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Abafi-Aigner, Lajos (Ludwig Aigner)

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Ludwig Aigner was born on the 11 February 1840 at Nagyjécsa, Torontál Shire, Transylvania, Hungary, now Romania. His family moved to Temesvár, a large town in Transylvania, where he received a formal education in commerce and begun his career as a book merchant. His family was of ethnic German stock and young Ludwig only learned Hungarian when, in 1858, they moved to Pozsony (now Bratislava and in the Slovak Republic), a large town with predominantly Hungarian inhabitants. From here he soon moved on to Pest (now Budapest) and in 1863, as it was the custom in those years, he wandered all over Austria and Germany. He completed his studies in Köln and Stuttgart before returning to Pest. He always had an interest in entomology and he became a keen amateur lepidopterologist. However, besides entomology, he had a great variety of other interests too, especially in the field of publishing, writing, historical research as well as aspirations in business. He found success in publishing and in establishing a popular bookshop. In 1870 he was initiated as a Freemason and eventually he rose to the highest positions in the Order. For 12 years he has worked on an extensive monograph of the history of Freemasonry. He used his Hungarian pen name "Abafi" in a hyphenated form with his original family name: Abafi-Aigner and changed his German Christian name "Ludwig" to the Hungarian equivalent "Lajos." However, despite his successes in publication and writing his business begun to decline in the 1880s and within a few years he faced financial difficulties, which ultimately led to the closure of his famous bookshop. Disillusioned, he discontinued most of his business activities, and from 1890 he devoted all his time and energy to lepidopterology. In 1895, he published the results of his studies in the *Természetrajzi Füzetek* (Notebooks of Natural History), the journal of the National Museum's Natural History Department and he was one of the authors of *Fauna Regni Hungariae* (Catalogue of Hungary's Fauna). He resurrected *Rovartani Lapok* (Entomological Papers), which was established in 1884 but ceased to exist in 1886. His treatment of the butterfly fauna of Hungary won the coveted Bugát Prize. Based on this work he published *Butterflies of Hungary* in 1907. The book was (and probably still is) one of the most popular entomological publications in Hungary. It has inspired countless young entomologists and made the name of Abafi-Aigner well known to every naturalist in the country. He passed away on the 19 June 1909.

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Horváth C (1990) A rovartan tudósa. E' let és Tudomány 45:290, 312

Abaxial Surface

The lower surface of a leaf (contrast with adaxial surface).

Abbott, John

John Abbott was born in London in 1751. In England, he was given drawing lessons and, through his drawing instructor, was introduced to Dru Drury, a collector of insects who had been president of the Linnean Society. These two encounters encouraged him to collect insects and draw them, but his father was training him to be an attorney. Finding legal paperwork not to his liking, he emigrated to Virginia in 1773. After 2 years in Virginia, he relocated to Georgia, where he served as a private in the Third Georgia Continental Battalion during the Revolutionary War. For his military service he received several hundred acres of land, and worked as a planter and schoolmaster. In Virginia he had collected American insects and bird skins, and drew and painted insects and birds. Some of the specimens and paintings were shipped to England for sale. Some of the paintings, after sale, adorned books on birds, insects, and spiders written by various authors, not necessarily with acknowledgment to Abbott. In all, Abbott produced over 3,000 drawings of a quality that was very high for that time. Some of the insect illustrations included not only adults, but also larvae and the plants on which they fed, and even observational notes. He died about 1840.

Reference

Mallis A (1971) American entomologists. Rutgers University Press, New Brunswick, NJ, 549 pp

Abbott's Formula

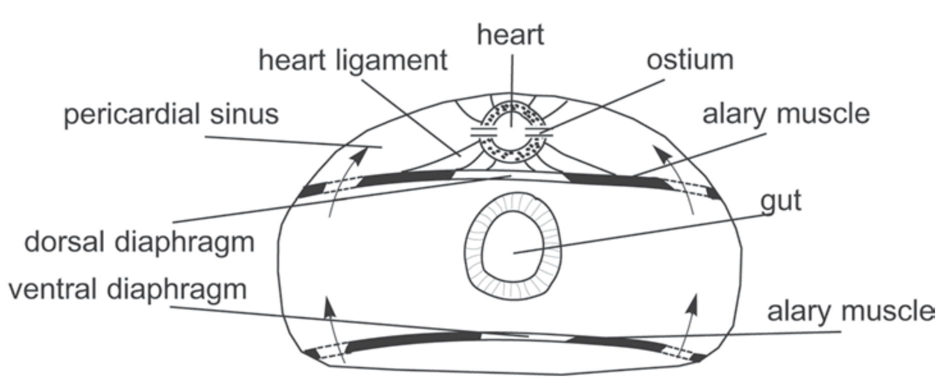
A mathematical technique commonly used to assess mortality in insecticide trials when there is need to correct for a change (decrease) in the background population density (i.e., in the check or control plots). The formula is:

% corrected control = 100 × (% alive in the check % alive in the treatment)/(% alive in the treatment)

Abdomen

The posterior of the three main body divisions of an insect (Fig. 1).

► Abdomen of Hexapods



Abdomen, Figure 1 **Cross section of an insect abdomen, showing components of the insect circulatory system and direction of hemolymph flow (adapted from Evans, Insect biology).**

Abdomen of Hexapods

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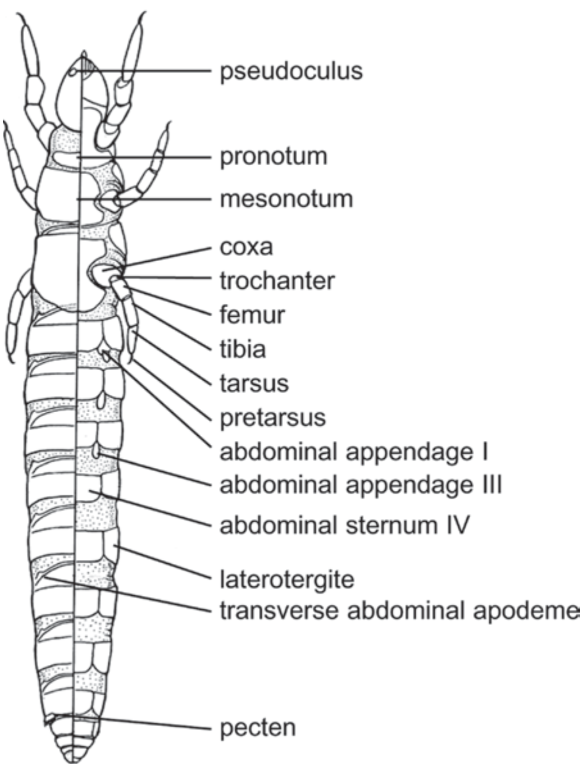
The abdomen constitutes the caudal tagma in the hexapods and is usually larger than the other two, the head and the thorax. This region is also referred to as a visceral area because it houses the visceral organs. Its form can vary depending on the group, and even on the species. The maximum number of observed segments is 11, although certain authorities consider a twelfth segment that in fact corresponds to a telsonic caudal region. In general, the number of segments decreases from the preimaginal phases to the adult stage, especially in those holometabolous insects in which the last segments of the adults are formed from imaginal discs during pupation. In the groups considered most primitive, the number of abdominal segments is usually greater, as occurs in the Protura with 11 segments (Figs. 2–5). An exception is the Collembola, which only possess six. In addition, it is necessary to keep in mind that, in certain cases, the total number of visible segments does not coincide with what a particular individual actually possesses, since some segments remain "invisible" upon being telescoped, particularly those of the posterior region of the abdomen.



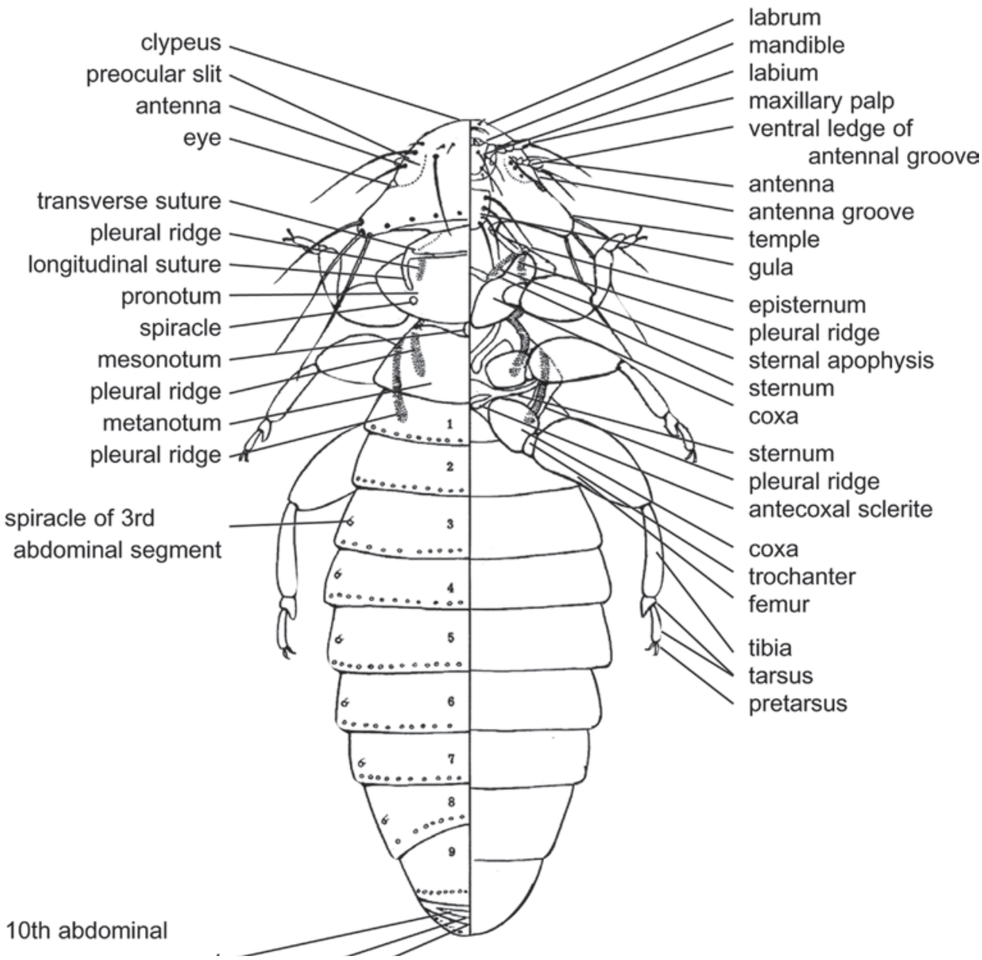
Abdomen of Hexapods, Figure 2 Diagram of a proturan (Protura) showing abdominal segments and appendages: dorsal view (left), ventral view (right).

According to Bitsch, a generalized abdominal segment would be limited anteriorly by a presegmentary domain, separated from the segmentary domain proper (of greater size) by a suture that begins an internal crest named the costa or antecosta. This crest anteriorly delimits an acrotergite or precosta in the tergal part and a presternite in the sternal part. In this idealized model, the muscles would be inserted in successive antecostas. No known structure is homologous to the thoracic furca.

The presence of the gonopore (double in Ephemeroptera) in segments VIII and IX (in VII in the case of Ephemeroptera), and fundamentally of the external structures related to reproduction (the genitalia), produce important modifications in those segments. Considering the presence of these genitalia, three regions of the abdomen are recognized: an anterior (pregenital or visceral region that includes the first eight segments), median (genital region, eighth and ninth segments), and caudal regions (postgenital region, tenth and eleventh segments plus the telsonic region).

The Pregenital Region

In the most generalized condition, the first abdominal segments conserve their basic structure, being easily distinguished from the thoracic segments. Nevertheless, the most frequent condition is that which produces morphological modifications that affect the thoracic-abdominal union. These modifications usually consist of reductions that affect the sternal region and involve a greater or lesser desclerotization of different structures and their

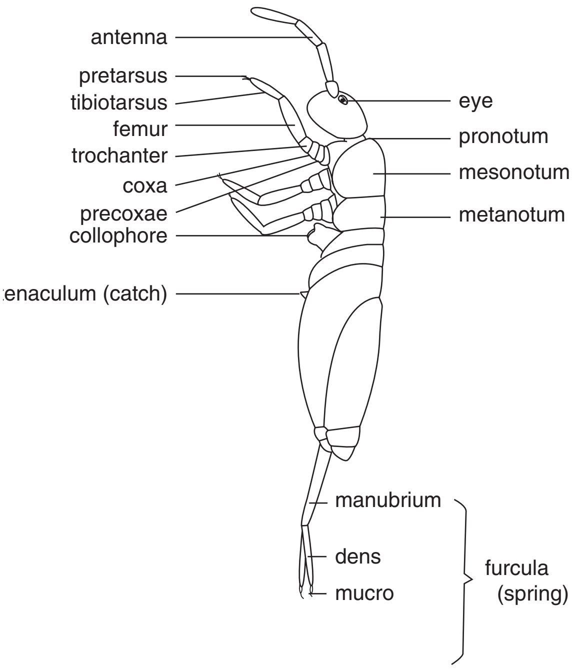


Abdomen of Hexapods, Figure 3 **Diagram of chewing louse (Mallophaga) showing abdominal segments, including numbering of segments: dorsal view (left), ventral view (right).**

incorporation to the metathorax. In this sense, the case of the Hymenoptera, Apocrita stands out, in which a narrowing is produced between the second and the third abdominal segments, which incorporate the thorax and is named the propodeum. The rest of the abdominal segments are called the gaster or metasoma. The region formed by the propodeum and the thorax constitutes the mesosoma. The narrowing allows a great amplitude of movements of the metasoma, which permits stinging in the capture of prey in aculeates. In some groups, like Formicidae and Sphecidae (Aculeata), one or two segments of the metasoma form a narrower zone called the petiole.

In the pregenital region, several appendicular structures can be found. Thus, three pairs of highly modified appendages exist in Collembola. In Archaeognatha, very developed coxites are differentiated, above which are inserted styli in a median position and the exsertile vesicles in the most internal position.

The styli are elongated pieces, articulated in their base above the external face of the coxite. They are unisegmentary and lack muscles inserted in their base, often presenting an apical spine. Taking into account their position and their embryonic development, the styli are considered by the majority of authorities as vestigial appendages, and more concretely as reduced telepodites. The exsertile vesicles are considered internal coxal formations (internal coxalia of some authorities).



Abdomen of Hexapods, Figure 4 Diagram of springtail (Collembola) showing furcular appendage at tip of abdomen.

In Pterygota the abdominal appendages remain restricted to the larval forms (Lepidoptera and Hymenoptera, Tenthredinoidea), although rough appendicular pairs already exist in the polypodous type of embryos. These abdominal appendages are named "false legs" or "prolegs" and are retractile, conical and membranous projections, with a circular planta that bears a crown, usually with hooks, to adhere to the substrate.

The Genital Region

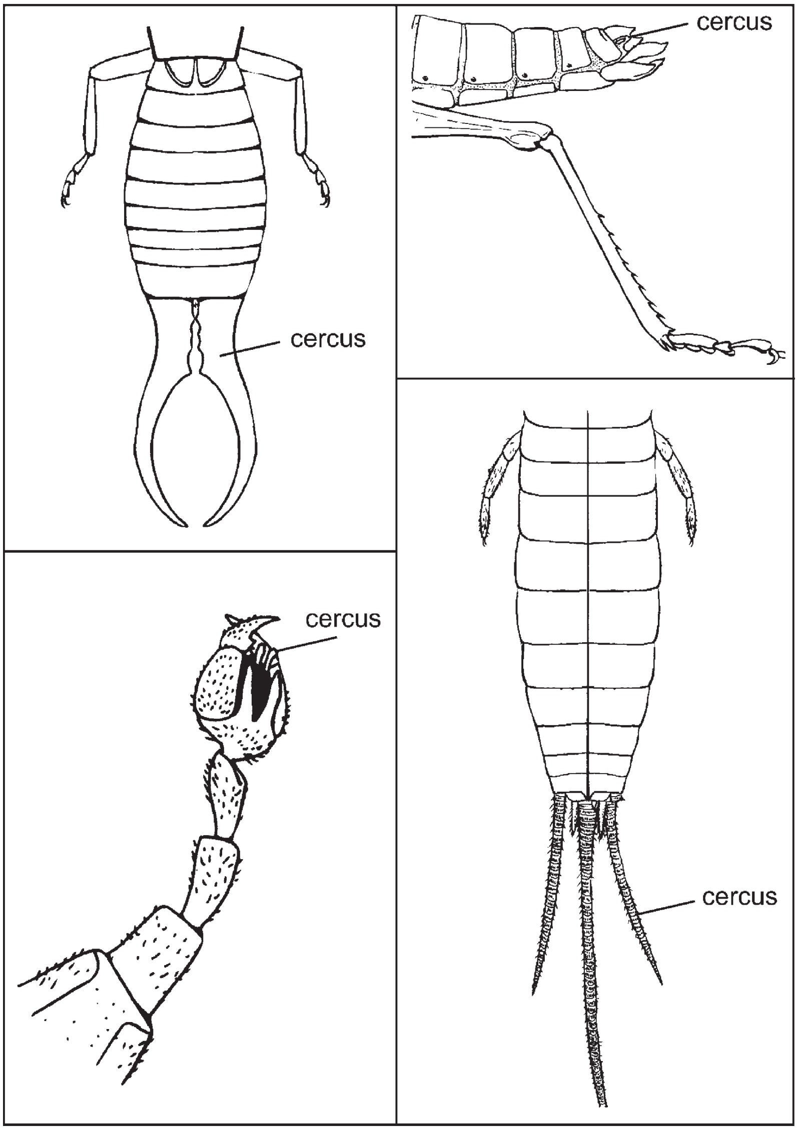
The transformations that affect the eighth and ninth abdominal segments are a consequence of the development of special external structures that in the case of the male serve in the transfer of sperm, and in the case of the female allow for oviposition. These structures together are known by the name genitalia.

The origin of the genitalia is controversial, although the majority of authorities accept that, at least in part, it is of appendicular origin. In this sense, it is clear that in the Archaeognatha the eighth and ninth segments are basically similar in males and females and their structures are homologous to those already indicated for the pregenital segments. Taking into account this relationship, the genitalia of Archaeognatha are considered primitive, and therefore fundamental to interpret the genitalia of Pterygota.

In the eighth segment of the Archaeognatha, the basal part of the appendicular structure is named first gonocoxa or gonocoxite and bears the first gonostylus; in the ninth is found the second gonocoxa with its corresponding stylus. In both segments (at times in the eighth, always in the ninth) formations homologous to the exsertile vesicles appear, which are called gonapophyses (parameters in the males and gonapophysis proper in the females). The fundamental difference between both sexes lies in the presence in the males of a phallic structure.

The female genitalia in the Pterygota constitute the ovipositor. The gonocoxites are incorporated into the lateral wall of the genital segments in a complete manner in the eighth segment, forming the first valvifer. In the ninth segment the basal part is incorporated into the lateral wall, originating the second valvifer, while the rest is extended, forming the third pair of valves (dorsal or lateral valves of some authorities), which are not homologous in Archaeognatha. The other two pairs of valves are the ventral valves, corresponding to the eighth segment, and the internal valves, corresponding to the ninth segment. These two pairs of valves are homologous to the gonapophysis of Archaeognatha. In the case of the generalized type of ovipositor like that of Orthoptera, these three pairs of valves are linked through the length of their course, forming in their interior a canal for oviposition.

Among the sclerites that are situated in the base of the valves (in addition to the valvifers already mentioned) are found the intervalves (intervalvulae of the authorities) by way of elongated transverse formations, one in the base of the valves of the eighth segment and another in the base of the valves of the ninth segment. The typical ovipositor



Abdomen of Hexapods, Figure 5 **Comparative development of cerci on earwig (Dermaptera, top left); grasshopper (Orthoptera, top right); scorpion fly (Mecoptera, lower left); silverfish (Zygentoma).**

that was just described can experience modifications according to the functions that it carries out; one of the most drastic is found in Hymenoptera, Aculeata, where it is transformed into a sting that serves the females as an attacking organ, either to capture prey or as a defense. On the other hand, the process of oviposition can be carried out through other, different structures, as occurs in the females of certain Diptera. In that case, the last segments are retractile and the intersegmental zones are highly developed, in such a way that they can become telescoped, forming oviposition tubes; this type of "ovipositor" is named the ovicauda. Not being homologous to the genitalia, many authorities call it terminalia.

The masculine genitalia present great morphological variability, which together with their taxonomic importance, have been the object of an infinity of descriptions, many of them without truly anatomical criteria. This has originated the use of very varied terminologies that have done nothing but complicate its study and impede the establishment of homologies even in the same group, creating in this way a great nomenclatorial chaos.

In the males, in addition to the genitalia proper, other structures (processes, lobes, etc). exist that intervene in functions other than those strictly related to the transfer of sperm; among the most common is the grasping of the female during mating. It has already been mentioned that the majority of authorities consider that the interpretation of the genitalia of Pterygota should be made by homology with the basic condition that is found in Archaeognatha. In this group, the phallic complex is formed by a median organ, the phallus or penis, and a pair of segmented pieces named parameres, that in the case of maximum development can exist in the eighth and ninth segments. The parameres correspond to the gonapophysis of the females (although the term gonapophysis is utilized indistinctly for both sexes by some authorities).

Many morphological models have been proposed to describe the male genitalia of Pterygota. The most complete, since it gathers and discusses early data, is that proposed by Bitsch. According to this author, what together forms the copulatory organ (phallus or penis) and the structures associated with the parameres (considered in the sense expressed by the Archaeognatha) is named the phallic complex.

