

# Biology and Evolution of Adelgidae

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## Key Words

Aphidoidea, complex life cycle, cyclical parthenogenesis, plant-insect interactions

## Abstract

The Adelgidae form a small clade of insects within the Aphidoidea (Hemiptera) that includes some of the most destructive introduced pest species threatening North American forest ecosystems. Despite their importance, little is known about their evolutionary history and their taxonomy remains unresolved. Adelgids are cyclically parthenogenetic and exhibit multigeneration complex life cycles. They can be holocyclic, with a sexual generation and host alternation, or anholocyclic, entirely asexual and without host alternation. We discuss adelgid behavior and ecology, emphasizing plant-insect interactions, and we explore ways that the biogeographic history of their host plants may have affected adelgid phylogeny and evolution of adelgid life cycles. Finally, we highlight several areas in which additional research into speciation, population genetics, multitrophic interactions, and life-history evolution would improve our understanding of adelgid biology and evolution.

*Two phenomena in the natural history of chermes [= adelgids] are especially striking; the parthenogenesis and the polymorphism: both of them attain such a high degree here as nowhere else in the animal kingdom. N.A. Cholodkovsky, 1915 (29)*

## INTRODUCTION

Adelgids (Hemiptera: Aphidoidea: Adelgidae), like their closest relatives, phylloxerans (Phylloxeridae) and aphids (Aphididae), exhibit cyclical parthenogenesis and have complex, multigeneration, polymorphic life cycles. The Adelgidae and Phylloxeridae are distinguished from the Aphididae by the absence of siphunculi and the retention of the ancestral trait of oviparity in all generations (78). While phylloxerans and many aphids feed on angiosperms, adelgids feed only on certain genera in the Pinaceae, retaining their ancestral relationship with gymnosperms (78, 157).

Adelgids, like their host plants, are endemic to Northern Hemisphere boreal and temperate environments. Despite the broad geographic distribution of their host plants, there are surprisingly few adelgid species: Fewer than 70 have been described in the entire family (15, 124, 145) (Table 1). However, there is considerable taxonomic uncertainty. Several described species may not represent unique taxa but are actually different morphological forms of the same species found on different host plants (15). It also is likely that cryptic species have yet to be described (76).

Work on adelgid biology and systematics has a long and rich history. After cyclical parthenogenesis and host alternation were discovered in adelgids between 1887 and 1889 (17, 18, 27, 42), a lively dialogue in the scientific literature established their natural history, life cycle terminology, and the morphological characters used in taxonomy, culminating in monographs by Cholodkovsky (28) in Russia, Börner (22) in Germany, Marchal (97) in France, and Annand (4) in North America. During the mid-

twentieth century, interest in adelgids peaked again. Eichhorn (45, 46) discussed population dynamics and predator-prey interactions. Steffan (144, 145) studied systematics, cytology, and life cycle evolution. Inouye (81) described the adelgid fauna in Japan, as did Carter (25) in Britain.

In recent decades, research on adelgids has focused mainly on two species, balsam woolly adelgid, *Adelges piceae* (69), and hemlock woolly adelgid, *A. tsugae* (103). They were introduced into North America from Europe (60) and Japan (76), respectively, and are serious threats to forest ecosystems. Recent research has therefore emphasized basic biology, plant-insect interactions, and potential biological control organisms to inform efforts to manage these two species. In this review, we give an overview of adelgid biology and systematics and discuss recent advances in understanding their evolutionary history. In particular, we focus on the evolution of adelgid life cycles and host plant use. By emphasizing patterns across the whole family, we hope to stimulate research on this unique group of insects, to inform control programs of current adelgid pest species, and to help prevent other species from becoming pests in the future.

## THE ADELGID HOLOCYCLE

In cyclically parthenogenetic organisms, a holo-cyclic species or lineage is one that includes a sexual generation in its life cycle. Life cycles that do not include a sexual generation are termed anholocyclic. Five generations make up the typical adelgid holocycle (Figure 1, center). Three are produced on the primary host, where sexual reproduction and gall formation occur; two are produced on the secondary host that supports a series of asexual generations. The entire cycle takes two years to complete. Spruce (*Picea* spp.) is always the primary host and another conifer genus (*Abies*, *Larix*, *Pseudotsuga*, *Tsuga*, or *Pinus*) is always the secondary host. Adelgids are highly host specific: A given species can survive and reproduce only on certain tree species within

**Table 1 List of described adelgid species, their life cycles, secondary hosts, and native ranges**

Species <sup>a</sup>	Life cycle <sup>c</sup>	Secondary host genus	Native range	Reference(s)
<i>Adelges (Sacchiphantes) abietis</i> (Linnaeus 1758)	Anholocyclic 1°	None	Europe	28, 118, 126
<i>Adelges (Adelges) aenigmaticus</i> Annand 1928	Unknown	<i>Larix</i>	Unknown	4
<i>Adelges (Gilletteella) cooleyi</i> (Gillette 1907)	Holocyclic	<i>Pseudotsuga</i>	Western North America	4, 30, 34, 67
<i>Adelges (Gilletteella) coweni</i> (Gillette 1907)	Anholocyclic 2°	<i>Pseudotsuga</i>	Western North America	35, 127, 145
<i>Adelges (Sacchiphantes) diversis</i> Annand 1928	Unknown	<i>Larix</i>	Unknown	4
<i>Adelges (Adelges) geniculatus</i> (Ratzeburg 1843)	Anholocyclic 2°	<i>Larix</i>	Europe	145
<i>Adelges (Gilletteella) glandulae</i> (Zhang 1980)	Holocyclic	<i>Abies</i>	China	168
<i>Adelges (Adelges) isedakii</i> Eichhorn 1978	Holocyclic	<i>Larix</i>	Japan	54
<i>Adelges (Adelges) japonicus</i> (Monzen 1929)	Anholocyclic 1°	None	Japan	54, 81, 113
<i>Adelges (Dreyfusia) joshii</i> (Schneider-Orelli & Schneider 1959)	Anholocyclic 2°	<i>Abies</i>	Western Himalayas	66
<i>Adelges (Sacchiphantes) karafutonis</i> (Kono & Inouye 1938)	Unknown	Unknown	Japan	54, 81
<i>Adelges (Adelges) karamatsui</i> Inouye 1945	Anholocyclic 2°	<i>Larix</i>	Japan	54, 81
<i>Adelges (Sacchiphantes) kitamiensis</i> (Inouye 1963)	Unknown	<i>Larix</i>	Japan	82
<i>Adelges (Dreyfusia) knucheli</i> (Schneider-Orelli & Schneider 1954)	Holocyclic	<i>Abies</i>	Western Himalayas	66, 91
<i>Adelges (Adelges) lapponicus</i> (Cholodkovsky 1889)	Anholocyclic 1°	None	Europe	28
<i>Adelges (Sacchiphantes) lariciatus</i> (Patch 1909)	Holocyclic	<i>Larix</i>	North America	4, 37, 117
<i>Adelges (Adelges) laricis</i> (Vallot 1836)	Holocyclic	<i>Larix</i>	Europe	23, 25, 33, 136, 168
<i>Adelges (Dreyfusia) merkeri</i> Eichhorn 1957	Holocyclic	<i>Abies</i>	Europe	43, 45, 49, 121
<i>Adelges (Dreyfusia) nebrodensis</i> (Binazzi & Covassi 1991)	Anholocyclic 2°	<i>Abies</i>	Italy	13
<i>Adelges (Dreyfusia) nordmanniana</i> (Eckstein 1890)	Holocyclic	<i>Abies</i>	Caucasus Mountains	51, 53, 97, 156
<i>Adelges (Cholodkovskya) oregonensis</i> Annand 1928	Unknown	<i>Larix</i>	Unknown	4
<i>Adelges (Aphrastasia) pectinatae</i> (Cholodkovsky 1888)	Holocyclic	<i>Abies</i>	Europe, China, Japan	54, 55, 81, 145
<i>Adelges (Dreyfusia) piceae</i> (Ratzeburg 1844)	Anholocyclic 2°	<i>Abies</i>	Europe	14, 97, 156
<i>Adelges (Dreyfusia) pindrowi</i> Yaseen & Ghani 1971	Anholocyclic 2°	<i>Abies</i>	Western Himalayas	164
<i>Adelges (Dreyfusia) prelli</i> (Grossmann 1935)	Holocyclic	<i>Abies</i>	Caucasus Mountains	63, 64
<i>Adelges (Sacchiphantes) roseigallis</i> (Li & Tsai 1973)	Anholocyclic 1°	None	China	93
<i>Adelges (Dreyfusia) schneideri</i> Börner 1932	Anholocyclic 2°	<i>Abies</i>	Caucasus Mountains	121, 145

