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benefit tremendously if methods can be developed that enable only male insects to be reared as required. For the medfly this
 genetically sexing technology is now available, leading to major
 improvements in program efficiency. As far as the process is
 concerned, more appropriate artificial diets for insect adults
 and larvae could make a major contribution through both
 improved economies and improved insect quality.

In many insect species, transgenic technology has been
developed and there is great interest in using it to improve the
SIT. A first application could be in replacing the use of fluore-
cent dyes by a transgenic marker. Suitable markers are available
and are currently undergoing evaluation in several pest species.
A second application is the use of transgenic technology to
develop molecular methods for genetic sexing. A caveat to the
use of any transgenic technology will be regulatory approval;
however, because the SIT uses sterile insects there is no risk of
vertical transmission of the transgene.

See Also the Following Articles
Agricultural Entomology • Biotechnology and Insects •
Integrated Pest Management • Rearing of Insects • Tsetse Fly

Further Reading
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Stenorrhyncha
(Jumping Plant Lice, Whiteflies, Aphids, and Scale Insects)

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The Stenorrhyncha is one of the suborders of the order
Hemiptera; it comprises some 16,000 described species.
It contains four major groups, all entirely phytophagous and
usually recognized as superfamilies: the Psylloidea (psylloids
or jumping plant lice), Aleyrodioidea (whiteflies), Aphidoidea
(aphids), and Coccoidea (scale insects or coccoids). The name
Stenorrhyncha (from the Greek sternon, meaning chest, and
rhynchos, meaning nose or snout) refers to the location of the
mouthparts on the underside of the insect, between the bases
of the front legs, although sometimes the mouthparts are
lacking in the adult.

OVERVIEW OF STENORRHYNCHA

Insects belonging to the Hemiptera are unique in having their
mouthparts forming a rostrum that comprises mandibles and
maxillae modified as needle- or thread-like styles lying in a
grooved labium. Two pairs of styles interlock to form two
canals, one delivering saliva and the other taking up plant or
animal fluid. The Stenorrhyncha is widely accepted as the
sister group to the rest of the Hemiptera. It is a well-defined
group diagnosed by the position of the rostrum and the presen-
tion of only one or two segments on each tarsus (the part of
the leg most distant from the body and bearing one or two claws);
in most other hemipterans there are three tarsal segments.

Stenorrhynchans use their styles to probe plant tissues
intracellularly (into or through plant cells) or intercellularly
(between plant cells). The tips of the styles always enter cells
at the site of ingestion, which is often phloem-sieve elements.
Generally, stylet penetration is accompanied by secretion of a
solidifying saliva that forms a sheath around the styles. Other
hemipterans mostly probe intracellularly, may or may not
secrete salivary sheaths, and ingest from a wider variety of plant
or animal tissues. Most stenorrhynchans are phloem feeders,
and thus have a diet rich in carbohydrates (sugars) and defi-
cient in amino acids and other nitrogenous compounds.
Generally, there is an intimate association with intracellular
bacteria, called endosymbionts, which are housed in special
tissue (bacteriomes or mycetomes) and contribute nutrition
to the insect host.

Stenorrhynchan excreta is often a sticky, sugary liquid
called honeydew that often contaminates foliage; it serves as
a substrate for the growth of black sooty mold fungi that can
impede photosynthesis and reduce plant vigor. Honeydew often
attracts ants that may protect the stenorrhynchans from their
natural enemies, especially predatory and parasitic insects.

Adult jumping plant lice, whiteflies, and many adult aphids
have two pairs of wings. All adult female scale insects and
most adult female aphids are wingless (apterous). Adult male
scale insects usually resemble small flies (order Diptera) in
having the hind wings reduced to small balancers (halteres),
although sometimes the halteres are absent; in a few scale
insect species males are apterous. The absence of wings in
adult females of scale insects and many aphids means that the
immature stages (nymphs) of these groups can be difficult to
distinguish from their adults.

Evolutionary interpretations of morphology have suggested
either that whiteflies are sister to aphids + scale insects, with
psylloids sister to all three, or that whiteflies + psylloids are sister to aphids + scale insects. Phylogenetic analysis of nucleotide sequences (of small subunit rDNA, also called 18S rDNA) supports the former hypothesis that Psyllioidea is the sister group to the other sternorrhynchnans. Some of the morphological traits shared by Aleyrodoidea and Psyllioidea are ancestral features (plesiomorphies), such as two, similar-sized, tarsal segments (the first tarsal segment is reduced or absent in aphids and coccoids) and good jumping ability. Also both groups have pedunculate eggs, i.e., one end of the egg has a short stalk or narrow extension (Fig. 1). Whiteflies, aphids, and scale insects all have Malpighian tubules (filamentous excretory organs) reduced in number or absent and their gut often has a well-developed filter chamber that allows most of the water in ingested sap to bypass the absorptive part of the midgut. In contrast, psylloids have four Malpighian tubules (an ancestral feature found in other Hemiptera) and possess only a rudimentary filter chamber.

