		C	S			*Conostegia*	Conconi (1973)
	D. xuani Messi et al.	TrM	Pe	ELA			C	L			*Ricinodendron*	Aléné et al. (2005a, 2005b)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Euphyllurini	*Euphyllura olivina* (Costa)	M	Pe	A	S		3+	S			*Olea*	Silvestri (1934), Ramirez Gomez (1958), Rapisarda (1990a), Conci et al. (1993), Del Bene et al. (1997), Arambourg and Chermiti (1986), Tzanakakis (2003, 2006)
	E. pakistanica Loginova	TrD	Pe	A	S		1+	S			*Olea*	Thakur et al. (1989)
	E. phillyreae Foerster	M	Pe	A	S		1	S			*Olea, Phillyrea, Osmanthus*	Loureiro Ferreira (1946), Ramirez Gomez (1958), Prophetou and Tzanakis (1977,1986), Stavraki (1980), Lauterer et al. (1986), Rapisarda (1991), Conci et al. (1993), Prophetou (1993,1997), Del Bene et al. (1997), Tzanakakis (2003, 2006)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Euphyllurini	*E. straminea* Loginova	M	Pe	A	S		2–3	S			*Olea*	Mustafa (1984, 1989a, 1989b), Mustafa and Najar (1985)
	Ligustrinia herculeana Loginova	TeM	Ps	A		C/L	1	S			*Ligustrum*	Konovalova (1976)
	Neophyllura arbuti (Schwarz)	TeM/M	Pe	EL	S		?	S/St		X	*Arbutus*	Ferris and Hyatt (1923)
Ctenarytainini	*Ctenarytaina eucalypti* (Ferris and Klyver)	TrS/M/TeM	Pe	ELA	S		up to 8	S			*Eucalyptus*	Fox Wilson (1924), Azevedo and Figo (1979), Bertaux et al. (1996), Malausa and Giradet (1997), Rapisarda (1998), Hodkinson (1999), Olivares (2000), Purvis et al. (2002)
	C. peregrina Hodkinson	TrS/TeM	Pe	ELA	S		M	S			*Eucalyptus*	Hodkinson (2007 and unpublished)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Ctenarytainini	*C. spatulata* Taylor	TrS/M	Pe	ELA	S		M	S			*Eucalyptus*	Mansilla et al. (2004), Costanzi et al. (2003), Perez Otero et al. (2005)
	C. thysanura (Ferris and Klyver)	TeM	Pe	ELA	S		3	S			*Boronia*	Mensah and Madden (1992a, 1992b, 1993a, 1993b, 1994)
Diaphorininae												
Diaphorinini	*Diaphorina citri* Kuwayama	TrS	Pe	ELA	S		8–16	S			*Citrus*	Hussain and Nath (1927), Atwal (1962), Mangat (1966), Catling (1970), Atwal et al. (1970), Pande (1971), Bigornia and Obana (1974), Shahid and Khan (1976), Mead (1977), Lakra et al. (1983), Tsai and Liu (2000), Liu and Tsai (2000), Nakata (2006)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Diaphorinini	*D. communis* Mathur	TrS	Pe	A		L	9	S			*Murraya*	Beeson (1941), Mathur (1975)
	D. lycii Loginova	M/TeD	Pe	ELA	S		5				*Lycium*	Boselli (1960) (as *putoni*), Rapisarda (1990a)
Psyllopseini	*Psyllopsis discrepans* (Flor)	TeM	Pd	E	S		1–2	L	R		*Fraxinus*	Lal (1934), Gegechkori (1984)
	P. distinguenda Edwards	TeM	Pd	E	S		2	L	R		*Fraxinus*	Lauterer (1982), Conci and Tamanini (1990)
	P. fraxini (L.)	TeM	Pd	E	S		1–2	L	R		*Fraxinus*	Heslop-Harrison (1942), Loginova (1954), Nguyen (1970b), Conci and Tamanini (1990)
	P. fraxinicola (Foerster)	TeM	Pd	E	S		1–2	L			*Fraxinus*	Lal (1934), Loginva (1954), Ramirez Gomez (1956), Conci and Tamanini (1990)
	P. machinosus Loginova	M/TeD	Pd	E	S		2	L	?		*Fraxinus*	Loginova (1968), Conci and Tamanini (1990)
	P. meliphila (Löw)	M/TeD	Pd	E	S		?	L			*Fraxinus*	Rapisarda (1998)
	P. narzykulovi Baeva	TeD	Pd	E	S		2	L			*Fraxinus*	Conci and Tamanini (1990)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Psyllopseini	*P. repens* Loginova	TeD	Pd	E	S		2	L	L		*Fraxinus*	Conci and Tamanini (1990)
	P. securicola Loginova	TeD	Pd	E	S		2	L	L		*Fraxinus*	Conci and Tamanini (1990)
Aphalaroidinae	*Baccharopelma baccharidis* (Burckhardt)	TrS	Pe	ELA	L		?	L	El		*Baccharis*	Espirito-Santo and Wilson Fernandez (1998, 2002)
Acizziinae	*Acizzia acaciaebaileyanae* (Froggatt)	TrD/M	Ps	ELA	S		M	S			*Acacia*	Conci et al. (1993), Rapisarda (1985,1993a), Rapisarda and Belcari (1999)
	A. melanocephala Burckhardt and Mifsud		Ps	ELA	S		M	S			*Acacia*	Palmer and Witt (2006)
	A. russellae Webb and Moran	TrD	Ps	ELA	S		M	S			*Acacia*	Hoffman et al. (1975), Webb (1977), Webb and Moran (1978)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Acizziinae	*A. uncatoides* (Ferris and Klyver)	TrD/M	Ps	ELA	S		M	S			*Acacia, Albizzia*	Heslop-Harrison (1949a) (as *Neopsyllia indica*), Munro (1965), Koehler et al. (1966), Madubunyi (1967), Madubunyi and Koehler (1974), Leeper and Beardsley (1976), Arzone and Vidano (1985), Rapisarda (1993a), Rapisarda and Belcari (1999)
Anomoneurinae	*Anomoneura mori* Schwarz	TeD	Pd	A	S		1	S			*Morus*	Chon (1964), Kuwayama (1971), Waku and Endo (1987), Arai (1991, 1993)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Ciriacreminae	*Heteropsylla cubana* Crawford	TrD	Ps	ELA	S		M (8–10)	S			*Leucaena*	Moxon (1984), Chazeau (1987), Oka and Bahgiawati (1988), Singh (1988), Yasuda and Tsurumachi (1988), Takara et al. (1990), Rauf et al. (1990), Patil et al. (1994), Austin et al. (1996), Ogol and Spence (1997), Geiger and Gutierrez (2000)
	H. spinulosa Muddiman et al.	TrS	Ps	ELA	S		<8	S			*Mimosa*	Willson and Garcia (1992)
	H. texana Crawford	TrS	Ps	ELA	S		C	S			*Prosopis*	Donnelly (2002)
Arytaininae	*Arytaina genistae* (Latreille)	TeM/M	Pe	A	S		2	S			*Cytisus*	Watmough (1968a, 1968b)
	A. africana Heslop-Harrison	M	Pe	E	S		2	S			*Adenocarpus*	Rapisarda (1988) (as *maculata*), Rapisarda (1990a), Conci et al. (1993)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Arytaininae	*Arytainilla barbagalloi* Rapisarda	M	Pe	E	S		1	S			*Genista*	Rapisarda (1989c), Conci et al. (1993)
	A. cytisi (Puton)	M	Pe	E	ST		1	S			*Genista Calicotome*	Rapisarda (1988, 1990a, 1990b), Conci et al. (1993)
	A. spartiicola (Šulc)	M	Pe	E	S		1	S			*Cytisus*	Conci and Tamanini (1985a), Conci et al. (1993)
	A. spartiophila (Foerster)	M	Pe	E	S		1	S			*Cytisus*	Heslop-Harrison (1951), Watmough (1968a, 1968b)
	Cyamophila astragalicola Gegechkori	TeD	C	A	?		1	S			*Astragalus*	Gegechkori (1984)
	C. caraganae (Loginova)	TeD	H	A	?		1	S			*Caragana*	Gegechkori (1984)
	C. caucasica (Baeva)	TeD	H	A	?		1	S			*Glycyrrhiza*	Gegechkori (1984)
	C. coluteae Baeva	TeD	C	A	?		2	S			*Colutea*	Gegechkori (1984)
	C. dicora Loginova	TeD	C	A	S		1	S			*Astragalus*	Naeem and Behdad (1988)
	C. glycyrrhizae (Becker)	TeD/M	H/C	A	?		2–3	S			*Glycyrrhiza*	Gegechkori (1984)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Arytaininae	*C. medicaginis* (Andrianova)	TeD/M	H	A	?		2	S			*Medicago*	Gegechkori (1984)
	C. megrelica (Gegechkori)	TeD	H/C	A	?		1	S			*Hedysarum*	Gegechkori (1984)
	C. prohaskai (Priesner)	TeM	H	A		C	1	S			*Anthyllis*	Conci and Tamanini (1986a, 1989b), Conci et al. (1993)
	Livilla bimaculata Hodkinson and Hollis	M	Pe	EL	S		1	S			*Genista*	Conci et al. (1993)
	L. cognata (Löw)	TeM	Pe	E/L?	S		1	S			*Chamaecytisu, Lemboptropis*	Conci et al. (1993)
	L. horvathi (Scott)	M	Pe	EL	S		1	S			*Genista*	Conci et al. (1993)
	L. magna Hodkinson and Hollis	M	Pe	L	S		2	S			*Genista*	Rapisarda (1988, 1990b), Conci et al. (1993)
	L. pyrenaea (Mink)	TeM	Pe	AE	S		1	S			*Genista*	Conci et al. (1993)
	L. retamae (Puton)	M	Pe	E/L	S		1	S			*Retama*	Rapisarda (1991, 1992), Conci et al. (1993)
	L. spectabilis (Flor)	TeM/M	Pe	A/E	S		1	S			*Spartium*	Rapisarda (1988, 1992), Conci et al. (1993)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Arytaininae	*L. variegata* (Löw)	TeM/M	Pe	E/L?	S		1	S			*Laburnum*	Conci et al. (1993)
	L. vicina (Löw)	TeM/M	Pe	A	S		1	S			*Cytisus*	Conci and Tamanini (1988), Conci et al. (1993)
	L. vittipennella (Reuter)	TeM/M	Pe	L	S		1	S			*Genista*	Conci et al. (1993)
Psyllinae	*Psylla alni* (L.)	TeM	Pd	E	S		1	S			*Alnus*	Lal (1934), Lauterer (1976), Gegechkori (1984), Ossiannilsson (1992)
	P. alpina Foerster	TeM	Pd	E	S		1	S			*Alnus*	Conci et al. (1993)
	P. betulae (L.)	TeM	Pd	E	S		1	S			*Betula*	Gegechkori and Djibladzne (1976), Gegechkori (1984), Ossiannilsson (1992)
	P. betulaenanae Ossianilsson	B	Pd	E	S		1	S			*Betula*	Ossiannilsson (1992), Hodkinson and Bird (In press)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Psyllinae	*P. borealis* (Horvath)	B	Pd	E	S		1	S			*Alnus*	Hodkinson and Bird (In press)
	P. cordata Tamanini	M	Pd	E	S		1	S			*Alnus*	Chiara et al. (1990), Conci et al. (1993), Rapisarda and Belcari (1999)
	P. floccosa Patch	TeM	Pd	E	S		1	S			*Alnus*	Patch (1909)
	P. fusca (Zetterstedt)	TeM	Pd	E	S		1	S			*Alnus*	Lauterer (1998), Ossiannilsson (1992), Conci et al. (1993)
	P. negundinis Mally	TeM	Pd	E	S		1	S			*Acer*	Mally (1894)
	P. trimaculata Crawford	TeM	Pd	E	S		1	S			*Prunus*	Osborn (1922)
	Baeopelma colorata (Löw)	M	Pd	E	S		1	S			*Ostrya*	Rapisarda (1990b), Conci et al. (1993)
	B. foersteri (Flor)	TeM	Pd	E	S		1	S			*Alnus*	Lal (1934), Lauterer (1976), Gegechkori (1984), Ossiannilsson (1992), Conci et al. (1993)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Psyllinae	*Asphagidella buxi* (L.)	TeM/M	Pe	EL	S		1	L	D		*Buxus*	Lal (1934), Wilcke (1941), Nguyen (1965,1968,1969), Sampo (1975), Malenovsky (1999)
	Spanioneura fonscolombei (Foerster)	TeM/TeD	Pe	EA?	S		1 or M?	L			*Buxus*	Ramirez Gomez (1956), Conci et al. (1993) (literature disagrees)
	S. caucasica Loginova	TeD	Pe	E	S		1	?			*Buxus*	Gegechkori and Djibladzne (1976)
	Cacopsylla sensu stricto											
	Cacopsylla mali (Schmidberger)	TeM	Pd	E	S		1	S			*Malus*	Brittain (1922a, 1922b, 1923a, 1923b), Speyer (1929), Przybylski (1970), Jonsson (1983), Gegechkori (1984), Lauterer (1999)
	C. peregrina (Foerster)	TeM	Pd	E	S		1	S			*Crataegus*	Missonnier (1956), Sutton (1983, 1984), Gegechkori (1984)
	C. sorbi (L.)	TeM	Pd	E	S		1	S			*Sorbus*	Conci et al. (1993)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Psyllinae	*C. ulmi* (Foerster)	TeM	Pd	E	S		1	S			*Ulmus*	Gegechkori (1984), Lauterer (1999), Ossiannilsson (1992), Conci et al. (1993)
	Cacopsylla (Hepatopsylla)* on *Salix											
	C. ambigua (Foerster)	TeM	Pd	E	S		1–2	S			*Salix*	Lal (1934), Lauterer (1976, 1999)
	C. brunneipennis (Edwards)	TeM/B	Pd	A		L	1	F/S			*Salix*	Gegechkori (1984), Hill and Hodkinson (1995), Lauterer (1999), Hill et al. (1998)
	C. compar (Loginova)	TeD	Pd	A		?	1	?			*Salix*	Gegechkori (1984)
	C. elegantula (Zetterstedt)	B	Pd	A		C	1	F/S			*Salix*	Ossiannilsson (1992), Lauterer (1999)
	C. fraterna (Gegechkori)	TeD	Pd	A		C	1	?			*Salix*	Gegechkori (1984)
	C. groenlandica (Šulc)	B	P/Cd	A		L	1	F/S			*Salix*	Hodkinson (1997), Hodkinson and Bird (In press)
	C. intermedia (Löw)	TeM	Pd	E	S		1	S			*Salix*	Lauterer (1999)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Psyllinae	*C. iteophila* (Löw)	TeM	Pd	A		C	1	F/S			*Salix*	Conci and Tamanini (1989a), Conci et al. (1993)
	C. macleani (Hodkinson)	B	Pd	A		L	1	F/S			*Salix*	Hodkinson et al. (1979)
	C. memor (Loginova)	TeD	Pd	A		?	1	?			*Salix*	Gegechkori (1984)
	C. moscovita (Andrianova)	TeM	Cd	A		L	1	F/S			*Salix*	Gegechkori (1984), Lauterer (1993c, 1999), Ossiannilsson (1992), Hill and Hodkinson (1996)
	C. nigrita (Zetterstedt)	B	Pd	A		C	1	F/S			*Salix*	Gegechkori (1984), Lauterer (1999), Ossiannilsson (1992)
	C. palmeni (Löw)	B	Pd/Cd	A		L	1	F/S			*Salix*	Hodkinson et al. (1979), Ossiannilsson (1992), Hill and Hodkinson (1995), Hill et al. (1998)
	C. parvipennis (Löw)	TeM	Pd/Cd	A		L	1	F/S			*Salix*	Ossiannilsson (1992)
	C. phlebophyllae (Hodkinson)	B	C	A		L	1	F/S			*Salix*	Hodkinson et al. (1979)
	C. propinqua (Schaefer)	B	Pd	A		L	1	F/S			*Salix*	Ossiannilsson (1992), Hill and Hodkinson (1995), Hill et al. (1998)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Psyllinae	*C. pulchra* (Zetterstedt)	TeM	Pd	A		C	1	F/S			*Salix*	Lauterer (1999), Ossiannilsson (1992), Conci et al. (1993)
	C. saliceti (Foerster)	TeM	Pd	A		C/L	1	F/S			*Salix*	Gegechkori (1984), Conci et al. (1993)
	C. zaecevi (Šulc)	B	Pd/Cd	A		L	1	F/S			*Salix*	Hodkinson et al. (1979), Ossiannilsson (1992)
	Other *Cacopsylla (Hepatopsylla)*											
	C. bidens (Šulc)	TeM	Pd	A	T		4–7	S			*Pyrus*	Lauterer (1979), Gegechkori (1984) (as *C. vasiljevi*)
	C. corcontum (Šulc)	TeM	Pd	A		C	1	S			*Sorbus*	Lauterer (1976, 1999), Ossiannilson (1992)
	C. hippophaes (Foerster)	TeM/TeD	Pd	E	T		1	S			*Hippophae*	Lauterer (1982, 1993a, 1999), Gegechkori (1984), Conci et al. (1993)
	C. ledi (Flor)	B	Pd	A	?		1	S			*Ledum*	Ossiannilsson (1992)
	C. notata (Flor)	M	Pd	A	T		M	S			*Pyrus*	Conci et al. (1993)
	C. myrtilli (Wagner)	B	Cd	E	S		1	S			*Vaccinium*	Lauterer (1999), Ossiannilsson (1992)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Psyllinae	*C. pyri* (L.)	TeM	Pd	A	T		2–8	S			*Pyrus*	Wille (1950), Bonnemaison and Missonnier (1955a, 1955b, 1956), Nguyen (1964, 1967a, 1967b 1970a, 1971, 1972a, 1972b, 1973, 1975), Wojnarowska et al. (1960), Nucifora (1969), Lazarev (1979), Deronzier (1981, 1984), Deronzier and Atger (1980), Atger (1982), Gegechkori (1984), Rieux and d'Arcier (1990), Lyoussoufi et al. (1988, 1992, 1994), Stratopoulou and Kapatos (1995a, 1995b), Souliotis and Broumas (1998), Kapatos and Stratopoulou (1996, 1999), Schaub et al. (2005)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Psyllinae	*C. pyricola* (Foerster)	TeM	Pd	A	T		3–5	S			*Pyrus*	Slingerland (1892), Ross (1919), Schaefer (1949), Siddiqui (1949), Wilde (1962, 1965), Wilde and Watson (1963), Wong and Masden (1967), Rasmy and MacPhee (1970), Burts (1970), Oldfield (1970), Radjabi and Behechti (1975), McMullen and Jong (1972, 1976, 1977), Fye (1983), Mustafa and Hodgson (1984), Savinelli and Tetrault (1984), Krysan (1990), Krysan and Higbee (1990), Horton et al. (1990a, 1990b), Horton, Higbee, et al. (1994), Horton et al. (1998), An et al. (1996)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Psyllinae	*C. rhododendri* (Puton)	TeM	Pd	E	S		1	S			*Rhododendron*	Conci et al. (1993)
	C. viburni (Löw)	TeM	Pd	E	S		1	S			*Viburnum*	Gegechkori and Djibladzne (1976), Gegechkori (1984), Lauterer (1999)
	C. visci (Curtis)	TeM	Par on Pd	E	S		2–3	S			*Viscum, Loranthus*	Bin (1970), Lauterer (1999), Hansen and Hodkinson (2006)
	C. zetterstedti (Thomson)	TeM/TeD	Pd	E	T		1	S			*Hippophae*	Lauterer (1982, 1993a, 1999), Ossiannilsson (1992), Conci et al. (1993)
	Cacopsylla (Thamnopsylla)											
	C. affinis (Löw)	TeM	Pd	A		C	1	S			*Crataegus*	Lauterer (1982, 1999), Sutton (1984) (as *subferruginea*)
	C. alaterni (Foerster)	M	Pe	ELA	S		up to 5	S			*Rhamnus*	Rapisarda (1989a, 1990a), Conci et al. (1993)
	C. albipes (Flor)	TeM	Pd	A		C	1	?			*Sorbus*	Gegechkori (1984), Conci et al. (1993)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Psyllinae	*C. breviantennata* (Flor)	TeM	Pd	A		?	1–2	S			*Sorbus*	Gegechkori (1984), Lauterer (1993c, 1999), Conci et al. (1993)