(Continued)

Table 1 (Continued)

Species <sup>a</sup>	Life cycle <sup>c</sup>	Secondary host genus	Native range	Reference(s)
<i>Adelges (Sacchiphantes) segregis</i> Steffan 1961	Anholocyclic 2°	<i>Larix</i>	Europe	138
<i>Adelges (Dreyfusia) tadomatsui</i> (Inouye 1945)	Anholocyclic 2°	<i>Abies</i>	Japan	54, 81
<i>Adelges (Adelges) tardoides</i> (Cholodkovsky 1911)	Holocyclic	<i>Larix</i>	Europe	23, 145
<i>Adelges (Adelges) tardus</i> (Dreyfus 1888)	Anholocyclic 1°	None	Europe	11, 145
<i>Adelges (Sacchiphantes) torii</i> (Eichhorn 1978)	Holocyclic	<i>Larix</i>	Japan	54
<i>Adelges (Aprastasia) tsugae</i> Annand 1924	Holocyclic	<i>Tsuga</i>	China, Japan, Western North America	4, 76, 166
<i>Adelges (Cholodkovskya) viridana</i> (Cholodkovsky 1896)	Anholocyclic 2°	<i>Larix</i>	Europe	143
<i>Adelges (Sacchiphantes) viridis</i> (Ratzeburg 1843)	Holocyclic	<i>Larix</i>	Europe	28, 136, 138
<i>Adelges (Cholodkovskya) viridula</i> (Cholodkovsky 1911)	Anholocyclic 2°	<i>Larix</i>	Northwestern Russia	145
<i>Pineus (Pineus) abietinus</i> Underwood & Balch 1964	Anholocyclic 2°	<i>Abies</i>	Western North America	155
<i>Pineus (Pineus) armandicola</i> Zhang, Zhong & Zhang 1992	Holocyclic	<i>Pinus</i>	China	94
<i>Pineus (Pineus) boernerii</i> Annand 1928	Anholocyclic 2°	<i>Pinus</i>	Unknown	4, 16, 99
<i>Pineus (Pineodes) boycei</i> Annand 1928	Unknown	Unknown	Unknown	4
<i>Pineus (Pineus) cembrae</i> (Cholodkovsky 1888)	Holocyclic	<i>Pinus</i>	Europe, Japan, China	28, 81, 168
<i>Pineus (Pineus) cladogenous</i> Fang & Sun 1985	Anholocyclic 2°	<i>Pinus</i>	China	56
<i>Pineus (Pineus) coloradensis</i> (Gillette 1907)	Anholocyclic 2°	<i>Pinus</i>	North America	4, 41, 99
<i>Pineus (Pineus) cortecicolus</i> Fang & Sun 1985	Anholocyclic 2°	<i>Pinus</i>	China	56
<i>Pineus (Pineus) engelmannii</i> Annand 1928	Unknown	Unknown	Western North America	4
<i>Pineus (Pineus) floccus</i> (Patch 1909)	Holocyclic	<i>Pinus</i>	Eastern North America	4, 117
<i>Pineus (Pineus) ghanii</i> Yaseen & Ghani 1971	Anholocyclic 2°	<i>Pinus</i>	Western Himalayas	164
<i>Pineus (Pineus) harukawai</i> Inouye 1945	Unknown	<i>Pinus</i>	Japan	81
<i>Pineus (Pineus) havrylenkoi</i> Blanchard 1944	Unknown	<i>Pinus</i>	Unknown	16a
<i>Pineus (Pineus) hosoyai</i> Inouye 1945	Unknown	<i>Pinus</i>	Japan	81
<i>Pineus (Pineus) kono-washiyai</i> Inouye 1945	Unknown	<i>Pinus</i>	Japan	81
<i>Pineus (Pineus) laevis</i> Maskell 1885	Unknown	<i>Pinus</i>	Unknown	98, 151
<i>Pineus (Pineus) matsumarai</i> Inouye 1945	Unknown	<i>Pinus</i>	Japan	81
<i>Pineus (Pineus) orientalis</i> (Dreyfus 1889)	Holocyclic	<i>Pinus</i>	Caucasus Mountains	86, 97
<i>Pineus (Pineus) patchae</i> Börner 1957	Unknown	None	North America	23

(Continued)

Table 1 (Continued)