PSYLLIOIDEA (JUMPING PLANT LICE)

Worldwide, there are about 2500 described species of psylloids or jumping plant lice. Sometimes the common name "psyllids" is applied to all jumping plant lice but this name may cause confusion because it is also the common name for one family of psylloids, the Psyllidae. The greatest abundance and species richness of psylloids are found in tropical and south temperate regions, where many new species await discovery. In the Northern Hemisphere, for example, fewer than 100 species occur in Britain and about 300 species are known from North America. Adult psyllids are small, ranging in length from 0.2 to 8.0 mm, and superficially resemble miniature cicadas or small leafhoppers, but are distinguished by their multisegmented antennae. Their common name derives from the ability of adults to jump backward when disturbed. All psylloids feed by sucking sap, mostly of woody dicotyledonous plants. They ingest sap from a variety of tissue sources, including phloem, xylem, and mesophyll parenchyma, and thus are not phloem specialists like most other sternorrhynchnans. Psyllid nymphs are either free living, gall inducing, or lep forming; lerps are manufactured sugary and starchy covers or scales under which the nymphs live. Some species of jumping plant lice are pests of cultivated plants, with damage resulting from loss of plant sap, toxins in the saliva, and/or disease caused by transmitted microorganisms.

Evolution and Classification

Historically, the classification of psyllids was based on the well-known, but relatively species-poor, Holarctic fauna. Expanding knowledge of the diverse tropical and south temperate faunas has led to better understanding of relationships and hence a more natural classification. The system used here is based on that of White and Hodkinson presented in 1985, with emendations suggested by D. Burckhardt and D. Hollis. In this system, six families of extant psyllid species are recognized (with each of the first four families listed here having 10 or fewer genera): Calophyidae, Carsididae, Homotomidae, Phacopteronidae, Psylidae (includes the Aphalaridae, Lividae, and Spondyliaispidae, recognized by some authors; about 120 genera), and Triozidae (over 40 genera).

Many species of the predominantly Neotropical and tropical/subtropical Asian family Calophyidae feed on plants in the Anacardiaceae. Carsididae is almost entirely pantropical in distribution and is restricted to the related plant families Bombacaceae, Malvaceae, and Sterculiaceae. The Homotomidae is predominantly from the Old World tropics and feeds almost exclusively on figs (Moraceae: Ficus). The Phacopteronidae occurs in tropical Asia, Africa, and the Americas and many species feed on plants in the Meliaceae. The Psylidae is the largest family, but it is heterogeneous morphologically. A large number of psyllids are associated with legumes (Fabaceae), although the speciose subfamily Spondyliaispidae specializes on Eugenia (Myrtaceae). Many species of Spondyliaispidae produce lerps or induce leaf galls that they plug with lerp substance. The Triozidae is cosmopolitan and has wide-ranging host preferences.

The fossil record of the Psyllioidea extends back into the Permian (>270 mya). The families Cicadopsyllidae, Liadopsyllidae, and Proteopsyllidae are known only as fossils, and the extant families probably diversified in the Cretaceous. Relationships among psylloid higher groups (families and subfamilies) are largely unresolved.

Life History

Reproduction is almost always sexual. There are seven life stages (Fig. 1): the egg, which is stalked; five instars; and the adult. With the sexes in about equal numbers. Eggs are either completely inserted into plant tissue or inserted by just the stalk (peduncle) through which water is absorbed. Depending on species, each female may lay as few as 20 to more than 1000 eggs. In cold temperate regions, psylloids frequently have only
a single generation per year (univoltine). In warmer climates, development continues year round, often with several to many generations per year. Species with multiple generations per year (polyvoltine) are more likely to have population outbreaks than univoltine or bivoltine species.

Morphology

Identification is based primarily on adult characteristics, with males being most important for species-level determinations, although features of the female terminalia are sometimes used. The fifth instar can materially aid identification in many groups. Adult males and females are morphologically similar, except that males are often smaller and have different genitalia and thus different abdominal shapes. In a few species the sexes are color dimorphic, and there is often a seasonal color dimorphism. Body coloration or the pattern of markings can be diagnostic of species. The size and shape of the head and its appendages provide useful taxonomic characters. Immature psyllids (Fig. 2) are usually characteristically flattened dorsoventrally and many secrete wax.

Behavior and Ecology

Adult psyllids disperse over short distances by jumping or flying, but many species may travel long distances on air currents. The adults of a number of species are known to stridulate as a method of mate attraction. Mating behavior is often rudimentary, but precopulatory darting movements and wing flicking have been observed in some species of Spondylaspisdinae.

The habits of nymphs vary among the different taxonomic groups. Nymphs of many species are naked, although often covered in waxy body secretions, and live exposed on the shoots of their host plant. Others induce galls of various complexity, from simple pits in leaves to round or elongate structures that totally enclose the nymphs. A third lifestyle is for the nymphs to develop on foliage but protected under scale-like covers called lerps. Each lerp is formed of substances eliminated from the insect’s gut (a special kind of liquid “feces” that is different from honeydew) or of a mixture of “feces” intermingled with wax filaments (exuded from pores in the anal plate). The “feces” of at least some species are composed of starch, especially amylose and amylopeptin, synthesized in the insect’s gut. The insect builds the lerp by moving its abdomen back and forth while squeezing out the liquid excreta (like glue from a tube), which rapidly hardens to form a lacework of filaments. Lerps have various shapes and sizes, from simple cones to fans or lacy shell-like structures, and often are of diagnostic use. They vary in color from white to cream or brown and may be opaque or transparent. Some lerp-formers (e.g., Glycaspis spp.) produce copious honeydew, whereas others (e.g., Cardiaspina spp.) produce very little or none.