	C. cotoneasteris (Loginova)	TeD	Pd	A		?	1	?				Gegechkori (1984)
	C. crataegi (Schrank)	TeM	Pd	A		C	1	S			*Crataegus*	Ramirez Gomez (1956), Nguyen (1963), Gegechkori (1984), Ossiannilsson (1992), Lauterer (1999)
	C. euxina (Loginova)	M	Pd	ELA	S		M	S			*Rhamnus*	Rapisarda (1989a)
	C. fasciata (Horvath)	TeD	Pd	A		C	2	S			*Spiraea*	Gegechkori (1984)
	C. incerta (Baeva)	TeD	Pd	A		C	1	S			*Rhamnus*	Gegechkori (1984)
	C. limbata (Meyer-Dur)	TeM	Pd	A		C	1	S			*Rhamnus*	Conci and Tamanini (1982, 1988), Conci et al. (1993)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Psyllinae	*C. melanoneura* (Foerster)	TeM	Pd	A		C	1	S			*Crataegus, Malus*	Lal (1934), Domenichini (1967), Lazarev (1972), Sutton (1983), Gegechkori (1984), Lauterer (1999), Conci et al. (1993), Tedeschi et al. (2002)
	C. myrthi (Puton)	M	Pe	ELA	S		up to 5	S			*Myrthus*	Conci et al. (1993)
	C. picta (Foerster)	TeM	Pd	A		C	1	S			*Malus*	Harisanov (1966b) (as *costalis*), Lauterer (1999)
	C. pruni (Scopoli)	TeM	Pd	A		C	1	S			*Prunus*	Harisanov (1966a), Gegechkori (1984), Ossiannilsson (1992), Lauterer (1999), Conci et al. (1993), Labonne and Lichou (2004)
	C. pulchella (Löw)	M	Pd	A		C	1	S			*Cercis*	Burckhardt (1999), Conci et al. (1993), Rapisarda and Belcari (1999)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Psyllinae	*C. pyrisuga* (Foerster)	TeM/M	Pd	A		C	1	S			*Pyrus*	Brocher (1926), Wojnarowska (1962), Lazarev (1975), Lauterer (1999), Ossiannilsson (1992)
	C. rhamnicola (Foerster)	TeM	Pd	A		C	1	S			*Rhamnus*	Gegechkori (1984), Lauterer (1999), Ossiannilsson (1992)
	C. steinbergi (Loginova)	TeD	Pd	A		C	1	?			*Ribes*	Gegechkori (1984)
	Cacopsylla (Chamaepsylla)											
	C. hartigii (Flor)	TW	Pd	E	S		1	S			*Betula*	Gegechkori (1984), Ossiannilsson (1992), Hodkinson (unpublished)
	Other Miscellaneous *'Psylla'* spp.											
	Psylla diospyri Ashmead	TrS	Pd	E	S		2	L	R		*Diospyros*	Ashmead (1881)
	Psylla isitis Buckton	TrS	Pe	ELA	S		C	S			*Indigofera*	Grove and Ghosh (1914), Maxwell-Lefroy (1913), Mathur (1975)
	Psylla nr. *simlae* Crawford	TrS	Ps	ELA	S		M up to 11	S			*Bauhenia*	Mathur (1935, 1975)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Spondyliaspididae												
Euphalerinae	*Euphalerus hiuri* Miyatake	TeM	Pd	E	T		1	L	Lf		*Caesalpinia*	Miyatake (1973)
	E. nidifex Schwarz	TrS	Pe	ELA	L		M	L		X	*Piscidia*	Mead (1967), Russell (1971)
	E. ostreoides Crawford	TrS	Pe	ELA	L		M	L	El		*Lonchocarpus*	Ferreira et al. (1990)
	E. vittatus Crawford	TrS	Pe	E	S		5	S			*Cassia*	Beeson (1941), Mathur (1935)
Pachypsyllinae	*Celtisapsis japonica* (Miyatake)	TeM	Pd	E	S		2	S		X	*Celtis*	Miyatake (1968b, 1980, 1994)
	C. usabai Miyatake	TeM	Pd	E	S		1	S		X	*Celtis*	Miyatake (1980, 1994)
	Pachypsylla celtidisgemma Riley	TeM	Pd	L	B		1	B/L	B/El		*Celtis*	Riley (1890), Weiss (1921), Walton (1960)
	P. celtidisinternis Mally	TeM	Pd	A	?		1	B	B		*Celtis*	Weiss (1921), Walton (1944), Smith and Taylor (1953)
	P. celtidismamma (Fletcher)	TeM	Pd	A	T		1	L	El		*Celtis*	Riley (1890), Smith and Taylor (1953), Heard and Buchanan (1998)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Pachypsyllinae	*P. celtidisvesicula* Riley	TeM	Pd	A	T		1	L	El		*Celtis*	Riley (1890), Smith and Taylor (1953)
	P. venusta (Osten-Sacken)	TeM	Pd	L	L		1	L	El		*Celtis*	Riley (1890), Smith and Taylor (1953)
	Tetragonocephala flava Crawford	TeM	Pd	A	T		1	L		X	*Celtis*	Riemann (1958)
Spondyliaspidinae	*Boreioglycaspis melaleucae* Moore	TrS	Pe	ELA	L		C	L			*Melaleuca*	Purcell et al. (1997), Wineriter et al. (2003)
	Cardiaspina albitextura Taylor	TrS	Pe	ELA	L		2–3	L		X	*Eucalyptus*	Clark (1962, 1963a, 1963b), Clark and Dallwitz (1975), Morgan (1984), Collett (2001)
	C. densitexta Taylor	TrS	Pe	ELA	L		3	L		X	*Eucalyptus*	White (1968, 1970b, 1970c, 1973), Morgan (1984), Collett (2001)
	C. fiscella Taylor	TrS	Pe	ELA	L		5	L		X	*Eucalyptus*	Campbell (1992)
	C. maniformis Taylor	TrS	Pe	ELA	L		4	L		X	*Eucalyptus*	Campbell (1992)
	Creiis costatus Froggatt	TrS	Pe	ELA	L		2+	L		X	*Eucalyptus*	Clark and Dallwitz (1975)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Spondyliaspidinae	*Glycaspis baileyi* Moore	TrS	Pe	ELA	L		2+	L		X	*Eucalyptus*	Moore (1961)
	G. brimlecombei Moore	TrS	Pe	ELA	L		2+	L		X	*Eucalyptus*	Clark and Dallwitz (1975), Morgan (1984), Brennan, Hrusa et al. (2001), Brennan and Weinbaum (2001a, 2001b, 2001c, 2001d)
	G. fuscovena Moore	TrS	Pe	ELA	L		M	L		X	*Eucalyptus*	Morgan (1984)
	G. prepta Moore	TrS	Pe	ELA	L		M	L		X	*Eucalyptus*	Clark and Dallwitz (1975)
	Spondyliapspis occidentalis Solomon	TrS	Pe	ELA	L		M	L		X	*Eucalyptus*	Solomon (1936)
Calophyidae												
Apsyllinae	*Apsylla cistellata* (Buckton)	TrM	Pe	L	S		1	S	Es		*Mangifera*	Mathur (1935, 1946), Mani (1948), Singh M (1959), Singh S (1954, 1960), Prasad (1957), Chaterjee and Sebastian (1965), Singh and Misra (1978), Monobrullah et al. (1998)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Mastigimatinae	*Mastigimas ernstii* (Schwarz)	TrM	Pe	ELA	L		M	L	R		*Cedrela*	Pintera (1982)
	Mastigimas schwarzi (Tuthill)	TrM	Pe	ELA	L		M	L	R		*Cedrela*	Pintera (1982)
Calophyinae	*Calophya nigra* Kuwayama	TeM	Pd	A		C	1	S			*Phellodendron*	Konovalova (1963), Miyatake (1992)
	C. nigrilineata Brown and Hodkinson	TrS	Pe	ELA	L		M	L	P		*Tetragastris*	Iglesias (1983), Brown and Hodkinson (1988, unpublished)
	C. rhois (Löw)	M/TeD	Pd	E or A	S		1	L	P/R		*Cotinus*	Gegechkori (1984), Conci et al. (1996)
	C. nigripennis Riley	TeM	Pd	L	T		1	L			*Rhus*	Weiss and Nicolay (1918)
	C. schini Tuthill	TrS/M	Pe	ELA	L		M	L	P		*Schinus*	Downer et al. (1988)
	C. shinjii Sasaki	TeM	Pe	A	S		1	L			*Picrasma*	Miyatake (1992)
	C. triozomima Schwarz	TeM	Pe	L	S		2	L	D		*Rhus*	Wheeler and Rawlins (1993)
Phacopteronidae												
	Phacopteron lentiginosum (Buckton)	TrS	Pe	L	L		3	L	El		*Garuga*	Mathur (1935, 1946), Raman (1987)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Homotomidae												
Homotominae	*Homotoma ficus* (L.)	M	Pd	E	S		1	L			*Ficus*	Boselli (1929a), Ramirez Gomez (1956), Gegechkori (1984) (and as *viridis*), Rapisarda (1989b) (as *viridis*), Conci et al. (1996b), Tuncer (2002), Gencer et al. (2007)
Triozaminae	*Triozamia lamborni* (Newstead)	TrM	Pe	ELA	S		M	S			*Antiaris*	Akanbi (1980)
Carsidaridae												
Carsidarinae	*Carsidara limbata* (Enderlein)	TeM	Pd	E	L		1–2	L			*Firmiana*	Ding et al. (1987)
	Mesohomotoma tessmannii (Aulmann)	TrM	Pe	ELA	S		M	S/F			*Theobroma*	Entwistle (1972), Kaufmann (1973), Igboekwe (1983), Igboekwe and Adenuga (1983), Messi (1983a, 1983b)
	Allocarsidara malayensis (Crawford)	TrM	Pe	ELA	S		M	S			*Durio*	Gadug and Hussein (1987)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Triozidae												
Triozini	*Bactericera acutipennis* (Zetterstedt)	TeM	Hel	A		C	2	L			*Comarum*	Lauterer (1982)
	B. albiventris (Foerster)	TeM	Pd	A		C	2	L			*Salix*	Gegechkori (1984), Lauterer (1976), Ossiannilsson (1992), Conci et al. (1996)
	B. atkasookensis (Hodkinson)	B	Pd	A		L	1	L			*Salix*	Hodkinson et al. (1979)
	B brassicae (Vasil'ev)	TeM	H	A	?		1	?			*Brassica*	Gegechkori (1984)
	B. bohemica (Šulc)	TeM	H	A		C	1?	L			*Geum*	Gegechkori (1984), Ossiannilsson (1992), Conci et al. (1996)
	B. bucegica (Dobreanu and Manolache)	TeM	H	A		C	1	L			*Ranunculus*	Conci and Tamanini (1991), Conci et al. (1996)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Triozini	*B. cockerelli* (Šulc)	TeD	C	ELA	L	L/C	3+	L		P/D	Solanaceae	Compere (1916), Essig (1917), Lehrman (1930), Knowlton and Janes (1931), Knowlton (1933, 1934), Knowlton and Thomas (1934), Davis (1937), Janes and Davis (1937), List (1939a, 1939b) Swenk and Tate (1940), Pletsch (1947), Wallis (1946, 1955), Liu and Trumble (2004, 2005, 2006, 2007), Liu et al. (2006)
	B. crithmi (Löw)	M/TeM	H	ELA	L		2+	L			*Crithmum, Ferula*	Conci et al. (1996), Mifsud (1997)
	B. curvatinervis (Foerster)	TeM	Pd	A		C	1?	L			*Salix*	Gegechkori (1984), Ossiannilsson (1992), Conci et al. (1996)
	B. femoralis (Foerster)	TeM	H	A		C	1–2	L			*Alchemilla*	Bin (1972), Gegechkori (1984), Ossiannilsson (1992), Conci et al. (1996)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Triozini	*B. harrisoni* (Wagner)	TeM	H	A		C	1	L			*Geum*	Conci et al. (1996)
	B. kratochvili Vondracek	TeM	G	LA	S		2–3	S			*Allium*	Lauterer (1965), Conci and Tamanini (1991), Conci et al. (1996)
	B. modesta (Foerster)	TeM	H	A		L	1–3?	L			*Sanguisorba, Poterium*	Lauterer (1991), Conci et al. (1996)
	B. nigricornis (Foerster)	TeM	H	A		C	2	L	D		*Solanum*	Heinz and Profft (1939), Ossiannilsson (1943), Biase (1983), Gegechkori (1984), Lauterer (1991), Conci et al. (1996)
	B. perrissii Puton	TeM	H	A		L/C	1	S			*Artemisia*	Lauterer (1982)
	B. reuteri (Šulc)	TeM	H	A	?	?	2?	L			*Potentilla*	Lauterer (1963), Ossiannilsson (1992)
	B. salicivora (Reuter)	TeM	Pd	A		C	?	L			*Salix*	Gegechkori (1984), Ossiannilsson (1992), Conci et al. (1996a, 1996b)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Triozini	*B. striola* (Flor)	TeM	Pd	A		C	2?	L			*Salix*	Gegechkori (1984), Ossiannilsson (1992), Conci et al. (1996a, 1996b)
	B. tremblayi (Wagner)	M/TeM	G	A		C	7–10	S	D		*Allium*	Tremblay (1958, 1961 (as *nigricornis*), 1965a, 1965b), Annunziata and Clemente (1980), Conci et al. (1996)
	B. trigonica Hodkinson	TeM	H	A		C	2–3	L	D		*Daucus*	Biase (1983), Lauterer (1993a), Conci et al. (1996)
	Phylloplecta tripunctata (Fitch)	TeM	Pd/C	A		C	1	S	D		*Rubus*	Sirrine (1895), Smith (1911), Felt (1906), Petersen (1923), Mead (1966a), Stuart (1991)
	P. trisignata (Löw)	TeM	Pd/C	A		C	1	L			*Rubus*	Conci and Tamanini (1984b, 1986b), Conci et al. (1996)
	Egeirotrioza ceardi (Bergevin)	TrS	Pe	L	L		1	L	El		*Populus*	Mathur (1935), Beeson (1941)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Triozini	*E. bifurcata* (Mathur)	TrS	Pe	L	S		1	S	Es		*Populus*	Mathur (1935, 1975)
	E. populi (Horvath)	E	Pe	L	S		1	St	Es		*Populus*	Pedata (1998)
	Epitrioza marginata Miyatake	TeM	Pe	A	L/S	C	1	L	R		*Eleagnus*	Miyatake (1978)
	E. mizuhonica Kuwayama	TeM	Pe	A	L/S	C	1	L	R		*Eleagnus*	Miyatake (1978)
	E. yasumatsui Miyatake	TeM	Pe	A	L/S	C	1	L	R		*Eleagnus*	Miyatake (1978)
	Eryngiofaga babugani Loginova	TeD	H	A		?	1	?				Gegechkori (1984)
	E. hungarica (Klimaszewski)	TeM	H	L	S		1	S			*Bupleurum*	Lauterer (1979, 1991)
	E. lautereri Loginova	TeM	H	L	S		2	S			*Bupleurum*	Lauterer (1965, 1979, 1991)
	Trichochermes walkeri (Foerster)	TeM	Pd	E	S		1	L	R		*Rhamnus*	Sampo (1975), Lauterer (1982), Ossiannilsson (1992), McLean (1993, 1994, 1998), Conci et al. (1996)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Triozini	*Leuronota trichiliae* Brown and Hodkinson	TrS	Pe	ELA	L		M	L	P		*Trichilia*	Brown and Hodkinson (1988, unpublished)
	Neotrioza tavearesi Crawford	TrS	Pe	L	L		1	L	El		*Psidium*	Butignol and Pedrosa (2003)
	Trioza sensu lato											
	T. abdominalis Flor	TeM	H	A		C	1?	L			*Achillea*	Gegechkori (1984), Ossiannilsson (1992), Conci et al. (1996)
	T. agrophila Löw	TeM	H	A		C	?	L			*Cirsium*	Gegechkori and Djibladzne (1976), Gegechkori (1984), Lauterer (1991), Ossiannilsson (1992)
	T. alacris Flor	M	Pe	A	S		1–4	L	R		*Laurus*	Essig (1917), Weiss (1917), Lizer (1918), Weiss and Dickerson (1921), Borelli (1920), Miles (1928), Sampo (1977), Conci and Tamanini (1985b), Ramirez Gomez (1958), de Meirleire (1971), Gegechkori (1984), Conci et al. (1996)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Triozini	*T. anthrisci* Burckhardt	TeM	H	A		C	1	L			*Anthriscus, Angelica*	Ossiannilsson (1992), Conci et al. (1996) (as *pallida*)
	T. apicalis Foerster	TeM	H	A	S		1	S	D		*Daucus*	Lundblad (1929), Bey (1931) (both as *viridula*), Balachowsky and Mesnil (1936), Laska (1964,1974), Rygg (1977), Gegechkori (1984), Ramert and Nehlin (1989), Ossiannilsson (1992), Ellis and Hardman (1992), Conci et al. (1996), Kristoffersen and Anderbrandt (2007)
	T. apicula Rapisarda	M	Pd/Pe	A		C	1?	L	P?			Rapisarda (1993b)
	T. binotata Conci and Tamanini	TeM	Pd	A	S		1	L			*Hippophae*	Conci and Tamanini (1984c)
	T. camphorae Sasaki	TeM	Pe	L	L		1	L	P		*Camphora*	Sasaki (1910), Sorin (1959a)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Triozini	*T. centranthi* (Vallot)	TeM	H/T	A or (ELA)	S	C	1 to M	L	D		*Centranthus, Valerianella*	André (1878), Ossiannilsson (1992), Conci et al. (1996)
	T. cerastii (L.)	TeM	C	A		C	1	S	D		*Cerastium*	Conci et al. (1996)
	T. chenopodii Reuter	TeM	H/T	A	S		2–5	L	D		*Chenopodium, Atriplex, Halimione*	Lauterer (1982), Baloch and Ghaffar (1984), Ossiannilsson (1992), Conci et al. (1996)
	T. chrysanthemi Löw	TeM	H	A		C	1	L	P		*Chrysanthemum*	Conci and Tamanini (1991), Conci et al. (1996)
	T. cinnamomi Boselli	TeM	Pe	ELA	L		1 to M	L	El		*Cinnamomum*	Miyatake (1969), Rajapakse and Kulasekera (1982)
	T. cirsii Löw	TeM	H	A		C	1	L			*Cirsium*	Conci and Tamanini (1990)
	T. diospyri (Ashmead)	TrS	Pd	E	S		2+	L	R		*Diospyros*	Mead (1966b)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Triozini	*T. erytreae* (Del Guercio)	TrS	Ps	ELA	L		M up to 8	L			*Citrus*	Moran and Blowers (1967), Moran (1968a, 1968b), Catling and Annecke (1968), Catling (1969a, 1969b, 1970, 1971), van Vuuren and Moll (1984), van den Berg and Villiers (1987), Samways (1987), van den Berg and Deacon (1988), van den Berg (1990), van den Berg, Anderson, et al. (1991), van den Berg, Deacon and Steenekamp (1991), van den Berg, Deacon and Thomas (1991a, 1991b), Messi and Tamesse (1999), Tamesse and Messi (2004)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Triozini	*T. eugeniae* Froggatt	TrS	Pe	ELA	L		M (3–5+)	L	P		*Syzygium*	Morgan (1984), Downer et al. (1991), Mead (1994), Dahlsten et al. (1995), Young (2003)
	T. flavipennis Foerster	TeM	H	A		C	1	L	P		*Aegopodium*	Löw (1880), Conci et al. (1996)
	T. fletcheri minor Crawford	TrS	Pe	ELA	L		C	L	El		*Terminalia*	Mathur (1935), Beeson (1941), Mani (1948), Das et al. (1988)
	T. galii	TeM	H	A		C/LL	1+?	S/L	D/R		*Galium, Aperula*	Boselli (1929b), Burckhardt and Lauterer (2006)
	T. hirsuta (Crawford)	TrS	Pe	E	S		2	L	R		*Terminalia*	Mathur (1935, 1975), Beeson (1941), Mani (1948), Dhiman and Singh (2003, 2004)
	T. ilicina (De Stefani Perez)	M	Pe	L	L		1	L	P		*Quercus*	Conci and Tamanini (1985c), Rapisarda and Belcari (1999), Conci et al. (1996)
	T. jambolanae Crawford	TrS	Pe	ELA	L		6–8	L	El		*Syzygium*	Raman (1991)