Species <sup>a</sup>	Life cycle <sup>c</sup>	Secondary host genus	Native range	Reference(s)
<i>Pineus (Pineus)<sup>b</sup> pineoides</i> (Cholodkovsky 1903)	Anholocyclic 1°	None	Europe	97, 140, 154
<i>Pineus (Pineus) pini</i> (Macquart 1819)	Anholocyclic 2°	<i>Pinus</i>	Europe	16, 97
<i>Pineus (Pineodes) pinifoliae</i> (Fitch 1853)	Holocyclic	<i>Pinus</i>	North America	9, 38, 95, 117
<i>Pineus (Pineus) piniyunnanensis</i> Zhang, Zhong & Zhang 1992	Anholocyclic 2°	<i>Pinus</i>	China	169
<i>Pineus (Pineus) sichuananus</i> Zhang 1980	Unknown	Unknown	China	168
<i>Pineus (Pineus) similis</i> (Gillette 1907)	Anholocyclic 1°	None	North America	26, 36, 67
<i>Pineus (Pineus) simmondsi</i> Yaseen & Ghani 1971	Anholocyclic 2°	<i>Pinus</i>	Western Himalayas	164
<i>Pineus (Pineus)<sup>b</sup> strobi</i> (Hartig 1937)	Anholocyclic 2°	<i>Pinus</i>	Eastern North America	41, 122
<i>Pineus (Pineus) sylvestris</i> Annand 1928	Unknown	<i>Pinus</i>	North America	4
<i>Pineus (Pineus) wallichianae</i> Yaseen & Ghani 1971	Anholocyclic 2°	<i>Pinus</i>	Western Himalayas	164

<sup>a</sup>The genus name in parentheses corresponds to the classification system of Börner & Heinze (23).

<sup>b</sup>Species placed in the genus *Eopineus* by Steffan (144).

<sup>c</sup>Holocyclic species host alternate in at least part of their range. Anholocyclic species complete their entire life cycle on either *Picea* (Anholocyclic 1°) or on a secondary host genus (Anholocyclic 2°). Some anholocyclic species may in fact be holocyclic, but forms on the alternate host have not been described.

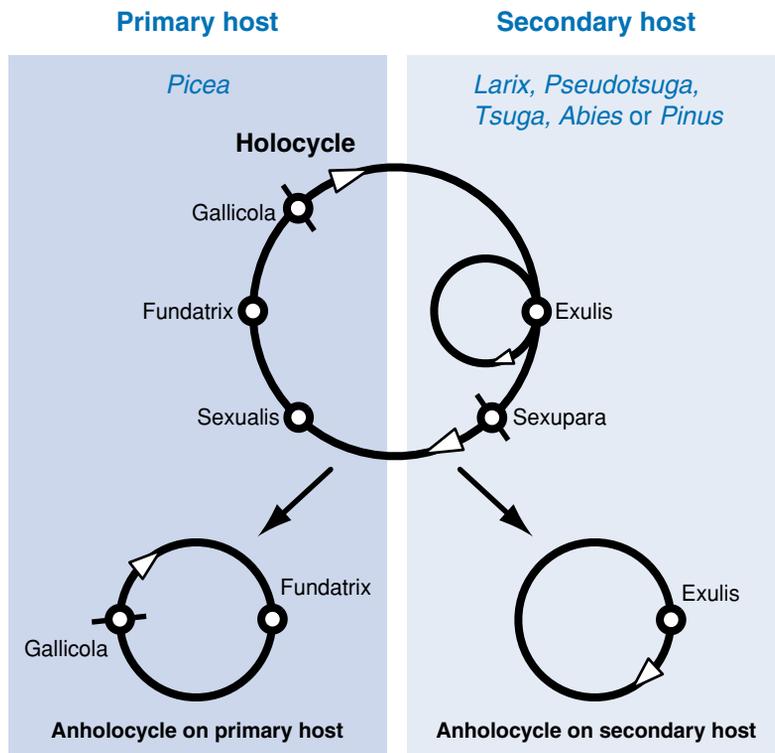
a single primary and secondary host genus. For example, *Pineus orientalis* can alternate between *Picea orientalis* and *Pinus sylvestris*, but it cannot survive on *Picea abies*, *Pinus strobus*, or *Pinus cembra* (145).

The nomenclature associated with the various adelgid generations can be confusing because different authors have used different systems. We use the nomenclature proposed by Marchal (97), which is the most concise and clearly defined and has been adopted by most adelgid researchers.

The winged individuals that migrate from the secondary to the primary host are called sexuparae (singular = sexupara; Latin for “those that bear the sexual generation”) (Figure 2). Upon arrival at a suitable *Picea* species, they lay eggs and die with their roof-like wings remaining to shelter the eggs (4). These eggs hatch and develop into the sexualis generation, consisting of mating females and males. Sexuales feed near the body of their dead mother and develop through four instars

(29, 95, 97; but see 34). They lack wings, are smaller than the parthenogenetic stages, and have relatively short stylets and long, slender, four-segmented antennae. Males are smaller, have longer legs, and are more active than females (4). After molting to the adult stage, sexuales of *A. cooleyi* (34) and *Pineus pinifoliae* (95) disperse toward the center of the tree where they mate and lay eggs.

After mating, a single, relatively large egg is laid that becomes the wingless fundatrix (Figure 3). Interestingly, mated females of some other taxa within the Aphidoidea, the Phylloxeridae (24, 68, 110), Pemphiginae (15), and Cerataphidini (92a), also lay only one egg. All these groups also host alternate and form galls. Reduction of fecundity to only one egg following the sexual generation is an unusual life-history strategy. This pattern has two consequences: It reduces the potential for genetic conflict in subsequent gall formation by ensuring that the progeny that form the gall belong to a single clone, and it allocates



**Figure 1**

Evolution of adelgid life cycles. Center: the host-alternating holocycle; lower left: the anholocycle on a primary host; and lower right: the anholocycle on a secondary host. Plain circles represent wingless generations and circles with bisecting lines represent winged generations. The sexualis, fundatrix, and gallicola are produced on a *Picea* primary host, and the exulis and sexupara are produced on an *Abies*, *Larix*, *Pseudotsuga*, *Tsuga*, or *Pinus* secondary host. The holocycle is ancestral and the anholocycles are derived. After anholocyclic lineages have lost the ability to migrate to the alternate host, they have permanently lost the sexual generation.

genetic variation among rather than within galls, making galls the effective units of selection at that stage of the life cycle.

The fundatrix crawls to and settles on or near a bud and then overwinters as an early-instar nymph. In the spring, she resumes feeding and induces swelling of the bud into a gall. After three nymphal instars the adult fundatrix lays a large clutch of eggs that become the gallicolae that migrate to and are enveloped by the developing gall. Formation of the basic gall structure is initiated by the fundatrix, and subsequent feeding by gallicolae stimulates further differentiation of gall tissue (114, 118, 126). The gallicolae feed inside the gall cham-

bers, where they pass through four nymphal instars (4, 135).