Most species are specialist feeders as nymphs, with many species restricted to one plant genus or even a single species and often to particular host structures (leaves, new shoots, etc.) or growth stages (either young or mature foliage). Almost all psyllids develop on dicots, a few on monocots or conifers, but none on ferns. In cool-temperate climates, some species overwinter as adults on evergreens, returning to their true hosts in spring, when eggs are laid. Host selection appears to involve taste rather than olfaction. Adults frequently are less discriminating than nymphs and thus host plants are defined as those on which nymphs can complete their development to adulthood. Nymphaal feeding frequently damages the host plant (e.g., premature leaf senescence), whereas adult feeding usually causes little injury. Large natural increases, or outbreaks, in psyllid populations appear to result from changes in the suitability of their food supply, rather than from reduction in numbers of predators or parasitoids. Many psyllid species have a mutualistic association with honeydew-seeking ants.

Notable Pest Species and Their Control

Some species of jumping plant lice have become pests of plantation trees. For example, since the mid-1990s, several species of Australian Psyllidae have become pests of South American plantations of Eucalyptus. In particular, the eucalypt shoot psyllid Blastopisylla occidentalis, the blue gum psyllid Ctenartryaina eucalypti, and Ctenartryaina spatulata have caused considerable damage. In western North America, Australian psyllid pests appeared in the early 1980s, with B. occidentalis, C. eucalypti, the tristania psyllid Ctenartryaina longicauda, the red gum lerp psyllid Glycaspis brimblecombei, and the lemon gum lerp psyllid Eucalyptolygma maidenii all established in California.

Two of the world’s most serious citrus pests are the Asian citrus psylla (or psyllid), Diaphorina citri (Psyllidae), and the African citrus psylla, Triozoa erytreae (Trioziidae). Damage to citrus derives from direct feeding (removing sap), development of sooty mold on honeydew, and, most importantly, from transmission of phloem-limited bacteria (Liberobacter africanum and L. asiaticum) that cause a disease called citrus greening.
The most characteristic symptom is a yellow-green mottling associated with dieback of shoots and leaves, followed by subsequent deterioration of fruit quality. Adults and nymphs of both psyllid species can transmit both diseases.

Other than the citrus pests, the most economically important psyllids of temperate and subtropical areas feed on cultivated apple and pear trees. *Cacopsylla mali* (Psyllidae) and related species cause various kinds of damage to apples. Pears also host a suite of *Cacopsylla* species, especially *C. pyricola*, which can transmit the virus that causes pear decline.

*Triozia* species (Triozidae) occur as pests on persimmons, cultivated fig, and carrots. *Paratriozia cockerelli* (Triozidae) feeds on potatoes, tomatoes, and other Solanaceae; nymphal saliva contains phytotoxins that cause "psyllid yellows" in potato (reducing tuber growth) and sometimes in tomato. The leucaena louse, *Heteropsylla cubana* (Psyllidae), which is native to the Caribbean, has become a pest of the tropical leguminous tree *Leucaena leucocephala* in several parts of the world where it is variously planted for timber, fuel, animal fodder, or shade for other crops and or because it fixes nitrogen and tolerates drought.

Recorded parasitoids are mostly psyllid specialists, but there is little evidence of parasitoid-host specificity. Worldwide a number of wasp species, especially from the families Encyrtidae (e.g., *Psyllaphagus* spp.) and Eulophidae (e.g., *Tamarixia* spp.), are parasitic on psyllids. In Europe, cecidomyiid flies (*Endopsylla*) are parasitic on some adult psyllid pests (e.g., *Cacopsylla* spp.).

**ALEYRODOIDEA (WHITEFLIES)**

Members of the Aleyrodidae derive their common name from the powdery, white waxy secretion preened over the body and wings of most adults. The Greek root *aleyro*-, found in many whitefly names, means flour. Adults of both sexes are tiny, delicate, and free flying. They have a wingspan of up to 4 mm, but usually about 2 mm, and resemble minute moths. They are a familiar sight to many home gardeners because, when infestations are heavy, the adults will fly up en masse if disturbed from the foliage of favored host plants. The group occurs worldwide, although few whiteflies occur in the cooler temperate regions. About 1450 species are described, with perhaps two or three times as many species awaiting collection and formal taxonomic study. All adults and nymphs feed by ingesting phloem sap and several species are serious plant pests.

**Evolution and Classification**

All whitefly species belong to one family, Aleyrodidae, which is divided into just two extant subfamilies, the Aleurodicinae and Aleyrodinae. The Aleurodicinae contains 17 genera and just over 100 described species, mostly from the Neotropics (Central and South America and the Caribbean). All other species (in more than 110 genera) belong to the Aleyrodinae, which has a mostly pantropical distribution. These two subfamilies are defined on both adult and nymphal features, whereas species and genera are diagnosed mainly or entirely on characters of the fourth instar, usually known as a puparium. The Aleurodicinae generally have larger adults with more complex wing venation than those of the Aleyrodinae (Fig. 3).

Whiteflies are rarely fossilized because they have small and delicate bodies. The known fossils are preserved mostly in Cretaceous and Tertiary amber with one record from the Upper Jurassic. The two modern subfamilies probably diverged during the Cretaceous, whereas the Aleyrodoidae may have originated in the Late Permian or even earlier.