The aedeagus is a sclerotized tube, situated above a largely membranous phallobase, although in more complex cases the phallobase presents an internal fold that remains membranous (endotheca) while the external part is sclerotized (phallotheca or theca). The aedeagus presents an invagination that forms a more or less developed internal chamber (the endophallus), which communicates with the gonopore at its base and in the other extreme communicates with the exterior through the phallotreme. In counter-proposition to the endophallus, the part formed by the external walls of the phallobase and the aedeagus forms the ectophallus. The phallic complex can present variable development, even being able to cause the aedeagus to disappear, or on the contrary, increase in complexity, developing spines and other types of processes named flagellum, virga or pseudovirga over the internal walls of the endophallus. When the endotheca and the endophallus are evaginated, the genitalia are converted into authentic intromittent organs.

The primitive position of the male genitalia can be displaced through different types of turns; one of the most showy cases is that which occurs in some Hymenoptera, Symphyta that present the condition called strophandric, which is characterized by a 180° rotation of the genitalia. Rotations have also been observed in males of Diptera.

The postgenital region, as was mentioned in the beginning of this section, comprises the tenth and eleventh segments plus the telsonic region. The tenth segment has been detected in Protura, Diplura, Archaoegnatha, Thysanura (Zygentoma), Ephemeroptera, Plecoptera, and some Orthoptera. The morphology of this segment is basically similar to the pregenital segments, although with certain frequency it can form a ring when the tergum and sternum unite, or the sternal region can be membranous. In embryonic forms, a pair of appendicular outlines is seen above this segment. In certain holometabolous insects, structures of uncertain meaning appear, such as the socii of some Hymenoptera.

The eleventh segment is recognized in the majority of embryonic phases of hexapods. In Archaeognatha and Thysanura it forms an annular structure from whose dorsal part is differentiated a long and narrow process called filum terminale, while from the lateroventral position are differentiated the cerci that in the adults possess numerous divisions. In the Pterygotes, the eleventh segment is formed by the epiproct (tergal region) and the paraprocts (in the lateroventral position); in the more primitive groups exist cerci (whose length and number of divisions are variable) situated in the membranous zones that exist between the epiproct and the paraprocts. The telsonic, asegmentary region constitutes the perianal membrane or periproct.

► Alimentary Canal and Digestion

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Abdominal Pumping

Contraction of the muscles associated with the abdomen can result in collapse and expansion of the air sacs. This forces relatively large volumes of air in and out of the insect through the spiracles, promoting ventilation. This is called active ventilation, in contrast with the more normal gas exchange mechanism of insects, diffusion or passive ventilation. To a small degree, abdominal pumping also promotes gas exchange through the trachea, but the trachea is quite resistant to change in shape. Abdominal pumping is more important for larger insects such as locusts, which display abdominal pumping almost continuously, but especially when active. In these insects air is sucked in through some spiracles and pumped out through others.

► Active Ventilation

Abiotic Disease

A disease caused by factors other than pathogens (e.g., weather or nutrition).

Abiotic Factors

Factors, usually expressed as factors affecting mortality, characterized by the absence of life. Abiotic factors include temperature, humidity, pH, and other physical and chemical influences.

Abnormality

In insect pathology, deviation from the normal; a malformation or teratology; a state of disease.

Abrocomophagidae

A family of chewing lice (order Phthiraptera).

► Chewing and Sucking Lice

Absolute Methods of Sampling

Techniques used to sample insect populations that provide an estimate per unit of area (e.g., per square meter, per leaf or per plant). Types of absolute methods include unit of habitat, recapture, and removal trapping. (contrast with relative methods of sampling).

► Sampling Arthropods

Acanaloniidae

A family of insects in the superfamily Fulgoroidae (order Hemiptera). They sometimes are called planthoppers.

► Bugs

Acanthmetropodidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Acanthopteroctetidae

A family of moths (order Lepidoptera). They commonly are known as archaic sun moths.

► Archaic Sun Moths
► Butterflies and Moths

Acanthosomatidae

A family of bugs (order Hemiptera).
► Bugs

Acaricide

A pesticide applied to manage mite populations. An acaricide is also called a miticide.
► Acaricides or Miticides

Acaricides or Miticides

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An acaricide or miticide is a pesticide that provides economic control of pest mites and ticks. Mites and ticks are collectively called either acari or acarina. Some products can act as insecticides or fungicides as well as acaricides.

An acaricide is a pesticide used to kill mites and ticks (Table 1). Always check with state and federal authorities to be sure products containing these active ingredients are registered for use. Always read labels carefully and follow the directions completely.

The toxicity of an acaricide is determined by a dose-response curve or a concentration-response curve. Such curves are obtained by exposing test mites or insects to increasing concentrations or doses of the pesticide and recording the resulting mortality after a given time interval. One estimate of toxicity used is the term LD_{50} (which is the dose required to kill 50% of the test population). The LC_{50} is the concentration required to kill 50% of the test population. If the dose is introduced through the insect's mouth it is an oral LD_{50}, if it is introduced through the skin or integument it is a dermal LD_{50}, and if it is introduced through the respiratory system it is the inhalation LD_{50}. A measured dose is applied to an arthropod by inserting a measured amount of toxicant into the gut or by applying a measured amount to the integument. The lower the LD_{50} or LC_{50}, the more toxic the poison.

An LC_{50} is obtained when a mite is exposed to a particular *concentration* of toxicant but the actual amount of toxicant the individual experiences is not determined. For example, if the pesticide is applied to foliage and the mite walks about on the foliage, the actual amount of toxicant the mite is exposed to depends on the activity of the mite, the amount taken up through the integument or by feeding.

Figure 6 shows a concentration-response curve in parts per million (ppm) for the acaricide Omite (propargite) exhibited by adult females from colonies of the Pacific spider mite *Tetranychus pacificus*. The concentration required to kill 50% of the individuals is the LC_{50}. The two types of F1 females (produced by crossing Chapla males and Bidart females, and vise versa) respond similarly and their concentration-response curves are about midway between those of the resistant (Bidart) and susceptible (Chapla) colonies, which indicates that resistance may involve a semidominant mode of inheritance. The term mode of inheritance describes how the trait is inherited; for example, the resistance can be determined by a single major dominant (only one copy of the gene is required for the mite to express the resistance) or recessive (two copies of the gene are required) gene. Or, the resistance can be a quantitative trait determined by multiple genes of equal and additive effect. In this example, the propargite resistance may be determined a single semidominant gene with modifying genes, but additional tests are required to resolve whether more than one gene actually contributes to this resistance.

Acaricide Classification

Pesticides are classified in several ways, including: (i) their mode of entry into the target pest, (ii) chemical structure, or (iii) source.

Acaricides or Miticides, Table 1 Acaricides (miticides) currently or recently available for general and restricted use to control mites and ticks*

Name** (chemical type) Some trade names	General Use (GU)*** Restricted Use (RU)	Potential use
Abamectin (avermectin B1a; produced from the bacterium Streptomyces avermitilis) Affirm, Agri-Mek, Avid, vertimec, Zephyr	GU, Class IV (practically nontoxic)	Also an insecticide; affects nervous system and paralyzes insects or mites; used in citrus, pears, nut tree crops
Amitraz (triazapentadiene) Acarac, Mitac, Ovidrex,Triatox,Topline	GU, Class III (slightly toxic)	Used in pears, cotton, and on cattle, and hogs to control insects, ticks and mites
Azadirachtin (tetranortriterpenoid extracted from the Neem tree) Align, Azatin, Turplex	GU, Class IV	Azadirachtin is similar to insect hormones called ecdysones, which control metamorphosis; also may serve as a feeding deterrent; used to control insects and mites on food, greenhouse crops, ornamentals and turf
Bifenazate (carbazate) **Floramite**	Class IV	Mites on greenhouse, shadehouse, nursery, field, field, landscape and interiorscape ornamentals, not registered in USA for use on food
Bifenthrin (pyrethroid) Talstar, Brigade, Capture	RU, Class II (moderately toxic)	Insecticide and acaricide that affects the nervous system and causes paralysis; used on greenhouse ornamentals and cotton
Carbaryl (carbamate) Adios, Bugmaser, Crunch, Dicarbam on formulation Hexavin, Karbaspray, Septene Sevin, Tornadao, Thinsec	GU, Class I, II or III, depending	General use pesticide to control insects on citrus, fruits, cotton, forests, lawns, nuts, ornamentals, shade trees, poultry, livestock and pets. Also works as a molluscicde and acaricide
Chlorobenzilate (chlorinated hydrocarbon) Acaraben, Akar, Benzilan, Folbex	RU, Class III, may cause tumors in mice	Used for mite control on citrus and in beehives; also kills ticks; use cancelled in USA
Chlorfenapyr (pyrrole) Pylon, Pyramite, Pirate	Class I	Used to control spider mites, broad ites, budmites, cyclamen mite, rust mites and some insects.
Cinnamon oil (cinnamaldehyde) Cinnamite	Exempt from registration under FIFRA	Broad spectrum miticide/ insecticide/fungicide controls or repels pests; could be phytotoxic in some cases; used in ornamentals, shade or nursery trees, vegetables, herbs and spices
Citronella oil	Exempt from FIFRA	Repels insects and ticks
Demeton-S-Methyl (organophosphate) Meta-Systox, Azotox, Duratox, Mifatox	No longer registered for use in USA; Class I, highly toxic	Systemic and contact insecticide and acaricide, widely used against diverse pests

Acaricides or Miticides, Table 1 **(Continued)**

Name** (chemical type) Some trade names	General Use (GU)*** Restricted Use (RU)	Potential use
Dicofol (organochlorine) Acarin, Difol, Kelthane, Mitigan	GU, Class II or III, depending on formulation	Miticide used on fruits, vegetables, ornamentals and field crops
Dicrotophos (organophosphate) Bidrin, Carbicron, Dicron, Ektafos	RU	Contact systemic pesticide and acaricide used to control sucking, boring and chewing pests on coffee, cotton, rice, pecans; used to control ticks on cattle
Dienochlor (organochlorine) Pentac, often formulated with other pesticides	GU, Class III	Contact material used for plant-feeding mites on ornamental shrubs and trees outdoors and in greenhouses; disrupts egg laying of female mites; use cancelled in USA
Dinocap (dinitrophenyl) Arathane, Caprane, Dicap, Dikar Karathane, Mildane	GU, Class III	Used as a fungicide and as an acaricide for ticks and mites; use cancelled in USA
Disulfoton (organophosphate) Disyston, Disystox, Dithiodemeton, Dithiosystox, Solvigram, Solvirex	RU, Class I, highly toxic	Systemic insecticide and acaricide used to control sucking insects/ mites on cotton, tobacco, sugar beets, cole crops, corn, peanuts, wheat, grains, ornamentals, potatoes
Endosulfan (chlorinated hydrocarbon) Afidan, Cyclodan, Endocide, Hexasulfan, Phaser, Thiodan, Thionex	RU, Class I	Contact insecticide and acaricide used to control many pests on tea, coffee, fruits, vegetables, grains
Ethion (organophosphate) Acithion, Ethanox, Ethiol, Nialate, Tafethion, Vegfru Foxmite	GU, Class II	Insecticide and acaricide used on wide variety of food, fiber and ornamentals, including greenhouse crops, citrus, lawns and turf
Eucalyptus oil	Exempt from FIFRA	Repels mites; repels fleas and mosquitoes
Fenamiphos (organophosphate) Nemacur, Phenamiphos, Bay 68138	RU, Class I	A nematicide that has some activity against sucking insects and spider mites
Fenbutatin oxide (organotin) Vendex	RU	Miticide used on perennial fruits, eggplant and ornamentals
Fenitrothion (organophosphate) Accothion, Cyfen, Dicofen, Fenstan, Folithion, Mep, Metathion, Micromite Pestroy, Sumithion, Verthion	GU	Acaricide and insecticide effective gainst a wide array of pests

Acaricides or Miticides, Table 1 (Continued)

Name** (chemical type) Some trade names	General Use (GU)*** Restricted Use (RU)	Potential use
Formothion (organophosphate) Aflix, Anthio, Sandoz S-6900	RU, Class II	Systemic and contact insecticide and acaricide, used against spider mites on tree fruits, vines, olives, hops, cereals, sugar cane, rice
Hexythiazox (ovicide, growth regulator) Savey	Class III	Ovicide/miticide effective against spider mites on tree fruits, christmas trees, strawberries, hops, peppermint, caneberries
Lambda cyhalothrin (pyrethroid) Charge, Excaliber, Granade, Hallmark, Icon, Karate, Matador, Saber, Sentinel	RU, Class II	Insecticide and acaricide used to control a variety of pests in cotton, cereals, hops, ornamentals, potatoes, vegetables; controls ticks
Lindane (organochlorine) Agrocide, Benesan, Benexane, BHC, Gammex, Gexane, HCH, Isotox, Kwell, Lindafor, Lintox, Lorexane, Steward	RU, Class II Most uses cancelled in USA because of potential to cause cancer	Insecticide and fumigant; used in lotions, creams and shampoos for control of lice and mites (scabies) in humans
Methamidophos (organophosphate) Monitor, Nitofol, Tamaron, Swipe Patrole, Tamanox	RU, Class I	Systemic, residual insecticide/acaricide/avicide with contact and stomach action, used to control chewing and sucking insects and mites in many crops outside the USA
Methidathion (organosphosphate) Somonic, Supracide, Suprathion	RU, Class I	Insecticide and acaricide with stomach and contact action used to control a variety of insects and mites in many crops
Methomyl (carbamate) Acinate, Agrinate, Lannate, Lanox, Nudrin, NuBait	RU, Class I	Broad spectrum insecticide and an acaricide to control ticks, acts as a contact and systemic pesticide
Mevinphos (organophosphate) Fosdrin, Gesfid, Meniphos, Menite, Mevinox, Mevinphos, Phosdrin, Phosfene	RU, Class I	Insecticide and acaricide effective against a broad spectrum of pests, including mites and ticks; use cancelled in greenhouses
Monocrotophos (organophosphate) Azodrin, Bilobran, Monocil 40, Monocron, Nuvacron, Plantdrin	RU, registration in USA withdrawn in 1988	Systemic and contact insecticide and acaricide
Naled (organophosphate) Bromex, Dibrom, Lucanal	GU, Class I	Contact and somach insecticide and acaricide, used against mites in greenhouses
Oxamyl (carbamate)	RU, Class I granular form is banned in USA	Insecticide/acaricide/nematacide that controls a broad spectrum of mites, ticks and roundworms on field crops, vegetables, fruits, ornamentals

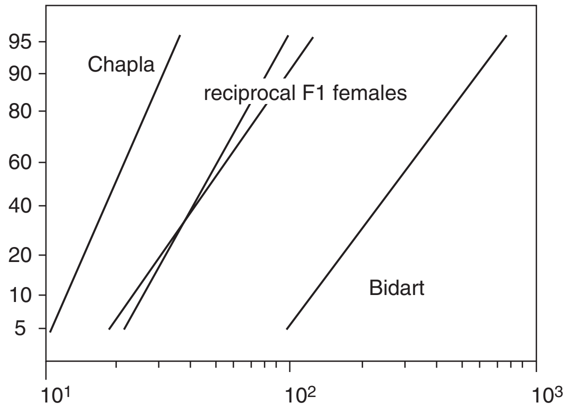
Acaricides or Miticides, Table 1 **(Continued)**

Name** (chemical type) Some trade names	General Use (GU)*** Restricted Use (RU)	Potential use
Neem oil Trilogy		Broad spectrum fungicide and acaricide in citrus, deciduous fruits and nuts, vegetables, grains
Permethrin (pyrethroid) Ambush, Cellutec, Dragnet, Ectiban, Indothrin, Kafil, Kestrel, Pounce, Pramex, Zamlin, Torpedo	Class II or III, depending on formulation RU in agriculture because of adverse effects on aquatic organisms	Broad spectrum used on nut, fruit, vegetable, cotton, ornamentals, mushrooms, potatoes, cereals, in greenhouses, home gardens, on domestic animals
Petroleum oils (refined petroleum distillate) Sunspray and others	Class IV	Kills by contact a wide range of mite and insects; complete coverage is essential; may act as a feeding or oviposition deterrent. Phytotoxicity can occur if plants are stressed, especially by lack of water; some plant cultivars are more susceptible than others. Used as dormant and as foliar sprays.
Phorate (organophosphate) Agrimet, Geomet, Granutox, Phorate Rampart, Thimenox, Thimet, Vegfru	RU, Class I	Insecticide and acaricide used on pests, including mites, in forests, root and field crops, ornamentals and bulbs
Phosalone (organophosphate)	GU, No longer for sale in USA due to carcinogenic effects	Broad spectrum insecticide/acaricide used on deciduous trees, vegetables, cotton.
Phosmet (organophosphate)	GU, Class II, some tolerances in foods changed in 1994 by EPA	Broad spectrum insecticide, used to control insect and mites on apples, ornamentals, vines; is used in some dog collars.
Propargite (organosulfide) Comite, Omite	GU	Acaricide used in many crops but not USA
Rosemary oil (rosemary essential oil) Hexacide	Meets requirements of USDA National Organic Program Exempt from FIFRA	Broad spectrum contact insecticide/miticide used in fruits, nuts, vegetables. Could be phytotoxic on some cultivars.
Soybean oil (essential oil)	Low acute toxicity to humans, generally recognized as safe	
Spinosad (macrocyclic lactone) Conserve		Broad spectrum insecticide and miticide used on ornamentals and in greenhouses.
Sulfur (sulfur) Cosan, Hexasul, Sulflox, Thiolux	GU, Check label for restrictions	Fungicide and acaricide; used to control plant diseases, gall mites, spider mites, used widely in food and feed crops, ornamentals, turf and residential sites; a fertilizer or soil amendment, mixing with oil can cause phytotoxicity

Acaricides or Miticides, Table 1 (Continued)

Name** (chemical type) Some trade names	General Use (GU)*** Restricted Use (RU)	Potential use
Triforine (piperazine derivative)	RU, Class I	Fungicide used on almonds, apples, asparagus, berries, cheeries, hops, ornamentals, peaches, rose; also controls spider mites
Wintergreen oil (contains methyl salicylate)	Exempt from FIFRA	Used to control mites (Varroa) in honey bees; causes contact mortality and reduced fecundity when mites feed on syrup

* The list is based on chemicals currently registered in the USA, which can change as new information regarding environmental impact and human health effects become available. Inclusion in this list does not necessarily indicate that the products are effective acaricides; application methods and resistance levels in individual mite populations can affect efficacy.
**Most have a variety of trade or other names, as well as different formulations, which can affect their toxicity.
***Restricted Use (RU) means that pesticides may be purchased and used only by certified applicators. Check with specific state regulations for local restrictions.



Acaricides or Miticides, Figure 6 This is a concentration-response curve showing the responses of a colony of *Tetranychus pacificus* resistant (Bidart) and susceptible (Chapla) to propargite (Omite). The mortality of adult females at different concentrations has been transformed into a straight line. The concentration-responses of the reciprocal F1 females in crosses between the susceptible and resistant populations are intermediate and similar.

Mode of Entry

A pesticide can enter and kill mites as stomach poisons, contact poisons, and or as fumigants. A systemic acaricide is absorbed into a plant or animal and protects that plant or animal from pests after the pesticide is translocated throughout the plant or animal.

Chemical Structure

Pesticides are classified as organic or inorganic. Inorganic pesticides do not contain the element carbon (but include arsenic, mercury, zinc, sulfur, boron, or fluorine). Most inorganic pesticides have been replaced by organic pesticides.

Source

Organic pesticides include botanicals (natural organic pesticides) produced by plants (such as natural pyrethrums, nicotine, rotenone, essential oils such as those from the neem tree, soybean oil). Essential oils are any volatile oil that gives distinctive odor or flavor to a plant, flower or fruit, such as lavender oil, rosemary oil, or citrus oil. Essential oils have been registered as pesticides since 1947 and at least 24 different ones are available in registered products. These are used as repellants, feeding depressants, insecticides, and miticides. Botanicals have relatively high LD50 values to mammals, so usually are considered safe to humans. Some newer pesticides are derived from microbes, such as avermectin or spinosad.

Synthetic organic pesticides are commonly used in pest management programs and can be separated into groups based on their chemistry. The main groups are: chlorinated hydrocarbons (such as DDT and chlordane, which are banned from use in most parts of the world), organophosphates (such as malathion, parathion, azinphosmethyl), carbamates (carbaryl, propoxur), pyrethroids (permethrin, fenvalerate),and a variety of newer products with very different chemistries including nicitinoids, pyrroles, carbazates, and pyridazinones.

Insecticides as Acaricides

Many insecticides have acaricidal properties. Sometimes an insecticide is more effective as an insecticide than as an acaricide (lower concentrations are required to kill the insect than are required to kill the mite species). Some products are more toxic (often for unknown reasons) to mites than to insects. We think that mites have the same fundamental physiological responses to toxic chemicals as insects, although mite physiology and responses to pesticides have been studied less often. Different mite species appear to respond differently to different products, which could be due to behavioral differences (feeding behavior, location on plant, activity levels), differences in cuticle thickness, differences in detoxification rates, or other biochemical, morphological or behavioral factors. Different formulations also can influence toxicity to different species of both insects and mites.

Many insecticides are effective acaricides (or at least they were before resistance to them developed). For example, many OPs (such as azinphosmethyl, parathion, ethion, dimethoate) were toxic to spider mites until resistance to these products developed. Likewise, carbamates, formamides, and many pyrethroids have both insecticidal and acaricidal properties. Other products have both fungicidal and acaricidal properties. The reasons as to why these products are effective on particular taxonomic groups are generally unknown.

Acaricide Types

Pesticide registrations change frequently so some of the materials listed here may be obsolete. Always check with state and federal authorities to be sure products containing these active ingredients are registered for use. Always read labels carefully and follow the directions completely.