Table 1. (*Continued.*)

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Triozini	*T. kiefferi* Giard	M	Pe	A	T/S		1	L	El		*Rhamnus*	Rapisarda (1989a), Conci et al. (1996)
	T. laserpitii Burckhardt and Lauterer	TeM	H	A		C	1	L			*Laserpitium*	Burckhardt and Lauterer (1982), Conci et al. (1996)
	T. machilicola Miyatake	TeM	Pe	L	L		1	L	P		*Machilus*	Miyatake (1968a)
	T. magnisetosa Loginova	TeM	Pd	A	?		2	L			*Rhamnus*	Gegechkori (1984)
	T. malloticola (Crawford)	TrS	Pe	L	L		2–3	L	El		*Mallotus*	Mathur (1935, 1975), Beeson (1941), Mani (1948)
	T. magnicauda Crawford	TrM	Pe	ELA	L		9–11	L			*Diospyros*	Chang et al. (1995)
	T. magnoliae (Ashmead)	TrS	Pe	L	L		1	L	P		*Magnolia, Persea*	Mead (1963), Leege (2006)
	T. munda Foerster	TeM	H	A		C	1?	L	P		*Knautia, Succisa, Scabiosa*	Gegechkori (1984), Ossiannilsson (1992), Conci et al. (1996)
	T. nana Gegechkori	TeM	H	A	?	?	1	L			*Valeriana*	Gegechkori (1984)

Table 1. (*Continued.*)

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Triozini	*T. neglecta* Loginova	TeM	Pd	A	?	?	2	L			*Eleagnus*	Lauterer and Janicek (1990), Lauterer (1993a)
	T. obsoleta Buckton	TrS	Pe	L	L		3	L	El		*Diospyros*	Vaishampayan and Bahadur (1980)
	T. pitiformis Mathur	TrS	Pe	L	L		4	L	P		*Mallotus*	Mathur (1935, 1975)
	T. proxima Flor	TeM	H	A		C	1	L	P		*Hieracium*	Conci et al. (1996)
	T. rapisardai Conci and Tamanini	TeM	H	A		C	1	L			*Laserpitium*	Conci and Tamanini (1984d, 1988), Conci et al. (1996)
	T. remota Foerster	TeM	Pd	A		C	1	L	P		*Quercus*	Sorin (1959b), Gegechkori (1984), Lauterer (1991), Conci et al. (1996)
	T. rhamni (Schrank)	TeM	Pd	A		C	2	L	P		*Rhamnus*	Löw (1877), Gegechkori (1984), Lauterer (1991), Conci et al. (1996)
	T. rotundata Flor (sensu Burckhardt and Lauterer)	TeM	H	A		C	1	L/St	P		*Cardamine*	Gegechkori (1984), Conci and Tamanini (1987, 1991), Conci et al. (1996), Burckhardt and Lauterer (2002)

Table 1. (*Continued.*)

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Triozini	*T. rumicis* Löw	TeM	H	A		C	1	F	F		*Rumex*	Sampo (1975), Gegechkori (1984), Conci et al. (1996)
	T. saxifragae Löw	TeM	H/G	A		C	1–2	L			*Saxifraga*	Conci and Tamanini (1986c), Lauterer (1993a), Conci et al. (1996)
	T. schrankii Flor	TeM	H	A		C	1	L			*Astrania*	Conci et al. (1996)
	T. scottii Löw	TeM	Pd/G	A		C	1	L	R		*Berberis*	Sampo (1975), Gegechkori (1984), Conci et al. (1996)
	T. senecionis (Scopoli)	TeM	H	A		C	1	L			*Senecio, Adenostyles*	Gegechkori (1984), Conci et al. (1996)
	T. soniae Rapisarda	M	Pd	A		C	1	L	P		*Quercus*	Rapisarda (1993b), Conci et al. (1996)
	T. tabebuiae Santana and Burckhardt	TrR	Pe	L	L		M	L	R		*Tabebuia*	De Queiroz Santana and Burckhardt (2001)
	T. tripteridis Burckhardt et al.	TeM	H	A		C	1	L	F		*Valeriana*	Burckhardt et al. (1991), Conci and Tamanini (1991), Conci et al. (1996)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Triozini	*T. urticae* (L.)	TeM	H	A		C	1–4	L			*Urtica*	Lal (1934), Zhangeri (1954), Onillon (1969), Davis (1973), Sampo (1975), Gegechkori (1984), Conci et al. (1996)
	T. valerianae Gegechkori	TeD	H	E	S		1	L			*Valeriana*	Gegechkori and Djibladzne (1976), Gegechkori (1984)
	T. viridula (Zetterstedt)	TeM	H	A		C	?	L			*Cirsium*	Gegechkori (1984), Ossiannilsson (1992)
	T. vitreoradiata (Maskell)	TeM	Pe	ELA	L		2–5	L			*Pittosporum*	Carter (1949)
Pauropsyllini	*Pauropsylla beesoni* Laing	TrS	Pe	L	L		2	L	El		*Litsaea*	Mathur (1935), Beeson (1941), Mani (1948)
	P. depressa Crawford	TrS	Pe	L	L		1–2	L	El		*Ficus*	Mathur (1935), Beeson (1941), Mani (1948), Abbas (1967), Negi and Bisht (1989)
	P. longispiculata Mathur	TrS	Pe	L	L		1	L	El		*Buchanania*	Thenmozhi and Kandasamy (1992)

Table 1. (*Continued.*)

Higher taxon	Species	Climate zone	Plant type	Overwintering stage	Overwintering on host	Overwintering elsewhere	Voltinism	Feeding site	Gall	Lerp former	Host plant(s)	References
Pauropsyllini	*P. purpurescens* Mathur	TrS	Pe	L	L		3	L	El		*Ficus*	Mathur (1935, 1975)
	P. trichaeta Petty	M	Pe	ELA	L		M	L	P		*Ficus*	Awadallah and Swailem (1971)
	P. udei Rübsaamen	TrS	Pe	ELA	L		M	L	El		*Ficus*	Hill (1982)

The relationship between the development rate of non-diapausing larvae and temperature is asymptotic for species such as *Agonoscena pistaciae*, *Diaphorina citri*, *Cacopsylla pyri* and *Cacopsylla pyricola* within the temperature range 5–35°C (McMullen and Jong 1977; Kapatos and Stratopoulou 1999; Liu and Tsai 2000; Nakata 2006; Mehrnejad and Copland 2006b). Development commences at the lower temperature threshold for development, rises approximately linearly to a maximum as temperature increases, but then falls back at higher temperatures, presumably in response to increasing thermal stress. By contrast, other species such as *Psyllopsis fraxini, Mesohomotoma tessmanni* and *Heteropsylla cubana* appear to show a linear response, although the maximum experimental temperatures tested (30–32°C) were lower than in the previous examples and thus probably less stressful (Nguyen 1970a; Messi 1983b; Patil et al. 1994; Geiger and Gutierrez 2000). A similar difference in response occurs between the development rate of eggs (linear) and larvae (asymptotic) of *C. pyri* over an identical temperature range, suggesting a divergence in thermal sensitivity of their respective development rate at higher temperatures (Kapatos and Stratopoulou 1999).

Temperature-specific development rates may also differ significantly among instars, although there appears to be little consistency in the trend. For example, in *Ctenarytaina thysanura* and *Trioza urticae*, at a given temperature, speed of development is highest in the early instars and progressively slows in the later instars (Onillon1969; Mensah and Madden 1993b). By contrast, development rates in other species such as *Heteropsylla cubana, Mesohomotoma tessmani, Trioza magnicauda, Trioza erytreae, Psyllopsis fraxini, Cacopsylla pyricola* and *Diaphorina citri*, appear highest in the intemediate instars (2–4) (Moran and Blowers 1967; Nguyen 1970b; An et al.1996; McMullen and Jong 1977; Messi 1983b; Patil et al. 1994; Chang et al. 1995; Geiger and Guttierez 2000; Tsai and Liu 2000; Liu and Tsai 2000).

The lower temperature threshold for larval development is comparatively low relative to ambient temperatures in tropical/subtropical species such as *Heteropsylla cubana* (9.6°C), *Trioza erytreae* (8.6–9.2°C) and *Diaphorina citri* (10.9–11.7°C) but significantly higher than in temperate species such as *Strophingia ericae* (c. 3°C), Trioza urticae (<6°C) and *Cacopsylla pyricola* (2–3°C) (Blowers and Moran 1968; Hodkinson et al. 1999; Kapatos and Stratopoulou 1999; Liu and Tsai 2000; Geiger and Gutierrez 2000).

Field development times from hatching egg to emerging adult in non-diapausing tropical/subtropical species including *Allocarsidara malayensis*, *Mesohomotoma tessmani*, *Diclidophlebia xuani*, *Heteropsylla cubana*, *Trioza erytreae* and *Trioza magnicauda* typically range between 9.5–23 days (Blowers and Moran 1968; Messi 1983b; Gadug and Hussein 1987; Patil et al. 1994; Chang et al. 1995; Tsai and Liu 2000). However, some less typical tropical species, such as *Euphalerus clitoriae* on *Clitoria* may take up to 34 days to complete development (Junior et al. 2005). By contrast, development times of equivalent warm to cool temperate species, including *Euphyllura olivina*, *Anomoneura mori*, *Asphagidella buxi*, *Cacopsylla melanoneura*, *C. pyricola* and *C. ambigua*, typically span around 22–44 days (Lal 1934; Loureiro Ferriera 1946; Kuwayama 1971). Development, however, can be significantly slower at temperatures just above the developmental threshold, extending to 190 days in *T. urticae* at 6°C, 56 days for *Psyllopsis fraxini* at 15°C and 47 days for *Cacopsylla pyricola* at 10°C (Onillon 1969; Nguyen 1970b; McMullen and Jong 1977).

Response to high temperature and drought

Psyllids in tropical/subtropical and desert ecosystems are often exposed to potentially lethal high temperatures, particularly when such temperatures are coupled with low humidity to produce a high Saturation Deficit Index (SDI). High temperatures/low humidity are known to influence strongly life cycle completion in several psyllid species, where it results in reduced fecundity, increased mortality and slower rates of development at temperatures above the optimum for the species in question. It may also limit the distribution of the psyllid within the broader range of its potential host plant.

Effect on mortality, reproduction and longevity

The link between high temperature, SDI and mortality is particularly well-documented in *Trioza erytreae* on Rutaceae, for which models have been produced to predict population densities from these climatic variables by defining particularly lethal SDI values (Moran and Blowers 1967; Catling and Annecke 1968; Catling 1969a, 1969b; van Vuuren and Moll 1984; Samways 1987; van den Berg, Anderson et al. 1991; Tamesse and Messi 2004). Similar links between high temperature and population crashes have been observed in *Heteropsylla cubana* (>36°C) and *Glycaspis baileyi* on *Eucalyptus*, notwithstanding that larvae of the latter species secrete a protective covering or lerp (Moore 1961; Yasuda and Tsurumachi 1988; Geiger and Gutierrez 2000).

The relationship between SDI and mortality at a given standard high temperature, however, is not linear. At a low SDI *Acizzia russellae* on *Acacia* died from thermal shock associated with low evaporative cooling of host leaves. Survival rose to an optimum at a moderate SDI as evaporative cooling became more effective but then declined as the SDI increased and desiccation became significant (Hoffman et al. 1975). *Trioza hirsuta* on *Terminalia* showed similar optimal survival within the range 70–90% relative humidity (Dhiman and Singh 2003).