**Life History**

Reproduction is usually sexual, with fertilized eggs producing females and unfertilized eggs producing males (arhenotoky or archeonotokous parthenogenesis); unmated females lay only haploid eggs. A few species produce only females (thelotoky or thletotokous parthenogenesis). There are six life stages (Fig. 4): the egg stage; the first instar, in which the nymph is often called a crawler; the second and third instars, in which the nymphs are sessile; the fourth instar or last nymphal stage, at the end
of which the insect is usually referred to as a "pupa," or a "puparium," (Fig. 5) although it is not a true pupa as seen in holometabolous insects as there is no molt to a totally non-feeding, "resting" stage; and, finally, the adult (or imaginal) stage. After the emergence of the adult, the empty cuticle (exuviae) is often called a "pupal case."

Whitefly eggs are usually attached to the underside of leaves by a short stalk, the pedicel, through which water is absorbed from the plant. Eggs are often laid in circles or arcs, and egg batches are frequently conspicuous because of a dusting of white wax. First instars usually settle adjacent to the eggs from which they hatched. In most species, development occurs on the underside of leaves. After the first molt the nymphs become immobile and cannot move to a new site if food quality deteriorates. During the fourth instar, feeding ceases and the insect transforms into the winged adult.

Species such as the greenhouse whitefly (Trialeurodes vaporariorum) can breed continually in greenhouses or indoors. Those whitefly species that have economic impact have several to many generations per year, but many species are thought to have only one or two generations annually.

Morphology

Historically, pupalial rather than adult characteristics have been used to recognize species and genera, although adults do display many taxonomically useful characteristics. Seasonal dimorphism, as seen in many aphid species, is uncommon but occurs in the puparia of a few temperate species. Male (Fig. 3) and female whiteflies are similar in appearance except for their genitalia, but males are often smaller than females of their own species. The body and wings are dusted with powdery wax emanating from large, paired wax plates on the underside of the abdomen and thus adults most commonly appear whitish or grayish even if the body color is yellow, brown, or red or if they are darkly sclerotized. The male genitalia (the claspers or parameres and the intromittent organ or aedeagus) are more informative taxonomically than the female genitalia (ovipositor and associated structures).

Nymphs of all stages (Fig. 4) superficially resemble scale insects (Coccoidea) and frequently have ornate wax secretions in later instars. First instars have functional legs, but nymphs of the subsequent three instars have vestigial appendages and are immobile. The anus of all nympha1 stages (and adults) opens in a special pit called the vasisiform orifice (Fig. 5), located dorsally near the posterior end of the abdomen. It comprises a depression with a sclerotized border, a dorsal flap (the operculum), and a tongue-shaped structure (the lingula). The anus opens under the operculum, which covers at least the base of the lingula; each droplet of anal excreta (honeydew) that accumulates is catapulted away by an upward flick of the lingula, which is the only mobile body part in instars II to IV.

Puparia are mostly oval or elongate-oval, 0.5 to 2.0 mm in length, with the body margin either smooth or variously sculptured. Color varies from transparent to white, brown, or black. Waxes also contribute to the puparial appearance and may be transparent, translucent, iridescent, or opaque, usually colored white or grayish; mechanical color (iridescence) may be blue, turquoise, bottle-green, or pearly white. Transparent wax occurs in a thin layer over the body or as a marginal fringe and/or dorsal "spines." Opaque wax may occur in powdery deposits, loose mats, or filaments, or be defined as tufts or rays, and is exuded from a variety of pores and tubes in the cuticle.

Behavior and Ecology

Adult males of a few whitefly species, especially Bemisia tabaci and T. vaporariorum, have been observed to display courtship
behavior prior to mating, including abdominal oscillations that result in acoustic signals caused by substrate-borne vibrations. Females may produce sex pheromones to attract males. Adult whiteflies will fly short distances, if disturbed from their host plant. They also undertake longer migratory flights, which are air-current dependent because whiteflies are weak fliers. They have complex host-finding and host-orientation behaviors, involving at least attraction to particular colors, especially yellow or yellow-green.

Whiteflies feed from plant vascular tissue and all feeding stages produce copious quantities of honeydew, yet relatively few species are ant attended. Most whitefly species appear to be oligophagous, with few known to be monophagous; however, polyphagous species are the best documented because they are most likely to be pests. Whitefly host plants are almost entirely flowering plants (angiosperms), especially woody dicots; relatively few species of whiteflies are found on herbs, grasses, ferns, or palms.

The morphology of the puparia of some species has been shown to vary depending on the species of plant that is acting as host, probably because of differences in the nature of the plant surfaces. For example, the size, number, and position of setae of the puparia can be correlated with leaf hairiness in some species (e.g., *B. tabaci*). These phenotypes of the same species often look very different from each other and this phenomenon can confound identification. This variation is especially a problem among polyphagous species in the genera *Bemisia* and *Trialeurodes*.

### Notable Pest Species and Their Control

The feeding activity of many whiteflies damages their host plants and some species are known or believed to transmit diseases, especially those caused by viruses. Feeding can cause excessive sap loss as well as physiological changes in host tissues, such as leaf discoloration, wilting and premature shedding, and fouling by honeydew. The most serious aleyrodid pests are those of orchards (especially citrus), greenhouse crops, and vegetable field crops, and a few pest species are almost cosmopolitan in distribution. The past 2 decades have seen an increase in the pest status of certain whiteflies, probably because of the development of aggressive strains that are more fecund, are more efficient virus vectors, and/or have broader host ranges. Successful whitefly control depends upon an appropriate integrated pest management program in which natural enemies are protected or augmented. A number of groups of parasitic wasps (particularly Eulophidae and Aphelinidae) specialize on whiteflies, and useful predators include some ladybird beetles (Coccinellidae). Whiteflies are attacked also by pathogenic fungi, especially *Achersonia* species.