Chlorinated Hydrocarbons

Dienochlor (Trade name = Pentac) is a chlorinated hydrocarbon acaricide with long residual activity. It has been used in greenhouses and on outdoor ornamentals. Pentac cannot be used on food crops and has short residual activity when used outdoors. It has a rapid effect on mites, stopping their feeding within hours. Endosulfan and DDT have also been used as acaricides (as well as insecticides).

Essential Oils

Soybean oil was first registered in 1959 for use as an insecticide and miticide. Three products currently are registered to control mites on fruit trees, vegetables and a variety of ornamentals. Soybean oil is not phytotoxic under most conditions. Many of these oils are approved for organic farming.

Inorganics

Sulfur is a good acaricide and fungicide, although it can be phytotoxic (cause plant injury), especially if plants are not well watered during hot weather. Sulfur is probably the oldest known acaricide. Sulfur (dusts, wettable p owders and flowable formulations) are usually highly effective acaricides for spider mites and rust mites, with two known exceptions.

Spider mites in California vineyards (*Tetranychus pacificus* and *Eotetranychus willamettei*) developed resistance to sulfur, probably because sulfur was applied up to 20 times a season over many years to control powdery mildew. After a number of years, these spider mites became pests because they were no longer controlled by the sulfur which had been applied to control powdery mildew. A number of years later, a predatory mite called *Metaseiulus occidentalis* was demonstrated to have developed a resistance to sulfur. The resistance to sulfur in this natural enemy of spider mites is based on a single major dominant gene; once the predator became resistant to sulfur it became an effective predator of spider mites in San Joaquin Valley vineyards in California.

The resistance to sulfur in *M. occidentalis* is unusual; even very high rates of sulfur are non-toxic to the resistant populations. Interestingly, populations of this predator collected from nearby almond orchards in California are susceptible to sulfur, indicating that populations are subjected to local selection and evolution. No genetic analyses have been conducted on the resistance to sulfur in the spider mites, so their mode of inheritance to sulfur resistance remains unknown. The biochemical mechanism of resistance is unknown for both spider mites and their predators.

Petroleum Oils

Petroleum oils are excellent insecticides/acaricides/fungicides for integrated mite management programs and have been used in pest management programs for over 100 years.

Different types of petroleum oils are used with different molecular weights. Most oils used are distillations of petroleum, although some oils derived from plants (sesame, almond, citrus) are used.

Crude petroleum oil is a complex mixture of hydrocarbons with both straight chain and ring molecules. Crude oil is separated into a range of products by distillation and refining. The lightest fractions include gasoline, kerosene, diesel and jet fuel. As these lighter fractions distill or boil, they are separated into different fractions. Spray oils are derived from the lighter lubricating oil fraction and distill at a temperature range of 600 to 900°C.

Currently used petroleum oils in the USA are narrow-range oils and have had the waxes, sulfur, and nitrogen compounds removed. Labels on sprays usually describe the degree to which the sulfur compounds have been removed and the percentage of active oil. The sulfur compounds are likely to cause phytotoxic effects, so the degree of removal of these compounds (called the UR rating) is an important piece of information on the label and commonly is greater than 92%. The composition of oil should be greater than 60%.

Since the mid-1960s, narrow-range horticultural oils have been used both as dormant or summer oil sprays. These highly refined and narrow range petroleum oils rarely cause phytotoxicity and increasingly are used for controlling both insect and mite pests on deciduous trees, citrus, and ornamental trees and shrubs. Oils have a wide range of activity against scales, mites, psyllids, mealybugs, whiteflies, leafhoppers, and eggs of mites, aphids and some Lepidoptera. Heavier dormant sprays are used to control overwintering pests in deciduous trees and vines. Summer oils are used to control pests during the growing season.

Oil kills mites and their eggs by contact. The toxicity appears to be due to suffocation of the pest, although it may also be due to chemical effects. Oils block spiracles, reducing the availability of oxygen and suffocation occurs within 24 h. Penetration and corrosion of tracheae, damage to muscles and nerves may also contribute to the toxicity of oils. Oils are sometimes a repellent to pests. Once the oil dries it is no longer toxic to most natural enemies; thus the very short residual activity of oil makes it a useful material for integrated mite management programs, although it also means that there is no residual toxicity to the pests.

No resistance to oils has been reported in pest arthropods, including mites, perhaps because oils have a relatively short residual activity. Oils are easy to apply, relatively inexpensive, and safe to handle. They are relatively harmless to vertebrates, dissipate quickly after spraying, and leave little or no residue on crops. Oils man be used by organic farmers.

A disadvantage to petroleum oils is that they have little residual activity and kill only upon contact, so thorough and precise coverage is necessary to achieve effective control. Phytotoxicity can occur even with these narrow-range oils, especially if plants are weakened or under moisture stress. Thus, applications should not be made during droughts, or periods of very high temperatures. Some varieties of plants are more susceptible to phytotoxicity than others, so caution should be taken when using oils for the first time on a particular crop or cultivar. Oils are not compatible with sulfur or some other pesticides, causing serious phytotoxicity problems.

Organosulfurs

Tetradifon (Tedion) and propargite (Omite, Komite) are organosulfurs. These products contain sulfur as a central atom with two phenyl rings. Tedion is particularly toxic to mites, but has very low toxicity to insects. Organosulfurs are often ovicidal as well as toxic to active stages. Propargite was used for many years (more than 20) and appeared to some to be immune to the development of resistance in spider mite populations. However, propargite resistance has now developed in many populations of spider mites around the world. Propargite is less toxic to beneficial phytoseiid predators than to pest spider mites, and thus could be used in integrated mite management programs, although at high concentrations it also is toxic to phytoseiid predators.

Organotins

Cyhexatin (Plictran) and fenbutatin-oxide (Vendex) are examples of tin compounds that are primarily acaricides and fungicides. Plictran (cyhexatin) was introduced in 1967 and was widely used for many years before resistance developed in spider mites. Some people had assumed that the organotins were immune to resistance problems. The organotins were useful products because they were more toxic to spider mites than to phytoseiids and thus were very useful in integrated mite management programs. Fenbutatin-oxide (Vendex) is another organotin. These products were taken off the market in the USA due to concerns about safety.

Insecticides with Acaricidal Activity

Organophosphorus Pesticides

The organophosphates (pesticides that include phosphorus) are derived from phosphoric acid and are the most toxic of all pesticides to vertebrates. They are, in fact, related to nerve gases by structure and mode of action. Organophosphorus pesticides (OPs) are less persistent in the environment than the organochlorines such as DDT.

Organophosphorus pesticides (such as azinphosmethyl, parathion, ethion, demeton, dimethoate) function by inhibiting important enzymes (cholinesterases) in the nervous system. Acetylcholine is the chemical signal that is carried across synapses (where the electrical signal is transmitted across a gap to a muscle or another neuron. After the electrical signal (nerve impulse) has been conducted across the gap by acetylcholine, the cholinesterase enzyme removes the acetylcholine so the circuit won't be kept on. When OPs poison an organism, the OP attaches to the cholinesterase so it cannot remove the acetylcholine. The circuits then remain on because acetylcholine accumulates. This gives rise to rapid twitching of the voluntary muscles and to paralysis, which is can be lethal if it persists in the vertebrate respiratory system.

Not all OPs are highly toxic to vertebrates; if the phosphorus is modified by esterification (adding oxygen, carbon, sulfur and nitrogen), six different classes of OPs can be produced. Some of these are relatively safe to vertebrates, such as malathion. The use of most OPs is being eliminated in the USA due to the Food Quality Protection Act.

Carbamates

Carbamates (aldicarb, carbofuran, methomyl, propoxur) are derivatives of carbamic acid. The mode of action of carbamates is to inhibit cholinesterase. The carbamates were introduced in the 1950s. Carbaryl (Sevin) is one of the most popular products available to home gardeners for controlling a variety of insect pests and has low mammalian oral and dermal toxicity. Methomyl (Lannate) and aldicarb (Temik) are examples of other carbamates.

Sevin is well known to induce outbreaks of spider mites after applications are made to control other pests. The outbreaks are due to two factors; (i) Sevin kills phytoseiid predators and other natural enemies of spider mites, and (ii) it stimulates reproduction of spider mites, a process called hormoligosis. Even very low doses of Sevin appears to act like a hormone to stimulate reproduction of the two-spotted spider mite *Tetranychus urticae*. It is likely that the use of carbamates also will be eliminated or greatly reduced in the USA due to the Food Quality Protection Act.

Formamides

Formamides include chlorodimeform (Galecron or Fundal), amitraz, and formetanate (Carzol). These products are effective against the eggs of Lepidoptera and also against most stages of mites and ticks. The mode of action of these products is unclear, but thought to be due to the inhibition of monoamine oxidase, which results in the accumulation of compounds called biogenic amines.

Pyrethroids

Many of the pyrethroids have acaricidal activity. Some (such as bioresmethrin, fenpropathrin and bifenthrin) are considered effective acaricides. Unfortunately, pyrethroids usually are very toxic to beneficial arthropods, including phytoseiid predators. These detrimental effects can be very long lasting because the residues persist a long time. Few have been found useful for integrated mite management programs for this reason. Laboratory selection of phytoseiids (*Amblyseius fallacis, Metaseiulus occidentalis, Typhlodromus pyri*) for resistance to two pyrethroid insecticides has been successful. The pyrethroid-resistant strains were developed for use in apple pest management programs using both laboratory and field selection methods.

Pyrroles

Pyridaben is a novel pyrrole pesticide that works as a mitochondrial electron transport inhibitor to block cellular respiration, causing pests to become uncoordinated and die. Can be used on both insects and mites.

Other Acaricides

Azadirachtin

This is a triterpenoid extracted from the seeds of the neem tree *Azadirachta indica*. Extracts include a combination of compounds, the proportion of which vary from tree to tree. Such variability in this natural product makes it difficult to predict the precise effect of the product when extracted by local people. Commercial products may be more consistent in their effect because they have been tested to confirm their quality and are blended to achieve a consistent product. Azadirachtin blocks the action of the molting hormone ecdysone.

Avermectin

Avermectin is a natural product containing a macrocyclic lactone glycoside that is a fermentation product of *Streptomyces avermitilus*, which was isolated from soil. Avermectin is actually a mixture of two homologs, both of which have biological activity. Avermectin has insecticidal and acaricidal properties and is closely related to ivermectin, which kills nematodes.

At appropriate rates, abamectin is less toxic to beneficial phytoseiids than to spider mites; it paralyzes active spider mite stages, but is not toxic to eggs. Avermectin has translaminar activity (meaning it is taken up by the plant tissue and subsequently by spider mites feeding on the plant tissues), but has a short residual toxicity to phytoseiids.

Resistance to this product has been reported in some populations of spider mites. A resistant strain of *M. occidentalis* was obtained after laboratory selection, suggesting that resistance mechanisms may be present in field populations.

The mode of action of avermectin involves blocking the neurotransmitter gamma-aminobutyric acid (GABA) at the neuromuscular junction. Mites that are exposed to abamectin become paralyzed and, although they do not die immediately, the paralyzed mites do stop feeding.

Clofentezine and Hexythiazox

These are very interesting growth regulators of mites; they kill eggs (ovicides) of spider mites, but not the active stages of spider mites. The products have different chemistries, but both are nontoxic to phytoseiid mite eggs or active stages! In fact, the phytoseiid mite *Metaseiulus occidentalis* can be fed a diet consisting solely of spider mite eggs that have been killed with these products and the predator females reproduce and their progeny develop normally. This selectivity makes the products particularly useful for integrated mite management programs because predators can be maintained while suppressing spider mite populations. Unfortunately, resistance to these products has developed in spider mite populations in several locations around the world, including Europe and Australia.

Tebufenpyrad

This is a phenoxypyrazole and has been evaluated under the trade name Pyranica in Australia, where it was shown to be useful in integrated mite management programs in apples because it is selective (relatively nontoxic) to phytoseiid predators.

Acaricides and Fungicides

Benomyl is a carbamate that has been used primarily as a fungicide, but also has acaricidal properties. Benomyl is interesting because it acts as a sterilant of phytoseiid predators. Adult phytoseiid females treated with benomyl survive, but they do not deposit eggs. This product apparently disrupts spindle fiber formation in cells and interferes in the synthesis of DNA, resulting in females that are unable to reproduce.

Resistance in Mites

Resistance to pesticides is an increasingly serious problem around the world. Resistance to one or more pesticides has been documented in more than 440 species of insects and mites. Spider mite and tick species have readily developed resistance to all classes of pesticides.

Resistance is a decreased response of a population of animal to a pesticide or control agent as a result of their application. It is an evolutionary or genetic response to selection. Tolerance is an innate ability to survive a given toxicant dose without prior exposure and evolutionary change. Cross resistance is a genetic response to selection with compound A that generates resistance to both compound A and other compounds (B and C). Multiple resistance is resistance to different compounds due to the coexistence of different resistance mechanisms in the same individuals. Multiple resistances usually are generated by sequential or simultaneous selection by more than one type of pesticide.

Methods for Evaluating Resistance

There are a variety of methods available for assessing resistance to pesticides in mites. The test method chosen will depend upon the goals of the researcher. Each method has strengths and weaknesses.

Resistance is a genetically-determined change in the ability to tolerate a pesticide. Therefore, one must have at least two different populations to test – one that is putatively resistant and one that exhibits the normal, wild type response. Unless these two populations can be compared under identical laboratory conditions, it is difficult to document resistance because historical data are of questionable value in assessing whether a population is resistant. This is because it is very difficult to conduct identical bioassays in two different laboratories, even when attempts are made to use the same methods. Small differences in techniques can result in very large differences in toxicity data. For example, spider mites tested on smooth leaves may respond very differently than spider mites tested on the same plant species but on a variety with hairy leaves. Small differences in formulations and temperature also influence responses of mites to pesticides. Small differences in age or feeding status also influence toxicity responses. Most conclusions about resistance should be based on comparative data obtained by the same researcher under identical conditions.

The apparent failure of a product to control a mite population under field conditions is NOT adequate evidence for resistance. Field failure is a reason to investigate further, but field failures can occur for a variety of reasons that have nothing to do with resistance. Failures could occur because the pesticide applicator may have mixed the product improperly, coverage may have been inadequate, the pH of the water used to mix the pesticide could have altered the toxicity of the product, and the product could have been old or degraded due to improper storage.

Slide Dip Bioassays

Slide dip bioassays of adult female spider mites and phytoseiids have been proposed as a standard method for assessing resistance or tolerance. This method involves placing adult female on their backs on to double-sided sticky tape applied to glass microscope slides and dipping the slides into a specific pesticide concentration. This method has the virtue of being relatively rapid and easy to conduct. However, measuring toxicity to adult females after 24 or 48 h is not an appropriate assay for many pesticide types (for example ovicides, growth regulators). Also, the results probably bear little relation to the field toxicity of the product. It is very likely that many products are much more toxic to the mites using this assay than they would be under field conditions, where mites can feed and move around and coverage is rarely complete, so this method may give no information about whether the resistance level induced is relevant to field concentrations used.

Leaf Dip or Leaf Spray Bioassays

Leaf dip or leaf spray bioassays involve placing mites on leaf disks, which are then sprayed or dipped into a specific concentration of pesticide. This type of bioassay provides an exposure that is more similar that the mites would experience under field conditions and it is possible to measure survival, fecundity, and ability to successfully develop on pesticide residues.

Whole Plant Bioassays

This approach, which involves spraying the entire plant, is very realistic, unless the plants (and pesticide residues) are not exposed to sunlight or rain.

Field Tests

Field trials are the most realistic method for assessing resistance, but it can be difficult to determine why the predators or spider mites died (did other tolerant predators fly in and eliminate the pest?). If adequately replicated over time and space, field trials provide very relevant information. The relevance of application method (high or low volume), coverage, and droplet size can be assessed. Unfortunately, field trials are the most expensive to carry out so the methods described above are often used to save time and funds.

- ► Insecticides
- ► Insecticide Toxicity
- ► Insecticide Formulation
- ► Detoxification Mechanisms in Insects
- ► Pesticide Resistance Management
- ► Pesticide Application

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Accessory Cell

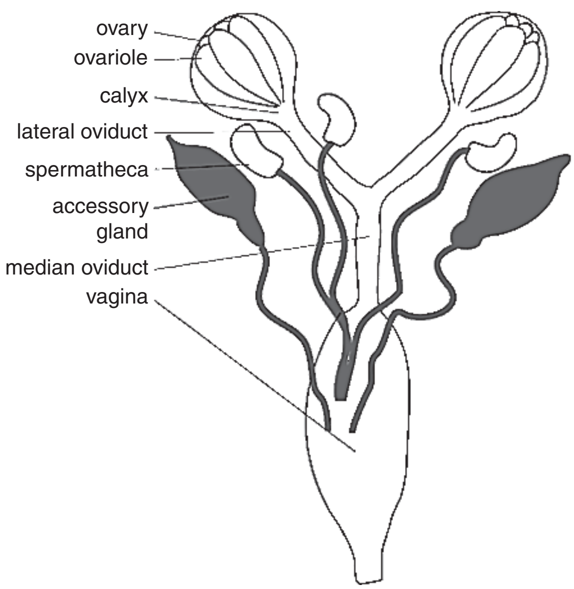
A wing cell not normally present in the taxon.

Accessory Circulatory Organ

Although the dorsal vessel (heart) is normally considered to be the organ responsible for blood circulation in insects, sometimes small sac-like structures are located at the base of appendages (antennae, legs, wings). These structures are capable of contractions independent of the dorsal vessel, and assist in circulation. This is also called "accessory pulsatile organ."

Accessory Gland

A gland associated with the male or female reproductive system, and producing substances associated with the sperm or eggs, respectively (Fig. 7). Male accessory glands produce such substances to



Accessory Gland, Figure 7 **Diagram of the female reproductive system, as found in *Rhagoletis* (Diptera) (adapted from Chapman, The insects: structure and function).**

facilitate sperm transfer, as a barrier to further insemination, as a means of altering female behavior, and as a means of providing nutrition to the female. Females produce substances for packaging their eggs, adhering them to a substrate, and providing a protective coating over the eggs.

► Sampling Arthropods

Accessory Vein

An extra branch of a longitudinal vein. Such veins normally are designated by a subscript of "a."

►Wings of Insects

Accessory Hearts

Pulsatile, sac-like organs that assist in circulation of the hemolymph into appendages such as the antennae, wings, and legs.

Accidental Host

A host in which the pathogenic microorganism (or parasite) is not commonly found.

Accidental Species

Species that occur with a low degree of consistency in a community type. Such species are not useful for community definition.

Acclimation

The adaptation of an organism' s physiological responses to existing environmental conditions. A nearly equivalent term is "acclimatization," though acclimation may be a more rapid or laboratory-based phenomenon, whereas acclimatization is a long term, field-based phenomenon.

Accuracy

A measure of the closeness of an estimate to the true mean or variance of a population.

Acephalous

The condition of lacking an apparent head. This term is usually applied to certain flies and wasps that lack a well-defined head.

Acerentomidae

A family of proturans (order Protura).

► Proturans

Acetylcholine

The synaptic transmitter substance found in the insect central nervous system. When released into the synaptic cleft, it is bound to a receptor, depolarizing the postsynaptic membrane and stimulating nervous excitation.

Acetylcholine Esterase

An enzyme that breaks down acetylcholine after it is released into the synaptic cleft of insect neurons. Interference with acetyl choline esterase, as by exposure to some insecticides, results in prolonged stimulation of the nerves.

Achilidae

A family of insects in the superfamily Fulgoroidae (order Hemiptera). They sometimes are called planthoppers.

► Bugs

Acleridiidae

A family of insects in the superfamily Coccoidae (order Hemiptera).

► Bugs

Acoustical Communication in Heteroptera (Hemiptera: Heteroptera)

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Acoustic signaling is found in many hemipteran families. It serves a variety of purposes, particularly defensive behavior such as repelling potential predators and signaling alarm or distress, but also for species spacing within a particular habitat, reproduction, and coordination of group actions. Vibratory signals for reproductive purposes may be produced by males and/or females, leading to aggregation to mate attraction, courtship and copulation. Non-receptive females may sing to reject copulation (male-deterring stridulation), as in the subfamily Triatominae (Reduviidae) and in Pentatomidae (e.g., *Nezara viridula*).

The vibratory signals produced by many insect species cannot be heard by the human ear because the sounds are low frequency and generally transmitted by mechanical vibrations through the substrate, and not by the air. The study of acoustical communication has greatly progressed in accordance with improvement of recording and analyzing equipment, including the necessary computer software.

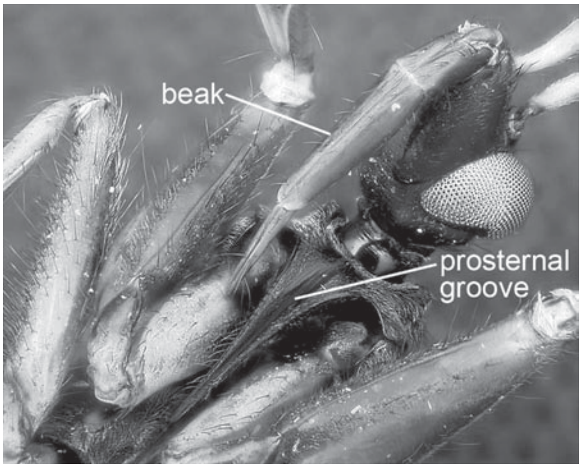
Production of Vibrational Signals and Songs

Vibrational signals and songs are produced by stridulation (stridulatory device, stridulatory organs), by body vibration, or by a simple tymbal mechanism. Stridulation occurs widely in Heteroptera, and is the act of producing sound or vibration by rubbing together certain body parts. The first systematic survey of sound-producing devices in the Heteroptera was that of Handlirsh in 1900. To stridulate, usually both a movable and a stationary portion are needed. The movable part is called the plectrum or scraper. The stationary portion may be called the stridulitrum, file, strigil (strigile, strigilis) or lima (pl., limae). The stridulitrum is typically striated or finely tuberculated, and the plectrum is a structure with a well-defined lip or ridge, tubercles, or provided with spines.