Among temperate species such as *Cacopsylla pyricola*, egg output per female and longevity are reduced at temperatures (<35°C) that exceed the optimum of 26.7°C. Similar suppression of egg production at high summer temperature is found in *Cacopylla pyri* (Stratopoulou and Kapatos 1995b; Souliotis and Broumas 1998). Even in tropical species, such as *Diaphorina citri*, the optima for oviposition and development are 25–28°C, with larvae failing to develop at 33°C (Liu and Tsai 2000).

Gall-forming species, despite living within humidity-buffered galls, are not immune from a high SDI, with species such as *Euphalerus ostreoides* on *Lonchocarpus* suffering high mortality among young larvae before gall formation (Ferreira et al. 1990). However, some species in cool temperate environments such as *Craspedolepta nebulosa* and *C. subpunctata* appear physiologically capable of withstanding at least short-term exposure, as older larvae, to high temperature (40°C), provided high humidity is maintained (Bird and Hodkinson 1999).

Often the precise choice of oviposition site on a plant determines whether or not a psyllid egg survives a low SDI. Those of *Cacopsylla pyricola*, for example are less susceptible to desiccation when laid along the mid vein rather than on the leaf lamina (Horton 1990a). This is probably linked to differences in the relative availability of water within the leaf tissue for absorption through the basal pedicel of the psyllid egg, which is inserted into the plant tissue (White 1968; Conci 2000).

Effects on distribution

Temperature and humidity may thus affect both the absolute distribution and the relative breeding success of a psyllid species across its range. *Megatrioza* species on *Pritchardia* in the Hawaiian Islands are confined to altitudes above 425m, where temperatures are lower and humidity is higher (Uchida and Beardsley 1988). The range of *Trioza erytreae* in South Africa is limited by high temperature/SDI and even within this restricted range populations tend to increase with altitude (Catling 1969b; Green and Catling 1971; Human and Bedford 1985).

Positive impact of drought

Not all effects of low water availability and high temperature are negative for psyllids. Periods of atypically low winter rainfall, for example, produce water stress in *Eucalyptus fasciculosa* that is strongly correlated with subsequent population outbreaks of the psyllid *Cardiaspina densitexta* (White 1969, 1971). Stress in this instance leads to increased mobilization of soluble nitrogen within the leaves, which in turn enhances their suitability for larval development (White 1969, 1971). The effect is similar to that observed in *Cacopsylla pyricola* when its host plant is fertilized with nitrogen (Pfeiffer and Burts 1983, 1984; Daugherty et al. 2007).

Seasonal polymorphisms

Morphological differences

Several species of psyllid display environmentally determined seasonal polymorphisms as part of their life cycle. This has, in the past, resulted in the seasonal forms being described as distinct species. Such polymorphisms are often closely linked to diapause and have major implications for life history completion, involving key differences in performance, life history parameters and dispersal characteristics in the species concerned. These implications are discussed in detail later in the context of the factors such as day length and temperature that determine onset and breaking of diapause. Seasonal polymorphisms occur in the adults of several multivoltine species within a number of distantly related taxa, including *Agonoscena pistaceae* on *Pistacia*, *Cacopyslla pyricola*, and *C. pyri* on *Pyrus*, *Celtisaspis japonica* on *Celtis*, *Bactericera acutipennis* on *Comarum* and *Trioza chenopodii* on various Chenopodiaceae (Bonnemaison and Missonnier 1955a; Wong and Madsen 1967; Oldfield 1970; Nguyen 1972a, 1985; Miyatake 1980; Lauterer 1982; Mustafa and Hodgson 1984; Rieux and d'Arcier 1990; An et al. 1996; Mehrnejad 2002; Mehrnejad and Copland 2005). Polymorhism may simply involve marked seasonal differences in overall size (*Acizzia uncatoides* and *A. acaciaebaileyani* on *Acacia*) or colour (*Acizzia* spp. and *Bactericera perrissii* on *Artemisia*) among generations (Koehler et al. 1966; Lauterer 1982; Rapisarda 1993a). More frequently it additionally involves differences in such things as the relative size, shape and venation of the forewing, the presence or intensity of forewing colour patterns, the distribution and density of surface spinules in the forewing cells, minor differences in the shape of the terminalia, dark or light body colouration, and the relative length of the antenna and its component segments. In *Cacopsylla pyricola*, *C. pyri* and *A. pistaceae* the morphs usually consist of a smaller lighter coloured spring form with little or less-intense wing colour pattern and an autumn form that is larger and darker, with a distinctive

darker wing colouration or pattern. Morph determination is, however, not absolute and intermediate generations often display transitional characteristics between the extremes, or a few autumn forms may be produced even in summer generations (Mustafa and Hodgson 1984; Nguyen 1985; Rieux and d'Arcier 1990; Mehrnejad and Copland 2005). There is evidence for *C. pyri* that different features of the polymorphism, such as wing pattern or body colour are controlled to different extents by particular temperature and photoperiod exposures acting during the larval stages (Nguyen 1972a). In contrast to the aforementioned species, *Trioza chenopodii* unusually has its darker autumn form characterized by shorter and broader wings (Lauterer 1982). The darker wing-patterned autumn morph of *Pachypsylla japonica* additionally shows strong sexual dimorphism in wing pattern. The adaptive significance of this is obscure, but such sexual pattern dimorphism also occurs sporadically in both other temperate (*Livilla pogii* on *Genista*) and tropical (*Euphalerus fossiconis*, host unknown) species (Conci and Tamanini 1984a; Brown and Hodkinson 1988). Other species, such as *Crastina loginovae* on *Tamarix*, show similar strong sexual dimorphism in general body colouration (Conci and Tamanini 1983).

Seasonal colour change in long-lived adults

Long-lived adults of many temperate univoltine species undergo marked colour changes throughout the season. This may have adaptive significance through camouflage (Sutton 1983). Changes can occur gradually over several months and are often associated with a reproductive diapause. In genera such as *Cacopsylla* and *Psylla*, for example, the general body colouration changes gradually from pale colours such as green or yellow to deep red, brown and black. Adults of *Cacopsylla peregrina*, for instance, are bright green on emergence in spring, matching the colour of the leaves of their host plant, *Crataegus monogyna*, on which they are initially found. As the season progresses sexually maturing adults move from the leaves on to the darker stems as a prelude to oviposition and this is accompanied by a change in body colouration to a more cryptic brown and red (Sutton 1983).

Consequences of size differences

Temperature-induced size polymorphism resulting from varying developmental rates has strong implications for life history completion at the edge of psyllid species' ranges. For example, *Craspedolepta nebulosa* and *C. subpunctata* are univoltine species feeding on *Epilobium angustifolium*. Both are widely distributed in the temperate northern hemisphere. *C. nebulosa* shows developmental flexibility by reducing its body size and increasing its developmental temperature reaction norm as the day degrees available for larval development decrease along an altitudinal transect. *C. subpunctata* shows no such flexibility and is thus restricted to lower altitudes, thereby occupying a smaller portion of the host-plant range than *C. nebulosa* (Bird and Hodkinson 2005; Hodkinson and Bird 2006b). Atypically high temperature may also affect psyllid size. Both egg length and wing length of *Heteropsylla cubana* on *Leucaena* in Thailand decreased with rising temperature over the range 20–30°C and this was thought to be a partial explanation for a population crash during unseasonably hot weather (Geiger and Gutierrez 2000).

Induction of seasonal morphs

The production of different seasonal morphs is primarly controlled by day length, with temperature often playing a secondary role. For example *C. pyricola* eggs reared experimentally under short days (LD 12:12 h) produce autumn/winter-form adults; those reared under long day length (LD 16:8 or 18:6 h) produce summer forms (Mustafa and Hodgson 1984). The precise day length inducing the winter form varies, however, between studies and localities, with winter forms being produced at day lengths between 11 and 14 h in California and British Columbia respectively (Wong and Madsen 1967; Oldfield 1970; McMullen and Jong 1976). Day length acts on the early larval stages, but larvae become progressively less susceptible to a sudden switch in day length as they develop, becoming insensitive by the fourth or fifth instar (Mustafa and Hodgson 1984; An et al. 1996). The process at the relatively high experimental temperatures used appears relatively insensitive to temperature (An et al. 1996). Seasonal polymorphism in *C. pyri* and *Agonoscena pistaceae* appears to be under similar control, with short day length (LD 12:12), but coupled with low temperature (15°C) acting on instars 1–3 to produce the autumn/winter form and long day length linked to higher temperatures (25°C) resulting in spring/summer forms (Bonnemaison and Missonnier 1955a, 1955b; Nguyen 1972a; Mehmejad and Copland 2005).

Significance of diapause

For tropical multivoltine psyllids species living in non-seasonal environments, such as *Diaphorina citri* in the Philippines, the host plant *Citrus* spp. remains suitable for psyllid development throughout the year and life cycle progression is usually uninterrupted (Bigornia and Obana 1974). However, for species living in seasonal environments, close phenological synchrony of development with that of the host plant is a prerequisite for successful life cycle completion. Diapause provides the timing and synchronization mechanism through which psyllids are able to survive unfavourable periods, such as extended periods of cold or drought, when their host plant becomes unfavourable for development. Diapause, which involves a slowing down or cessation of development, may occur in one or more of the egg, larval and adult stages, depending on species and circumstances. It is usually controlled by environmental cues, such as photoperiod and temperature, which signal changes in the favourability of the external environment that will, when mediated through the host plant, affect psyllid development. The mechanisms that instigate and control adult diapause are well understood for a few economically important multivoltine psyllids such as *Cacopsylla pyricola* and *C. pyri* but remain unknown for the vast majority of species. Interestingly, diapausing adult *C. pyricola* are more insecticide tolerant than non-dipausing adults and this has implications for population contol of economically important species (Unruh and Krysan 1994).

Developmental diapause in eggs and larvae

Egg diapause occurs most frequently in univoltine species associated with deciduous trees and shrubs in which eggs laid on exposed shoots and branches one year overwinter, and hatch the following year. Examples include *Psyllopsis fraxini* on *Fraxinus*, *Cacopsylla peregrina* on *Crataegus* and *Psylla alni* on *Alnus* (Lal 1934;

Nguyen 1970b; Bonnemaison 1956). Overwintering by diapausing larvae on bare shoots is less frequent but not unknown; *Calophya triozomima*, for example, overwinters at the base of the bud of its host *Rhus* (Wheeler and Rawlins 1993). Larval winter diapause is more frequently found in free-living species that overwinter on evergreen hosts such as *Strophingia ericae* on *Calluna, Livilla magna* on *Genista* and *Asphagidella buxi* on *Buxus* (Nguyen 1968; Conci et al. 1993; Miles et al. 1998; Butterfield et al. 2001). Larvae cease development in the autumn and recommence in spring.

This period of suspended development may in some species also embrace a large part of the previous summer. Several leaf-gall forming species, for example, *Trioza camphorae* on *Camphora*, *Trioza cinnamomi* on C*innamomum*, *T. machilicola* on *Machilus*, and *T. obsoleta* on *Diospyros* hatch in spring and develop to early-stage larvae before entering diapause: development to adult only recommences the following spring (Sorin 1959a; Miyatake 1968a, 1969; Vaishampayan and Bahadur 1980). A similar extended larval diapause is found in several *Craspedolepta* species including *C. nebulosa* and *C. subpunctata* on *Epilobium*, but in these latter species there is a larval migration onto the roots or the overwintering shoots of their herbaceous perennial host (Bird and Hodkinson 1999, 2005). In these examples diapause serves to retard the production of adults and synchronize the life cycle of the psyllid with the optimum spring period for oviposition on the host. Summer larval diapause as in *Trioza saxifragae* on *Saxifraga* and species of *Acaerus* on *Calligonum* probably facilitates summer survival in particularly dry habitats (Loginova 1970, 1976; Lauterer 1993a). By contrast, diapause in *T. remota* and *T. soniae* on *Quercus* leaves and *Trioza kiefferi* on *Rhamnus*, which delay adult emergence until autumn, probably corresponds with a period when mature host leaves have become unsuitable for development. Subsequent leaf senescence in autumn then releases the soluble amino acids required for development through to overwintering adult (Conci et al. 1996).

Reproductive diapause in adults

Adult reproductive diapause, in which egg development by females is postponed, again achieves similar ends in different species. In several univoltine species of *Cacopsylla* sensu stricto, such as *C. mali* on *Malus, C. sorbi* on *Sorbus* and *C. peregrina* on *Crataegus*, and *Psylla* species such as *P. betulaenanae* on *Betula* and *P. borealis* on *Alnus*, adults emerge in late spring but egg development and oviposition on stems and branches is delayed until autumn (Brittain 1922a; Sutton 1983; Hodkinson and Bird in press). A possible advantage of postponed oviposition is that eggs are not exposed to predation or desiccation throughout the summer, although this must be offset against the probability of reduced female survival throughout this period.

Many psyllid species overwinter as adults, either on their host or on shelter plants (see later), and reproductive diapause ensures that eggs are not matured and laid until the following spring when the host becomes suitable for larval development. Thus, species that move onto shelter plants during winter undergo an extended diapause that delays sexual maturation of eggs until the flight to and the return from the winter host are completed. In multivoltine species such as *Cacopsylla pyricola*, *Cacopsylla pyri* and *Bactericera nigricornis* it is the autumn generation that

undergoes this reproductive diapause (Nguyen and Ledoux 1973; Nguyen 1975; Mustafa and Hodgson 1984; Krysan 1990; Krysan and Higbee 1990; Lyoussoufi et al. 1994; Horton et al. 1998). Many adult overwintering psyllids, including, for example, several *Cacopsylla* species on *Salix*, *Livia junci* on *Juncus*, *Aphalara* species on Polygonaceae, *Euphyllura phillyreae* Foerster on *Olea* and *Togepsylla matsumurana* on *Lindera* are, however, univoltine (Heslop-Harrison 1949b; Miyatake 1970; Lauterer 1976, 1979; Prophetou and Tzanakakis 1977 (as *olivina*); Hill and Hodkinson 1996; Tzanakakis 2003; Del Bene et al. 1997). They emerge in the previous spring or early summer, necessitating an even longer period of reproductive diapause to ensure host synchrony the subsequent year. Diapause may also play a role in survival during summer dry periods. *Diaphorina lycii* on Sardinia has up to five generations per annum, but breeding on the host *Lycium* is concentrated into the wetter spring and autumn and adults undergo reproductive diapause during the intervening summer (Rapisarda 1990a).

Control of diapause

Egg and larval diapause

Little is known about the control of diapause in psyllid eggs and larvae. Among the few species studied, the univoltine *Asphagidella buxi* on *Buxus* overwinters in southern France as a first instar larva beneath the chorion of the egg from which it has emerged in autumn. September–December represents a period of true diapause initiated by cues unknown (Nguyen 1968). This is followed by a reactivation phase that leads up to the moult to second instar in March. Prolonged exposure to temperatures between 0–10°C for 10–30 days is necessary to break diapause but once broken the development rate during the reactivation phase is positively correlated with temperature (Nguyen 1968). Developmental inhibition, acting at different stages of larval development of *Strophingia ericae* on *Calluna* at high or low altitudes, controls whether the species undergoes a one or two year life cycle. At both altitudes eggs hatch over an extended summer period. In annual lowland populations, which overwinter predominantly in instar 3, long days (LD18:6 h) retard development through instars 1–3, and development through to adult is delayed until the following spring. Instars 4 and 5 respond positively to elevated temperature and long days, from mid-winter onwards. In biennial upland populations development is slower at lower temperatures and larvae overwinter predominantly in instars 1 and 2. Development continues the following year but is inhibited by short autumn day length (LD 12:12 h) in instar 5, ensuring synchrony within the population and adult emergence in spring of the following year (Miles et al. 1998; Butterfield et al. 2001).

Adult diapause

In seasonally polymorphic multivoltine species, such as *C. pyricola*, *C. pyri* and *A. pistaciae*, the factors such as photoperiod and temperature that induce the autumn morphological forms are the ones that simultaneously initiate ovarian diapause in overwintering female adults (Wong and Madsen 1967; Oldfield 1970; McMullen and Jong 1976; Mustafa and Hodgson 1984; Mehmejad and Copland 2005). Less is known about the factors inducing ovarian diapause in spring emerging adults,

although photoperiod, temperature and possibly host-plant condition are again likely to be involved. In *Euphyllura straminea* on *Olea* a mean temperature of >20°C rather than photoperiod or host-plant quality is thought to induce summer diapause (Mustafa and Najar 1985). For overwintering adult female psyllids ovarian diapause is usually broken at some point during the winter to be followed by a period of quiescence at low temperature when ovarian development continues to be depressed but once spring temperatures rise then egg development takes place. Adult longevity during this late-winter period may, however, decline as temperatures rise (Hill and Hodkinson 1996).

For species with an extended long ovarian diapause commencing in the previous spring, such as *Euphyllura phillyreae*, then a succession of summer, winter and spring conditions are necessary to terminate diapause (Prophetou and Tzanakakis 1986; Tzanakakis 2003). A combination of increasing day length coupled with rising temperature during winter, however, is still necessary to break ovarian diapause in the univoltine *Cacopsylla moscovita* overwintering on *Salix* (Hill and Hodkinson 1996).

For multivoltine species such as *C. pyricola* and *C. pyri* the effectiveness of long photoperiod in breaking female diapause diminishes as the winter progresses and the importance of rising temperature increases (Nguyen 1964, 1967a, 1967b, 1968, 1975; Fields and Zwick 1975; McMullen and Jong 1976; Horton et al. 1998). However, in the latter species exposure to temperatures above 25°C breaks diapause irrespective of photoperiod. The temperature required to terminate ovarian diapause generally differs both within and among species and habitats, depending on the characteristic temperatures that the species normally experience and the relative length of the winter period.