Adelgid galls, often described as pineapple galls because of their characteristic shape (**Figure 4**), are formed from spruce buds in which the developing leaves enlarge laterally and the margins merge into each other, forming multiple chambers inside which the insects feed (126). Feeding by the fundatrix induces a change from regular shoot tissue to gall tissue with increased nutrients and decreased defensive chemicals. Gall tissue contains larger cell nuclei, more lipids and starch (118, 126), less reducing sugars (130), and less phenolic compounds (90) than ungalled tissue.



**Figure 2**

*Adelges tsugae*  
sexupara on *Tsuga*  
*canadensis*.

Differences in the structure and appearance of galls among adelgid species on the same tree are due to differences in their stylet-probing behavior, settling site, and phenology (126).

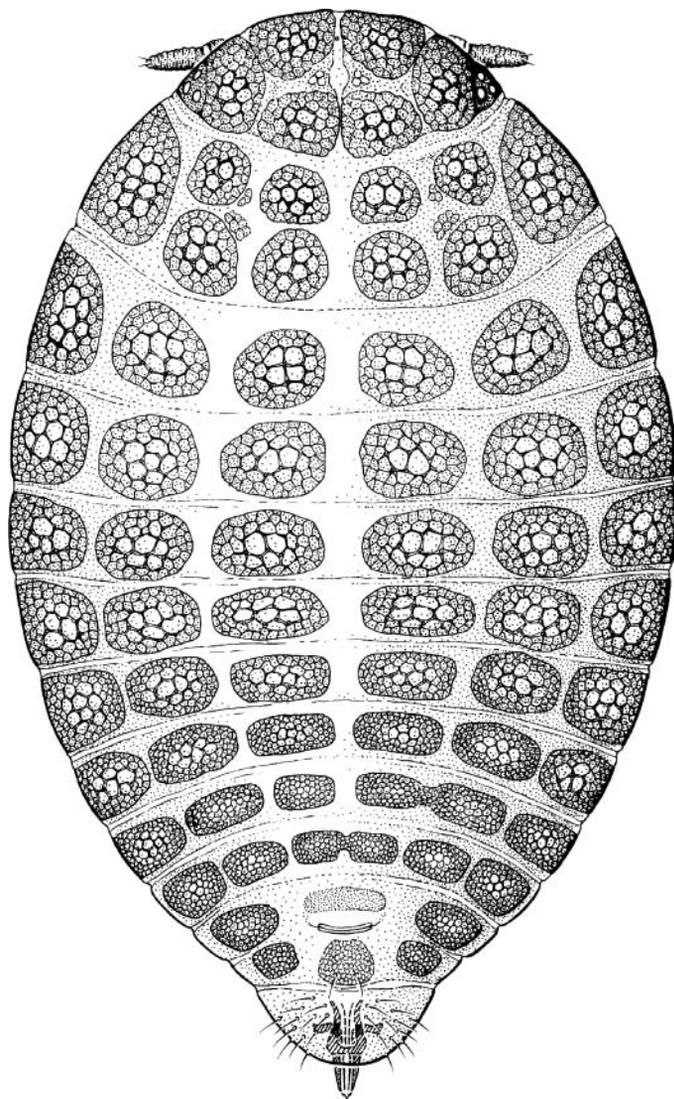
Arthur Church, a botanist who studied the evolution of plant structures, noted developmental and morphological similarities between the galls formed by *A. viridis* and primitive seed cones, especially of *Thuja* (Cupressaceae) (32). He suggested that gall formation involves the same chemical factors required for cone development. Galls can be induced by a fundatrix that is settled several centimeters from a bud (134) and by injection of adelgid salivary gland extracts (118), indicating that gall induction involves a chemical component. Whether the fundatrix produces a chemical stimulant de novo, or plant hormones are somehow manipulated, is not yet known.

Gall size is positively correlated with the number of insects in the gall and therefore has been used to estimate fundatrix fitness (104, 113, 133). Galls are larger when they are formed on shoots with more needles, are surrounded by more ungalled shoots, and are higher in the tree (57, 58, 115). Fay & Whitham (58) found that *A. cooleyi* fundatrices

preferentially settle on lower branches. Those that settle on the uppermost branches produce more than twice as many progeny but suffer much higher winter mortality.

In mid-summer the gall dries, causing the chambers to open. The gallicolae emerge, undergo a final molt into winged adults, and migrate to a secondary host. There they lay eggs and die within hours of settling on a suitable tree (62). The offspring of the gallicolae begin a series of generations consisting of wingless, parthenogenetic exules (singular = *exulis*; Latin for “one who is banished”) (Figure 5) on the secondary host.

Marchal (97) introduced the term sistentes (singular = sistens; Latin for “to halt”) for exules that have a period of diapause during the first instar and the term progredientes (singular = progrediens; Latin for “to proceed”) for exules that do not diapause and that molt from the first to second instar with no delay. Sistentes can be distinguished from progredientes by some or all of the following characters: heavier sclerotization, longer rostral stylets, fewer wax glands (but see Reference 100), reduced versus well-developed antennae, and three versus four molts (4, 8, 97, 122). Phenotypes that are intermediate between



**Figure 3**

*Adelges cooleyi* fundatrix showing the distribution of wax pores.

sistentes and progredientes have also been reported (136); consequently, care should be taken when distinguishing them on the basis of morphology alone, as the nomenclature properly refers to the behavior in addition to morphology.

Some adelgid species have a strict alternation of sistens and progrediens generations (e.g., *A. viridis*). Other species (e.g., *A. nordmanniana*) exhibit more plasticity, and over-

wintering sistens can give rise either to more sistens or to progredientes from the same clutch (2, 47, 116), the proportions of each being determined maternally (47) and regulated by photoperiod and temperature (128).

Newly hatched adelgids in all generations start out as crawlers that have longer legs and antennae than other instars and actively locate settling sites on the tree. With the exception of winged adults, the crawler is the only mobile stage in the adelgid life cycle. Depending on species and generation, exilis crawlers settle on needles (e.g., *A. cooleyi*, *A. pectinatae*), at the base of needles (e.g., *A. tsugae*), at the base of buds (e.g., *A. laricis*), or on the bark (e.g., *A. piceae*, *P. strobi*). Their stylets are inserted intercellularly and terminate inside cortical parenchyma cells, where they feed on the plant's stored nutrients (8, 118, 126, 165), or in phloem, where they feed on sap (1, 8, 116, 134), as is typical of most aphids (7).

The choice of settling site of exilis crawlers is due likely to a combination of environmental and chemical cues. *P. strobi* crawlers are positively phototactic (122). *A. piceae* crawlers are negatively geotactic, but this can be overcome by attraction to diffuse light; however, they are repelled by direct sunlight (8). The settling site can also depend on the adelgid generation within a species. For example, *A. cooleyi* progrediens crawlers prefer to settle on current-year needles of *Pseudotsuga menziesii*, while sistens crawlers prefer to settle on previous years' foliage (137). Crawlers and eggs disperse between trees passively via wind, small mammals, birds, deer, or humans (6, 8, 101, 163).