Different parts of the body may be involved to function as the stridulatory device. The forewing edge is most commonly used as a stridulitrum (file), while the hind femur is the most usual structure used as a plectrum (scraper). Other stridulitrum may be located in the head, associated with the mouth (labium, maxillary plate), the thorax (propleurum, metapleuron, prosternal groove), the wings (metathoracic wing vein, hypocostal lamina or articulatory sclerite, underside of clavus), the legs (forecoxa, mesotrochanter, tibia, femora), and the abdomen (sternum, the connexival margin, posterior margin of the pygophore). There are also a variety of locations for the plectrum or scraper: the rostrum, the legs (forecoxal cavity, coxal peg, hind tibia, and fore-, middle or hind femur) or the abdomen. Some stridulatory devices are present in several families, whereas others are only known from a few genera or even a single species.

Examples of stridulation devices are that of the Corixidae (spinose area inside the front femur against the clypeus, genitalia against abdomen segments), Scutelleridae (wart-like, toothed tubercles in the hind tibia against the femur), Reduviidae (tip of the labium against a cross-striated furrow (Fig. 8) in the prosternal groove), some Pentatomoidea and Lygaeiodea (dorsal abdominal files against teeth on the under-sides of the hindwings), some Miridae, Lygaeidae, Largidae and Alydidae (hind femur against forewing edge) and some other Pentatomoidea (tubercles on the hind femora against strigose regions on abdominal sterna).

Morphological differences in the stridulatory device may, in some cases, be related to differences in the songs emitted by either males or females, as



Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 8 The stridulatory apparatus in Reduviidae: the tip of the labium is rubbed against a cross-striated furrow in the prosternal groove.

occurs in the burrower bugs (Fig. 9) *Scaptocoris castanea* and *S. carvalhoi*. In *S. castanea*, males have a longer stridulitrum than females. However, in *S. carvalhoi* the stridulitrum length does not differ between sexes. Instead, in *S. carvalhoi* the male stridulitrum has more teeth than in the female stridulitrum. There are no intersexual differences for this latter morphological trait in *S. castanea.*

Differences in the stridulatory apparatus may be related to interspecific differences, with a specific diagnostic value. In the genus *Triatoma* (Reduviidae), it is possible to distinguish between *T. guazy* and *T. jurbergi* at any nymph stage or in the adults by studying the stridulatory sulcus (stridulitrum). As *T. jurbergi* is naturally infected with *Trypanosoma cruzi*, the causal protozoan of Chagas disease (American trypanosomiasis), identification of specimens along their whole life cycle is of great medical importance.

In other instances, morphological differences in the stridulatory device do not cause differences in their song patterns. For example, in Reduviidae of the subfamily Triatominae, individuals of the same species have stridulatory grooves with different inter-ridge distances, though the frequency spectra and repetition rates are similar.

A tymbal is formed by abdominal tergal plates fused together and which vibrate over a hollow chamber within the abdomen. The tymbal is activated by muscular contractions and produces body vibrations that are low frequency. Tymbals have been found in Piesmatidae, Pentatomidae, Acanthosomatidae, Cydnidae, Lygaeidae, Coreidae and possibly Reduviidae, and similar vibration-producing mechanisms have been found in Plataspidae and Rhopalidae. Differences exist about precise abdominal parts and muscle contraction mechanisms among the tymbals of different families. For example, the description of the *N. viridula* tymbal follows: The first and second abdominal tergites are fused into a forward-backward movable tymbal-like plate that is loosely fixed, anterior and posterior, to the thorax and to the third abdominal tergum, by a chitinous membrane, and more firmly, laterally, to the pleurites. Longitudinal and lateral compressor muscles contract synchronously and in phase with these vibratory waves.

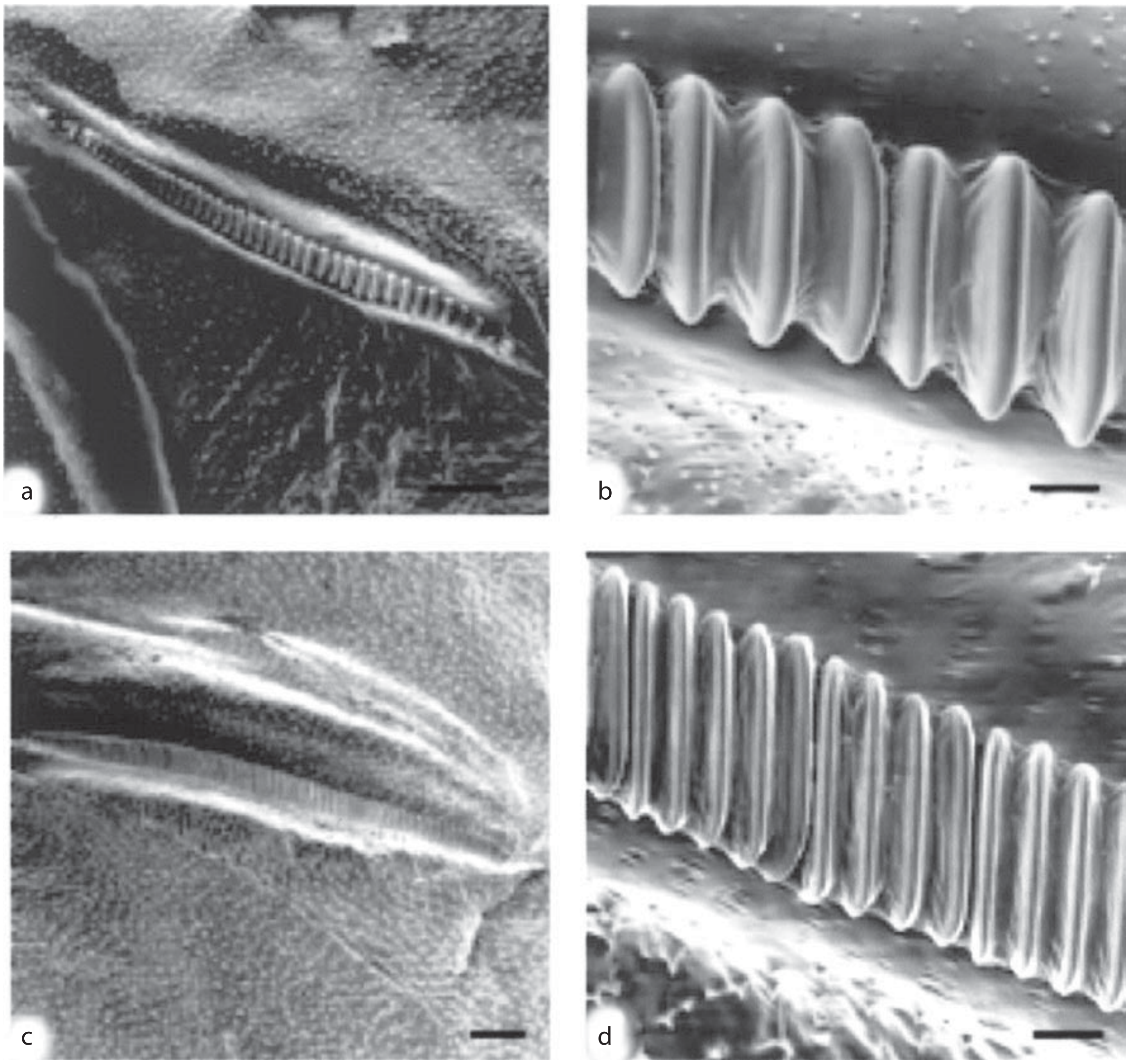
All Heteroptera species investigated so far emit low frequency narrow-band signals by body vibration, and/or broadband signals produced by stridulation. For example, in Cydnidae and Pentatomidae, vibratory mechanisms produce a low frequency vibration (around 100 Hz), and the stridulatory vibration extends up to 10 kHz.

Reception of Vibrational Signals and Songs

Although sound production is found quite widely in Heteroptera, it is not common to find structures specialized for sound reception. Sound reception in Heteroptera is possible due to the presence of either scolopophorous organs or tympanal organs.

Scolopophorous organs are mechanoceptors, and they occur widely in insects. They are composed of sensory sensilla (scolopodia), which may be arranged in groups, and are distally attached to a membrane in the body wall or to the body wall itself. Scolopophorous organs may be located in antennae (Johnston's organ), legs (subgenual organ, joint chordotonal organ), thoracic pleura, or abdominal terga.

Legs are the site of sensory organs that detect vibratory signals with highest sensitivity. For example, at the dorsal side of each leg of *N. viridula* there are four scolopodial organs: femoral, tibial, tarsopretarsal and subgenual organs. The receptor neurons may be low frequency (most sensitive between 50 and 100 Hz) or high frequency sensitive (there are two types: middle frequency neurons being sensitive around 200 Hz, and higher frequency



Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 9 **Interspecific differences in the stridulatory devices found in females of the burrower bugs *Scaptocoris castanea* and *S. carvalhoi* (Hemiptera: Cydnidae). Images a and b are *S. castanea*; images c and d are *S. carvalhoi*. Images a and c show the stridulitrum in the postcubital vein of the hind wings (scale bar = 100 μ); images b and d show the central section of the stridulitrum, showing details of the teeth (scale bar = 10 μ) (adapted from Čokl et al (2006) Physiol Entomol 31:371–381).**

neurons sensitive around 700–1000 Hz). Also, the Johnston's organ of *N. viridula* has several vibratory sensitive organs which respond in the frequency range between 30 and 100 Hz. When standing on its host plant, the male of *N. viridula*, by different combinations of legs and antennae, may compare the vibratory signals on two branches of the host plant, and choose the best one in order to locate the singing female. The most probable mechanism underlying resolution of direction by vibratory cues (vibratory directionality) may be time-of-arrival differences (perception of vibratory signals by two different receptors in the insect). For example, when legs of the receptor bug are separated by 2 cm, a time-of-arrival difference between 0.125 and 0.250 ms is created, very close to that found in scorpions, where vibrational directionality is well known. Reduviidae also receive vibratory signals via legs and antennae. Fewer data are available on leg vibratory receptor organs in other land bug species. Among land bugs, no sensory organs for airborne sound have been found.

Tympanal organs have been found in the mesothorax of the Corixidae, and are in contact with the physical gill air bubble. They are able to catch airborne sounds, and to respond to stridulation frequencies produced by conspecific bugs.

Transmission of Vibratory Signals and Songs

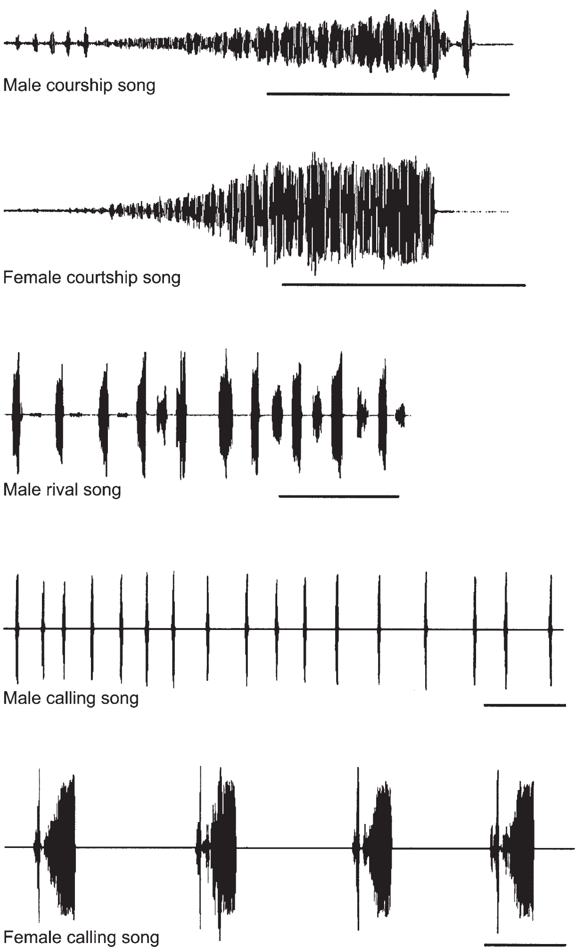
Independent of their mode of production, vibrational signals may be transmitted by the substrate (substrate-borne vibrations) or by the air (airborne vibrations). The signals may travel a short or long distance, or travel at a low or high speed. Low-frequency components are more suitable for longer-range communication through plants. Low frequency signals travel longer distances, but slowly; high frequency signals travel shorter distances, but quickly. Long-range vibratory songs are associated with pre-mating calling and vibrational orientation, and close-range vibratory songs are associated with courting rivalry and repelling.

Substrate-borne vibrations are less costly to the emitter. Also, substrate-borne vibrations are more far-reaching signals for intraspecific communication and not easily perceived by a potential predator or parasitoid. Usual substrates to transmit vibrational signals are plants or soil.

The characteristics of plants as transmission media for insect-produced vibrations have been described, and in many respects they determine signal production and the mode of reception. Depending on the physical properties of the host plant, the vibratory signals are transmitted effectively or not. Vibrations can be transmitted all along the stem, but the physical properties of a plant (e.g., elasticity, water content) affect resonance of insect vibrations. For transmission through plants, insects commonly emit broadbanded-mixed stridulatory and vibratory signals. Higher-frequency signals produced by stridulation are less relevant for long-distance communication through plants. However, narrow-band and low frequency songs are efficient in long-distance communication when well tuned to the resonant spectra of their host plants. The vibrational pulse reflects when attaining both the root area and top of the plant, and reflected waves travel up and down the stem several times. Reflections change the patterns of the input signal. Abiotic factors (temperature, rain, wind) may significantly modify plant resonance, masking insect vibratory signals and thus the effectiveness of the signal. Plant-borne vibrations seem to be important in the success of group-living, herbivorous insects for locating and remaining in a group of conspecifics, for locating food resources, and to avoid predation. Also, small insects that are not able to emit airborne sounds efficiently at low frequencies in many cases communicate with vibratory signals transmitted through plants.

In the stink bug *Nezara viridula* (Pentatomidae) (Figs. 10 and 11), a species which has become a model for all Pentatomorpha in relationship to acoustical communication, its vibratory signals were recorded and described first as airborne sound. However, further investigations showed that their most important mode of transmission is as substrate-borne vibrations. In *N. viridula*, a male could perceive a female calling in a *Cyperus* stem 2 m away from him, mechanically coupled only by roots and the surrounding earth. Below the leg of the singing bug, the intensity of signals was about 4 mm s^{-1}. On the bottom of the same stem (a distance of 80 cm) it decreased to around 3 mm s^{-1}, and at the place of the receiving bug, 200 cm away, it was approximately 0.5 mm s^{-1}.

When transmitted through the soil, signals travel a shorter distance and are more attenuated than when transmitted through a plant stem. For example, in *Scaptocoris* species (Cydnidae) the velocity of soil transmitted signals varied between 1.5 and 12.9 ms^{-1} at a distance of 0.5 cm.



Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 10 Oscillograms of songs emitted by males and females of the southern green stink bug, *Nezara viridula* (Pentatomidae) (adapted from Čokl, Virant-Doberlet (2003) Annu Rev Entomol 48: 29–50).

Acoustic Characteristics of Vibrational Signals

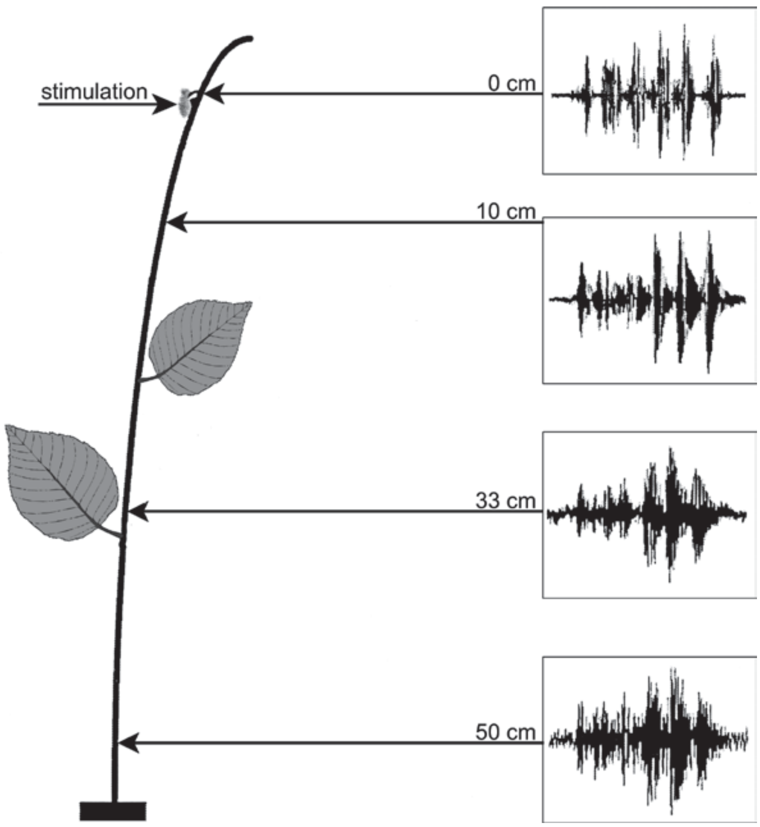
A vibrational signal may be characterized by its temporal (pulse train duration, repetition times, inter-pulse intervals) (Fig. 12) and spectral characteristics (dominant frequency). All of these characteristics may be measured by the receptor insect, who may modify its behavior in response to the message. The dominant frequency of signals produced by the vibratory mechanism lies between 50 and 200 Hz in most Heteroptera. Between species, songs differ in their time structure and amplitude modulation of their units. On the other hand, spectrally and temporally different pulse trains trigger the same male behavior in *N. viridula*.

In *Rhodnius prolixus* (Reduviidae), the male-deterring call has a main carrier frequency of about 1500 Hz, and the disturbance stridulation has a main carrier frequency of about 2200 Hz. In *Rhinocoris iracundus* (Reduviidae), low-frequency components of carrier frequency below 200 Hz are exchanged with frequency-modulated stridulatory components whose dominant frequency lies between 1 and 2 kHz. In *Triatoma infestans* (Reduviidae), distress songs have a peak of frequency between 700 and 800 Hz, although in other reduviids the carrier frequency may reach about 2000 Hz.

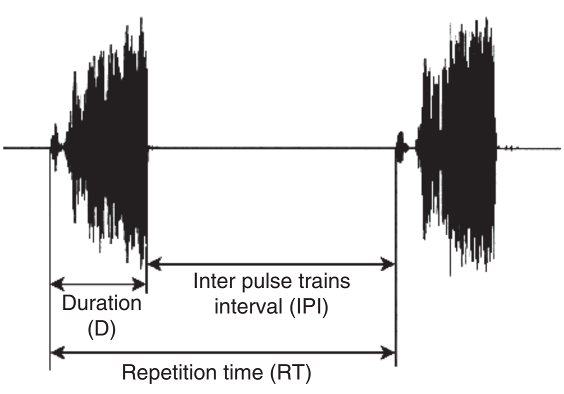
In *N. viridula*, dominant frequencies between 80 and 150 Hz were found in songs either as airborne sounds, or substrate or body vibrations. Body vibrations are around 100 Hz, and lie close to the range of best frequency sensitivity of low frequency receptor cells.

Specificity and Variability of Vibratory Signals

Sounds, especially those involved in the reproductive process (attraction, courtship, copulation),



Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 11 Laser vibrometer recordings taken from a plant fed upon by *Nezara viridula* showing the pattern of recordings at various distances (in cm) from the point of stimulation (adapted from Miklas et al (2001) J Insect Behav 14: 313–332).



Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 12 Temporal parameters of a vibratory signal (adapted from Miklas et al (2003) Behav Process 61: 131–142).

can be very complex and highly species-specific, and may be used as taxonomic characters of land bugs. In contrast, signals are much less specific when they provide information about enemies, rival mates, or serve as distress (disturbance or alarm) signals.

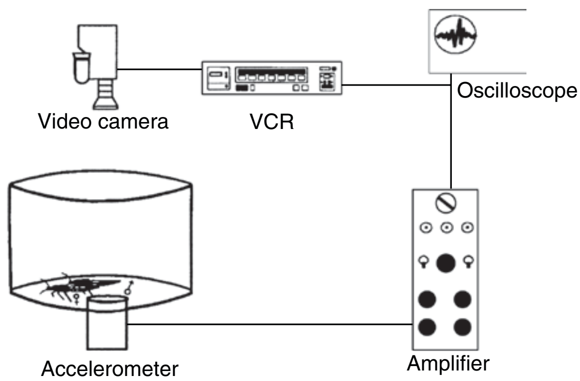
Females of *N. viridula* sing to trigger the male approach, and to evoke emission of the male courtship song. Females coming from populations of different geographic origin emit different calling songs, which can be differentiated by males. Females of *N. viridula* may emit a song that rejects copulatory attempts of males and stops their courting, and this is also known in the reduviid *Rhodnius prolixus*. The courtship songs of both males and females in different populations are not markedly different, but the calling songs may differ in some features and may be the source of reproductive isolation among populations. *Nezara viridula* produces four different species and sex-specific songs, and two of them play a vital role in mate location. There is song variability within populations (inter-individual variability). To assess those differences, the temporal song (pulse train duration, repetition times, inter-pulse intervals) and spectral song characteristics (dominant frequency) may be measured. Males usually show a preference for the females of their own population, although they may recognize females from other populations as potential partners.