By contrast with the reproductively suppressed females, newly emerged males of the autumn diapausing form of *C. pyricola* have active sperm in the testes and seminal vesicles, but rates of insemination are depressed at short photoperiod (LD 10:14). Initially, an exposure for 10 days at long photoperiod (LD 16:8) is required to release sexual activity but the exposure time required decreases as the winter progresses (Krysan 1990; Krysan and Higbee 1990). Repeated mating and insemination of females on the overwintering host is evidenced by the presence of multiple spermatophores (mean 5.3 to 16.5 per female), with each spematophore representing one copulation (Burts and Fischer 1967; Krysan 1990; Krysan and Higbee 1990). Psyllids collected from conifers on warm days during late winter show similar promiscuous tendencies suggesting that, for psyllids, the overwintering period is far from being a quiescent and relatively unimportant phase of the life cycle. Mating, however, does not always lead to insemination (Van den Berg, Deacon and Thomas 1991a).

Mating, before or immediately after adult diapauses, usually ensures that egg development and maturation are completed ahead of the host plant becoming suitable for oviposition, provided the temperature is sufficiently high. This applies to both summer diapausing species such as *Euphyllura straminea* and winter diapausing species such as *Cacopsylla moscovita*, *Cacopsylla pyricola* and *Euphyllura phillyreae* (Prophetou and Tzanakakis 1977, 1986; Mustafa and Najar 1985; Lyoussoufi et al. 1994; Hill and Hodkinson 1996; Horton et al. 1998). Mature eggs of *C. moscovita* first developed in the field, for example, 6 weeks before the *Salix* catkins on which they were to be laid (Hill and Hodkinson 1996).

The larger size of overwintering morphs of multivoltine psyllid species has implications for both reproductive performance and dispersal ability of individuals. There are often major differences in the main parameters of reproduction between summer and post-diapause winter morphs of the same species, including the length of the pre-reproductive and oviposition periods, the mean number of eggs produced per female and adult longevity. For example, optimum mean fecundity in *Agonoscena pistaceae* varied between 893 and 1087 eggs per female in summer and winter morphs respectively (Mehmejad and Copland 2005). The difference is even more marked in pear psyllids with corresponding figures for *C. pyricola* of 212 (summer) and 486 (winter) in Canada and 387 and 486 in South Korea (McMullen and Jong 1977; Butt and Stuart 1986; An et al. 1996). *C. pyri* exhibits similar variation (342 and 471) (Nguyen 1970a; Kapatos and Stratopoulou 1996).

The optimum temperature for maximum fecundity may also shift between generations to match the prevailing ambient temperature. In laboratory experiments, egg output per female of *C. pyricola* was optimal at 15.6°C in the winter form but maximal at between 21.1 and 26.7°C in the summer form (McMullen and Jong 1977). The pre-reproductive period is generally shortest in summer forms, but longevity is greatest in winter forms. The net result of these variations is that egg output tends to be maximized at the start of the host-plant growing season. There may also be behavioural differences between the morphs, with summer forms showing a strong ovipositional preference for leaves but winter forms preferring dormant bud-bearing stems (Butt and Stuart 1986).

Development of cold-hardiness

Overwintering psyllids in temperate, montane and boreal habitats are frequently exposed, often over long periods, to sub-zero temperatures that may potentially damage or ultimately freeze the body tissues. Freeze tolerance is unknown among psyllids and survival depends on the ability of individual species, whether in the egg, larval or adult stage, to resist freezing by lowering the supercooling point (SCP) of their body tissues. Adult and larval stages may mitigate the effects of low air temperature to some extent by seeking out overwintering sites beneath a protective snow blanket or, in the case of adults, on evergreen trees such as conifers (Bird and Hodkinson 1999).

Eggs

Overwintering eggs, however, are often exposed on tree branches to the full rigour of winter. Those of *Cacopsylla mali* in Norway, for example, display a mean SCP that varies between −28.0°C and −38.8°C, depending on whether or not eggs have been acclimated at sub-zero (−5°C) temperature (Skanland and Sömme 1981). This allows eggs to avoid freezing, even at the very low winter temperatures recorded. The lowered SCP is achieved partly by the synthesis of cryoprotectants such as glycerol within the egg, with highest concentrations found in midwinter (Skanland and Sömme 1981).

Larvae

Recorded mean SCPs for overwintering instars include *Strophingia ericae* (range=−21.6 to −27.3°C), *S. cinereae* (−23.6 to −23.7°C), *Craspedolepta nebulosa*

(−21.6 to −23.5°C) and *C. subpunctata* (−21.8 to −23.5°C) (Cannon 1983; Bird and Hodkinson 1999; Hodkinson et al. 1999). SCP was slightly lower in upland populations of *S. ericae* than lowland populations, although there was no difference between the mean SCP of the *S. ericae* and *S. cinereae* where they occurred together at the same site, despite the latter species being more typically Mediterranean than its congener. Similarly there was little variation in SCP of populations of *C. nebulosa* in lowland UK and Tromsø, northern Norway. SCPs of all species studied to date, despite their varying evolutionary and geographical origins, fall within a narrow range, suggesting that larvae may posses attributes that predispose them to surviving cold. Sap feeding, in particular, ensures that ice-nucleating food particles are absent from the gut. There is, however, evidence for all the aforementioned species and for *Asphagidella buxi* that the SCP should only be taken to indicate the lower limit of cold-hardiness (Nguyen 1969; Bird and Hodkinson 1999; Hodkinson et al. 1999). In both long and short time survival experiments at sub-zero temperatures, mortality accrues above the SCP as temperatures fall: mortality is related to the period of exposure as well as to temperature *per se*. Furthermore, prior acclimation at high sub-zero temperatures (−5 or −10°C) enhances survival of fifth-instar *A. buxi* larvae at −15°C compared with controls at −15°C. Survival at low temperatures in species such as *A. buxi* may differ among overwintering instars, with later instars performing better. However, in the aformentioned *Strophingia* and *Craspedolepta* species, such differences were not apparent (Bird and Hodkinson 1999).

Adults

Overwintering adults of *A. buxi* and *Cacopsylla melanoneura* are significantly less cold-hardy than eggs or larvae, as previously discussed. The SCP of *C. melanoneura*, for example, varied between −6.8 and −14.7°C when acclimated at up to 11 days at 6°C compared with −11.1 to −15°C when acclimated at −7°C (Nguyen 1969, Jackson et al. 1990). SCP values for adults of the overwintering form of *Cacopsylla pyricola* (−18 to −22°C), however, were comparable with larval values cited earlier and *Trioza apicalis* adults show high survival (71–87%) when exposed to −18°C for 7 days (Rygg 1977; Horton et al. 1996; Lee et al. 1999). Freeze susceptibility, however, was markedly increased (SCP changed from −15°C to −2–15°C) when *C. pyricola* was placed in contact with surface moisture or bacteria such as *Pseudomonas syringi*, which act as ice-nucleating agents (Horton et al.1996; Lee et al. 1999).

One of the mechanisms by which freeze susceptibility can be lessened is for overwintering psyllids to reduce freezable body water content before the onset of winter, as occurs in adult *C. melanoneura* and *Euphyllura straminea* (Mustafa 1989b; Jackson et al. 1990). Psyllids that become active during winter and begin fluid feeding during temporary warm spells thus run the risk of lowering their resistance to cold. Even in non-feeding adults, metabolic production of water from stored fat reserves may again potentially increase cold susceptibility (Jackson et al. 1990; Hill and Hodkinson 1996).

Psyllids have thus evolved a variety of mechanisms to prevent winter mortality in cold environments that appear largely independent of phylogeny.

Metabolic adaptations

In passing through their life cycles, psyllids incur the metabolic cost of respiration: energy expended in maintaining body tissue becomes unavailable for growth, development and reproduction. It is thus advantageous to minimize basal metabolism during periods of seasonal inactivity or growth cessation, especially when this is linked to diapause. Metabolic energy expenditure for individual species, measured as oxygen uptake, is influenced significantly by ambient temperature, body size and sex (Krawczyk and Migula 1979; Migula et al. 1980).

Adult male psyllids generally tend to be smaller and more active than females and, within any given species, have a higher metabolic rate per unit body weight. Similarly across adults of species representing the larger psyllid families Psyllidae and Triozidae there is a negative relationship between log respiration and log body mass, indicating that smaller species tend to respire less "efficiently" than larger species.

There are, however outliers to this general pattern: *Rhinocola aceris* and *Livia junci* (Psyllidae) have much lower rates of metabolism than might be predicted from their body size, possibly indicating their more sedentary nature (Migula et al. 1980). When measured over the range 15–25°C an array of species belonging to *Aphalara*, *Craspedolepta*, *Rhinocola*, *Livia*, *Psyllopsis*, *Arytaina*, *Psylla*, *Cacopsylla*, *Trioza*, *Trichochermes* and *Bactericera*, genera with differing degrees of phylogenetic relatedness and contrasting life history patterns, all showed significantly increasing respiration with temperature. The rate of increase, however, varied significantly among species, resulting in considerable differences in metabolism among species at a given ambient temperature.

While the species sample size is small, and the temperature range examined rather high, there is clear evidence for differences in metabolic rate among individual species with different life history adaptations (Migula et al. 1980). For example, widely distributed multivoltine species such as *Bactericera nigricornis*, *Trioza urticae* and *Cacopsylla pyri* tend to have higher metabolic rates than their univoltine congeners (Migula et al. 1980). Similarly, *Aphalara* species tend to have higher metabolism than the related *Craspedolepta*, which may reflect differences in their speed of development following overwintering as adults and larvae respectively. Among several species overwintering on conifers, such as *Aphalara exilis* and *Bactericera nigricornis*, metabolism is higher by between 20–38% during spring reproductive activity than in autumn before overwintering (Migula et al. 1980).

Phenological synchrony with host-plant growth and host quality

Under both temperate and tropical conditions a high degree of phenological synchrony between psyllid and host-plant growth is required for successful life cycle completion. Among temperate psyllids that overwinter as eggs, such as many *Cacopsylla*, *Psylla* and *Psyllopsis* species, egg hatch is generally timed to coincide with bud burst, although the precise mechanisms maintaining this synchrony are poorly understood (Nguyen 1970b; Lal 1934). In *Cacopsylla mali* and *C. peregrina*, for example, on *Malus* and *Crataegus* respectively, larvae hatch within a few days of the first buds breaking and move on to the newly developing plant tissues, especially the flower clusters (Przybylski 1970; Jonsson 1983; Sutton 1984; Lal 1934). This synchrony is generally strictly maintained among different sites and years

(Przybylski 1970). The importance of such close synchrony for the psyllids is emphasized in *Crataegus* by the rapid decline in the quality of their food resource, with soluble nitrogen concentrations of shoots and leaf clusters falling from around 0.5 mg N dry weight^{-1} at bud burst to less than 0.1 mg N dry weight^{-1} 1 month later (Sutton 1984). Timing of egg hatch in *Homotoma ficus* on *Ficus* appears to determine subsequent larval abundance (Gençer et al. 2007). *Cacopsylla ambigua* on *Salix*, in contrast to the aformentioned species, is unusual in that eggs hatch well ahead of bud burst and the larvae remain quiescent beneath the bud scales (Lauterer 1999).

Non-gall-forming univoltine psyllids that overwinter as adults and which already contain fully developed eggs by early spring, such as *Cacopsylla moscovita* mentioned earlier, have the advantage of ovipositing directly onto newly emerging foliage as soon as it appears. This is a more precise procedure with less natural wastage than one involving small newly emerged larvae seeking out actively growing tissues. Eggs laid, however, may then take further time to hatch. *Cacopsylla affinis* and *C. melanoneura* larvae, for example, emerge 7–14 days after *C. peregrina* on the same host (Sutton 1984). This direct spring oviposition strategy is employed by a diversity of species including *Gyropsylla ilicis* on *Ilex*, several *Aphalara* species on Polygonaceae and is probably best exemplified by *Cacopsylla* species feeding on willow (*Salix*) (Mead 1983; Hodkinson et al. 1979; Hill and Hodkinson 1995; Hill et al. 1998; Hodkinson 1997).

Many of these latter species develop on female *Salix* catkins and life cycle completion within a narrow phenological window is vital. Willow catkins are of short persistence, developing early in the year before drying out and dehiscing once the seed has developed. Catkin ''life'' for six species of willow in northern Alaska varied between 37–43 days, depending on species. The associated psyllids, *Cacopsylla palmeni* and *C. phlebophylla* developed from egg to adult within 36–41 days, an exceedingly tight phenological schedule (Hodkinson et al. 1979). Development rates of psyllid and host are, nevertheless, independently temperature-dependent. Later studies of *C. palmeni, C. propinqua* and *C. brunneipennis* along altitudinal transects in Norway showed that life cycle completion was determined by the available thermal budget and its differential effect on psyllid and host development rates (Hill et al. 1995). Each psyllid had a wide distribution along the transect but failed to complete its life cycle at a characteristic upper altitudinal limit because host growth became too slow to support development or the psyllid developed too slowly to exploit the phenological window available. The upper limit for *C. palmeni* was, however, significantly higher than that for C. *brunnepennis* (Hill et al. 1995). Soluble nitrogen concentrations within catkins declined slightly with increasing altitude but the decline over time during catkin development at a given altitude was far steeper, implying a rapidly narrowing time window for psyllid development as catkins aged (Hill et al. 1998; Hodkinson et al. 2001).

MacLean (1983) extended these ideas to propose a simple temperature-driven phenological model of psyllid and host-plant development on a wider geographical scale. The latitudinal distribution of nearly all Alaskan psyllid species is more restricted than that of their host plants (MacLean and Hodkinson 1980). The model demonstrates how a psyllid's northern limit might be set by the failure of its host plant to develop and grow sufficiently quickly to support life cycle completion within one season. The southern limit, by contrast is determined by the plant developing too quickly to permit psyllid development through to maturity. Furthermore, psyllids

may, because of phenological contstraints, exploit different host plants in separate parts of their range or even exploit different tissues on the same host species. The Greenland willow psyllid *Cacopsylla groenlandica*, in the relatively benign climate of southern Greenland, reproduces on four different *Salix* species, developing on both catkins and growing shoot tips (Hodkinson 1997). Further northwards the thermal budget available for development decreases and the psyllid life cycle can be completed only on the catkins of one species, *Salix glauca*, despite other species often being present.

Among temperate species that overwinter as larvae on evergreen plants, such as *Strophingia ericae* on *Calluna* and *Asphagidella buxi* on *Buxus*, phenological synchrony is probably less important: once diapause is broken: the psyllids simply recommence development as the host plant resumes growth in the spring (Hodkinson 1973b; Nguyen 1968). Consequently, by contrast with the aforementioned *Salix*-feeding species, *S. ericae* is less dependent on precise host synchrony and occupies the full altitudinal range of *Calluna* (Hodkinson et al. 1999).

Several psyllids, particularly *Craspedolepta* species, feed and overwinter as larvae on perennial herbaceous plant species that die back each year and pass the winter with the perennating buds usually present as small rosettes at the soil surface (Hemicryptophytes) or on tubers (Geophytes). These plants, frequently associated with xerophytic conditions, often grow rapidly and flower early in the year, presenting a time-limited opportunity for psyllid exploitation. Overwintering sites of the associated psyllid larvae are usually at or below the soil surface on the rosette buds (*Craspedolepta nervosa*), on fine roots (*C. nebulosa* and *C. subpunctata*) or at the base of old woody stems (*C. eas*) (Wheeler 1994; Bird and Hodkinson 2005). In spring late instar larvae migrate to the rapidly growing shoot and quickly complete development. Larvae of the next generation then migrate back down to the overwintering site before entering a long larval diapause, usually before mid-summer. Close phenological synchrony is thus maintained and long exposure to dry summer conditions avoided.

Many species of psyllid in tropical and subtropical regions do not undergo an extended diapause and reproduction is continuous. However, many of their host species do not produce new shoots and leaves continuously but put out flushes of new growth in response to variations in ambient temperature and moisture availability. Flushing cycles may be irregular and non-synchronous within species and may vary over short geographical distances. Even within individual host plants there may be marked differences in leaf quality between sun and shade leaves. *Diclidophlebia xuani* on *Ricinodendron*, for example, tends to attain higher population density on unshaded leaf shoots whereas psyllid galls on *Persea* tend to be more numerous on shade leaves (Aléné et al. 2006; Leege 2006). This again presents synchrony problems in psyllids that need to seek out suitable tissues on flushing trees on which to complete their life cycle.

The relationship between the flushing cycle of tree and shrub species and the breeding success of their associated psyllid species has been widely documented. Good examples include *Diclidophlebia harrisoni* on *Triplochiton*, two *Phytolyma* species on Milicia, *Diaphorina citri* and *Trioza erytreae* on *Citrus*, *D. lycii* on *Lycium*, *Acizzia uncatoides* on *Albizzia*, several *Cardiaspina* and *Glycaspis* species on *Eucalyptus*, *Mesohomotoma tessmanni* on *Theobroma*, *Protyora* and *Diclidophlebia* species on *Argyrodendron*, and *Heteropsylla cubana* on *Leucaena* (Moore 1961; Clark

1962; White 1967; Catling 1969a; Entwistle 1972; Osisanya 1974a, 1974b; Bigornia and Obana 1974; Clark and Dallwitz 1975; Leeper and Beardsley 1976; Lakra et al. 1983; Cobbinah 1986; van den Berg and Villiers 1987; Rapisarda 1990a; Basset 1991). Similar examples have also been observed in milder temperate regions including *Ctenarytaina eucalypti* on planted *Eucalyptus* in Europe and *Trioza vitreoradiata* on *Pittosporum* in New Zealand (Carter 1949; Purvis et al. 2002).