Some of the offspring of the overwintering sistens become winged sexuales that migrate back to the primary host, thus completing the cycle. The proportion of winged to wingless individuals is positively density-dependent and determined by postnatal cues (47, 102, 116, 156). Increased thigmotactic stimulation (52) and reduced dietary amino acids (116) have been suggested as the specific cues associated with crowding, but these have not been confirmed. The wingless exiles



**Figure 4**

Dried and opened gall of an unknown adelgid species in Shaanxi Province, China.

that do not migrate can overwinter as early-instar nymphs and therefore contribute to a continuous cycle of exules on the secondary host.

Frolowa (65) and Speyer (136) observed that sexuparae give rise to either all males or all females, resulting in parallel male and female cycles. Steffan (139) confirmed this and suggested that cytological factors are responsible. Eichhorn (50, 51) and Alles (2) questioned this result on the basis of field observations and rearing experiments, noting that exules from locally anholocyclic populations produce sexuparae that lay eggs that become all males, all females, or both males and females. Less is known about the behavior and population structure of the sexuales than any other generation, and the factors that influence sex ratio are not known. If adelgid sex ratios are indeed highly variable, then it would be interesting to explore its causes, constraints, and fitness consequences (74).

### ADELGID ANHOLOCYCLES

Adelgid species and populations that are anholocyclic experience only parthenogenetic reproduction on either a primary or secondary host. Sexual reproduction and host alternation

are strictly linked in all known adelgids: All host-alternating lineages have a sexual generation and all lineages that do not host alternate are entirely asexual.

The anholocyclic life cycle on *Picea* consists of two parthenogenetic generations, fundatrices and gallicolae (**Figure 1**, lower left). The entire cycle is completed within one year. As in the holocycle, fundatrices overwinter as



**Figure 5**

*Adelges cooleyi* exulis with eggs on *Pseudotsuga menziesii*.

nymphs and galls are formed in the spring. Winged gallicolae can disperse or can stay to lay eggs near the gall from which they emerged (84).

*Pineus pineoides* is unique among adelgid species in that it is restricted to *Picea* but does not produce galls (97, 154). The life cycle consists of only wingless parthenogenetic individuals that reside on the bark. Morphologically they are more similar to exules on secondary hosts than to the fundatrices or gallicolae normally found on spruce (140). *Pineus similis* which is anholocyclic on *Picea* is also unique in that gallicolae can sometimes be wingless and can occasionally settle, feed, and even lay eggs inside the gall (26, 36).

The anholocyclic life cycle on a secondary host (**Figure 1**, lower right) consists of a simple series of parthenogenetic exulis generations. The number of generations per year ranges from two to six depending on the species and on climate and host condition (5, 94, 97, 105). The pest species, *A. piceae* and *A. tsugae*, have this type of life cycle in their introduced ranges.

## ENDOSYMBIONTS

Endosymbiotic bacteria have been found in adelgids but have not been studied in nearly as much detail as in aphids. Adelgid primary endosymbionts are housed in special cells called bacteriocytes, while secondary endosymbionts are generally found outside of bacteriocytes (20). Profft (119), Steffan (144, 146), and Shields & Hirth (131) examined endosymbiont ultrastructure and their location in the insect. Recent work on sequencing bacterial genes and in situ hybridizations with specific probes has detected two types of endosymbionts within bacteriocytes of several *Adelges* and *Pineus* species; these bacteria belong to the same lineages as endosymbionts of aphids and other Sternorrhyncha (C. von Dohlen, personal communication).

Adelgid primary endosymbionts are transmitted vertically through the ovaries from mother to egg (131, 150). In aphids, primary

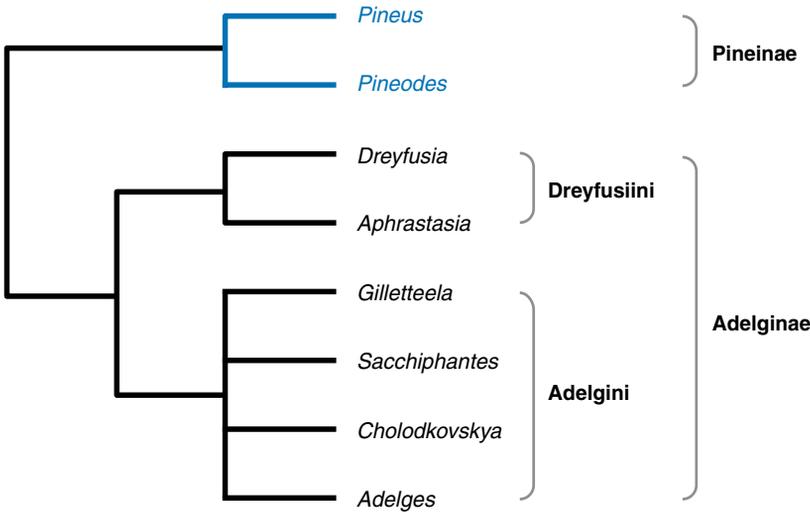
endosymbionts are necessary for survival because they synthesize essential amino acids that the insects cannot produce themselves (10), and secondary endosymbionts have been implicated in defense from parasitoids and pathogens (112, 129). The specific role of adelgid endosymbionts is not known, but treatment of *A. tsugae* with antibiotics killed their endosymbionts and resulted in death of the adelgids, suggesting that endosymbionts play a critical role in nutrition (131).