In *Tritoma infestans*, stridulation songs differ in their syllable durations, repetition rate and main carrier frequency, depending on the song function. Differences come from rubbing their rostrum (scraper) at different speeds on the prosternal file. Also in *Rhodnius prolixus*, the different frequency between deterrent and disturbing signals can be explained on the basis of a different rubbing velocity by the proboscis against the prosternal stridulatory organ (Fig. 13).

In *Scaptocoris carvalhoi* and *S. castanea* (Cydnidae), two sympatric burrower bugs, high individual variation of the dominant frequency was observed in both male and female emissions (Fig. 14).

Vibratory Signaling in the Families of Heteroptera

Vibratory signaling has been reported in several Dipsocoromorpha and Leptodomorpha, but has been better studied in the following families: Veliidae (Gerromorpha), Nepidae, Corixidae, Notonectidae (Nepomorpha), Reduviidae, Miridae, Tingidae, Nabidae (Cimicomorpha), Aradidae, Acanthosomatidae, Cydnidae, Pentatomidae, Scutelleridae, Tessaratomidae, Thaumastellidae, Colobathristidae, Lygaeidae, Piesmatidae, Largidae, Alydidae, Coreidae, Rhopalidae (Pentatomorpha) (Figs. 15 and 16). Selected examples follow:



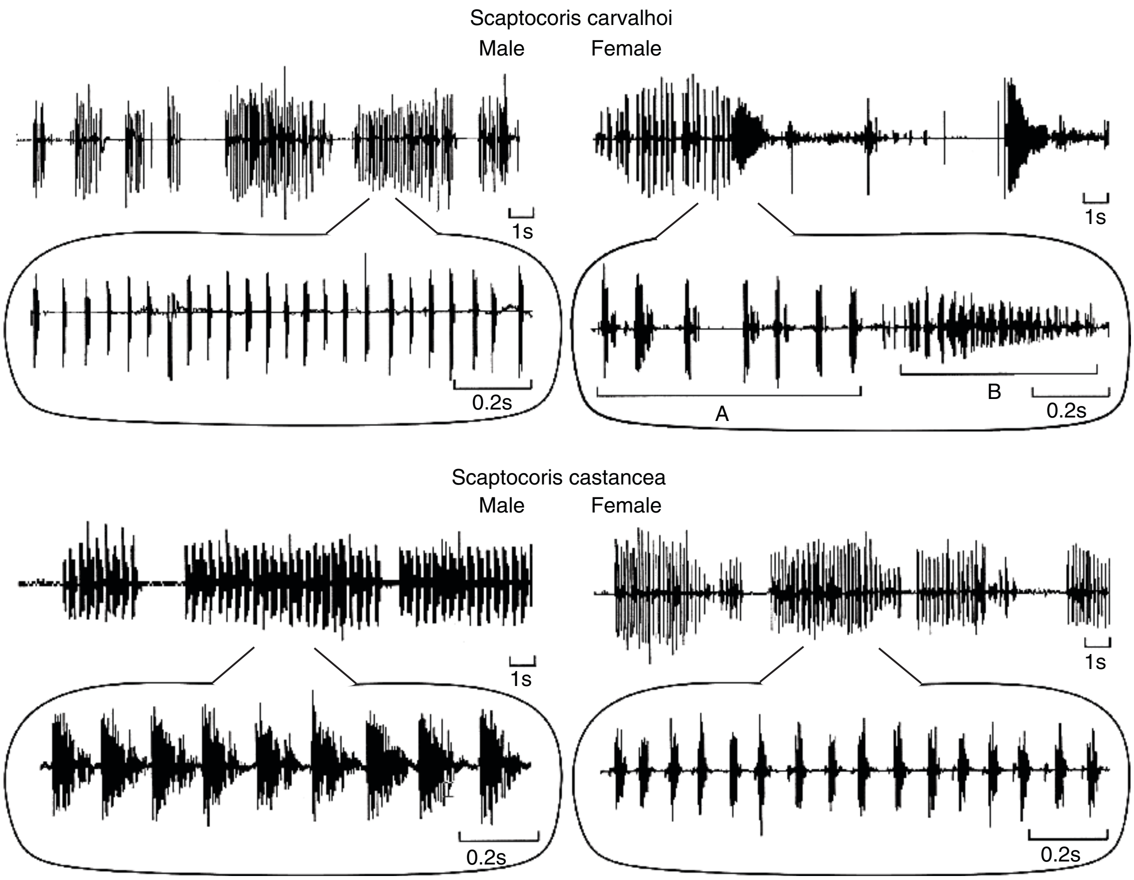
Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 13 Experimental setup used to study substrate-borne signals produced by stridulation in *Rhodnius prolixus* (Hemiptera: Reduviidae). The accelerometer generated a signal with voltage proportional to the instantaneous acceleration of the moving object, electrical signals were amplified and monitored by an oscilloscope, then this information was stored in the sound track of a videotape. Also, the behavior of the bugs was simultaneously videotaped (adapted from Manrique, Schilman (2000) Acta Trop 77:271–278).

Corixidae

In Corixidae, males or both sexes use species-specific sound for mate attraction and in courtship. The sounds are produced by stridulation, i.e., rubbing together specially modified parts of the body, or the partner's body.

Notonectidae

In Notonectidae, males produce species-specific courtship sounds by rubbing roughened parts of their front tibiae and femora against a special stridulatory region at the base of the rostrum (Fig. 17). In genus *Buenoa*, the sound can be heard at a distance of several meters. While next to the female, but before clasping her, the sound pattern can change.

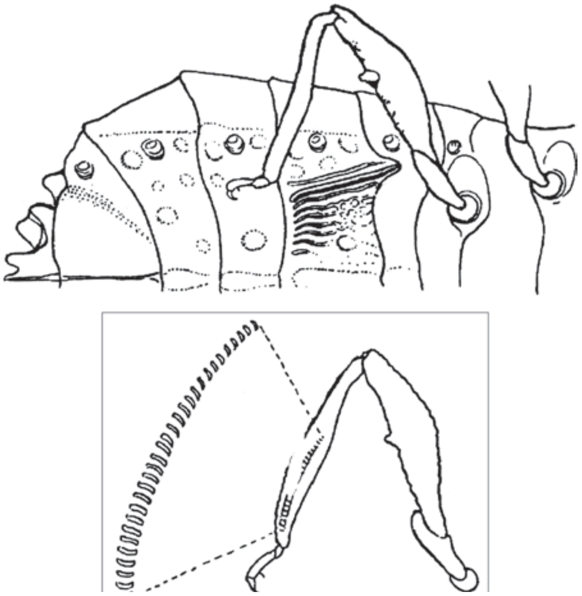


Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 14 Vibratory emissions of male and female burrower bugs *Scaptocoris carvalhoi* (above) and *S. castanea* (below) (Hemiptera: Cydnidae). A and B designate the two types of female song found in *S. carvalhoi*. Time scales are marked below oscillograms (adapted from Čokl et al. (2006) Physiol Entomol 31:371–381).

Reduviidae

Distress (disturbance or alarm) signals in Reduviidae may be produced either as nymphs or adults (males and/or females). In *Panstrongylus rufotuberculatus* (Reduviidae), stridulation occurs only under conditions of extreme provocation. Its sound is audible by the human ear, which is unusual among stridulating Triatominae, and is similar to the sound of sandpaper scraping wood. The tip of the rostrum is rubbed along the transversely ridged prosternal groove with an anterior-posterior movement; the return stroke (posterior-anterior) is silent. Stridulation lasts for about 5 min, although the insect remains immobile when held for a longer time. In a silent environment, the sound is audible at about 1 m away. A disturbance call has been described in the following triatomine species: *Dipetalogaster maxima*, *Triatoma infestans*, *T. guasayana*, *T. sordida*, *Panstrongylus megistus* and *Rhodnius prolixus*.

In the spined assassin bug, *Sinea diadema*, agonistic interactions between adult females may be resolved by stridulation in 33% of the cases. Stridulating individuals retreated more often than their non-stridulating opponents, indicating that stridulation may be a startle mechanism employed by temporarily disadvantaged individuals to escape from encounters. Together with other signs, stridulations provide information on the identity and relative fitness of the opponent.

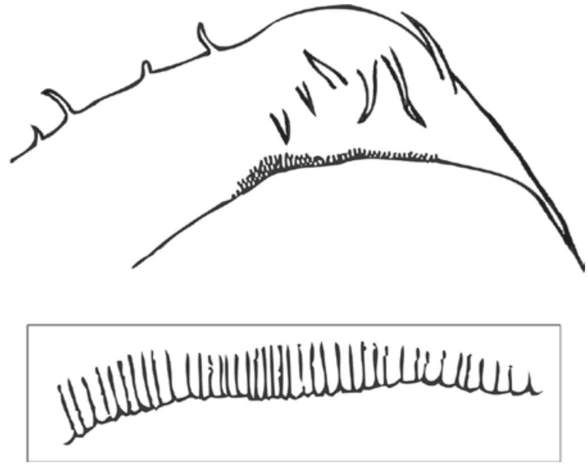


Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 15 ***Artabanus lativentris*** **(Hemiptera: Aradidae): (above) ventral view of abdomen, with file (stridulitrum), (below) hind leg with detail of scraper (plectrum) in the interior surface of the hind tibia (adapted from Schuh and Slater 1995 True bugs of the world (Hemiptera-Heteroptera): classification and natural history. Cornell University Press, Ithaca, NY, 335 pp).**

The acoustic repertoire of the ambush bug, *Phymata crassipes*, is quite large and may be displayed by females, males or nymphs. Its vibrational songs may be emitted in response to, and alternating with, calls from conspecifics, or even human speech or whistle. Sound emission is related to disturbance, interaction with other males and females, or courtship. Signals are produced by locomotory, stridulatory and/or vibratory mechanisms. Airborne signals directly or indirectly stimulate vibrational receptors. Bugs within a group respond to each other only via substrate, even in close proximity.

Miridae

Although a stridulatory device has been described in several tribes and subfamilies, the functions of acoustical communication in Miridae are still unknown.



Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 16 ***Phyllomorpha laciniata*** **(Hemiptera: Coreidae): (above) dorsal view of pronotum with scraper (plectrum) at its margin, (below) detail of spines of scraper (adapted from Moulet 1995 Faune de France 81).**

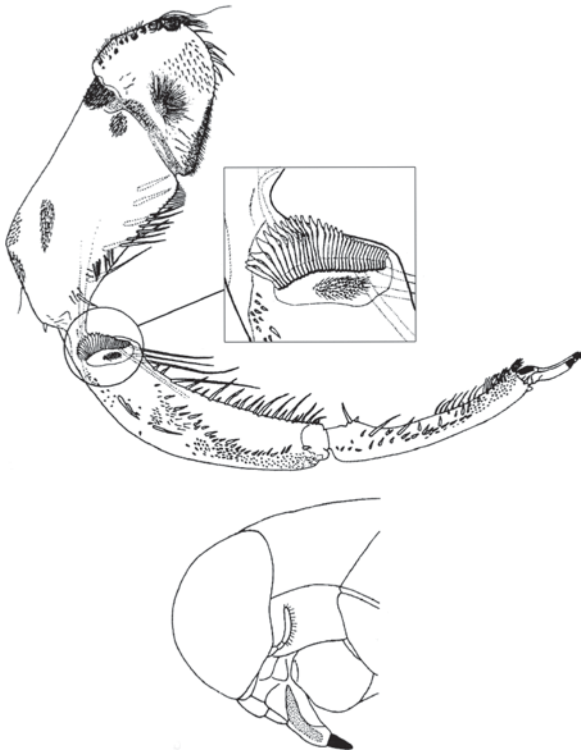
Tingidae

In the tingid *Corythuca hewitti*, vibrational signaling during group movements may occur as groups of nymphs are attended by a female. It has been reported that a disturbance of the leaf where *C. hewitti* aggregated caused feeding to stop and dispersal by the bugs, with occasional stopping of the bugs to vibrate the abdomen in a vertical plane, a behavior followed by conspecifics.

Cydnidae

In cydnids, the low species and sex specificity of pure stridulatory signals indicates that these vibratory emissions may play a role in disturbance (defensive) behavior, as in *Tritomegas bicolor*. Stridulatory signals are also related to aggregation or some other unspecific behavioral context. Cydnid bugs engage in rival singing and also distress (disturbance or alarm) signals, either as nymphs or adults (males and/or females).

Courtship, acceptance and rivalry songs show higher specificity and in most cases are



Acoustical Communication in Heteroptera (Hemiptera: Heteroptera), Figure 17 **Male *Anisops megalops* (Hemiptera: Notonectidae): (above) foreleg with detail of scraper (plectrum) in the interior surface of the fore-tibia, (below) lateral view of the head with file (stridulitrum) on the labium (adapted from Schuh and Slater 1995 True bugs of the world (Hemiptera-Heteroptera): classification and natural history. Cornell University Press, Ithaca, NY, 335 pp).**

produced by low frequency body vibration and/or by stridulation. *Tritomegas bicolor* produces courtship, mating, and male rivalry calls by stridulation and body vibration. In *Sehirus luctuosus*, the male's courtship call is produced by body vibration, giving a drumming song. Two types of species-specific male courtship songs, produced by stridulatory and vibratory mechanisms, have been described. The first type triggers female response, a species-specific agreement song. The second type stimulates pair formation.

In the group-living species of genus *Scaptocoris*, the absence of low frequency components of the emitted signals and the uniformity of songs indicate that calling and courtship may be mediated by signals of other modalities. The lack of low frequency signals may be explained by the direct contact of the bug with soil, which mechanically prevents free vibration of the abdomen.

Pentatomidae

Pentatomid bugs engage in rival singing. For example, *Nezara viridula* and *Rhapigaster nebulosa* may alternate rival songs until one or both stop singing, and in *P. lituratus*, males perform rival singing. Vibrational directionality has been demonstrated in host or prey searching in the predatory stink bug *Podisus maculiventris*.

The general pattern of singing during pre-mating behavior is similar for all Pentatomoidea. Calling starts with the emission of the female calling song, which triggers males to respond with calling and courtship songs, activates them to walk on the plant, and enables directional movement toward the female. Alternation of male and female songs may result in more or less complex duets, as is the case in *N. viridula*. *Nezara viridula* vibrates its body as part of intersex communications (courtship, directional cue for locating the mate, mate recognition), which implies that substrate-borne signals are highly species-specific. The female song causes the male to walk, to respond with the calling and courtship songs, and to approach the source of the song with characteristic search behavior. In contrast, females show no reaction to vibratory stimulation and no vibrational directionality.

► Insect Acoustics
► Cicada Acoustics
► Vibrational Communication

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Acoustic Aposematism (Clicking) by Caterpillars

Adult Lepidoptera are well known to perceive sound, such as the ultrasonic cries of insectivorous bats. Some even produce sounds that are used for social communication. Less well known is the sound production and reception of larvae. Some caterpillars employ vibrational signals with ants (e.g., Lycaenidae and Riodinidae), communicate about space with conspecifics (e.g., Gracillariidae), or detect insect predators or parasitoids (e.g., Noctuoidea and Gracillariidae). However, "clicking" sounds are an audible sound produced by caterpillars of silk moth (Saturniidae) and hawk moth (Sphingidae). This noise has also been described as "squeaking" or "crackling," and originates with the mandibles. Defensive sounds are usually categorized as startle or warning behaviors; startle sounds warn a potential predator, causing momentary hesitation and escape of the potential prey, whereas warning sounds alert a potential predator that it is inadvisable to attack. Associated with the clicking sound is regurgitation behavior, and both actions follow disturbance of the larva. Regurgitant usually is adverse to predators, and is a widespread defensive behavior among insects. Thus, clicking is thought to warn potential predators of an unpleasant experience if predation is attempted, but it is also possible that clicks function as startle sounds, allowing escape. This latter explanation seems unlikely, however, as caterpillars usually move very slowly, so escape is not very likely.

► Acoustic Communication in Insects
► Vibrational Communication

Reference

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Acoustic Communication in Insects

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Sound is used by a wide variety of insects for diverse purposes. It is difficult to evolve an acoustic communication system. There must be modifications to produce sound, transmit the sound in the environment and modify the sound to specific biological purposes, as well as the evolution of structures that will receive and decipher the signals. Arthropods are one of only two major groups of animals (along with the vertebrates) that have evolved acoustic communication and insects are the primary group of arthropods to exhibit acoustic behavior. At least ten orders of insects possess species that produce acoustic signals.

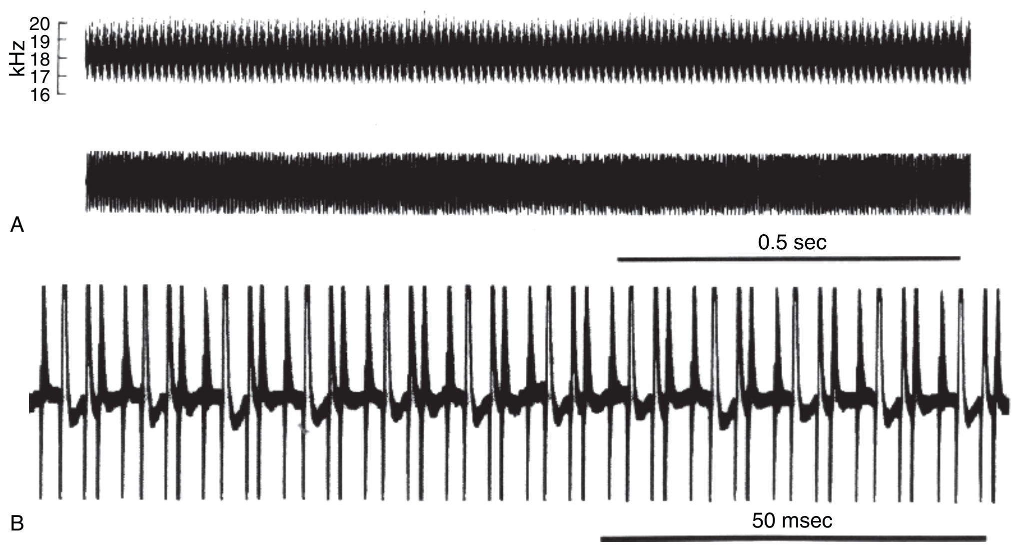
Sound

Sound is generated by causing the repeated compression and rarefaction of an elastic medium. The waves of compression produced will then travel through the medium to the receptor or target. The medium can be air, water or a substrate – so sound also encompasses vibrations. As the sound energy travels through the environment, it is modified by various interactions with the components of that environment. In addition, sound waves are reflected as they move through any environment. This bending of sound waves can initiate interactions among the waves. The signal begins to deteriorate as a result of these wave interactions and with the variations in the signal initiated due to temperature and humidity. Acoustic energy is also lost as it is absorbed by structures in the environment and as a result of spherical spreading from the sound source. The loss of signal integrity due to these environmental interactions is termed the excess attenuation of the signal. The amount of excess attenuation varies with the habitat and the original signal properties.

To complicate matters, the small size of insects requires that they use high frequencies (Fig. 18) to transfer energy efficiently to the signal. This will limit the range of a given signal because higher frequencies attenuate more rapidly in the environment. To use lower frequencies, insects must modify their bodies or behaviors to increase the efficiency of sound production. For example, tree crickets (Gryllidae) create a baffle by inserting their body in a leaf to decrease the acoustic short circuiting of a small dipole sound source, mole crickets (Gryllotalpidae) dig burrows which act as loudspeakers that amplify and direct their calls skyward, and the hollow abdomen of male cicadas (Cicadidae) acts as a resonating structure to amplify the acoustic signals produced by the tymbals.

The sound producing systems of insects are generally vibrating structures. These structures are necessary because muscles cannot contract rapidly enough to produce high frequency sounds. The sound generating structures vibrate multiple times for each muscle contraction, so the sound producing systems act as frequency multipliers. Once the vibrations are initiated, the sound can be modified by attached resonant structures.

There are many different schemes that can be employed to describe insect calls. The variety of sound production mechanisms has led to a variety of terminologies. No one terminology has been successful in describing the different sound production mechanisms or phylogenetic relationships of insects. When sounds are recorded and analyzed in any acoustic work, each analysis of acoustic signals in



Acoustic Communication in Insects, Figure 18 **Acoustic signal produced by the cicada *Beameria venosa* (Uhler). (a) Sonogram of calling song illustrating energy distribution of the call. Middle trace is an oscillogram illustrating the temporal pattern of the call. (b) Expanded oscillogram to show individual sound pulses within the call.**

insects should provide a detailed description of the terminology used to describe the signals, and illustration of the terminology on any oscillogram or sonogram in the work.

Sound Production

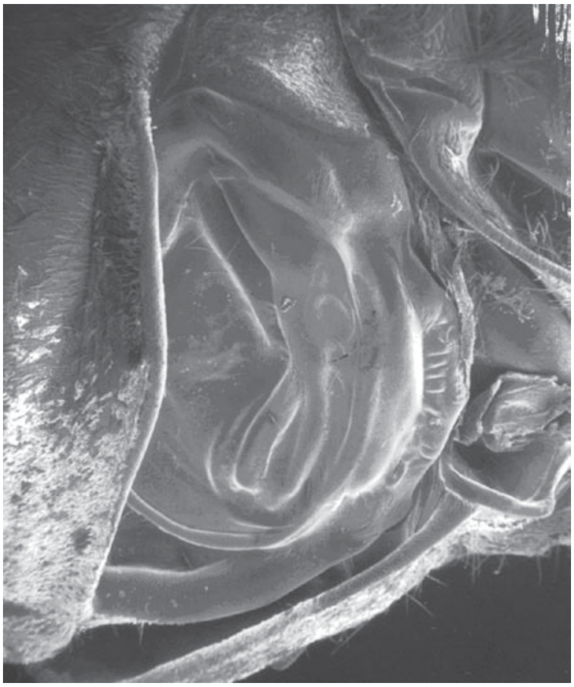
There are several different types of sound production mechanisms that have evolved in insects. The relatively low muscle contraction frequency means that additional structures had to evolve in order to produce the high frequency sounds that small body size will require to generate acoustic signals efficiently.