In both the aforementioned set of species and those non-tropical multivoltine species with a winter diapause and several summer generations, such as *Cacopsylla pyricola*, successful host-plant usage depends on females correctly discerning the physiological state and condition of the host-plant tissue at the time of oviposition (White 1970a; Nguyen 1972b; Moran and Buchan 1975; Butt and Stuart 1986; Stuart et al. 1989; Horton 1990a, b; Horton and Krysan 1990, 1991; van den Berg, Anderson, et al. 1991; Mensah and Madden 1992a; Puterka et al. 1993; Luft and Paine 1997). Selection must favour young growing tissues rather than older mature leaves and shoots. For certain pest species, such as *Cacopsylla pyricola* on *Pyrus*, for which detailed information is available on the temperature dependence of diapause termination, pre-reproductive period, oviposition period and development rates, phenological models can be used to predict psyllid population growth characteristic and densities for the following summer period (Schaub et al. 2005). This can help determine when subsequent population control measures should be applied.

Many species of psyllid persist within enclosed or roll-leaf galls on the mature leaves of their host throughout much of the year. Even in these species, however, the timing of oviposition and subsequent gall initiation, to correspond with the flushing cycle of new growth, is important (Raman 1994, 2003). Gall induction usually involves the active modification of growth in young rapidly growing plant tissue and plants are thus most susceptible to galling at time of flushing (Kumar et al. 1981). Subsequent growth of plant tissue through to maturity would normally correspond with a period of declining quality for psyllid feeding that is overcome by the metabolic changes induced within the leaf as a result of psyllid feeding that allow continued development within the gall.

The close correspondence between new tissue growth and gall initiation, and increasing gall mortality on maturing leaves, has been observed in many psyllids representing several different families, including *Pachypsylla* species on *Celtis*, *Phacopteron lentiginosum* on *Garuga*, *Schedotrioza* and *Glycaspis* species on *Eucalyptus*, *Trioza simplifica* on *Terminalia*, *Trioza gigantea* on *Vaccinium*, *Calophya* spp and *Tainarys sordida* on *Schinus* and *Baccharopelma baccaridis* on *Baccaris* (Smith and Taylor 1953; Walton 1960; Kandasamy 1980; Kandasamy and Krishnan 1981; Taylor 1987; Espirito-Santo and Wilson Fernandez 1998, 2002; Saiz and Nunez 2000). In many of these species adult emergence from the gall is timed to correspond with a predictable seasonal flush of new growth and often involves a larval or adult diapause designed to maintain host-plant synchrony.

A similar situation pertains in several leaf pit-gall forming species of *Trioza* including *T. camphorae*, *T. cinnamomi*, *T. machilicola*, *T. obsoleta* and *T. ilicina* in which oviposition occurs on new flush spring growth and larval diapause corresponds with summer/winter leaf maturity (Sorin 1959a; Miyatake 1968a,1969; Vaishampayan and Bahadur 1980; Rapisarda and Belcari 1999). Synchrony and survival may be further enhanced in species such as *Pachypsylla venusta* on *Celtis* and *Trioza tabebuiae* on *Tabebuia* in which the presence of galls prevents galled

leaves being shed during normal autumn abscission and thus remaining on the host tree (Smith and Taylor 1953; De Queiroz Santana and Burckhardt 2001). However, contrary to this trend, *Celtis laevigata* displays early abscission of leaves with *Pachypsylla* galls and this may serve as a plant defence mechanism (Stromgren and Lanciani 2001). Even in tropical tree species, including *Milicia excelsa*, staggered loss of leaves by adult trees allows small populations of associated psyllids (e.g. *Phytolyma fusca*) to survive as galls through the dry season when the majority of trees are leafless (White 1967).

Development on different hosts

The relative success of a psyllid species in completing its life history may vary significantly among different potential host species or even among different provenances within the same host species. Breeding success is determined by the initial attractiveness of a particular host, the extent to which oviposition occurs and the survival of these eggs through to adult emergence.

In large-scale host-plant trials psyllids are often found to oviposit on a much wider range of plant species than those on which they can successfully complete development (Baloch and Ghaffar 1984). *Prosopidopsylla flava*, for example, oviposited on 57 of 58 host species (Leguminosae and Rosaceae) tested but developed successfully on just four species of *Prosopis* (Leguminosae) (van Klinken 2000). Similarly, *Boreioglycaspis melaleucae* laid eggs on 27 out of 43 species of Myrtaceae but developed successfully on just two or three species of *Melaleuca* (Purcell et al. 1997; Wineriter et al. 2003).

Different species of plant within a given host range often vary in their susceptibility to the associated psyllid species, ranging across a spectrum from highly susceptible to near resistant. Examples include *Glycaspis brimblecombei* on *Eucalyptus* spp, *Ctenarytaina thysanura* on *Boronia* spp *Cacopsylla pyricola* on *Pyrus* and *Heteropsylla cubana* on *Leucaena* spp (Williams et al. 1963; Westigard et al. 1970; Mensah and Madden 1991; Brennan, Hrusa, et al. 2001; Mullen and Shelton 2003; Pasqualini et al. 2006; Center et al. 2007).

Similar variation in susceptibility also occurs across provenances, cultivars and varieties *within* single species of host plant, as in *Phytolyma lata* on *Milicia excelsa*, *Acizzia melanocephala* on *Acacia nilotica*, *Cacopsylla pyricola* and *C. pyri* on *Pyrus communis, Heteropsylla cubana* on *Leucaena leucocephala* and *Bactericera cockerelli* on *Lycopersicon* (Harris 1973; Chang and Philogene 1976; Butt et al. 1989; Cobbinah and Wagner 1995; Berrada et al. 1995; Baldassari et al. 1996; Puterka 1997; Mullen and Shelton 2003; Finlay-Doney and Walter 2005; Liu and Trumble 2006; Pasqualini et al. 2006; Palmer and Witt 2006). Such variation forms the basis for selective breeding for host-plant resistance against pest psyllid species or identifying varieties of invasive weed species susceptible to biological control (e.g. Nguyen and Messi 1973; Lahiri and Biswas 1980; Palmer and Witt 2006; Center et al. 2006).

Sometimes the within-species variation in plant susceptibility may be as great or greater than the between-species variation. *Asphagidella buxi*, for instance, breeds naturally on *Buxus sempervirens* var *arborescens* but not on var *rotundifolia*, yet it breeds successfully on *B. macrophylla* (Nguyen 1965). Comparable apparent anomalies are found in the host range of *Heteropsylla cubana* (Mullen and Shelton 2003). Differences in susceptibility may even occur among plants of the same

provenance. The most striking example occurs in species of Myrtaceae that display heteroblasty, strong morphological differentiation between juvenile and mature foliage related to tree age (Brennan, Weinbaum, et al. 2001). *Ctenarytaina eucalypti*, for example, oviposits and develops on juvenile shoots of *Eucalyptus globulus* whereas *C. spatulata* develops primarily on the mature foliage (Brennan and Weinbaum 2001a, 2001b, 2001c).

Variation in psyllid development success among host species and cultivars can usually be explained by differences in the initial attractiveness of the foliage, differential oviposition rates, larval survival rates and larval development period. *Diaphorina citri*, when tested using four host *Citrus* species, developed most successfully on *C. paradisi* as a result of higher fecundity, faster development time in the final instar and higher larval survival (Tsai and Liu 2000; Nava et al. 2007). *Heteropsylla cubana* developed more successfully on *Leucaena leucocephala* than on *L. collinsii* in which slower colonization resulted in 46–63% fewer eggs being laid, a 67% reduction in larval survival and the production of smaller, probably less fecund adults (Lapis and Borden 1993a, 1993b). The host preference hierarchy in *Bactericera cockerelli* on *Lycopersicon* is similarly based on rates of oviposition, development and survival, although these parameters may differ between native and invasive populations of the psyllid (Liu and Trumble 2004, 2005, 2006, 2007). There are, however, apparently anomalous examples in which a host plant that is most attractive for oviposition is not the most suitable for larval development. *Trioza erytreae*, for example, oviposits preferentially on *Citrus limon* but the development period is shorter and the adult size attained is greater on indigenous Rutaceae such as *Vepris* and *Clausena* (Moran 1968a, 1968b).

The precise mechanisms that determine the preference hierarchy of host plants appear to vary among psyllid species. In *Cacopsylla pyricola*, when offered three host plant species in the laboratory, host acceptance for oviposition appeared determined by interactions among plant species, female egg load and the time for which the psyllid was deprived of a suitable host (Horton and Krysan 1991). Cues received during probing and settling released oviposition but egg laying ceased earlier on lower hierarchy species, suggesting that further cues received during oviposition were also involved in prolonging egg laying.

Other factors implicated in establishing preferences include host species phenology (*Euphyllura phillyreae*), amount of glaucous wax on the leaf surface (*Glycaspis brimblecombei*), physical hardness of the terminal shoot (*Ctenarytaina thysanura*), leaf colour (*Mesohomotoma tessmanni* and *G. brimblecombei*), the presence of attractive chemicals such as caryophyllene (*Heteropsylla cubana*) and low concentrations of repellent chemicals such as phenolics (*Cacopsylla pyricola*), terpenoids (*Boreioglycaspsis melaleucae*) or glucosinolates (undescribed "*Aphalara*" sp.) (Moran and Brown 1973; Louda and Rodman 1983; Messi 1983a; Ullman and McLean 1988a; Mensah and Madden 1991; Luft and Paine 1998; Luft et al. 2001; Brennan and Weinbaum 2001a, 2001c, 2001d; Finlay-Doney and Walter 2005; Wheeler and Ordung 2005; Prophetou 1997). In *Bactericera cockerelli* on *Lysopersicon* jumping and leaf avoidance behaviour was greatest on the most resistant cultivars, suggesting active repellence and not just an antixenosis response (Liu and Trumble 2004). A single gene (Mi-1.2) from wild tomato, *Solanum peruvianum*, confers resistance to *B. cockerelli* in some commercial tomato varieties (Casteel et al. 2007).

Host-plant amelioration, disease transmission and endosymbionts

Host plants, particularly when leaves are mature, provide a low quality source of soluble nutrients, especially available nitrogen in the form of amino acids, for sap-feeding psyllids. This frequently results, as noted earlier, in lower rates of reproduction, slower development and reduced longevity on mature versus young or senescing foliage (Nguyen 1972b). Psyllids, however, often display mechanisms through which they enhance, ameliorate or partly circumvent the condition of their mature host plant for larval growth and development (White 1970b).

Feeding involves the injection of saliva and its associated enzymes, such as amylase, into the host, most frequently into the phloem and its associated tissues or into leaf mesophyll (Pussard 1939; Williams and Benson 1966). This may or may not result in wider salivary translocation within the plant. Species of *Cardiaspina*, *Glycaspis*, *Creiis* and *Lasiopsylla* on *Eucalyptus blakeleyi* and *E. melliodora* induce localized symptoms of varying severity in phloem tissues that resemble premature senescence (Woodburn and Lewis 1973). In mesophyll-feeding species such as *Cardiaspina retator* on *Eucalyptus camaldulensis* feeding similarly produces cell degeneration that resembles senescence and involves the mobilization of lipids, amino acids and soluble proteins (Crawford and Wilkens 1996).

Some psyllids, including known pest species such as *Trioza apicalis* (on carrot) and *Bactericera cockerelli* (on potato and tomato), induce a wider systemic phytotoxaemia within their host, resulting in severe growth distortion, cellular necrosis and yellowing of leaves (Richards and Blood 1933; Eyer and Crawford 1933; Eyer 1937; Sanford 1952; Laska 1964; Markkula and Laurema 1971), which again resemble senescence, with the associated mobilization of soluble nitrogen and increasing the availability of nutrients to the psyllid (Laurema 1989). This may, as in *T. apicalis*, be accompanied by an increase in leaf monoterpenes concentrations and result in reduced root growth (Nissinen et al. 2005, 2007). It may also be associated with the transmission of plant diseases, particularly mycoplasmas (see next section). Gall formation, which is largely outside the scope of this review, similarly brings about improvements in host tissue quality for feeding psyllid larvae through the creation of metabolic sinks within the plant tissue (e.g.Raman 1987; Rajadurai et al.1990; Mani and Raman 1994; Yang et al. 2006).

Enhanced amelioration may occur when psyllids feed in groups rather than singly. *Cacopsylla pyri* on *Pyrus communis* and *Cardiaspina densitexta* on *Eucalyptus fasciculosa*, for example, showed higher reproduction, greater longevity or enhanced survival with increasing feeding group density up to an optimum (White 1970b; Nguyen 1971). Galls of *Pachypsylla celtidismamma* on Celtis similarly grew larger when more than one gall was present per leaf (Heard and Buchanan 1998). However, feeding by some species at high densities, such as *Boreioglycaspis melaleucae* on *Melaleuca* may promote increased leaf abscision and a decline in host quality (Morath et al. 2006). Similarly, feeding-induced changes in the concentrations of leaf nutrients, chlorophyll, minerals and phenolics may lead to an ultimate reduction in food quality for *Cacopsylla* species on *Pyrus* (Scutareanu and Loxdale 2006).

Significance of disease transmission

Several psyllids are known vectors of plant diseases and as such are regarded as noxious pests. However, psyllids often show close association with these pathogens.

When viewed from the psyllids' perspective, the association may prove highly beneficial by bringing about pathogen-induced changes in the host plant that makes it more acceptable or more nutritious for psyllid development (Weintraub and Beanland 2006). Pathogens may, for example, induce physiological changes resembling the premature senescence noted previously or produce reduced levels of defensive chemicals. However, our knowledge of these psyllid–pathogen relationships is confined to just a few crop plants but similar pathogens occur widely in wild hosts where the insect–vector relationships remain to be established (Weintraub and Beanland 2006).

The main plant diseases associated with and transmitted by psyllids (Table 2) are viruses, and bacteria within three main groups, the liberibacters, the phytoplasmas (previously known as mycoplasma-type organisms) and fireblight. Several of the causative agents are taxonomically poorly defined, being identified solely from their RNA, and are included in the *Candidatus* category of the bacterial classification. The disease organisms are initially ingested during psyllid feeding and are then later re-injected back into other plants with the psyllid saliva. Phytoplasmas and liberibacters in particular are restricted to the phloem sieve tubes and circulate with the plant sap, making them ideal candidates for transmission by psyllids. Within the insect they cross the gut wall, multiply in the haemolymph and migrate into the salivary glands ready for onward transmission in the saliva (Hibino et al. 1971; Chen et al. 1973; Cousin and Boudon-Padieu 2002; Hung et al. 2004; Weintraub and Beanland 2006).

Both larvae and adults appear capable of transmitting phytoplasmas (Carraro, Loi, et al. 1998; Tedeschi and Alma 2004). Some evidence exists for transovariole transfer of these bacteria between female psyllids and their offspring in psyllids such as for Phytoplasma prunorum in *Cacopsylla pruni* (Tedeschi et al. 2006). However, Liberibacter asiaticum in *Diaphorina citri* and Phytoplasma mali in *Cacopylla melanoneura*, by contrast, do not appear to be vertically transmitted between generations (Hung et al. 2004; Tedeschi et al. 2006). Interestingly, infection of potato by a virus provides cross-protection against psyllid yellows phytoplasma transmitted by *Bactericera cockerelli* (Staples 1968).

Psyllids may also benefit from a general weakening of the plant caused by sooty moulds growing on the larval excreta or honeydew deposited on the leaf or shoot surface. Examples include *Cacopsylla pyricola* on *Pyrus* and *Ctenarytaina thysanura* on *Boronia* (Savinelli and Tetrault 1984; Mensah and Madden 1992b).

Significance of endosymbionts

Endosymbiotic bacteria also play a more direct role in the nutrition of psyllids, which in common with aphids, whiteflies and pseudococcids, support such bacteria within, or associated with, specialized cells (bacteriocytes) that aggregate to form a bacteriome within the insect's body cavity (Tarsia in Curia 1934; Chang and Musgrave 1969; Waku and Endo 1987; Fukatsu and Nikoh 1998; Thao et al. 2000a). Phloem sap, on which many psyllids feed, is rich in sugars but poor in amino acids and it is thought that the endosymbionts synthesize essential amino acids and vitamins such as riboflavin that then become available to the psyllid (Thao et al. 2000a; Thao et al. 2001).

Table 2. List of plant diseases transmitted by psyllid vectors.