## PHYLOGENY AND SYSTEMATICS

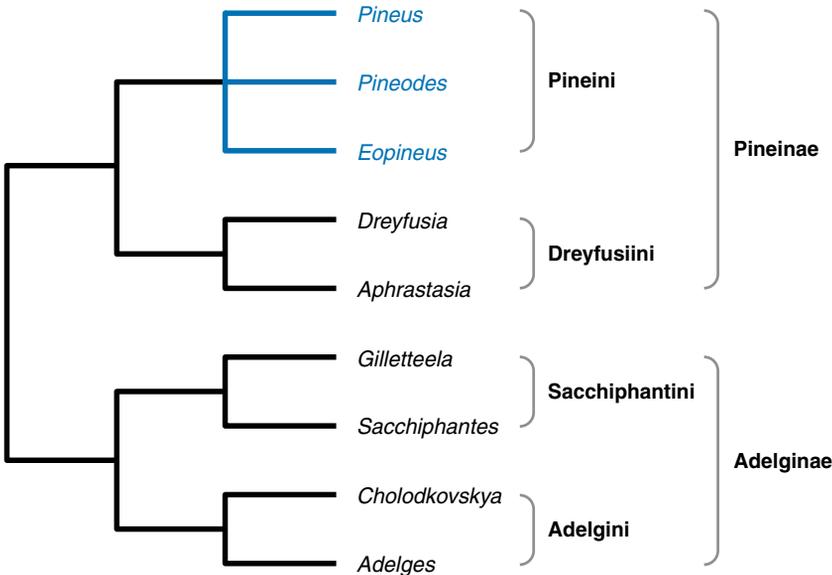
Adelgids are minute insects with simple morphology (**Figure 3**). First instars are typically 0.4 to 0.5 mm long, wingless adults 0.6 to 1.3 mm, and winged adults 1 to 2 mm (4, 15). Classification of adelgids based on morphology is difficult because their complex life cycles include many different forms within a single species. Adelgids also have more reduced morphology and less interspecific variation than their aphid relatives, perhaps because they have evolved smaller body sizes compared with the common ancestors of adelgids and aphids (109). The most important characters for species recognition are host plant information and the shape and distribution of the dorsal sclerites, wax plates, and wax glands of the first-instar settled sistentes (15, 23). Interspecific morphological differences are less apparent in adult insects, although it is possible in some cases to distinguish closely related species with adult characters (4, 12).

Currently, two systems are used to arrange adelgids into genera. The older system, developed primarily by Börner (22) and Cholodkovsky (29) and presented by Börner & Heinze (23), places adelgid species into eight genera. Annand (4) lumped adelgids into two genera distinguished by four (*Pineus*) or five (*Adelges*) pairs of abdominal spiracles. This system is preferred because the differences used to distinguish genera in the other system are considered too slight for this level of classification (4, 15, 61).

### Börner and Heinze 1957



### Steffan 1968



**Figure 6**

Graphical representations of adelgid classification from Börner & Heinze (23) and from Steffan (144). Blue branches correspond to *Pineus* and black branches correspond to *Adelges* from Annand (4).

While Börner (22) and Annand (4) agreed that five pairs of abdominal spiracles is ancestral and four is derived, their classification schemes are typological and not necessarily meant to reflect a hypothesis of

phylogenetic relationships. To our knowledge, Steffan proposed the only explicit hypothesis of phylogenetic relationships within Adelgidae (Figure 6). He used morphology, number of chromosomes, and the appearance

and location of endosymbiotic bacteria to modify Börner's taxonomy to reflect this hypothesis (144, 146).

A recent phylogenetic analysis used DNA sequence data from three mitochondrial and one nuclear gene to reconstruct relationships among adelgids (75a). The resulting phylogenetic tree recovered separate monophyletic groups of adelgid species associated with each secondary host genus (or, in the case of species that are anholocyclic on *Picea*, that are derived from a holocyclic species associated with that genus). Host plant specificity seems to have persisted through the history of Adelgidae, constraining the radiation of this group of insects and perhaps contributing to its low diversity. The molecular phylogeny also recovered two major clades corresponding to *Pineus* and *Adelges* of Annand (4), or Pineinae and Adelginae of Börner & Heinze (23). At the level of tribe and above, the molecular phylogeny agrees with the classification of Börner & Heinze (23) but differs from that of Steffan (144), who included *Dreyfusia* and *Aphrastasia* in Pineinae, erected a new tribe, Sacchiphantini, for *Gilletteela* and *Sacchiphantes*, and erected a new genus, *Eopineus*, for two species, *E. strobi* and *E. pineoides* (Figure 6). Several results of the molecular phylogeny differ from those of Börner & Heinze (23) and Steffan (144) at the genus level. For example, the authors place *A. tsugae*, which is associated with *Tsuga*, and *A. pectinatae*, which is associated with *Abies*, in the genus *Aphrastasia*. These species do not cluster in the molecular phylogeny, making *Aphrastasia* a polyphyletic taxon. A taxonomic revision is needed to reconcile the conflicting classification systems by incorporating new information about relationships in the Adelgidae.

Several groups of species in the Adelgidae have similar or identical morphologies but different life cycles. For example, *A. viridis*, which alternates between *Picea* and *Larix*, is morphologically similar both to *A. abietis*, which is only on *Picea*, and to *A. segregis*, which is only on *Larix* (141). Likewise, *A. nordmanniana* alternates between *Picea* and *Abies* while

*A. piceae* and other related species are only on *Abies* (44), and *P. orientalis* alternates between *Picea* and *Pinus* while *P. pini* is only on *Pinus* (97). Adelgid taxonomists have debated whether anholocyclic species that are morphologically identical to holocyclic species should be described as different species only on the basis of their difference in life cycle (21, 29, 141, 142). Ideally, designation of parthenogenetic lineages as separate species should be based on knowledge of their evolutionary history and the presence of clearly discernable, biologically significant differences (59). In general, adelgid taxonomists have considered it appropriate to describe an anholocyclic lineage as a new species if it has lost the ability to migrate to the alternate host and is therefore genetically isolated from its holocyclic counterpart, and if there are consistent morphological differences that distinguish the holocyclic lineage from its anholocyclic counterpart (50, 139). Current adelgid taxonomy reflects the best efforts to apply these criteria using rearing experiments and morphological comparisons. The addition of molecular methods could help resolve some of the outstanding taxonomic issues related to changes in life cycle by comparing morphological variation, behavior, and population genetics.

## BIOGEOGRAPHY

The fossil record of the Adelgidae is sparse, but some representatives have been found from the Pliocene and Pleistocene (79), and a fossilized adelgid gall from the Pleistocene was found in Japan (87). The extinct Elektraphididae, described from fossils dated to the Pliocene and Oligocene back to the Cretaceous-Tertiary boundary (77, 147), are thought to be the sister to the Adelgidae.

Examination of the historical biogeography of adelgid host plants may help explain phylogenetic patterns within Adelgidae. Some host-associated clades, such as those on *Larix* and *Pinus*, have representative species that are endemic to North America, Europe,

China, and Japan. For species associated with *Larix*, Steffan (138) proposed that during the Cretaceous, ancestral *Picea* and *Larix* were continuous across Eurasia and North America. During the Oligocene and Miocene, the climate changed, spruce and larch migrated and became disjunct in each of the three continents, and cospeciation between adelgids and their hosts occurred separately in each region. Other adelgid clades have more restricted distributions. For example, there are no adelgid species associated with *Tsuga* or *Abies* endemic to eastern North America (Table 1). The resulting lack of coevolved tree resistance and specialized natural enemy complexes is likely the reason that introduced adelgids have become such serious pests in this region.