The primary mechanism used by insects to produce sound is a stridulatory apparatus. The chitinous exoskeleton and jointed appendages of insects are preadapted for modification into stridulatory apparati. Each stridulatory apparatus is composed of a file and plectrum or scraper. The file is generally a row of small cuticular teeth that is rubbed against a ridge or blade (the plectrum) on some other body part (Fig. 19). The teeth are bent as they catch on the plectrum and pop forward as they release from the plectrum. The release causes the teeth to vibrate alternately compressing and expanding air molecules producing sound. In general, these vibrations will occur in a single plane, resulting in a dipole being formed that produces an asymmetrical sound field at close range. The joints and exoskeleton of insects have permitted stridulatory apparati to evolve in many locations on the body. There are file and scrapers found between antennal segments (Phasmatodea), separate mouthparts (Orthoptera), head and thorax (Coleoptera), abdominal segments (Hymenoptera), wings and thorax (Lepidoptera, Hemiptera), body parts and legs (Hemiptera, Orthoptera), legs and wings (Orthoptera, Lepidoptera, Coleoptera), legs and legs (Thysanoptera, Hemiptera), between wings (Orthoptera), and between segments on the genitalia (Lepidoptera, Hemiptera). A tymbal organ is a specialized sound production organ. It is a ribbed, chitinous membrane attached to a tymbal

Acoustic Communication in Insects, Figure 19 **Stridulatory apparatus of the cicada *Tettigades undata* Torres. The file (illustrated) is located on the mesothorax in this group of cicadas. The plectrum is located on the tegmina. Sound pulses are produced as the tegmina is rubbed over the series of mesothoracic ridges.**

muscle (Fig. 20). The tymbal buckles as the tymbal muscle contracts. Sound pulses are produced when the tymbal buckles, when individual ribs buckle and potentially when the tymbal returns to its relaxed position. The unbuckling of the tymbal is assisted by the resilin within the tymbal. The resonant frequency of the tymbal determines the frequency of the sound pulses produced. Additional structures such as the opercula, tymbal covers, various muscles and the abdominal air sacs can modify the sound produced. The abdominal air sacs can become rather large as in the bladder cicada *Cystosoma saundersii* Westwood whose abdomen is so large, to resonate at a low frequency, that the male has difficulty flying. The tymbal is a common organ in the Hemiptera and acts as the ultrasonic pulse generator in the Lepidoptera.

Percussion is another mechanism of sound production used by insects. Crepitation, a clicking sound produced by the wings, is another percussion mechanism in insects. The wings are clapped together or banged on the substrate to produce a sound pulse in some Hemiptera. It is relatively rare for airborne signals which are generally produced as a by-product of flight. The wings may strike each other or the legs



Acoustic Communication in Insects, Figure 20
Tymbal organ of the cicada *Beameria venosa* (Uhler). The internally attached tymbal muscle buckles the tymbal to produce a sound pulse.

during flight-producing sound pulses as in the acridid grasshoppers (Orthoptera). However, specialized percussive sound production systems have evolved. A castanet is found on the costal margin of the tegmina in some moths (Lepidoptera) which produces a pure tone when struck. The acridid grasshopper *Paratylotropidia brunneri* Scudder can snap their mandibles together to generate sound. Percussion has been observed in Hemiptera, Isoptera, Plecoptera, Lepidoptera, and Orthoptera.

Tremulation is the vibration of unspecialized body parts to generate sound. The abdomen is often moved dorso-ventrally or laterally to send vibrations through the legs to the substrate. This mechanism has been well studied in the lacewings (Neuroptera). Wing vibrations can also be used to send information over short distances. This type of signal is produced by members of the Diptera (flies and mosquitoes) and Hymenoptera.

The expulsion of tracheal air is the final and relatively rare mechanism of insect sound production in insects. This method of sound production has been described in a number of insects, most notably the Madagascan hissing cockroach (*Gromphadorhina portentosa* [Schaum]), the Death's Head hawk moth (*Acherontia atropos* [L.]) and some African Sphingids (Lepidoptera).

In addition to the airborne signals produced by acoustic insects, it has now been shown that vibrational signals are also produced by sending information through the substrate. These vibrational signals are primarily produced by tremulation but also can be important in deciphering an airborne signal, particularly at close range to the sound source. Vibrational signals have been identified in members of the Neuroptera, Diptera, Hemiptera, Plecoptera, Coleoptera, Orthoptera, Mecoptera, Raphidioptera, Lepidoptera and Hymenoptera.

Sound Reception

A receptor for acoustic signals is necessary for a communication channel to exist. Because sound is produced by changing air pressure, a modified mechanoreceptor is needed to sense the acoustic information. The receptors can be classified as either a pressure detector or a particle detector. Pressure detectors are membranes that bend when pressure is unequal on the two sides of the detector. Particle detectors are long structures that move when impacted by many particles moving in the same direction. The movement of the particle detector alternately stretches and compresses sensory cells at the base of the organ.

The primary type of pressure receptor organ is a tympanum, which has evolved independently in at least eight orders of insects. Tympana are generally a thin membrane system stretched over a closed cavity. The tympanum bends away from the side of higher pressure setting up oscillations as the sound waves strike the membrane. Each tympanum has a resonant frequency based on its thickness, size and shape. The resonant frequency is generally tuned to the carrier frequencies of the communication channel to increase the efficiency of information transfer.

The tympana are associated with other mechanoreceptor organs to transduce the signal for the nervous system. As the tympana oscillate, vibrations are sent to various types of receptors, generally a specialized chordotonal organ called a scolopidial organ, which act as the input site to the central nervous system. There can be elaborate structures associated with the tympana to transduce energy into the central nervous systems such as the crista acoustica of the crickets and katydids (Orthoptera) and Müller's organ of locusts (Orthoptera), which provides frequency discriminating abilities. These pressure receptors are generally found in pairs, one on each side of the body. This provides an animal with a means to determine the direction from which the sound originated.

The sensory structures for vibrational signals are trichoid sensilla generally found on the feet or cerci or through specialized subgenual and metatarsal organs located in the legs. The subgenual organs are located just distal to the femoral-tibial joint in all six legs to promote detection and directional hearing. They are similar to tympana in that they are chordotonal organs but lack the tympanal membranes and tracheal air sacs of the tympanal system.

Particle receptors are generally specialized structures found in specific groups of insects. For example, female fruit flies (Diptera) sense the courtship signals produced by the male with a special antennal segment called an arista. Male mosquitoes and midges (Diptera) have plumose antennae which detect the species-specific wing beat frequencies produced by females. Johnston's organ is a more complex chordotonal organ found in the antennal pedicel of some Diptera and Hymenoptera which is stimulated by the vibration of the antennal flagella. The long bristles and antennae provide a mechanical advantage to the sensory cells increasing the sensitivity of the receptor.

Functions of Acoustic Signals

Sound has many potential benefits in that the signals can be used day or night, can be modified quickly, and can travel a significant distance even if conditions are not optimal for other signal pathways. However, sound is energetically costly to produce and advertises your position to potential predators as well as potential mates. Even with these potential problems, insects have evolved diverse functions for acoustic signals. Acoustic signals are used for a variety of purposes in insects including sexual signaling, courtship signals, aggression, social recruitment and defense.

A primary function of acoustic signals is as an intraspecific communication channel. Sounds are used to attract mates and to isolate species reproductively. Each species has a characteristic call that can prevent related species from cross mating. The calls produced by individual signalers can be compared by receivers providing the opportunity to select a mate who is producing a call that exhibits specific characteristics. This is particularly true when callers have congregated into localized areas, which is another function of acoustic signaling. Mates may be selected based on the number of calls, the temporal patterns, loudness, etc. The specific characteristics used by a given species are usually chosen based on their ability to demonstrate the viability of the caller. Duets between individuals (either intrasexual or intersexual) can also act as mechanisms to determine mate choice. The signals often change as potential mates approach. These courtship sounds are modified advertisement calls which provide further opportunities for mate assessment. Acoustic signals can also be used intraspecifically to space individuals in the environment, as aggression signals, or as competitive signals to jam the signal of a neighbor. Eusocial insects use acoustic signals as warnings, to recruit a defensive response within the colony, and to recruit foragers to specific food sources.

Predator deterrence is another significant function of acoustic signals. The loud sounds produced by many insects (e.g., cicadas [Hemiptera]), can startle a potential predator giving the insect a chance to escape. The percussion sounds produced by acridid grasshoppers (Orthoptera) are thought to be defensive displays. Sound production has evolved specifically for this anti-predator function in click beetles (Coleoptera). The acoustic systems that use air movement in the Death's Head moth (Lepidoptera), cockroaches (Blattodea) and grasshoppers (Orthoptera) also have anti-predator functions. Moths (Lepidoptera) have evolved a sound production system that is used to jam the ultrasonic signals of the bats that prey upon them. The arctiid moths emit ultrasonic pulses as bats approach which act to confuse the bat as to the exact location of its target. This gives the moth a chance to escape while the bat circles around for another attempt at capturing the insect. These pulses may also have an aposomatic function warning bats of a potentially distasteful meal.

Insects have also evolved specialized acoustic receptors as a means of avoiding predation. Bat-detectors have evolved independently in geometrid, noctuid and hawk moths (Lepidoptera), lacewings, (Neuroptera), praying mantises (Mantodea), beetles (Coleoptera), crickets, locusts and katydids (Orthoptera). These bat-detectors provide an early warning system for the insects that a bat is nearby giving the insect a chance to escape before the bat can sense an insect in the vicinity.

► Sound Production in the Cicadoidea
► Acoustic Aposematism
► Drumming Communication and Intersexual Searching Behavior of Stoneflies (Plecoptera)

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Acrididae

A family of grasshoppers (order Orthoptera). They commonly are known as shorthorned grasshoppers.

► Grasshoppers, Katydids and Crickets

Acriology

The study of grasshoppers, katydids, crickets and their relatives (Orthoptera). This is sometimes expanded to include the orders of insects related to Orthoptera (the Orthopteroids) such as cockroaches (Blattodea), mantids (Mantodea), stick insects (Phasmatodea), earwigs (Dermaptera), and gladiators (Mantophasmatodea).

► Classification
► Grasshoppers, Katydids and Crickets

Acrobat Ants (Hymenoptera: Formicidae)

A term applied to ants of the genus *Crematogaster*. Typically they are small, shiny brown or black, and possess a pedicel with two nodes. They elevate the gaster (tip of the abdomen) over the thorax or head when alarmed. Acrobat ants usually are found in association with wood or trees, including the tunnels of termites and wood boring beetles. They are omnivorous and tend aphids. Their bite can be painful.

► Ants (Hymenoptera: Formicidae)
► Ant-Plant Interactions

Acroceridae

A family of flies (order Diptera). They commonly are known as small-headed flies.

► Flies

Acrolepiidae

A family of moths (order Lepidoptera). They commonly are known as false diamondback moths.
► False Diamondback Moths
► Butterflies and Moths

Acrolophidae

A family of moths (order Lepidoptera). They commonly are known as tube moths.
► Tube Moths
► Butterflies and Moths

Acron

A preoral, unsegmented portion of the body, anterior to the first true body segment. This is also known as the prostomium.

Acrosternite

The narrow marginal region at the anterior edge of a sternite. It appears to be the posterior edge of the preceding sternite, and includes the intersegmental fold. It is found on the abdominal sterna, but absent from the thoracic sterna.

Action Threshold

A level of pest abundance that stimulates action to protect plants from serious damage.
► Economic Injury Level (EIL) and Economic Threshold (ET) Concepts in Pest Management

Active Dispersal

The redistribution of animals caused by their own actions such as flying or walking. The wings of insects allow active dispersal frequently (contrast with passive dispersal).

Active Ingredient (A.I.)

The toxic component of an formulated pesticide. It also is known as the toxicant.

Active Space

The area or space in which the concentration of pheromone (or other behavioral chemical) is at or above threshold concentration necessary to elicit a response from the receiver.

Active Ventilation

Although most gas exchange in insects occurs through diffusion (passive ventilation), in some cases it is inadequate to meet the oxygen needs of insects, particularly large or flying insects. Thus, muscular contractions acting via hydrostatic pressure (pressure on the hemolymph) compress the trachea and air sacs to force carbon dioxide out and allow more rapid intake of air. The exact mechanism varies among taxa, but usually involves contraction of the abdomen, and synchronization of opening and closing of the spiracles.
► Abdominal Pumping

Aculae

Small spines on the wing membrane of Lepidoptera.

Aculeus

This term has several meanings depending on the taxon of insects under consideration. In Hymenoptera, it is synonymous with the sting, an eversible hollow cylindrical structure at the tip of the abdomen used to deliver venom. Though derived from the ovipositor, it is not used to deliver eggs. Among Diptera, this term is sometimes used to refer to a pointed, sclerotized structure associated with the reproductive system in males. Among Lepidoptera, this term refers to hair-like structures on the body and wings of primitive moths; these also are known as microtrichia.

Acute

Of short duration, characterized by sharpness or severity.

Acute Bee Paralysis

A disease of honey bees caused by a picornavirus. Symptoms include trembling, sprawled appendages, and sometimes hairlessness (contrast with chronic bee paralysis).

Aculeate

Pertaining to the stinging Hymenoptera (suborder Aculeata), a group including the bees, ants, and many wasps.

► Wasps, Ants, Bees and Sawflies (Hymenoptera)

Acute Toxicity

The toxicity of a pesticide determined after 24 h. The toxicity resulting from a single dose or exposure.

► Insecticide Toxicity
► Insecticides

Adaptation

This term has at least two meanings: changes in the form or behavior of an organism during its life, and natural selection of organisms in evolutionary time. In entomology, usually the latter definition is intended.

Adaptation of Indigenous Insects to Introduced Crops

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Host range expansion, or adaptation of insects to new crops, is a world-wide phenomenon that has been observed repeatedly and extensively. It is particularly well documented in North America, where forests and prairies consisting of indigenous plants were planted extensively to introduced cultivated crops only after European emigrants arrived in the eighteenth century. Although many new insect pests were also accidentally introduced from Europe into Canada and the United States, many species of native insects adapted to the new crops and became economically important pests (Table 2).

Prior to widespread introduction of cultivated crops, some species of native insects fed on a wide range of plants and therefore might be expected to accept the new crops readily. Although polyphagous insects such as grasshoppers (Orthoptera: Acrididae), wireworms (Coleoptera: Elateridae), and cutworms (Lepidoptera: Noctuidae) readily accepted corn, wheat and other crops, not all of the species within these groups became agricultural pests. For example, several hundred species of cutworms and grasshoppers are present, but only about a dozen species in each group have achieved regular pest status.

Other native insect species had a narrower host range, and therefore adapted to a more narrow range of crops, or perhaps only a single crop. In the south the boll weevil, *Anthonomus grandis grandis* Boheman (Coleoptera: Curcullionidae), originally fed on native plants in Mexico related to cultivated cotton, and dispersed northward into the new cotton belt of the southeastern United States as cotton was planted extensively. In the north, the wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), fed on hollow-stemmed wild grasses, and within 10 years after tillage began in Alberta, wheat was damaged from

Adaptation of Indegenous Insects to introduced Crops, Table 2 Examples of American insect pests that have adapted to introduced crops

Insects with wide host ranges	Old host plant	New host plant
Apple maggot, *Rhagoletis pomonella* (Walsh) Diptera: Tephritidae	Hawthorne	Apple
Chinch bug, *Blissus leucopterus leucopterus* Heteroptera: Lygaeidae	Grasses	Corn
Western corn rootworm, *Diabrotica virgifera virgifera* LeConte Coleoptera: Chrysomelidae	Grasses	Corn
Western bean cutworm, *Loxagrotis albicosta* (Smith) Coleoptera: Chrysomelidae	Solanaceous weeds	Corn, beans
Colorado potato beetle, *Leptinotarsa decemlineata* (Say) Coleoptera: Chrysomeliodae	Buffalo burr	Potato
Carrot weevil, *Listronotus oregonensis* (LeConte) Coleoptera: Curculionidae	Umbelliferous weeds	Carrots, etc.
California red scale, *Aonidiella aurantii* (Maskell) Hemiptera: Diaspididae	Shrubs and trees	Citrus
Boll weevil, *Anthonomus grandis* Boheman Coleoptera: Curculionidae	Malvaceous weeds	Cotton
Insects with wide host ranges	**Old host plant**	**New host plant**
Sugar beet wireworm, *Limonius californicus* Coleoptera: Elateridae	Weeds, grasses	Field and vegetable crops
White grubs, *Phyllophaga* spp. Coleoptera: Scarabidae	Weeds, grasses	Field and vegetable crops
False chinch bug, *Nysius raphanus* Howard Hemiptera: Lygaeidae	Weeds, grasses	Field and vegetable crops
Tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois) Hemiptera: Miridae	Weeds, grasses	Field and vegetable crops
Army cutworm, *Euxoa auxiliaris* (Grote) Lepidoptera: Noctuidae	Weeds, grasses	Field and vegetable crops
Yellow striped armyworm, *Spodoptera ornithogalli* (Guenée) Lepidoptera: Noctuidae	Weeds, grasses	Field and vegetable crops
Redlegged grasshopper, *Melanoplus femurrubrum* (de Geer) Orthoptera: Acrididae	Weeds, grasses	Field and vegetable crops

Adaptation of Indegenous Insects to introduced Crops, Table 2 (Continued)

Insects with wide host ranges	Old host plant	New host plant
Migratory grasshopper, *Melanoplus sanguinipes* (Fabricius) Orthoptera: Acrididae	Weeds, grasses	Field and vegetable crops

the Canadian prairie provinces south into Montana and North Dakota. In the eastern United States the apple maggot, *Rhagoletis pomonella* (Walsh) (Diptera: Tep hritidae), expanded its host range to included newly introduced cultivated fruits, especially apples. The Colorado potato beetle, *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae) originally fed on solanaceous weeds in Mexico or the southwestern United States, and quickly spread across the United States on potatoes once it gained access to potato acreage. These are just a few examples of insects accepting new hosts, and the same phenomenon is well documented for important tropical crops such as sugarcane and cacao, and other crops, as they were introduced and cultivated in various locations around the world.

Some of the native insect populations originally occurred at low levels because their host plants were relatively sparse. Large acreage of new monocrop habitats therefore resulted in an abundant food supply, excellent survival, and eventually in pest population outbreaks. Also, the native environments were relatively stable, and supported a wide range of beneficial insects suppressed herbivorous insects. However, soil tillage within the agricultural environments produced highly disturbed systems, and pests with high fecundity were not effectively suppressed by predators and parasitoids.

America's native insects displayed considerable plasticity in acquiring new hosts. This trend has been noted everywhere agriculture is practiced, and we can expect the number of pests to increase with time, and especially with the area planted to each particular crop, as indigenous species adapt to imported host plants or crops are exposed to additional potential pests in new geographic areas. However, species accrual occurs most rapidly soon after plant introduction, and the number of species feeding on a plant (species richness) does not increase indefinitely, leveling off after less than 300 years if there is not an increase in crop acreage.

We can observe insects with both broad and narrow host selection behavior expanding their host range to include introduced crop plants. This is not surprising for generalist species, which feed broadly on many plants, but it is quite interesting when insects with a narrow host range adopt new hosts. In such cases the species with a narrow host range usually are pre-adapted to accept the foreign crops because they feed on plants in the same family as the introduced crop. North America possesses close relatives to nearly all the introduced crops among its indigenous flora, so it is not surprising that insects associated with the native plants would adapt to the introduced crops. The presence of secondary plant metabolites (allelochemicals) such as alkaloids, terpenoids, and cyanogenic glycosides often serves to keep non-adapted insects from feeding extensively on plants, but may serve as chemical cues or stimulants for insects that are adapted. Thus, insects that specialize on cruciferous weeds and crops are attracted to allylisothiocyanate, and insects that feed on cucurbitaceous weeds and crops are attracted to cucurbitacin.

Host selection behavior by insects is not a static situation, nor is it as simple as the single-chemical scenario presented above. It is constantly evolving in response to various biotic characteristics such as herbivory, and even to crop cultural practices. Some natural selection of insect strains may have occurred during the adaptation from native to introduced plants. In the northern Great Plains, wheat matures earlier in the season than wild grasses. Therefore, after a century, adult wheat stem sawflies are now active nearly a month earlier than previously, and now are more effective in utilizing wheat.

Changes in farming practices that have also impacted populations of native insect pests in croplands. Originally, horses were used for farming, and oats were needed for their feed. Later, the horses were replaced by tractors, and the need for oats was reduced. Oats are resistant to wheat stem sawflies, and when oats was eliminated from the cropping system, the vast acreages of wheat resulted in a population explosion of the sawflies. More recently, canola has been included in the Canadian Prairie Provinces, and populations of grass-feeding insects are somewhat disrupted by the presence of a non-host, cruciferous crop. Other water and soil conservation practices such as alternate-year summer fallow, strip cropping, and chemical fallow have affected the prevalence of both pest and beneficial insects.

Beneficial insect populations were also impacted by tillage and cultural practices, and changes in the chemical constituency of crop plants. Parasitoids have complex host searching behavior that begins with finding plant environments in which their hosts could occur. Therefore, it was necessary for the parasitoids to learn that the new crops could be sources of hosts. In the case of the wheat stem sawfly, only two of the known parasitoid species have currently adapted from wild grasses to wheat. Parasitoids may be more favored by one plant cultivar than another, or less favored by a crop than a similar weed. The availability of food for the adult parasitoid or predator, either nectar from blossoms or extra floral nectaries or pollen from blossoms, is often implicated in differential survival of beneficial insects among different plants.