Organism	Disease	Psyllid vector	Reference
Bacteria			
***Candidatus* status**			
Liberibacter asiaticus (in Asia and Florida)	Citrus Huanglongbing (HLB)=Greening Disease	*Diaphorina citri*	Halbert and Manjunath (2004), Davis et al. (2005), Das et al. (2007)
Liberibacter africanus (in Africa)	Citrus Huanglongbing (HLB)=Greening Disease	*Trioza erytreae*	Van den Berg et al. (1987), Anon. (1988)
Liberibacter americanus (in S. America)	Citrus Huanglongbing (HLB)=Greening Disease	*Diaphorina citri*	Teixeira et al. (2005)
Phytoplasma	Peach Yellow Leaf Roll (PYLR)	*Cacopsylla pyricola*	Purcell and Suslow (1984), Blomquist and Kirkpatrick (2002)
Phytoplasma prunorum	European Stone Fruit Yellows (ESFY)=Apricot Chlorotic Leafroll	*Cacopsylla pruni*	Carraro, Osler, et al. (1998), Jarausch et al. (2001), Carraro et al. (2004), Labonne and Lichou (2004), Delic et al. (2005)
Phytoplasma mali	Apple Proliferation (AP)	*Cacopsylla picta* *C. melanoneura*	Frisinghelli et al. (2000), Jarausch et al. (2003), Tedeschi et al. (2002), Tedeschi and Alma (2004)
Phytoplasma pyri (in Europe and N.America)	Pear Decline (PD)	*Cacopsylla pyricola* *C. pyri*	Jensen et al. (1964), Ullman and MacLean (1988b), Davies et al. (1992), Giunchedi et al. (1994), Carraro et al. (1998), Ben Khalifa et al. (2007)
Phytoplasma (in Taiwan)	Pear Decline (PDTW)	*Cacopsylla qianli* *C. chinensis*	Liu et al. (2007)
Phytoplasma	Carrot Stolbur	*Bactericera trigonica*	Font et al. (1999), Weintraub and Beanland (2006) Léclant et al. (1974) (misidentification as *B. nigricornis*?)
'Rickettsia type organism'			
	Wissadula Proliferation (WP)	*Paracarsidara dugesii* (Löw)	Dabek (1983) (as *concolor*)
Family Enterobacteriaceae			
Erwinia amylovora	Fireblight of orchard trees	*Cacopsylla pyricola* Psyllids generally	Wilde et al. (1971), Hildebrand et al. (2000)
Virus			
(SB26/29)	Potato Rugose Stunting Virus	*Russelliana solanicola*	Tenorio et al. (2003)
Undetermined			
	Zebra chip disease	*Bactericera cockerelli*	Munyaneza et al. (2007)

The psyllid endosymbionts fall into two main groups, primary (P) and secondary (S). The P endosymbionts, found within the bacteriocytes, are genetically similar throughout the psyllids, suggesting that they have colonized the psyllids just once, and then co-evolved with their hosts (Thao et al. 2000b). They are defined as a single taxon *Candidatus* Carsonella ruddii (Thao et al. 2001; Spaulding and von Dohlen 2001). The S endosymbionts, by contrast, are present in cells associated with the bacteriocytes and appear to be multiply derived, consisting of several distinct groups within the Eubacteriaceae (Spaulding and von Dohlen 1998; Thao et al. 2001; Fukatsu and Nikoh 1998). Their function in psyllid nutrition is less clear than for the P endosymbionts (Thao et al. 2001). Secondary endosymbiont infection levels may vary greatly among populations, as in *Glycaspis brimblecombei*, where infection appears more associated with levels of parasitism than with nutrition (Hansen et al. 2007).

Dispersal

Effective dispersal is a key element in the life history of psyllids irrespective of the habitat within which they are found. In insects that are capable of flying only limited distances under their own power, it serves several important purposes. In particular, it enables a species to track the changing spatial distribution of its host plant and/or the temporal availability of the food resource that it relies on for breeding success. It allows psyllids to move between different host-plant species and to exploit non-host-plant species as overwintering sites and it permits species to escape the effects of strong intraspecific competition and natural enemies. Among economically important species, such as *Trioza erytreae*, it expedites rapid colonization of cultivated *Citrus* hosts (metapopulation sinks) by psyllids originating on indigenous host plants within the surrounding area (metapopulation sources) (van den Berg, Deacon and Steenekamp 1991).

Dispersal distance

There is strong evidence to suggest that, as a group, the psyllids are highly effective dispersers over both short and long distances, although in almost all cases dispersal is wind assisted. Dispersing psyllids belonging to the genera *Cardiaspina*, *Ctenarytaina*, *Eucalyptolyma*, *Psylla* sensu lato and *Bactericera* have been taken in drogue nets towed behind light aircraft in Australia, the Galapagos Islands and the USA or in kite mounted nets in the Canary Islands (Glick 1939; White 1970a, 1973; Ashmole and Ashmole 1988; Peck 1994). Psyllids form a major component of the insect flotsom found on the surface of the sea at sites around the UK coastline and off the west coast of the USA (Cheng and Birch 1978; Hardy and Cheng 1986). Species belonging to several genera including *Aphalara*, *Craspedolepta*, *Livia*, *Cacopsylla*, *Euphalerus* sensu lato, *Acizzia*, *Bactericera* and *Trioza* are a common component of aerial deposition on high altitude snowfields in California and Tenerife (Papp and Johnson 1979) or early successional volcanic areas in the Azores (Ashmole et al. 1996). Thirty-seven species have been recorded as vagrants in yellow water traps in northern Italy and several, including *Cacopsylla melanoneura*, *C. affinis*, *Bactericera albiventris* and *Trioza urticae*, overwinter on *Pinus* in northern England at a distance of around 13km from the nearest host plant (Hodkinson 1972,

1983c). *Trioza apicalis* similarly moves up to 1km on to its overwintering shelter plants (Kristoffersen and Anderbrant 2007).

Tropical forest species may also move considerable distances. The coastal mangrove-feeding *Limbopsylla laguncullariae* has been taken inland in central Panama, many kilometres from the coast (Brown and Hodkinson 1988). Populations of *Boreioglycaspis melaleucae*, newly introduced for the biological control of *Melaeuca*, spread at a rate of up to 10km per year. Further testimony to the rapid dispersal powers of psyllids is the time (<10 years) in which *Heteropsylla cubana* spread from an origin in Central America to colonize virgin plantings of its forage legume host *Leucaenca leucocephala* in the Pacific, Asia, Australia and Africa (Hodkinson 1988b).

Experimental studies suggest that in species such as *Arytainilla spartiophila*, *Acizzia russelli* and *Trioza erytreae* females disperse further than males, as evidenced by an increase in the female: male sex ratio with increasing distance, 90–1500m depending on species, from the source (Dempster 1968; Webb 1977; van den Berg and Deacon 1988). However, this would be an ineffectual strategy in species with a post-dispersal ovarian diapause. For psyllids living on short herbaceous plants, such as *Trioza urticae*, the effective dispersal boundary layer, within which most directed dispersal movements take place, is probably less than 1m (Omole 1980). It is the individuals that stray above this height that are more likely to be wind dispersed.

Adaptive significance of dispersal

Multivoltine psyllids often show differences in dispersal behaviour among generations. Summer and autumn emerging adults of *Cardiaspina densitexta* in Australia, for example tend to show what White (1970c) calls "concentrative" behaviour. Adults blown out of a given *Eucalyptus* tree usually fly back into the same tree, and appear to neglect adjacent trees with significantly lower populations. This results in some trees supporting high psyllid densities while other nearby trees have low-density populations. By contrast, long-distance "dispersive" behaviour is a characteristic feature of the spring generation that has developed at shorter day length and lower temperatures. This parallels certain multivoltine north temperate species, such as *Cacopsylla pyricola* in which the winter morph, with its relatively longer wings produced under short day length, shows significantly greater dispersive behaviour than the spring or summer generation (Hodgson and Mustafa 1984; Horton, Burts, et al. 1994). The actual duration of the flight activity period is similar in the two morphs but flight frequency is much greater in the former (Horton and Lewis 1996). The actual rate of dispersal of these winter forms out of pear orchards tends to be correlated with the rate of leaf fall, lower temperature and density (Fye 1983; Horton, Burts, et al. 1994).

Univoltine species moving onto overwintering shelter plants, by comparison, exhibit both an autumn and a spring period of peak dispersal as they move to and from their winter host. Where significant dispersal occurs in summer generations, as in *Arytainilla spartiophila*, *Acizzia russellae* and *Trioza erytreae* it is usually associated with interspecific competition arising from high populations and declining host-plant favourability or increasing pressure from natural enemies (Dempster 1968; Webb 1977; van den Berg, Anderson, et al. 1991). Psyllids disperse to new, more favourable plants.

Dispersal opens up the opportunity for host-plant alternation in multivoltine psyllids but this behaviour, so typical of many aphid species, is rare in psyllids, with just two known examples. *Bactericera crithmi* on Malta undergoes a winter generation on *Ferula* during the period when its normal host *Crithmum* is dormant (Mifsud 1997). It moves back to *Crithmum* in spring. Similarly, the vector of psyllid yellows disease of potato, *Bactericera cockerelli* overwinters as source populations on *Lycium* and other wild Solanaceae in the warmer southern USA. In spring there is a general northwards wind-assisted dispersal of adults to establish sink populations breeding on potato (*Solanum*) in regions far to the north (Knowlton 1933; Knowlton and Thomas 1934; Swenk and Tate 1940; Wallis 1946, 1955).

Dispersal allows psyllids to track spatial and temporal changes in the availability of host-plant tissues suitable for growth and development. Many psyllids require flushes of young, rapidly growing leaf tissues on which to breed. As these leaves mature they become unsuitable for psyllid development and the psyllid must seek out new breeding sites. This is most acute where individuals of particular tree species drop leaves completely but asynchronously. In some Australian species, such as *Cardiaspina densitexta* and *C. albitextura*, this can result in progressive waves of psyllid outbreak and decline spreading across the landscape as psyllids track the flushing pattern of their host *Eucalyptus* (Morgan 1984). This precludes the need for diapausing stages. The problem may be particularly acute for tropical rainforest psyllids where individual host plants are usually sparsely distributed within a highly species diverse tree community and often flush asynchronously. A high level of dispersive behaviour by psyllids is necessary constantly to track the spatial and temporal availability of their food resource (Brown and Hodkinson 1988; Hodkinson and Casson 2000).

Even in temperate regions individual host plants may vary markedly in suitability between successive years. Many species of Rosaceae, for example, exhibit biennial or irregular patterns of flowering by individual plants that may affect their suitability as psyllid hosts (Sutton 1984). It is unsurprising, therefore, that highly dispersive psyllids like *Cacopsylla melanoneura* and *C. affinis* are associated with one such rosaceous plant species, namely *Crataegus* (Sutton 1984).

Overwintering on shelter plants

Many temperate species of psyllids are known to disperse to, and overwinter as adults on, evergreen shelter plants before moving back onto their true host in the spring (Reuter 1909; McAtee 1915; Hodkinson 1972; Hågvar and Hågvar 1975; Kristoffersen and Anderbrandt 2007) (Table 1). Such hosts are usually conifers, primarily species of *Pinus*, *Picea*, *Abies*, *Taxus*, *Tsuga*, *Cupressus* and *Juniperus* but may also include thorny evergreen shrubs such as *Ulex*. In *Trioza apicalis* there appears to be a distinct order of preference, with *Picea* supporting higher populations than *Pinus* or *Juniperus* (Kristoffersen and Anderbrandt 2007). The period spent on shelter plants, which usually matches periods when the host is dormant or unfavourable for psyllid development, is normally accompanied by an ovarian diapause. This adaptive overwintering strategy is found in almost all temperate psyllid families but is most frequent among species of *Aphalara*, *Livia*, *Cacopsylla*, *Bactericera*, *Phylloplecta* and *Trioza*. It is, however, recorded more sporadically in a wider range of genera including *Pachypsylla*, *Calophya*, *Camarotoscena*, *Togepsylla*, *Ligustrinia*, *Cyamophila*, *Livilla* and *Epitrioza* (Table 1).

Psyllids on conifers are easily caught and observed whereas those overwintering in leaf litter or grass tussocks are much less obvious. Careful studies on some species such as *Bactericera perrisi*, *Aphalara avicularis*, *A. exilis* and *A. longicaudata* show that individuals overwinter both on conifers and in litter, perhaps raising the question for other species of what actual proportion of the overwintering population is on conifers (Lauterer 1976, 1982, 1991). Furthermore, several species of *Aphalara*, *Cacopsylla* and *Trioza*, known to overwinter on conifers, can also be overwintered successfully in grass tussocks maintained in pots (Heslop-Harrison 1937). These individuals tend to be much lighter coloured than those spending winter on conifers (Heslop-Harrison, 1937).

One question that has not been fully answered is whether overwintering psyllids feed on conifers or other shelter plants. Experiments in our laboratory using *Pinus* shoots labelled with C_{14} and P_{32} repeatedly failed to provide definitive evidence for winter feeding by *Cacopsylla melanoneura*, although the maintenance of body condition and levels of hydration suggest that some feeding must take place (Jackson et al. 1990). There is, however, some evidence that overwintering *Cacopsylla pyricola* may feed on transitory hosts such as *Prunus persica* (Ullman and McLean 1988b).

Mate finding and aggregation on host plants

Small dispersive insects, such as psyllids, are faced with the problem of finding suitable mates, either on their breeding or overwintering host plants. Species are frequently found as highly-aggregated, mixed-sex colonies on the tissues of their host. Several are known to emit species- and gender-specific stridulation calls or to make drumming sound or vibrations with their tarsi on leaf surfaces (Campbell 1964; Ossiannilsson 1950; Heslop-Harrison 1961; KL Taylor 1985; Carver 1987; Tishechkin 1989, 2005, 2007; Percy et al. 2006), which are thought to aid mate location and aggregation. There is also some evidence for chemical mechanisms leading to aggregation and mate finding. Male *Cacopsylla pyricola* are attracted to volatile chemicals emanating from pear shoots with receptive post-diapause females present or from shoots that have recently supported populations of such females. The precise nature of the chemical stimulus is unknown and it remains to be determined whether the chemicals involved originate from the psyllid, the host plant, or a combination of both (Horton et al. 2007; Horton and Landolt 2007). However, in some other species, such as *Cardiaspina albitextura*, host-plant tissues previously occupied by psyllids appear less favourable for oviposition than formerly unfrequented sites (Clark 1962, 1963b).

Variation in fecundity among species

It might be predicted that the fecundity of psyllid species is related to their type of life cycle, with species having larvae living in protective galls or lerps producing fewer eggs than those living on exposed growing tips. There is, however, surprisingly little pattern in the fecundity of psyllid species (Table 3). Experimentally measured fecundity differs widely, even among species within the same genus or family. Where repeated measures have been made on the same species in different localities or at different times, such as in *Trioza erytreae*, *Heteropsylla cubana* or *Diaphorina citri*, mean fecundity may differ by a factor of two or more (Table 3). Furthermore, there is little to suggest major differences in fecundity related to taxonomic position.

Table 3. Fecundity of selected psyllid species on preferred host, illustrating variation in potential reproductive output across the group. Numbers given are mean and maximum egg production per female under non-limited experimental conditions.

Family	Species	Maximum	Mean	Reference
Psyllidae	*Aphalara polygoni*		c. 300	Lauterer (1982) (as *rumicicola*)
	Paurocephala psylloptera		640†	Hsieh and Chen (1977)
	Diclidophlebia eastopi		502	Osisanya (1974a)
	Diclidophlebia harrisoni		131	Osisanya (1974a)
	Diclidophlebia xuani		532–758	Aléné et al. (2005a)
	Ctenarytaina thysanura		86–92	Mensah and Madden (1992a, 1993b)
	Agonoscena pistaceae		893–1087	Mehrnejad and Copland (2005)
	Gyropsylla spegazziniana	180	108*	Leite and Zanol (2001)
	Diaphorina citri	807	630†	Hussain and Nath (1927)
	Diaphorina citri		748	Liu and Tsai (2000)
	Diaphorina citri		858	Tsai and Liu (2000)
	Diaphorina citri	700	266	Mangat (1966)
	Diaphorina citri	520	210–300	Pande (1971)
	Cacopsylla melanoneura	116	84	Domenichini (1967)
	Cacopsylla pyricola		664	Burts and Fischer (1967)
	Cacopsylla pyricola		445	McMullen and Jong (1977)
	Cacopsylla pyricola		665	Rasmy and MacPhee (1970)
	Cacopsylla pyricola		387–486	An et al. (1996)
	Cacopsylla pyri		47–406	Kapatos and Stratopoulou (1996)
	Cacopsylla pyri	2527		Lyoussoufi et al. (1988)
	Cacopsylla pyri		471	Nguyen (1970a)
	Cacopsylla pyri		588	Nguyen (1973)
	Acizzia uncatoides		463†	Koehler et al. (1966)
	Acizzia uncatoides		986	Madubuny and Koehler (1974)
	Arytaina genistae	962	435	Watmough (1968a)
	Arytainilla spartiophila	354	93	Watmough (1968a)
	Heteropsylla cubana		758	Patil et al. (1994)

Table 3. (*Continued.*)

Family	Species	Maximum	Mean	Reference
	Heteropsylla cubana	857	394	Takara et al. (1990)
	Heteropsylla texana	100		Donnelly (2002)
	'Psylla' isitis	828	479†	Grove and Gosh (1914)
Spondyliaspididae	*Euphalerus clitoriae*		1148	Junior et al. (2005)
	Cardiaspina albitextura	220	124*	Clark (1962, 1963b)
	Cardiaspina albitextura	290	45	Morgan and Taylor (1988)
	Boreioglycaspis melaleucae		78	Purcell et al. (1997)
Calophyidae	*Apsylla cistellata*		141–150	Monobrullah et al. (1998)
	Apsylla cistellata		141	Prasad (1957)
Carsidaridae	*Carsidara limbata*	1701		Ding et al. (1987)
	Allocarsidara malayensis		50	Gadug and Hussein (1987)
	Mesohomotoma tessmanni	61	48†	Igboekwe and Adenuga (1983)
Triozidae	*Phylloplecta tripunctata*	202	94–164	Petersen (1923)
	Trioza erytreae	560	327	Moran and Blowers (1967)
	Trioza erytreae		787	Van den Berg, Deacon and Thomas (1991a)
	Trioza erytreae		827	Van den Berg (1990)
	Trioza eugeniae	331	198	Young (2003)
	Trioza hirsuta	180	99	Dhiman and Singh (2004)
	Trioza magnicauda		692	Chang et al. (1995)
	Bactericera cockerelli	1176	439	Pletsch (1947)
	Bactericera cockerelli	1300	318	Knowlton and Janes (1931)
	Bactericera tremblayi	803	431	Tremblay (1965b)
	Schedotrioza multitudinea		487	GS Taylor (1985, 1987)
	Trichochermes walkeri	279	201	McLean (1998)
	Neotrioza taveresi		219	Butignol and Pedrosa (2003)
	Pauropsylla depressa		>150	Abbas (1967)

Note: occasionally, where means were not calculated in the original paper, they are calculated as (minimum+maximum)/2 (indicated by*); alternatively, some means (indicated by†) are calculated directly from raw data given in the original paper; a range of values indicates recorded differences in means among seasons.