## EVOLUTION OF ADELGID LIFE CYCLES

### Evolution of Host Alternation

Host alternation in most Aphididae usually involves migration between a woody primary host, where they undergo sexual reproduction and overwinter as cold-hardy eggs, and an herbaceous secondary host, where they produce a series of parthenogenetic generations (107). Woody plants are more nutritious in the spring and herbaceous plants are more nutritious later in the summer, suggesting a selective advantage to a one-year cycle that maximizes host nutrition (92). In addition, in temperate climates, the return to a woody primary host each fall is necessary because herbaceous hosts die back in the winter (132). In contrast, adelgids have a two-year cycle, have primary and secondary hosts with synchronous rather than complementary growth, and can overwinter as nymphs on either host. Cyclical parthenogenesis and polymorphism were preadaptations for the evolution of host alternation in all Aphidoidea (107), but a set of adaptations and constraints different from those in aphids are needed to explain host alternation in adelgids.

When considering the evolution of complex life cycles, it is helpful to bear in mind that selection can act simultaneously at different levels of organization: the individual, the clone, and the entire life cycle (80, 83, 149). In a multiple-generation complex life cycle, different phenotypes occupy different ecological niches, and the decoupling of developmental processes that determine phenotypic traits allows the different morphological forms to respond independently to different selective forces, resulting in increased fitness across the life cycle (107).

As in most host-alternating aphid taxa (40), the primary hosts of adelgids are more closely related to each other than are the secondary hosts. This finding, along with the restriction of the specialized sexual and gall-forming generations to *Picea*, has led adelgid taxonomists to assume an ancestral association with *Picea* followed by diversification as host alternation to other secondary hosts evolved (29, 109, 141). Why did ancestral adelgids evolve migration between alternate hosts rather than staying on their tree of origin or migrating to another tree of the same species? The number of extant lineages that do not host alternate makes clear that this is a viable evolutionary alternative under the right conditions. A host-alternating clone must have higher fitness than a clone that does not host alternate if alternation is to persist when primary and secondary hosts are present. Explanations for the evolution and maintenance of host alternation in aphids, which could also apply to adelgids, are fundatrix constraint (106, 109, 148, 157), enemy escape (158), bet hedging (71), and induced responses (160); they are not mutually exclusive. We focus here on the last hypothesis because more is known about the effects of induced plant responses on adelgid populations than about the factors implicated in the other hypotheses.

Induced responses are changes in plant suitability to herbivores that result from herbivore feeding. Rapidly induced responses are those that affect the herbivore generation causing the response, and delayed induced

responses are those that affect subsequent generations (75, 85). Delayed induced responses can have strong impacts on adelgid populations feeding on secondary hosts. Feeding by *A. piceae* on *Abies* causes an initial increase in adelgid survival corresponding to increased protein content of the bark, followed by bark resinosis, deformation of xylem, depletion of nutrients, death of phloem cells, disruption of water flow, rapid decline in adelgid survival, and often death of the tree (3, 31, 70). Similarly, populations of *A. tsugae* in eastern North America increase rapidly after infesting a healthy tree. This causes reduction in new growth the following year, forcing the adelgids to feed on less nutritious old growth and causing the population to crash (102). Populations of the holocyclic species *P. pinifoliae* are remarkably synchronized such that populations are almost entirely on either *Picea* or *Pinus* in alternate years (38, 39, 95). *Pinus* branches with alternating long and short internodes testify to the impact of adelgids in alternate years when radial growth is inhibited by heavy infestations (38).

The induced response to adelgid fundatrices feeding on *Picea* is a rapid, hypersensitive reaction that does not have the same delayed impact. Resistant tree genotypes have higher constitutive levels of phenolic compounds (153) that increase locally in the area surrounding the feeding site and are associated with the collapse and death of affected cells, whereas feeding on susceptible trees induces a gall (125, 152).

On secondary hosts, production of migrants allows an adelgid clone to escape crowded trees where nutrition is reduced. Regular alternation between tree species allows the primary host to recover while the population is on the secondary host, and vice versa. Migrating to another tree of the same species carries the risk of landing on a tree with equal or higher adelgid density, whereas switching to a different species decreases competition for resources. Even if the uninfested alternate host is not as nutritious as an un-

infested primary host, it may be better than an infested primary host. If adelgid fitness is measured as the number of individuals left at the end of a population cycle (159), a host-alternating clone could out-compete a clone that does not host alternate if selection at the level of the clone is strong enough to overcome the individual risk of mortality during migration.

This dynamic can be likened to a metapopulation (73) that is divided into subpopulations on discrete resource patches: primary and secondary hosts. The interaction between the insect and plant is unstable because of the delayed induced response on the secondary host, yet the population persists because individuals disperse to colonize the alternate host. Complementary host nutrition across years, rather than within a year, as in aphids, may be driving the host-alternating cycle.

Once this dynamic is in play, synchronization of population cycles between alternate hosts would emerge, dictated by the intensity of host plant response, the insect population growth rate, and the response to crowding. Parry and Spires (116) noted that *A. nordmannianae* produced a much higher proportion of winged migrants than did *A. cooleyi* at similar population densities. The species-specific reaction norm that relates crowding to production of winged migrants is expected to evolve to maximize clonal fitness depending on host-specific induced responses and the probability of landing on a suitable alternate host.

Once regular cycles emerge, different generations that are developmentally separate but still share a clonal genome can independently adapt to better utilize the different host plants and perform different tasks. This specialization leads to developmental and evolutionary constraints imposed on the possible sequence of morphological forms. In adelgids, only sistenteres can produce sexuparae, and only sexuparae can produce sexuales, resulting in the strict link between host-alternation and sexual reproduction that is evident in the extant Adelgidae.

## Loss of Host Alternation

Of the 50 adelgid species with well-described life cycles, 19 are holocyclic, 8 are anholocyclic on *Picea*, and 23 are anholocyclic on secondary hosts (**Table 1**). Some anholocyclic populations have retained the ability to migrate to an alternate host but have no suitable alternate hosts in proximity, whereas others have become obligately anholocyclic. For example, *A. tsugae*, which was introduced into eastern North America approximately 50 years ago from Japan (76), where it is presumed to be holocyclic, continues to produce sexuparae in the introduced range in a density-dependent manner despite the absence of a suitable primary host (100). *A. nordmannianae*, which is holocyclic in the Caucasus Mountains but anholocyclic on *Abies* in Europe, was able to complete its life cycle after its primary host, *Picea orientalis*, was planted in Switzerland (48). Other species appear to have had a longer separation from a suitable alternate host and are less likely to produce migrants. For example, *A. piceae* is anholocyclic on *Abies* in Europe (8). It is morphologically similar to the holocyclic *A. nordmannianae*, but some consistent differences allow discrimination between them (44). *A. piceae* does not typically produce sexuparae, but there are records of limited occurrence in Italy (12) and Canada (19). Likewise, *P. strobi*, which is anholocyclic on *Pinus*, rarely produces winged sexuparae (122). It seems likely that the ability to develop migratory forms would be lost quickly from a population of adelgids living in a region with no suitable alternate hosts because the migrants die without reproducing, creating strong selection against this trait.