Overall, adaption by herbivorous insects to new host plants is a dynamic and widespread phenomenon. Though sometimes it is difficult to determine whether it is the change in the constituency of the host plant that accounts for insect acceptance, or it is some other factor such as widespread host plant availability that accounts for insect abundance, it is clear that the relationship between insects and plants is not static, resulting in a continuing stream of new pest problems for crop plants.

► Host Plant Selection by Insects
► Allelochemicals
► Plant Resistance to Insects

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Adaxial Surface

The upper surface of a leaf (contrast with abaxial surface).

Adeheterothripidae

A family of thrips (order Thysanoptera).

► Thrips

Adelgidae

A family of insects in the order Hemiptera. They sometimes are called pine and spruce aphids.

► Aphids
► Bugs

Adelidae

A family of moths (order Lepidoptera). They commonly are known as long horned fairy moths.

► Long horned Fairy Moths
► Butterflies and Moths

Adephaga

One of four suborders of beetles (Coleoptera), and one of two suborders that contain numerous and important beetles (the other is suborder Polyphaga). It is comprised of about nine families, the principal ones being Carabidae, Gyrinidae, and Dytiscidae. Nearly all groups are predatory, and many are aquatic.
► Beetles (Coleoptera)

Aderidae

A family of beetles (order Coleoptera). They commonly are known as antlike leaf beetles.
► Beetles

Adfrontal Areas

A pair of narrow oblique sclerites on the head of a caterpillar. The adfrontal areas border the front, which normally is triangular, so the adfrontal areas take on the shape of an inverted "V."
► Head of Hexapods

Adelphoparasitism

A type of hyperparasitism occurring in Hymenoptera: Aphelinidae in which the males are parasitoids of females of their own species (the females parasitize Hemiptera).

Adherence

The ability of a material such as a pesticide to stick to a surface.

Adipohemocyte

A type of hemocyte, ovoid in shape and likely secretory in function.
► Hemocytes of Insects: Their Morphology and Function

Adipokinetic Hormone (AKH)

A decapeptide hormone synthesized in neurosecretory cells of the corpora cardiaca and important in the regulation of lipid metabolism, and sometimes carbohydrate or proline metabolism and other physiological functions.
► Adipokinetic and Hypertrehalosemic Neurohormones

Adipokinetic and Hypertrehalosemic Neurohormones

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The adipokinetic hormones and hypertrehalosemic hormones of insects comprise a family of peptide hormones that primarily regulate the levels of energy metabolites, such as trehalose, diacylglycerol and proline that circulate in the hemolymph. These peptide hormones are products of neurosecretory neurons located in the corpora cardiaca, neuroendocrine glands attached to the brain. The structural organization of the insect corpora cardiaca is similar to the hypothalamus-neurohypophysis of the vertebrate endocrine system.

Historical Perspective

The existence of hypertrehalosemic hormones was discovered with the observation that injections of extracts of corpora cardiaca elevated the concentration of trehalose in the hemolymph of cockroaches (hypertrehalosemia). Unlike vertebrates that use glucose as the major blood carbohydrate, the hemolymph of insects generally contains the disaccharide trehalose, an α-1-1-gluco-glucoside, as its major circulating carbohydrate. In addition, the enzyme glycogen phosphorylase in the fat body of cockroaches was demonstrated to be activated when these insects were injected with an extract from the corpora cardiaca. Subsequently, studies in locusts showed that injections of corpora cardiaca extracts elevated hemolymph diacylglycerols, instead of trehalose, and this action was referred to as an adipokinetic or hyperlipemic effect. Injections of locust corpora cardiaca extracts into cockroaches produced the hypertrehalosemic response, and vice versa. Hence, it was likely that the adipokinetic hormone (AKH) of locusts and the hypertrehalosemic hormone (HrTH) of cockroaches were related, or identical, peptides.

The locust adipokinetic hormone was isolated and characterized first. It was obtained from the migratory locust, *Locusta migratoria*, and its primary structure consisted of ten amino acids. It was designated Locmi-AKH-I according to the newest nomenclature for naming insect neurohormones. The amino acid composition and sequence of Locmi-AKH-I had a remarkable similarity to a previously reported red pigment-concentrating hormone (Panbo-RPCH) obtained from the shrimp *Pandalus borealis* and later found in various crustaceans. It was shown that Locmi-AKH-I was also present in the desert locust, *Schistocerca gregaria*.

Subsequently, both *L. migratoria* and *S. gregaria* were shown to contain a second adipokinetic hormone (Locmi-AKH-II and Schgr-AKH-II, respectively) that differed from each other by the amino acids in position 6. The two locust AKH-IIs were octapeptides with sequences similar to those of Locmi-AKH-I and Panbo-RPCH. A third octapeptide AKH (Locmi-AKH-III) was also found in *L. migratoria* and a similar octapeptide (designated Phymo-AKH-III) occurs in pyrgomorphid and pamphagid grasshoppers, but an AKH-III is missing in *S. gregaria*. Subsequently, three research groups ultimately reported, in the same year, the presence of two octapeptides from the corpora cardiaca of the American cockroach, *Periplaneta americana*, that were structurally related to the locust AKHs and the crustacean RPCH. These two peptides were isolated on the basis of myotropic or heartbeat acceleration bioassays and are referred to as cardio acceleratory hormones (Peram-CAH-I and Peram-CAH-II), but they also produced hypertrehalosemia in the cockroach and represent the hypertrehalosemic hormones. These pioneering studies, along with numerous subsequent studies, demonstrated that there are, so far, about forty structurally related, but distinct, peptides with adipokinetic and hypertrehalosemic effects in the insects and one in crustacean (Table 3). The name adipokinetic hormone/red pigment-concentrating hormone (AKH/RPCH) family was coined for this general family of peptides, which likely encompasses the arthropods.

Chemistry of the AKH/RPCH Family

The members of the adipokinetic hormone/red pigment-concentrating hormone family share numerous structural features. They consist either of eight, nine or ten amino acids, depending on the insect species from which they are isolated. They are blocked by pyro-glutamate at the N-terminus and by an amide moiety at the C-terminus. Presumably, blocked termini prevent degradation of the neuropeptides by amino- and carboxypeptidase enzymes while circulating in the hemolymph. Aromatic amino acids, usually phenylalanine and tryptophan, always occupy positions 4 and 8, respectively, but aromatic amino acids can also occupy other positions. The peptides are usually neutral under physiological conditions, but a few have a negatively charged aspartate at position 7. Glycine is always present at position 9 as deduced from cDNA analysis of the precursor. The terminal glycine is converted to the amide moiety on the tryptophan in the octapeptides.

Adipokinetic and Hypertrehalosemic Neurohormones, Table 3 **Representative sequences of adipokinetic/hypertrehalosemic peptides from various insect orders**

Order	Peptide name	Genus	Structure										
			1	2	3	4	5	6	7	8	9	10	
Odonata	Libau-AKH	*Libellula, Pantala, Orthetrum*	pGlu	Val	Asn	Phe	Thr	Pro	Ser	Trp	NH_2		
	Anaim-AKH	*Anax, Aeshna*	pGlu	Val	Asn	Phe	Ser	Pro	Ser	Trp	NH_2		
	Psein-AKH	*Pseudagrion, Ischnura*	pGlu	Val	Asn	Phe	Thr	Pro	Gly	Trp	NH_2		
Blattodea Blattidae Blaberidae Blattellidae	Peram-CAH-I[a]	*Periplaneta, Blatta*	pGlu	Val	Asn	Phe	Ser	Pro	Asn	Trp	NH_2		
	Peram-CAH-II[a]	*Periplaneta, Blatta*	pGlu	Leu	Thr	Phe	Thr	Pro	Asn	Trp	NH_2		
	Bladi-HrTH	*Blaberus, Nauphoeta*	pGlu	Val	Asn	Phe	Ser	Pro	Gly	Trp	Gly	Thr	NH_2
		Leucophaea, Blattella											
		Gromphadorhina											
Mantodea	Emppe-AKH	*Empusa, Sphodromantis*	pGlu	Val	Asn	Phe	Thr	Pro	Asn	Trp	NH_2		
Phasmatodea	Carmo-HrTH	*Carausius, Sipyloidea, Extatosoma*	pGlu	Leu	Thr	Phe	Thr	Pro	Asn	Trp	Gly	Thr	NH_2
Mantophasmatodea	Manto-AKH	Not known	pGlu	Val	Asn	Phe	Ser	Pro	Gly	Trp	NH_2		
Orthoptera, Caelifera	Locmi-AKH-I	*Locusta, Schistocerca*	pGlu	Leu	Asn	Phe	Thr	Pro	Asn	Trp	Gly	Thr	NH_2
	Locmi-AKH-II	*Locusta*	pGlu	Leu	Asn	Phe	Ser	Ala	Gly	Trp	NH_2		
	Schgr-AKH-II[a]	*Schistocerca, Phymateus*	pGlu	Leu	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		
	Locmi-AKH-III	*Locusta*	pGlu	Leu	Asn	Phe	Thr	Pro	Trp	Trp	NH_2		
	Phymo-AKH-III	*Phymateus*	pGlu	Ile	Asn	Phe	Thr	Pro	Trp	Trp	NH_2		
Orthoptera, Ensifera	Grybi-AKH[a]	*Gryllus, Acheta, Gryllodes*	pGlu	Val	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		
	=Schgr-AKH-II	*Tettigonia, Decticus*	pGlu	Leu	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		

Isoptera	Micvi-CC	*Microhodotermes*	pGlu	Ile	Asn	Phe	Thr	Pro	Asn	Trp	NH_2		
Dermaptera	=Grybi-AKH	*Labidura, Forficula*	pGlu	Val	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		
Hemiptera/Homoptera	Placa-HrTH	*Platypleura, Munza, Cacama, Magici-cada, Diceroprocta*	pGlu	Val	Asn	Phe	Ser	Pro	Ser	Trp	Gly	Asn	NH_2
Hemiptera, Heteroptera	Pyrap-AKH	*Pyrrhocoris, Disdercus*	pGlu	Leu	Asn	Phe	Thr	Pro	Asn	Trp	NH_2		
	=Peram-CAH-II	*Pyrrhocoris, Disdercus*	pGlu	Leu	Thr	Phe	Thr	Pro	Asn	Trp	NH_2		
	Corpu-AKH	*Corixa*	pGlu	Leu	Asn	Phe	Ser	Pro	Ser	Trp	NH_2		
	Letin-AKH	*Lethocerus*	pGlu	Val	Asn	Phe	Ser	Pro	Tyr	Trp	NH_2		
	Nepci-AKH	*Nepa*	pGlu	Leu	Asn	Phe	Ser	Ser	Gly	Trp	NH_2		
Neuroptera	=Grybi-AKH	*Palpares*	pGlu	Val	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		
Coleoptera	Scade-CC-I	*Scarabaeus, Gareta, Onitis*	pGlu	Phe	Asn	Tyr	Ser	Pro	Asp	Trp	NH_2		
	Scade-CC-II	*Scarabaeus, Gareta*	pGlu	Phe	Asn	Tyr	Ser	Pro	Val	Trp	NH_2		
	Oniay-CC	*Onitis*	pGlu	Tyr	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		
	=Peram-CAH-I	*Leptinotarsa*	pGlu	Val	Asn	Phe	Ser	Pro	Asn	Trp	NH_2		
	=Peram-CAH-II	*Leptinotarsa*	pGlu	Leu	Thr	Phe	Thr	Pro	Asn	Trp	NH_2		
Lepidoptera	Manse-AKH[a]	*Manduca, Vanessa, Bombyx, Heliothis*[b]	pGlu	Leu	Thr	Phe	Thr	Ser	Ser	Trp	Gly	NH2	
	Helze-HrTH	*Heliothis*[b]	pGlu	Leu	Thr	Phe	Ser	Ser	Gly	Trp	Gly	Asn	NH_2
Hymenoptera	Tenar-HrTH	*Tenthredo*	pGlu	Leu	Asn	Phe	Ser	Thr	Gly	Trp	Gly	Gly	NH_2
	=Schgr-AKH-II	*Xylocopa, Bombus*	pGlu	Leu	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		
	=Grybi-AKH	*Vespula, Vespa*	pGlu	Val	Asn	Phe	Ser	Thr	Gly	Trp	NH_2		
	=Manse-AKH	*Apis*	pGlu	Leu	Thr	Phe	Thr	Ser	Ser	Trp	Gly	NH_2	

Adipokinetic and Hypertrehalosemic Neurohormones, Table 3 Representative sequences of adipokinetic/hypertrehalosemic peptides from various insect orders (Continued)

Order	Peptide name	Genus	Structure										
			1	2	3	4	5	6	7	8	9	10	
Diptera	Phote-HrTH	*Phormia, Drosophila*	pGlu	Leu	Thr	Phe	Ser	Pro	Asp	Trp	NH_2		
	Anoga-AKH	*Anopheles*	pGlu	Leu	Thr	Phe	Thr	Pro	Ala	Trp	NH_2		
	Tabat-AKH	*Tabanus*	pGlu	Leu	Thr	Phe	Thr	Pro	Gly	Trp	NH_2		
Crustacea	Panbo-RPCH	*Pandalus*	pGlu	Leu	Asn	Phe	Ser	Pro	Gly	Trp	NH_2		

[a]Note that the peptide in certain orders is identical. For example: Peram-CAH-I and -II of the Blattodea, Blattidae is also present in Coleoptera (Leptinotarsa); Schgr-AKH-II of Orthoptera, Caelifera is present in Orthoptera, Ensifera and in Hymenoptera (***Xylocopa***, ***Bombus***); Grybi-AKH of Orthoptera, Ensifera is also present in Dermaptera, Neuroptera and Hymenoptera, etc.

[b]***Heliothis*** is revised to ***Helicoverpa.***

Some of the members of this peptide family have additional post-translational modifications besides the blocked termini. For example, two HrTH decapeptides are present in the corpora cardiaca of the stick insect, *Carausius morosus*; one of these decapeptides is glycosylated and has a unique C-glycosylation where the sugar is linked to the C-2 atom of the indole ring of tryptophan. Another unusual modification has been found in an AKH of the protea beetle, *Trichostetha fascicularis*: the corpora cardiaca contain two AKHs, one of which is an octapeptide with a phosphothreonine at position 6.

The relationships between individual AKH and HrTH peptides and insect species are complex. There are no clear rules concerning which peptide occurs in which order of insects. Several species within an order may share the same peptide and have other species-specific sequences, and the same peptide may be present in species of different orders. As described above, the two locust species, *S. gregaria* and *L. migratoria*, share an identical decapeptide (Locmi-AKH-I); each species possesses a second, unique octapeptide (Locmi-AKH-II; Schgr-AKH-II); and *L. migratoria* contains a third octapeptide (Locmi-AKH-III) that does not have a complement in *S. gregaria*. Cockroach species of the families Blattellidae and Blaberidae share a single hypertrehalosemic decapeptide hormone (Bladi-HrTH), whereas cockroaches of the family Blattidae contain two octapeptide hormones (Peram-CAH-I and -II). In addition, there is overlap between orders. Grybi-AKH is present in certain crickets and in species of Neuroptera, Dermaptera and Heteroptera. Peram-CAH-I and -II of the blattid cockroaches are also found in the Colorado potato beetle, *Leptinotarsa decemlineata*, and Peram-CAH-II is shared with the heteropteran bug, *Pyrrhocoris apterus*. Whereas Peram-CAH-I and -II mobilize glycogen from the fat body of the cockroach to increase hemolymph trehalose, the same or similar peptides increase hemolymph proline in beetles to serve as the major flight substrate.

Unlike the complex situation in insects, the crustaceans apparently possess only the single Panbo-RPCH peptide which has a chromatophorotropic effect. Panbo-RPCH has also been found in an insect species, the heteropteran stinkbug, *Nezara viridula*, where it has an adipokinetic effect.

Phylogenetic relationships of the HrTHs have been proposed for the cockroaches based on morphological, behavioral and physiological characters congruent with the distribution of the various structures of the HrTHs within the order.

Physiological Actions

The general physiological action of the adipokinetic and hypertrehalosemic hormones in insects is to elevate the hemolymph metabolites that are used by the muscles and other tissues as a source of energy, regardless of the nature of the metabolites. This is accomplished by stimulating the fat body, which is the hormone's target tissue, to convert its stores of triacylglycerides or glycogen to diacylglycerides or trehalose, respectively, or to synthesize proline. The diacylglycerides, trehalose or proline are released from the fat body to increase their respective levels in the hemolymph. The same peptides that elevate diacylglycerides in locusts elevate trehalose when administered to cockroaches, and vice versa, and the hormones of locusts and cockroaches elevate proline in the Colorado potato beetle. The decision as to whether lipid-, carbohydrate-, or proline-mobilizing pathways are activated is a species-related function of the enzyme composition in the fat body.

Muscular activity for animal locomotion can involve either long-term or short-term events. Long-term activities might entail sustained, nonemergency actions such as migration or persistent searching for food, mates or shelter. Short-term activities might consist of local searching activities but may also require immediate, brief, emergency responses such as evading attack by a predator or defending a breeding territory. Long-term events require a steady supply of energy metabolites, whereas short-term events may be brief but intense, and, if successful, they can be followed by a period of recovery to replenish exhausted metabolites.

The adipokinetic hormones are often involved in prolonged, constant muscular activity such as migration. This is characteristically true for the locusts whose migratory behavior has been described since biblical times. Migration is a sustained flight activity that uses muscular oxidation of fatty acids to produce energy, since fatty acids deliver more energy per mole than carbohydrates. However, carbohydrate serves as the major source of muscular energy during initial flight, and lipid becomes the major source for energy as flight persists and becomes sustained. Based on differing physiological effects, it is speculated that the three AKHs may exert different regulatory actions on metabolite mobilization and use during the different stages of migration. Locmi-AKH-II is likely to be the major carbohydrate-mobilizing hormone that provides trehalose for initial flight; Locmi-AKH-I is the major hormone responsible for fat mobilization during sustained flight and Locmi-AKH-III may be responsible for regulating energy metabolism during rest. Furthermore, during lipid mobilization, AKH performs several distinct but related actions. In the fat body, AKH activates lipase for triacylglyceride degradation; this is achieved by binding of the AKH to a G-protein coupled receptor at the cell membrane, activation of adenylate cyclase resulting in the second messenger cAMP which, in conjunction with Ca^{2+}, is responsible for lipase activation. In the hemolymph, AKH increases the lipid-carrying capacity of lipophorins (proteins) resulting in increased amounts of low-density lipophorin for shuttling lipids from the fat body to the muscles. At the flight muscle level, AKH increases the rate of lipid oxidation. Recent research on a number of terrestrial and aqueous heteropteran bugs that have various feeding patterns (plant sap sucking, predators, obligatory hematophagous), also established a lipid-based activity (flight and/or swimming) metabolism that is regulated by the respective AKHs of these insects.

By contrast, insects such as cockroaches, bees and flies use only carbohydrate (trehalose) as the primary source of energy for muscular activity and locomotion. These species do not migrate and lack the adipokinetic response, but they are faced with emergency situations of predator evasion, and in such cases, the hypertrehalosemic hormone mobilizes trehalose in response to the emergency. However, injections of hypertrehalosemic hormone show that significant elevation of the hemolymph trehalose may take as long as 10–30 min. This delay in elevating hemolymph carbohydrate is too long to significantly assist the insect in evading capture. Furthermore, the open circulatory system of insects does not efficiently direct circulating metabolites to the muscles in the manner of the closed circulatory system of vertebrate animals. Energy metabolites, such as trehalose, must constantly be maintained at high levels in the hemolymph to meet urgent, immediate demands. Hence, the role of the hypertrehalosemic hormone appears to be to replace depleted hemolymph trehalose and maintain it at high levels. Maintenance of high trehalose levels allows the insect to make quick responses to elude capture that may require only seconds, or at most, several minutes to conclude. If the insect is successful at escape, the hormone stimulates the degradation of fat body glycogen to restore the high trehalose levels by activating specifically the enzyme glycogen phosphorylase after the hormone has bound to a G-protein coupled receptor on the membrane of a fat cell and had activated a phospholipase C, resulting in the production of inositol trisphosphate and the release of Ca^{2+} from internal stores (influx of external Ca^{2+} is also activated by HrTH) which sets in motion a cascade of activation of kinases and, finally, glycogen phosphorylase. Removal of the hypertrehalosemic hormone does not affect the ability of such insects to be active for the short term (several minutes), but after exhaustion, lengthens their recovery time.

Tsetse flies and various beetle species fuel their flight metabolism by the partial oxidation of proline and the production of alanine. For continuous flight or replenishment of proline reserves in the fat body a unique system exists in these insects to synthesis proline: the respective AKHs activate a lipase in the fat body and the fatty acids that are liberated from triacylglyerols undergo β-oxidation, and the resulting acetyl CoA units are used in conjunction with alanine to synthesize proline. Alanine, which is derived from the partial oxidation of proline, is re-used for proline synthesis and can be viewed as a shuttle system for the transport of acetyl units.

Although the mobilization of energy for flight and other metabolically intense situations is likely the major function for the adipokinetic and hypertrehalosemic hormones, the hormones exhibit pleiotropic actions. The hypertrehalosemic hormones were isolated originally based on their cardioacceleratory action on the heart. This is a logical action for the hormone since elevated heartbeat rate would facilitate distribution of the energy metabolites throughout the body and assure their ready access to the muscles. In keeping with the stimulatory action of AKH on lipid degradation in locusts, lipid synthesis is inhibited by AKH. Other, less well characterized actions include: inhibition of RNA and protein synthesis related to vitellogenesis in locusts and crickets, and the stimulation in cockroaches of the oxidative capacity of mitochondria during fat body maturation, and of gene expression for a fat body cytochrome P450 related to lipid oxidation. These latter actions by the hormones may be equally important as their effects on mobilization of energy metabolites, but they are poorly elucidated because of insufficient research, and they cannot yet be placed into perspective as to their physiological significance. Other actions in which AKHs seem to be involved are an enhanced activation of the locust immune system and, possibly, in the activation of an antioxidant protection mechanism in potato beetles.