Typically mean fecundity per female ranges from 40–50 to over 1000, with a majority of species lying within the range 200–800. Lowest values (40–50) occur in some but not all Spondyliaspididae and Carsidaridae but highest values are often found in pest species of Psyllidae and Triozidae such as *Agonoscena pistaciae*, *Trioza erytreae* and *Bactericera cockerelli* in which some individual females produce up to 1300 eggs.

Oviposition usually occurs over an extended period with females often maturing successive batches of eggs (An et al. 1996; Dhiman and Singh 2004). In species such as *Cacopsylla pyricola*, *Trioza erytreae* and *Agonoscena pistaciae*, repeated mating is necessary for a female to produce a full egg complement (Burts and Fischer 1967; van den Berg, Deacon and Thomas 1991a; Mehrnejad 1998; Mehrnejad and Copland 2006a), emphasizing the importance of continuous mate finding for successful life cycle completion.

Factors influencing fecundity

Several factors influence fecundity, including temperature, day-length and season, host condition and crowding. Fecundity, as noted earlier, tends to decline above and below an optimum temperature, as in *Acizzia uncatoides*, *Agonoscena pistaciae*, *Cacopsylla pyri* and *Bactericera cockerelli* (List 1939a; Madubunyi and Koehler 1974; Nguyen 1970a; Mehrnejad and Copland 2006a). In multivoltine species such as *Agonoscena pistaciae*, *Diclidophlebia xuani*, *Cacopsylla pyri*, *Cacopsylla pyricola* egg output per female also varies significantly between seasons, with day length as well as temperature often an important determining factor (Nguyen 1970a; Kapatos and Stratapoulou 1996; Mehrnejad and Copland 2005; Aléné et al. 2005b). Moderate crowding initially enhances fecundity in species such as *Trichochermes walkeri*, *Cardiaspina albitextura*, *Cacopsylla pyri* and *Arytaina genistae* but increasing density beyond the optimum leads to declining fecundity (Watmough 1968a, 1968b; Clark 1963a; Nguyen 1971, 1973; McLean 1998). The presence of eggs also acts as a deterrent to oviposition in *Trioza eugeniae* (Luft and Paine 1997).

The previous discussion of life history parameters shows that psyllid species exhibit considerable variation in their life history characteristics and their adaptive response to their environment. It is now appropriate to examine the distribution of characteristics across the Psylloidea and to identify how the life cycle parameters are combined within the life histories of species both within and among higher taxa.

Analysis of psyllid life history characteristics

Table 1 shows the detailed life history characteristics of 342 psyllid species culled from the literature. Species are arranged in descending taxonomic sequence by family, tribe and genus. The key references from which data are drawn are listed. In the large genus *Cacopsylla* the *Salix*-feeding species with similar life histories are separated from the other species, which themselves are split into subgenera. Information is provided for each species on the major climatic zone within which it is found, the functional growth form of its host plant, the overwintering stage(s), the overwintering site, either on or off the host, voltinism, feeding site on the host and whether or not the larva forms galls of a particular type or lerps on the host plant. A full explanation of the various life history categories and their abbreviations as used in this table are listed in the note of Table 1.

Methods of coding and analysis

The categorical life history data in Table 1 were numerically coded as the basis for a full analysis of the dataset, with each category of each characteristic given a separate numerical code. Voltinism presented a slight problem of coding and species were coded as semivoltine, univoltine or multivoltine, depending on the maximum life history duration. Taxonomic status of the psyllids was coded at the family, tribe and genus level. The basic objective of the analyses was to test whether there were recognisable and consistent patterns in the data linking particular life history traits with specific psyllid groups.

Three separate multivariate analyses were employed to explore the structure of the dataset using the MINITAB 14 statistical package, namely Multiple Correspondence Analysis (MCA), Linear Discriminant Analysis (LDA), and Cluster Analysis (CA) of both the descriptive variables and of the species.

MCA attempted to measure the extent to which different characters correspond with each other across the dataset and whether particular sets of characteristics correspond to particular taxonomic groupings within the psyllids. Analyses were initially conducted using life history characters alone to explore relationships among these variables and then repeated with psyllid groupings added. These analyses used the full dataset for all species.

LDA tests whether suggested groupings of species are justified on the basis of the measured life history variables. This analysis was conducted three times using genus, tribe and family as the suggested species grouping. The output displays how many species are correctly or incorrectly allocated objectively to the proposed grouping. A high level of correct prediction indicates that life history characteristics tend to be relatively uniform within the group and are good predictors of taxonomic position. A low level suggests that life history characteristics are highly variable within proposed groups and thus poor predictors. This may, however, indicate greater adaptive flexibility as species have evolved differing life cycles to exploit varying opportunities within different environments. In conducting these analyses it is necessary to remove monobasic genera and tribes from the dataset, where necessary, as a single taxon cannot form a group.

CA measured similarity among taxa or among variables within the main dataset using Euclidean distance: clustering was by average linkage.

Results of analyses

CA of variables (Figure 1) indicates two major groupings of characters and two outliers. The first grouping links voltinism and overwintering stage, not unexpectedly, to climate. The second links feeding site and overwintering site to plant functional type. The two outlying characters are gall type and lerp formation. Their separation from other characters appears to lie in the fact that lerp formation is largely concentrated within one family, the Spondyliaspididae, while gall instigation/type is spread broadly but rather haphazardly across taxa.

Overall, the level of correspondence among characters in MCA (Table 4) was low, with cumulative correspondence across species along the first five axes totalling only 26%. Introducing psyllid tribe as an additional character actually reduced correspondence further (19%). Gall and lerp formation were again the main outlying characters.

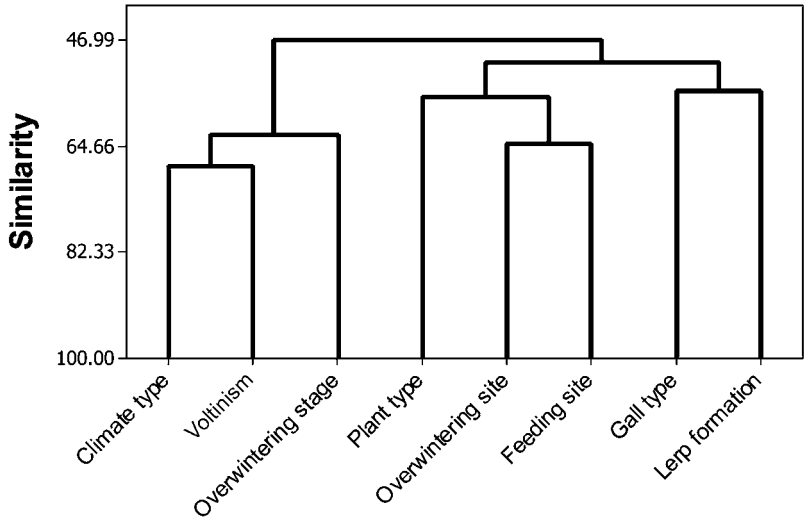

Figure 1. Dendrogram illustrating the level of correspondence among life history parameters measured across psyllid species. Note: similarity is measured by Euclidean distance; clustering is by average linkage.

The total percentage of species allocated to the correct tribe by LCA was generally around a weighted mean of 47% (Table 5) but this hid wider variation among taxa, with one large group the Triozini in particular, dragging the total down but with other smaller tribes, such as Acizziini, Gyropsyllini, Mastigimatini and Phytolymini, showing good predictability. However, the correlation between group size and predictability (%) was non-significant ($r=0.01$, $p>0.05$). Despite wide variability among taxa, predictability increased stepwise from the genus ($n=302$, 40% correct) to the family level ($n=322$, 50% correct). This suggests that differentiation and thus discrimination among taxa, related to life history traits, increases with taxonomic level.

Discussion and conclusions

Within the Psylloidea there is considerable variation in the body form of the larvae related to phylogeny and one might predict that particular physiognomies are best

Table 4. Results of multiple correspondence analysis across species showing percentage of cumulative correspondence explained by the first five axes.

	Cumulative Variation (%)				
	Axis				
Character set	1	2	3	4	5
Excluding tribe	7	13	17	22	26
Including tribe	5	9	12	16	19

Note: analyses are presented both with and without the inclusion of psyllid tribe as a character.

Table 5. Percentage of species allocated to their correct tribe using linear discriminant analysis based on life history characteristics. *n* is the number of species on which the percentage is based.

	n	% correct
Acizzini	3	100
Aphalarini	27	67
Arytainini	25	16
Calophyini	7	43
Ciriacremini	3	0
Ctenarytainini	4	25
Diaphorinini	3	33
Diclidophlebiini	7	100
Euphalerini	4	0
Euphyllurini	6	17
Gyropsyllini	2	100
Liviini	4	75
Mastigimatini	2	100
Mesohomotomini	2	50
Pachypsyllini	8	13
Pachypsylloidini	11	100
Paurocephalini	3	66
Pauropsyllini	6	33
Phytolymini	2	100
Psyllini	72	68
Psyllopseini	9	89
Rhinocolini	6	33
Spondyliaspidini	11	91
Strophingiini	2	100
Triozini	86	16
Total	**315**	**47**

adapted to exploiting plants in different ways (Loginova 1982; White and Hodkinson 1985). Thus, for example, larvae of many Triozidae and Calophyidae are strongly flattened and rounded and one might expect them to be best adapted for a sedentary existence, living on the surface of leaves or within open pit galls on the leaf surface. By contrast, larvae of many Psyllidae and Spondyliaspididae are less flattened and more robust, with relatively longer legs. They appear best adapted for a free living existence on expanding shoots or developing within larger enclosed leaf galls. While many species conform to this expected typology others do not. Thus, many Triozidae and Calophyidae live on growing shoots or within enclosed galls while several Psyllidae form pit galls and many Spondyliaspididae live on leaf surfaces. It is against this phylogenetic history that interpretations and conclusions regarding psyllid life history adaptations can now be made.

Several important conclusions can be drawn from the analyses of the life history data. Firstly, and perhaps most significantly, the linkage between phylogenetic grouping and life history characteristics, while discernible, is not of overriding significance in determining the type of life history a psyllid undergoes. The phylogenetic signal, as revealed by MCA is marginally stronger at the family level

than at the generic level but at best only explains about a quarter of the total variation observed. Similarly, LDA on average, using life history characteristics as predictors, only allocates species to the correct genus, tribe or family group with at best 50% mean accuracy. This again suggests high within group variation in life history characteristics, even at ascending taxonomic levels. However, within these average figures there do appear to be individual taxa that display a higher level of predictability, such as *Craspedolepta*, *Aphalara* and *Psyllopsis*, but this is compensated for by others such as the large genus *Trioza* that show low predictability. Nevetheless, these general findings accord with Danks (2006, p. 9) who reviewed published data on life history traits across the Insecta. He concluded that: "…phylogenetic history of a group or species does determine the core structure of seasonal responses… but that perhaps more striking is the large number of traits linked to habitat or its seasonal components that have evolved many times independently." Among such traits he lists diapause, cold-hardiness, reproductive pattern, paedogenesis, gall formation etc. (see also Danks (2002, 2005, 2007)). He concludes (2006, p. 9) that: "…how the different responses are integrated to provide coherent, seasonally relevant development trajectories can be understood only by reference to ecological demands."

Extending these conclusions to the psyllids we can observe the manner in which environmental and host-plant factors overlay the phylogenetic signal to produce the wide variation observed in psyllid life history traits observed today. Thus, the CA for life history variables recognizes two major groupings of linked parameters. First, voltinism and overwintering stage is linked to climatic environment. Second, larval feeding site and overwintering site is linked to plant functional type. Gall formation, by contrast appears to have evolved independently on several occasions across disparate psyllid taxa. Lerp formation is more tightly constrained within the family Spondyliaspididae. It should be noted, however, that plant functional type is itself largely a plant response to climate.

It now becomes possible to suggest how environmental and ecological constraints have led to the observed diversification of psyllid life histories and to draw together the various threads into a coherent exposition of psyllid life history adaptation on a global stage. Global temperature and moisture gradients and the adaptive biology of host plants provide the backdrop against which such psyllid adaptations have evolved.

Psyllid species living within tropical moist habitats, as typified by lowland tropical rainforest, probably suffer the least constraint on their development. They are usually associated with *evergreen* phanerophytes and chamaephytes, undergo continuous reproduction and are thus typically multivoltine. However, even in these benign habitats, host tree species frequently display cycles of flushing of suitable tissues for larval development, with individual trees at different stages of the flushing cycle at any one time. In such high diversity forests, a continuous life cycle demands continuous and effective population dispersal to seek out the sparsely distributed trees of the host species in an appropriate phenological state for reproduction to continue (Hodkinson and Casson 2000; Brown and Hodkinson 1988). It may also select for small and highly dispersive species (Hodkinson and Casson 2000).

In tropical habitats with increasing seasonality of rainfall an increasing proportion of host tree and shrub species are *deciduous*, with some host species being leafless for several months of the year and some tree species showing various

levels of deciduousness between individuals. Under these circumstances adult and/or egg diapause allows associated psyllids, independent of taxonomic provenance, to arrest their life cycle and therby align development with the phenology of their host, but at the expense of a reduced number of generations per year. As tropical habitats become even more seasonally dry then deciduousness among hosts becomes the norm and seasonal diapause responses assume even greater significance for psyllid survival. Here again successful dispersal over a wide area may be necessary to relocate hosts following periods of inactivity.

As one moves from the wet tropics into the moist temperate regions or at higher altitudes within the tropics a number of developments and trends in psyllid life cycles are observed. There is a general reduction in the temperature threshold for development, development rates are often slower, voltinism is reduced and life histories become strongly seasonal, with developmental or reproductive diapause becoming increasingly important for maintaining developmental synchrony with the host plant. Some species display morphologically distinct seasonal forms. Winter survival mechanisms, involving increased levels of cold-hardiness, assume increasing significance. There is also an increase in the availablity and use of herbaceous host-plant species falling within the hemicryptophyte and geophyte functional categories. Typically the growing tips of these plants overwinter at or below the soil surface, produce a flush of growth each year and then die back in the autumn. This necessitates a psyllid overwintering strategy that involves movement onto the winter bud or root or hibernation away from the host plant and movement back onto the new foliage in spring.

Psyllids living on temperate phanerophytes and chamaephytes have alternative life history possibilities. Many psyllid species on *deciduous* phanerophytes overwinter as diapausing eggs on the buds or apical shoots where they are exposed to the full rigours of winter. Hatching is timed to coincide with spring bud burst. Alternatively, adults may overwinter either on the host or on shelter plants. In both cases a reproductive diapause is necessary to delay oviposition until the spring growth of the plant commences. Movement onto and from winter shelter plants necessitates the development of two phases of pre-reproductive dispersal in autumn and spring.

On *evergreen* phanerophyte/chamaephyte species many psyllid species overwinter as diapausing larvae on the green shoots or leaves. On such plants the requirement for precise phenological synchrony with plant growth is less demanding as larval growth simply recommences as shoots or leaves resume growth in the spring. Development time can, as a consequence, be potentially extended beyond one year. Overwintering as mixed populations of eggs, larvae and adults also becomes feasible on such plants.

Within temperate regions, where rainfall becomes strongly seasonal, as in areas of Mediterranean climate, periods of psyllid development and reproduction often become compressed into the short period of the year, such as early spring, when temperatures are sufficiently high but not too hot and when rainfall is adequate to stimulate the flushing of new plant growth. Such compression of life histories, with long periods of spent inactive as diapausing eggs, larvae or adults, becomes even more pronounced in psyllid species associated with host plants growing in steppe and desert environments.

As one moves north from the temperate to the cold boreal regions psyllid faunas become much less diverse and individual species are usually associated with

prominent host taxa such as *Salix*, *Alnus* and *Betula* on which they typically undergo rapid annual life cycles during a short summer growing period. These woody host plants almost invariably exhibit a low chamaephyte growth form: other herbaceous hemicryptophytes and geophytes appear less commonly as hosts. Overwintering is either as eggs on growing shoots or as adults that overwinter in leaf litter around the base of the plants, often covered by a protective snow layer.

It is reasonable to conclude on the previous evidence that the two prime environmental variables, temperate and moisture availability, acting within an ecological context, are either directly, or mediated through the physiognomy and ecological adaptations of host plants, the major pressures acting on the evolution of psyllid life histories. Together they have frequently resulted in similar strongly convergent life histories across taxonomically disparate sets of psyllid species and divergent life histories among related species. Danks's (2006) conclusions regarding the comparatively low importance of group phylogenetic history in determining life history parameters are well supported by the psyllid data.

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