Lack of migrants may not be the only isolating mechanism between holocyclic and anholocyclic lineages. Cholodkovsky (29) noted that gallicolae of the anholocyclic *A. abietis* that remain on *Picea* have long stylets, whereas those of the holocyclic *A. viridis* that migrate to *Larix* have short stylets. He suggested that this difference was the result of adaptation to their respective host plants. Like-

wise, Steffan (141) suggested that cytological factors prevent the production of sexual forms and therefore are involved in keeping holocyclic and anholocyclic lineages separate. Comparison of these traits with other potentially isolating mechanisms between holocyclic and anholocyclic species pairs would help us understand how obligately parthenogenetic adelgid species arise.

It is difficult to determine the degree of genetic isolation between holocyclic and anholocyclic lineages using only morphology and rearing experiments. Detailed population genetic analyses using rapidly evolving nuclear markers such as microsatellites could reveal genealogy, population structure, and the signatures of sexual versus asexual reproduction. This has been done successfully with some aphids (72, 161) and would be a powerful way to investigate adelgid speciation and to help resolve outstanding taxonomic questions.

The greater number of species that are anholocyclic on secondary hosts than on *Picea* suggests that this is a more likely route to obligate parthenogenesis in the Adelgidae. Evolution of anholocycly on a secondary host simply requires loss of the migratory form and continuation of the already existing exulis cycle, whereas evolution of anholocycly on *Picea* involves changes in gallicola behavior and reproduction. Gallicolae must shift from migrating to the secondary host to remaining on the primary host, and from producing exules to producing fundatrices. All the adelgid species that are anholocyclic on *Picea* are either in the *Larix*-associated clade or in the *Pinus*-associated clade (75a). *Larix* is unique in Pinaceae because it is deciduous, and adelgids that feed on *Larix* alternate between needles and stems to compensate for this. *Adelges laricis* sistentes settle at the base of larch buds, where they lay eggs that hatch into crawlers that migrate to the needles (29, 136). This behavioral similarity to the fundatrices that settle on *Picea* buds may explain why adelgids associated with *Larix* are more likely than those associated with other secondary host genera

to generate anholocyclic lineages on *Picea*. It may be easier for offspring of gallicolae that remain on *Picea* to produce galls, and thus complete the anholocycle, if their behavior is already similar to the behavior required for gall formation.

A possible cause of transition from holocyclicly to anholocyclicly is the separation of primary and secondary host geographic ranges due to climate change (108, 119, 138). Anholocyclic lineages arise in refugia that contain only a primary or a secondary host, and holocyclic lineages persist only in regions where suitable primary and secondary hosts remain in proximity. Theory suggests that asexual lineages will not persist for long periods because their decreased ability to purge deleterious mutations and to evolve resistance to parasites reduces their fitness relative to sexual lineages (88, 111). In the evolutionary history of Adelgidae, lineages that continue to be holocyclic are expected to persist longer than those that become obligately anholocyclic. The current low diversity of adelgids may therefore be a result of the high extinction rate of asexual lineages and limited opportunities for persistence of sexual lineages.

A complete reconstruction of the historical range expansions and contractions of *Picea* and secondary host genera compared with adelgid phylogeny, geographic distributions, and host associations would greatly advance our understanding of adelgid evolution. Although much progress has been made in elucidating conifer biogeography by using fossil and pollen deposits and by inferring migration patterns from the genetic relationships of extant tree populations (89, 123), the picture is still fragmented. We can use the European adelgid fauna to examine the effects of host plant biogeography on adelgid evolution because the historical range shifts of European conifers have been relatively well studied. Approximately 75,000 to 100,000 years ago, prior to the last glacial period, *Picea*, *Abies*, *Larix*, and *Pinus* had broad distributions in Europe (123). Subsequent periodic glaciation resulted in range shifts, with a maximum

contraction of *Picea* approximately 15,000 to 17,500 years ago (123). During the subsequent expansion of plant distributions during the warming period, *Picea*, *Larix*, and *Pinus* had similar recolonization patterns, whereas the ranges of *Picea* and *Abies* remained disjunct for a longer time, perhaps owing to competition (123). This may explain why there currently are indigenous adelgid species in the European Alps that alternate from *Picea abies* to *Larix* or to *Pinus* but only anholocyclic species on *Abies* (Table 1). Not only can comparisons of this sort help explain the life cycles of the adelgid species indigenous to a region, but the life cycles of the adelgids can also be used to make inferences about which conifer species have remained in overlap.

## PERSPECTIVES AND FUTURE RESEARCH NEEDS

Studies that explore the bottom-up interactions between adelgids and their host plants, the top-down interactions between adelgids and their natural enemies, and the tri-trophic interactions that unite them, are all important for understanding the ecology and evolution of Adelgidae. Efforts to control pest adelgids have focused on bottom-up strategies such as development of resistant tree genotypes and on top-down strategies such as biological control. We have focused on bottom-up rather than top-down interactions in this review because space was limited, not because of a lack of interesting and active research in this area. In fact, a remarkable feature of adelgid biology that has made biological control difficult to achieve is that the entire family lacks hymenopteran parasitoids (120, 162). This is surprising considering the number of aphid parasitoids and their importance in regulating aphid populations. It is not known whether this is simply a result of historical phylogenetic factors (96) or whether adelgids possess a unique defense against parasitoids.

We hope that by compiling this review, we have highlighted some appealing topics for which information is lacking and in which

more work could be done to further advance our knowledge of adelgid biology and evolution. Some of these areas include:

- The relative importance of host phylogeny and biogeography versus host chemistry in shaping phylogenetic relationships within Adelgidae is not known. Molecular phylogenetic studies that include a more complete sampling of adelgid species are needed to fully understand the history of the adelgid-conifer interaction.
  - A taxonomic revision of Adelgidae is critical. Proper association of all morphological forms in the life cycles of each species has not yet been achieved, and there is a need for reliable keys to distinguish adelgid species. Accurate taxonomic information is essential for
- Population genetic studies using nuclear DNA markers such as microsatellites could determine the degree of population differentiation, dispersal, and gene flow among populations and answer questions about the speciation process in Adelgidae.
  - Adelgids offer a unique system for studying the evolution of complex life cycles and life-history evolution. The factors that contribute to the maintenance of host alternation and sexual reproduction in adelgids have yet to be examined experimentally or with rigorous evolutionary models.

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