One of the most important pests is the polyphagous tobacco or sweetpotato whitefly, *B. tabaci*, which occurs predominantly in tropical and subtropical regions and on protected crops elsewhere. It feeds on numerous fiber, food, and ornamental plants, and damage is exacerbated by its ability to vector more than 70 different viruses. *B. tabaci* exists in many biotypes or strains, and one virulent form, biotype B, sometimes is recognized controversially as a separate species, named *Bemisia argentifolii* (the silverleaf whitefly). Effective biological control of *Bemisia* whiteflies is possible using host-specific parasitoids, such as wasps of *Encarsia* and *Eretmocerus* species (Aphelinidae).

The polyphagous greenhouse whitefly, *T. vaporariorum*, occurs worldwide in greenhouses and on indoor plants; the aphelinid wasp parasitoid *Encarsia formosa* is an important biological control agent. *Aleurodicus destructor* and spiraling whitefly, *A. dispersus*, are polyphagous pests with abundant wax secretions covering the puparia. Spiral whiteflies are parasitized by wasps of *Aleurotonus vitatus* (Eulophidae) and *Encarsia* species, including *E. guadeloupae* (Aphelinidae), which can reduce the whitefly populations. *Siphoninus phillyreae*, perhaps of Middle Eastern origin, and *Parabemisia myricae* from Japan are pests of fruit trees and have extended their ranges into the Mediterranean region and parts of the United States. The Indian species *Vasavadius* (formerly *Auleurococcus*) *indicus* now attacks rice in West Africa. The woolly whitefly, *Aleurothrixus floccosus*, which is endemic to the Americas, has been introduced accidentally into Africa and Southeast Asia, where it is a pest, especially of citrus. *Dialeurodes citri* and *Singiella* (formerly *Dialeurodes*) *citrifoli* are widespread pests of citrus, with *D. citri* attacking a wider range of other plants than does *S. citri*.

### APHIDOIDEA (APHIDS)

Aphids are small soft-bodied insects, ranging from 1 to 8 mm in length. They are usually found living in aggregations on rapidly growing parts of their host plants and occur predominantly in the northern temperate regions of the world. More than 4400 species are known. The life cycles of aphids are frequently complex and usually include parthenogenetic (or asexual), but often also sexual, reproduction; many species display host alternation in which cyclical parthenogenesis is combined with the obligate use of two unrelated host plants. Also many aphids produce either eggs or living young at different parts of the cycle. Adults may be winged (alate) or wingless (apteral). Most aphids can increase their population size rapidly because of parthenogenetic production of live young combined with "generational telescoping," whereby a mother aphid carries both her daughters and their daughters (i.e., embryos within embryos). Aphid feeding activities can have deleterious effects on their host plants mainly via sap removal and/or virus transmission.

### Evolution and Classification

The Aphidoidea contains three families: *Phylloxeridae*, *Adelgidae*, and *Aphididae*. Strictly speaking, the common name of the entire group should be "aphidoids," but "aphids" is used almost universally as a collective name. Very occasionally the name "aphids" has been applied to just members of
the Aphididae, which should more properly be referred to as "aphidids."

The Phylloxeridae contains about 75 species, in eight genera, divided between two tribes. The Phylloxerini has seven genera, feeding mostly on oaks (Fagaceae: Quercus), or hickory and pecans (Juglandaceae: Carya), but with one pest species on grape vines (Vitaceae: Vitis). The Phylloxerini has a single genus associated with the willow family (Salicaceae). The Phylloxerae is probably the oldest extant family, although only one fossil (Palaephylloxera from the Lower Miocene) is known. Many phylloxerid species induce galls on their host plants; only a few species are host alternating.

Conifer woolly aphids, the Adelgidae, belong to two genera and about 50 species and are entirely Holarctic in distribution. Adelgids induce galls on their primary host, spruce (Picea), and move to other conifers as alternate hosts.

The largest family, Aphididae, has been divided into a number of subfamilies and tribes, but different authors frequently use different classifications. The 10 subfamilies listed here are those recognized in the monographs by R. L. Blackman and V. F. Eastop: Anoeicinae (34 species), Aphidinae (over 2700 species), Calaphidinae (including the Drepanosiphinae, Thelaxinae, and several other groups treated as subfamilies by some other authors; 400 species), Chaitophorinae (164 species), Eriostomatinae (formerly Pemphiginae: 319 species), Greenideinae (151 species), Hormaphidinae (176 species), Lachninae (355 species), Mindarininae (5 species), and Phloeomyzinae (1 species).

The oldest aphid fossils are from the Triassic (at ca. 230 mya) but aphids may have originated in the Permian. Phylogenetic analysis of molecular data suggests that aphids underwent a rapid radiation into the current tribes after shifting from gymnosperms to angiosperms some time during the Upper Cretaceous. Furthermore, the ancestral aphid probably had a simple life cycle with host alternation evolving independently in each of the families and perhaps several times within the Aphididae.

Life History

There are six stages in the life history of an individual aphid: the egg or embryonic stage, four instars, and the adult. Aphids have evolved a range of annual or biennial life cycles and other adaptive strategies that often vary within as well as among species. This complexity can complicate the study of aphid biology. Furthermore, aphidologists have developed a special nomenclature for the different life stages and types. Life cycles are called holocyclic (Fig. 6) if a sexually reproducing generation is present or anholocyclic if the sexual generation is absent. A typical complete cycle (holocycle) consists of a single generation of sexual morphs (sexuales) and several to many generations of only parthenogenetic females. In the sexual generation, males mate with females to produce fertilized eggs, which are all female. Each egg gives rise to a wingless "foundress" or "stem mother" (fundatrix) that gives rise to a lineage of parthenogenetic females. The parthenogenetic descendants of a single foundress are called collectively a clone and are identical genetically but may be of different
phenotypes (morphs). The adults may be apterae or alatae, depending on environmental conditions. In Aphididae, parthenogenetic females (viviparae) give birth to live young, whereas the sexual females (oviparae) lay eggs. In Adelgidae and Phylloxeridae, females lay eggs during both the sexual and the asexual phases of reproduction. The phenomenon of cyclical parthenogenesis is a key feature of aphid biology. Some aphids have lost, or can facultatively lose, the sexual part of the life cycle (a condition then called anholocycly). It is common for aphids to have 15 to 20 generations per year, with up to 40 in tropical climates.

Most aphids are monoecious (Fig. 6A), i.e., they undergo all phases of their life cycle on one host plant or on a small number of closely related hosts. About 10% of aphids are heteroecious (Fig. 6B), having more complex life cycles involving host alternation (heteroecy). The sexual morphs mate and the oviparae lay eggs on the primary host (often a woody plant); however, a regular move occurs to another, unrelated plant, the secondary host (which may be either herbaceous or woody), on which the parthenogenetic generations live. The aphids must return to their primary host for the next sexual generation. Host alternation may occur as part of a 1-year (annual) life cycle, as in many Aphididae, or as a 2-year (biennial) life cycle, as in Adelgidae. In the Aphididae, in temperate climates, alternation is frequently obligate, overcoming the twin problems of poor sap flow in woody primary hosts in summer and the death of many herbs in winter.

Morphology

Aphids are highly polymorphic, with most species occurring in several different forms or morphs. In individuals destined to be winged as adults, the wing buds are usually apparent after the second nymphal molt. Most common aphid species are soft-bodied and green in color, but dark and brightly colored species and a few hard-bodied species also occur. Nymphs superficially resemble adults except that they are smaller in size and never have wings. Aphids usually have two prominent, tube-like structures on the posterior dorsum of the abdomen, called siphunculi or cornicles (Fig. 7), which can discharge defensive lipids and alarm pheromones. In some species, these structures are reduced to pores or are absent. Another structure unique to the aphids is a posterior projection on the tip of the abdomen called the cauda, equivalent to the lingula in whiteflies. Protective wax secretions are common.

Behavior and Ecology

Both adults and nymphs can travel short distances by walking, but dispersal of alatae occurs by both active flight and passive long-distance movement on air currents. Apterinae and nymphs are frequently transported by attendant ants. In sexual morphs, males are attracted to females by sex pheromones released from glands on the female’s legs. Altruistic behavior has been reported in the few aphid species that have a sterile soldier “caste,” which is a special kind of first or second instar that defends the family group against competitors and natural enemies.

Aphids generally live in aggregations on the buds, stems, and/or leaves of their host plants. Some species induce galls and a few others live underground on roots. Almost all aphids are phloem feeders, producing copious quantities of honeydew, and thus many species are attended by ants. Some aphids feed from both phloem and parenchyma tissue, and adelgids are largely parenchyma feeders. In general, aphids are quite host specific, with each genus being associated with a particular host-plant family and each species with one genus or species of host plant or at least closely related plant genera. In host-alternating species, however, the primary and secondary hosts are usually unrelated and the specificity to the primary host is generally higher than to the secondary host(s). Pest aphids, especially those of agricultural crops, often feed on plants in a number of unrelated families.

Notable Pest Species and Their Control

Infestations of aphids can grow rapidly to enormous size and cause plant debilitation through nutrient deprivation. But even small numbers of aphids can transmit viruses to uninfected plants. Pest aphids often are more polyphagous than nonpest species and frequently are species exotic to the area where they are of most economic concern. Cosmopolitan pest species are frequently anholocyclic, i.e., reproducing continually by parthenogenesis on their crop hosts, and thus are particular pests in the tropics.

One of the most notorious aphidoid pests is the grape phylloxera, Daktulosphaira vitifoliae (Phylloxeridae), which induces galls on V. vinifera. Damage in vineyards results mainly...
from the rotting of roots when infestations are heavy, rather than sap loss per se. The main method of control is the use of resistant grape rootstocks.

Genera of Aphididae that contain significant pests of crops include *Aphis*, *Brevicoryne*, *Macrostigmum*, *Myzus*, and *Riopolisphum*; the species listed below all transmit plant viruses. There are a number of serious pest species of *Aphis*, including the cowpea aphid *A. craccivora* (Fig. 7), bean aphid *A. fabae*, and melon or cotton aphid *A. gossypii*. The cabbage aphid, *B. brassicaceae*, attacks members of the Cruciferae. The potato aphid *Ma. euphorbiae* and the rose aphid *Ma. rosea* both use roses as primary hosts. The polyphagous shallot aphid *My. australis* appears to be exclusively anholocyclic. The primary hosts of black cherry aphid *My. cerasi* and green peach aphid *My. persicae* are *Prunus* fruit trees; secondary hosts include a range of economically important plants. The corn leaf aphid *R. maidis* is a worldwide pest of cereal crops, particularly maize, sorghum, and barley, and is habitually anholocyclic in most places. Important tree pests include *Pineus* species (Adelgidae) on pines; *Cerataphis franseni* (Hormaphidinae) on coconut and other palms; *Cinara* species (Lachninae) on a wide range of conifers; *Dysaphis*, *Myzus*, and *Brachycaudus* species (Aphidinae), many of which utilize roseaceous trees as their primary hosts, causing unsightly leaf curling/galling in spring; and *Eriosoma lanigerum* (Eriosomatinae), which develops woolly colonies on apple branches and trunks.

The most common aphidophagous predators are ladybird beetles (Coccinellidae), lacewings (Neuroptera), some hover flies (Syrphidae), a few gall midges (Cecidomyiidae, especially the widespread *Aphidoletes aphidimyza*), and certain predatory bugs (Anthocoridae). Wasps of the large family Aphelinidae and several genera of Aphelinidae are endophagous parasitoids of Aphididae; Adelgidae and Phylloxeridae are not parasitized.

**COCOIDEA (SCALE INSECTS)**

The scale insects (also called coccoids) occur worldwide. They are mostly small (less than 5 mm in length) and often cryptic in habit. There are estimated to be about 7500 described species. Many scale insects are economically important pests of agriculture, horticulture, and forestry. Male scale insects display complete metamorphosis, whereas female development is neotenous (adults resemble nymphs). A number of taxa display remarkable diversity in their genetic systems (e.g., parthenogenesis, hermaphroditism, and paternal genome elimination) as well as in chromosome number, sperm structure, and types of endosymbioses. The name "scale insect" derives both from the frequent presence of a protective covering or "scale" and from the appearance of many of the female insects themselves. Most species produce a waxy secretion that covers the body either as a structure detached from the body (a scale or test) or as a substance that adheres to the body surface. Some coccoid species have been used as sources of candle wax, lacquers such as shellac, or dyes. Scale insects are more diverse in terms of major evolutionary lineages (families), species richness, and morphology than any of the other sternorrhynchan groups.

**Evolution and Classification**

Scale insects have been assigned variously to 20 or more families, but the family-level classification is controversial. Often the Coccoidea is divided into two major, informal groups, the archaeococcoids (or archaeococcids) and the neococcoids (or neococcids). The extant archaeococcoids comprise the Margarodinae *sensu lato* (with over 400 species and sometimes treated as several families), Ortheziidae (ensign scales; about 155 species), Carayonomidae (4 species), Phenacoleachidae (2 species), and perhaps the genus *Puto* (about 60 species, sometimes placed in their own family, Putoidea, or otherwise in Pseudococcidae). Collectively, the above archaeococcoid families number only approximately 80 genera and 600 species. Some of the morphological features that define the archaeococcoids occur more widely in the Hemiptera, and monophyly of archaeococcoids is uncertain.

The neococcoids, which comprise all of the other extant families (usually 17 are recognized) and most of the species of scale insects (about 7000), are a monophyletic group characterized by derived features, including a chromosome system involving paternal genome elimination, needle-like apical setae on the labium, and loss of abdominal spiracles. Among neococcoids, most families (with the exception of the Eriococcidae) are well characterized morphologically. In contrast, relationships among families are largely unknown or not supported well by available data. The three largest families of neococcoids, in order of size, are the Diaspididae (armored scales; about 2400 species), Pseudococcidae (mealybugs; about 2000 species), and Coccidae (soft scales; over 1000 species). The other neococcoid families are the Eriococcidae (felt scales; about 550 species); Asterolecaniidae (over 200 species), Lecanidiidae (about 80 species), and Coccidae (about 70 species) (these 3 families collectively are called pit scales); Kerriidae (Tachardiidae) (lac insects; about 100 species); Kermeidae (gall-like scales; about 90 species); Acclidae (flat grass scales; about 50 species); Conchococcidae (about 30 species); Halimiococcidae (about 20 species); Stictococcidae (16 species); Beesonidae (9 species); Dacylopidae (cochline insects; 9 species); Micrococcidae (8 species); and Phoenico-coccidae (1 species).

The oldest fossil scale insects are from the Lower Cretaceous but the group is at least of Triassic and probably of Permian age. The earliest radiation involved the archaeococcoids, with the neococcoids apparently diversifying in conjunction with flowering plants.

**Life History**

The reproductive repertoire of scale insects includes hermaphroditism, seven kinds of parthenogenesis, and six major types of sexual chromosome systems. In the vast majority of coccoid
species, the males are functionally (because of inactivation or elimination of paternal chromosomes), and sometimes actually, haploid.

Each individual female scale insect has four or five growth stages (Fig. 8): the egg, two or three immature (nymphal) instars, and the adult (imaginal stage). The female lays eggs (ovipary) either in a cavity under her body or in a waxy covering (ovisc; Fig. 9E) that may be attached to her body, or the eggs may be retained in her reproductive tract until the young are ready to hatch (ovovivipary). The mobile first instars, called crawlers, are the main dispersal agents for Coccoidea; other immature instars generally are sessile. Adult females may live for an extended period (months to several years).

After hatching from the egg, male scale insects have a total of four immature or preimaginal instars including their own specially derived form of a complete metamorphosis (holometabolous) involving one or two pupa-like stages (Fig. 8). These are called the prepupa and pupa and develop either under a scale cover or inside a waxy cocoon or test that is produced by the second instar. Neither the pupa-like instars nor the adult male feed; adult males are short-lived (at most a few days) and have limited time to seek out the sedentary females for mating.

Host-alternating life cycles, as seen in some aphids, are unknown. The number of annual generations varies among and often within species and ranges from fewer than one to up to seven or eight per year. Annual life cycles are common in cool-temperate regions and numerous annual generations, typical of many aphids, do not occur in scale insects.

**Morphology**

Morphologically, scale insects are among the most unusual of insects. There is a very marked dimorphism between the adult male and the adult female and identification is based almost entirely on the long-lived adult female. Adult females (Fig. 9A) are sac-like without a well-defined head, thorax, or abdomen, and they are neotenic, that is, the adult resembles an immature individual. Adult females are wingless, may be winged or may not have legs, but usually have well-developed mouthparts. The anus opens posteriorly and usually is surrounded by a chitinized ring and often anal plates (Fig. 9A) or anal lobes flank the opening. Species that have a scale cover (e.g., armored scales; Fig. 9B) usually incorporate it into the dorsal part of the cast-off cuticle from the previous growth stage. If the body wax is of the adhering type, then it may vary from a thin translucent sheet (many soft scales) to a thick, wet mass (e.g., wax scales), a cottony secretion (e.g., some margarodids) or a powdery, white dusting (many mealybugs; Fig. 9C). Species that produce waxy tests (e.g., felt scales; Fig. 9D) often also have a dusting of powdery body wax. Wax is produced by epidermal glands and is exuded from a great variety of cuticular pores and ducts and sometimes also from glandular setae. Typically the body also is covered in setae that may be hair-like, spine-like, or other shapes, often with several types present on each species.

Adult males resemble small, delicate flies (Fig. 8) and have a distinct head, thorax, and abdomen. Most have a pair of membranous forewings and a pair of vestigial hind wings (balancers or halteres), although adult males of some species are wingless. The mouthparts of the prepupa, pupa, and adult males are reduced or absent.

Crawlers (Fig. 8) are usually ovoid or elongate ovoid and flattened dorsoventrally. Their antennae, legs, and mouthparts are well developed and various kinds of pores, ducts, and setae
are present on the body and its appendages; often a fringe of setae surrounds the body margin.

Behavior and Ecology

The first instars either seek suitable feeding sites on the natal host plant or disperse on the wind; some crawlers display behaviors that increase their chances of becoming airborne. Adult males probably locate their sessile conspecific females using sex pheromones but the presence of these chemicals has been demonstrated experimentally for very few species.

Scale insects primarily feed from either the phloem or the parenchyma, and their host associations range from monophagous to polyphagous. Sap removal is the main cause of plant damage, but a few species (especially mealybugs and armored scales) also transmit plant pathogens and/or toxins that may further reduce plant vigor and eventually kill the host. Furthermore, most scale insects (except armored scales and a few others) produce honeydew and are ant attended; associations are usually facultative but a number of obligate ant–coccid relationships have been described.

Cochineal scales (Dactylopius spp.) and certain mealybugs and lac insects have been used as biological control agents for particular noxious weeds; e.g., cochineal insects can assist with the control of prickly pear cacti, Opuntia species.

Notable Pest Species and Their Control

Some scale insects are serious plant pests, especially of perennial agricultural plants. They can cause damage to nut and fruit trees, forest or plantation trees, glasshouse plants, woody ornamentals, house plants, and sometimes sugar cane and even grass in lawns. Pests are usually either polyphagous (e.g., certain wax scales, Ceroplastes species; the pink hibiscus mealybug Macarbellicoccus hirsutus; and the cottony cushion scale Icerya purchasi) or oligophagous (e.g., the beech scale Cryptococcus fagisuga on beech trees or Matsuococcus species on pines). The cryptic habits and small size of most scale insects mean that they may not be detected until plant damage is substantial. Also, if populations on plants are low, they can be notoriously difficult to detect during quarantine inspections. Most pest scales belong to the Diaspididae (e.g., California red scale Aonidiella aurantii on citrus, Boisduval scale Diaspis boisduvalii on orchids, euonymus scale Unaspis euonymi on ornamentals, and black pine leaf scale Nucraspis californica on pines), Coccidae (e.g., certain polyphagous Ceroplastes, Coccus, Pulvinaria, and Saissetia species), and Pseudococcidae (e.g., many species of Dysmicoccus, Pseudococcus, and Planococcus on a wide range of plants), but a few significant pests belong to other families, such as the Margarodidae (especially polyphagous Icerya species), Eriococcidae (e.g., certain Eriococcus species on ornamental plants), and Asterolecaniidae (e.g., Bambusaspis bambusae on bamboo).

The most important predators of scale insects are ladybird beetles (Coccinellidae; especially Rodolia, Chilocorus, and Cryptolaemus). The main parasitoids of scale insects are chalcidoid wasps, especially species of Aphelinidae (e.g., species of Aphytis, Encarsia, and Coccopteryx) and Encyrtidae (e.g., species of Anagrus, Leptomastix, and Metaphycus), although some scale insects are attacked by flies that may be either parasitic (e.g., Cryptochetidae) or egg predators (e.g., a few Cecidomyiidae).

See Also the Following Articles
Auchenorrhyncha • Cicadidae • Honeydew • Parthenogenesis • Procthetidae • Rostrum • Symbionts Aiding Digestion

Further Reading

Stonfly

see Plecoptera

Stored Products as Habitats

Rudy Plarre
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University of Wisconsin

The protection of stored food against attack by insects and molds has been a necessity since the dawn of agriculture,