In summary, the adipokinetic-hypertrehalosemic-hyperprolinemic hormones constitute a family of peptides that are adapted to the individual biology of the insect species in which they are found. They display a unique relationship with their target tissue in that the hormone carries the endocrine message to the target tissue (fat body) to mobilize energy stores, but the target tissue determines which metabolic pathways are activated depending on the biology of the species. It is this biology that determines the nature of the muscular activity (prolonged–migration; brief–predator evasion) and its metabolic need for consuming carbohydrates, lipids or proline as a source of energy.

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Adjuvants

Chemicals added to insecticides to improve their effectiveness. Examples of adjuvants include toxicity, stability, and adhesion.

► Insecticide Formulations

► Insecticides

Adoption Substance

A secretion presented by a social parasite that induces the host insects to accept the parasites as members of their colony.

► Social Insect Pheromones

Adult

The sexually mature stage of an animal. The adult is usually the winged stage in insects. With rare exceptions, the adult does not molt again.

► Metamorphosis

Adulticide

A pesticide used to kill adult insects. This term often is used to describe products used to kill adult mosquitoes. (contrast with larvicide)

► Insecticides

Adultoid Reproductive

In higher termites, a supplementary reproductive that in indistinguishable morphologically from the reproductive.

Adult Transport

A behavior in which social insects (usually ants) drag or carry their nestmates to a new location. This normally occurs during colony emigration.

Adventitious Veins

In some insects, additional wing veins are present which are neither secondary nor intercalary veins. They usually are the result of the lining up of cross veins.

► Wings of Insects

Adventive

An organism that has arrived in an area from elsewhere. It is not native, and likely arrived as an invader or accidental introduction. It is also known as nonindigenous.

► Invasive Species

Aedeagus

The intromittent (copulatory) organ of the male; the distal portion of the phallus. Sometimes referred to as the penis.

► Abdomen of Hexapods

Aenictopecheidae

A family of bugs (order Hemiptera).

► Bugs

Aeolothripidae

A family of thrips (order Thysanoptera). They commonly are known as broad-winged thrips or banded thrips.

► Thrips

Aepophilidae

A family of bugs (order Hemiptera). The sometimes are called marine bugs.

► Bugs

Aeshnidae

A family of dragonflies (order Odonata). They commonly are known as darners.

► Dragonflies and Damselflies

Aetalionid Treehoppers

Members of the family Aetalionidae (order Hemiptera).

► Bugs

Aerial Photography

In pest management, photographs taken by an airplane or satellite that are used to identify variations within fields/crops to help make management decisions.

Aeropile

The opening in the egg surface (chorion) through which air enters.

Aerosol

The air suspension of liquid or solid particles of small diameter. This is a common formulation for flying insects or for household use where no additional formulation or preparation is desired.

► Insecticides

► Insecticide Formulations

Aesthetic Injury Level

The level of pest abundance above which aesthetic, emotional, or sociological considerations require pest control actions. Economic considerations are not relevant.

► Economic Injury Level (EIL) and Economic Threshold (ET) Concepts in Pest Management

Aesthetic Pest

A pest which, through its presence or actions, is deemed objectionable and in need of elimination even though it causes no economic loss. The presence of some insects in homes or on ornamental plants are examples of aesthetic pests, though in the latter case if they inhibit the ability to market plants then the same insect can be come an economic pest.

► Economic Injury Level (EIL) and Economic Threshold (ET) Concepts in Pest Management

Aestivation

A state of inactivity or curtailment of normal activity during the summer months. Diapause

Aetalionidae

A family of insects in the order Hemiptera. They sometimes are called aetalionid treehoppers.

► Bugs

► Treehoppers

African Armyworm, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae)

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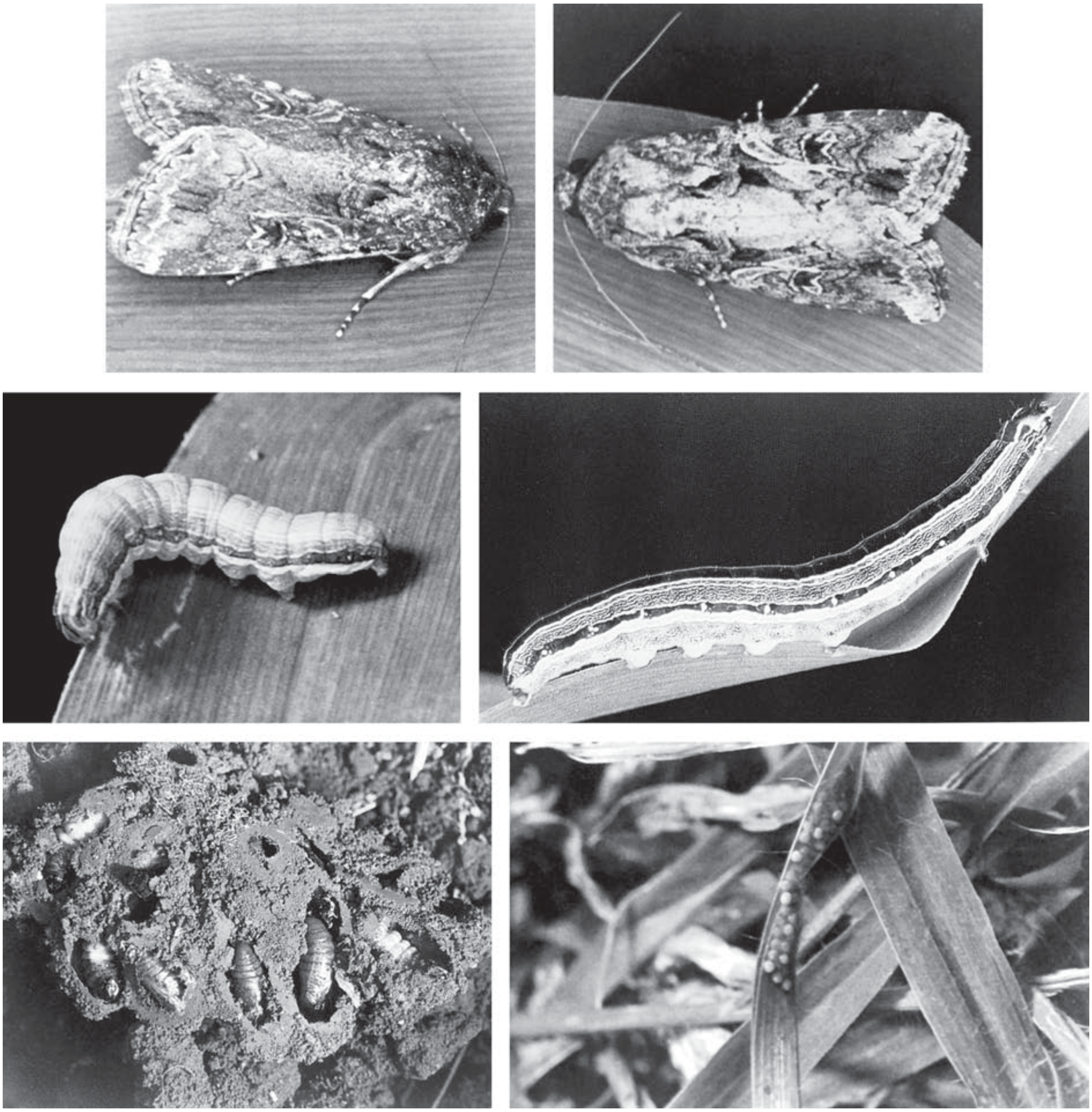
The African armyworm (Fig. 21) is a larva of a nocturnal moth, *Spodoptera exempta* (Walker). This species, although commonly referred to as the African armyworm, occurs rather widely in the grasslands of tropical and subtropical Africa and Asia. In Africa, where *S. exempta* is of major economic importance, its occurrence is confined to countries south of the Sahara: Tanzania, Kenya, Uganda, Ethiopia, Somalia, Malawi, Zimbabwe, Zambia and South Africa. Outside Africa, *S. exempta* has been reported from southwest Saudi Arabia in the republic of Yemen, southeast Asia, Australia, New Zealand and Hawaii.



African Armyworm, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae), Figure 21 **African armyworm: top left, adult female, top right, adult male; middle left, solitary form of larva; middle right, gregarious form of larva; lower left, pupae in soil; lower right, eggs on foliage.**

During an armyworm outbreak, larvae of *S. exempta* march together in long columns, akin to army columns, in search of susceptible plant material. This is the basis for the name "armyworm." When susceptible plant material is found, it is often voraciously devoured to ground level. In typical armyworm outbreaks, larval density may exceed 1,000 per m^2 over areas covering tens or even hundreds of square km.

In Africa, *S. exempta* is adapted for survival on seasonal grasslands by combining a high intrinsic rate of increase with "migration" to places of rainfall where grasses are suitable for survival of its caterpillars. Because of its capability to move over long distances, hundreds and sometimes thousands of km across national boundaries freely, *S. exempta* is truly an international pest. Often times it appears sporadically and suddenly in dense outbreaks capable of causing extensive and enormous damage to susceptible rangeland grasses, cereal crops and sugarcane. Because of its ability to appear suddenly and then disappear equally suddenly, the African armyworm has sometimes been referred to by farmers as the "mystery worm." The scale of devastation to crops and pastures by armyworm is comparable only to that caused by locusts. Thus, the armyworm is greatly feared wherever it occurs.

Biology and Ecology

Adult moths of *S. exempta* have a wing span in the range of 20–37 mm. The forewings are characterized by an overall dull gray-brown appearance. The hind wings are whitish with dark veins. The two sexes can be distinguished by examining the number of bristles on the frenulum (the mechanism that couples the fore and hind wings during flight), which are single in the males and multiple in the females. A characteristic feature of the African armyworm is the presence of racquet-shaped scales at the tip of the abdomen of the males and black scales on the tip of the body of the females.

Females of *S. exempta* lay between 100 and 400 eggs per night in a mass covered by black scales from the tip of their abdomen. Eggs are small, 0.5 mm in diameter, whitish in color, but then turn black prior to hatching. Eggs are often laid on the lower side of leaves and hatch in about 2–4 days after oviposition. There are six larval instars extending over a larval period of between 14 and 22 days depending on the temperature and the host plant on which the larvae have been reared. Fully grown sixth instar larvae are often 25–35 mm long. Pupation occurs 2–3 cm below the soil surface. This process is often preceded by a sudden and synchronized disappearance of larvae that quickly burrow into the ground, particularly if soil conditions are moist enough.

Adults emerge within 7–12 days after pupation and can live up to 14 days if appropriately fed. In their lifetime, females can lay up to 1,000 eggs. *Spodoptera exempta* is not known to enter into any type of diapause. This probably explains why this species has to migrate soon after emergence.

Spodoptera exempta exhibits a phenomenon called polyphenism, or phase polymorphism (i.e., the occurrence in a population of two or more phenotypes due to exposure to different environmental conditions). For example, up until the third molt, all larvae of *S. exempta* remain green in body color. However, at this stage, depending on whether there are many larvae or just a few, they will turn black or remain in various shades of green or brown. If there are large numbers of larvae present as in a typical outbreak situation, larvae tend to be characteristically velvety black on top with pale lines on each side and greenish-yellow underside; this phenotype is called the gregarious phase. It is during this phase that *S. exempta* is most devastating to crops. Larvae in the gregarious phase tend to be very active and often march on the soil in one direction only looking for fresh food. They also feed high on the plant during the day.

However, if not crowded, the developing larvae remain one of the many shades of green, pink or brown color until they pupate. In contrast to black gregarious larvae, they are sluggish, living mostly at the bases of plants and are not as destructive to crops. Although their appearance is so different, they are the same insect and one may easily be converted into the other. Nevertheless, because moths derived from gregarious and solitary larvae exhibit the same level of readiness to fly, phase change in *S. exempta* is construed as being merely a stress phenomenon associated with crowding. It is unknown whether this aspect of phase polymorphism is of any evolutionary significance to *S. exempta*. In the case of locusts, it is thought that the solitary form is the one that enables the populations to persist at a low level during the dry season when there are no outbreaks occurring. It is worth speculating, in the case of *S. exempta*, that at such low densities, its populations continue to breed during the dry season in areas where grasses remain green, such as in the cool highland areas and, more especially, the coastal areas where it is hot and there are periodic showers during the dry season. This form may, therefore, be of some critical survival value for this pest.

Seasonal Movements and Armyworm Outbreaks

Upon emergence, adult moths of *S. exempta* are fully capable of movement from their breeding sites to new areas. Such flights can be very short, or very long, depending on whether they are carried in a downwind direction or not. Nevertheless, because they are one-way journeys, they cannot, therefore, be regarded as migration in its strict ethological sense – where there is invariably a return flight to breeding sites.

The question of how armyworm outbreaks start has baffled scientists and farmers alike for a long time. Because moths emerge over a period of up to 12 days, and can also fly off on "migration" at different times, they become widely dispersed and do not form swarms as occurs with locusts. Moreover, the moths are weak fliers and are often carried in a downwind direction. Thus, moths disperse in space and time downwind. For purposes of this narrative, an armyworm outbreak is simply described as the sudden appearance of larval infestations, often simultaneously on many farms in one region.

Two hypotheses, the continuity and the concentration hypotheses, have been put forward in order to explain how outbreaks begin during an armyworm season. The continuity hypothesis, which is based on biogeographical analyses of past outbreaks, proposes that much of the armyworm population is always at crowded, outbreak densities, and that the seasonal absence of reports represents not a real absence of outbreaks, but a temporary loss of contact with the main population in remote and perhaps uninhabited areas. This continuity implies that the first outbreaks to appear in East Africa are due to the migration of parent moths from the north at the end of the season. Although there is ample evidence of adult dispersal on the wind over distances up to several hundred km in a few successive nights, there is little evidence in support of a southward dispersal at the start of an armyworm outbreak in East Africa.

The concentration hypothesis, on the other hand, postulates that because of occasional capture of moths in traps during the off-season, as well as the finding of rare caterpillars after concerted searches, *S. exempta* persists during such times of year as uncrowded populations (the solitary phase, in which caterpillars remain green and unreported), and that the first outbreaks of the season are due to concentration of moths before the synchronized mating and egg laying.

Thus, there seem to be two types of armyworm outbreaks: primary and secondary outbreaks. During primary outbreaks, sources of outbreaks are the low density populations that survive and breed during dry seasons in green areas of the coast and the highlands. Secondary outbreaks occur downwind from the coast near the first highlands. During years of serious armyworm outbreaks, the first outbreaks often start in Tanzania, Zimbabwe and Malawi at about the beginning of the wet season in December, and are followed by a progression of outbreaks at about one generation time-intervals from Tanzania through Kenya, Uganda, Ethiopia, Somalia to the Yemen and from Zimbabwe to South Africa. Wind convergence plus localized weather and moth behavior provide the mechanism for transporting and concentrating moths emerging from primary outbreaks.

Flight mechanisms of *S. exempta* prior to outbreaks have been the subject of extensive studies. After drying and hardening their wings, moths first move up into the trees. Then, when they are ready, they fly up several hundreds of meters into the air, where if caught up by prevailing wind, are carried away downwind. When dawn arrives, the moths descend and hide on the ground in the grass, but at dusk they take off again. They will continue to do this for several days, either until they die, or until they come to an area where rain is falling. Rain causes the moth to descend to the ground. The winds coming out of the rainstorm have the effect of concentrating the moths, rather as though they were being swept together with a brush. This is the reason why armyworms occurring during outbreaks are not evenly distributed. Upon descent to the ground, moths tend to drink water if this is available, mate and then lay their eggs. At this stage dispersal will have come to an end.

In Africa, seasonal rains are brought by the meeting of large scale winds from the northeast and the southwest at the Inter-Tropical Convergence Zone (ITCZ). The position of the ITCZ moves with the sun across the tropical zone twice each year, from north to south between July and December and from south to north between January and June. The first outbreaks, designated as primary outbreaks in East Africa, usually occur in central Tanzania in November or December. Occasionally they occur further south, in Mbeya, Mtwara and Lindi regions of Tanzania. More rarely, they occur in southeastern Kenya.

Moths produced by these primary outbreaks are then carried by the wind towards the ITCZ, which has meanwhile moved north. The moths are thus concentrated in areas where the rains are just beginning, and so they breed and multiply yet again. If conditions are suitable, they will increase at an enormous rate. Although the first outbreaks are only a few hectares in extent, by February and March there may be outbreaks of hundreds of square km.

Thus, as the ITCZ takes the rains northwards, so the moths, carried by the prevailing wind, move with it, bringing new armyworm outbreaks, designated secondary outbreaks, to northern Tanzania, Kenya, Somalia, Ethiopia, Sudan and eventually Yemen. Armyworm outbreak seasons vary greatly in severity, extent and timing in each of these countries.

From September to November, there are seldom armyworm outbreaks in any part of eastern Africa. The armyworm seems to disappear during the dry season. But since they have no diapause, they must be living and breeding somewhere. It has now been established that they survive in quite low numbers along the coastal area, where some rain falls in every month of the year. When the rains begin again in central Tanzania, small numbers of moths migrate inland from the coast and it is these that cause the first outbreaks.

Economic Importance of Outbreaks of *S. exempta*

During armyworm outbreaks, feeding damage by *S. exempta* to cultivated and wild host plants is almost entirely restricted to the leaves, although when food is scarce, the young stems or flowers, particularly of wild grasses, may also be eaten up. The young larvae at first eat the upper and lower surface tissue of the leaves, which results in the skeletonization, or windowing, of the leaves. As a rule, armyworm larvae tend to prefer young plants and recently germinated crops, often defoliating them to ground level. It is estimated that two larvae can completely destroy a 10-day-old maize plant with 6–7 leaves and a single larva can consume 200 mg of dry mass of maize leaves in the course of the sixth instar.

Destruction of cereal crops such as maize, rice, wheat or sorghum often necessitates replanting of the entire affected crop. *S. exempta* larvae are most damaging to cultivated and wild host plants during outbreaks when gregarious bands of larvae travel together on the ground. Such armyworm outbreaks are often capable of causing total crop loss within hours at the local level. Thus, crop losses as a result of armyworm outbreaks can be potentially devastating to local and national economies as they occur in some of Africa's most impoverished economies. Losses are sometimes difficult to assess quantitatively because of hidden costs such as effects of forage destruction, damage to subsistence farms, the expense of additional seed and, most importantly, food aid from international donors.

Survey and Control

Circumstantial evidence from light and pheromone traps shows that long distance migrations occur between moth emergence and the next breeding areas which are in the vicinity of seasonal passages of low-level wind convergence such as Inter-tropical Convergence Zone or African Rift Convergence Zones. Furthermore, increasing levels of moth catches in light and pheromone traps have been found to be followed by increased probability of infestations of larvae occurring 2–4 weeks later at up to 200 km from the trap.

Because primary outbreaks of *S. exempta* originate from moths taken downwind from sources nearest the coasts of eastern Africa, and concentrate where heavy rains are falling, control of this pest involves accurately detecting primary outbreaks and eliminating them before the subsequent moths emerge and move downwind causing secondary outbreaks in another region or country. The major objective is to kill as many armyworms as possible on pasture or crops before subsequent moths emerge and move downwind. Normally, the largest and densest outbreaks are attacked first. This approach is referred to as "strategic control." However, because primary outbreaks often remain unnoticed until after secondary outbreaks have occurred, direct elimination of the latter becomes the main objective in multiple outbreak situations.

Monitoring possible sources of the moths that cause primary outbreaks has involved deployment of a network of light and pheromone traps, as well as ground searches for low-density larvae in the off-season in areas historically known to be sites of primary outbreaks. In addition, for all primary outbreak areas, rainfall stations must report on a weekly or daily basis the amount of rainfall during the first month of the rainy season. Recently, there have been attempts to introduce predictive models that integrate African Real Time Environmental Monitoring and Information System (ARTEMIS) and satellite imagery and synoptic weather data that has been applicable for detection and elimination of gregarious locusts. The major challenge associated with armyworm monitoring, forecasting and control in countries most ravaged by this pest is the inadequacy of funding for these operations.

Because elimination of all primary outbreaks is almost impossible to achieve, management strategies for *S. exempta* tend to focus more on suppression of secondary outbreaks. This approach has invariably been dependent on the application of pesticide sprays. To date, a series of low toxicity pesticides are often used (e.g., synthetic pyrethroids, carbamates and organophosphates). Previously, highly toxic, persistent and broad spectrum pesticides such as DDT, BHC, dieldrin and a series of others were used due to lack of alternative, safer products. However, due to the need for rapid intervention and coverage of fairly extensive areas during outbreaks, newer oil-based pesticides are being applied as ultra-low volume (ulv) formulations using hand held, battery driven applicators. Nevertheless, suppression tactics are only cost-effective when applied in a timely manner on farmland. Outbreaks occurring on uncultivated land often remain unchecked.

Unfortunately, control of armyworms by less toxic means has received far less attention than in the case of other international migratory pests such as locusts, which have been the targets for tests involving fungi, protozoa and even viruses.

Extensive studies in eastern Africa have confirmed that all life stages of the armyworm are subject to attack by a diversity of natural enemies. For example, up to 90% of armyworm caterpillars in the last instar can be killed by a nuclear polyhedrosis virus (NPV). Similarly, pupal and prepupal stages can be killed by a cytoplasmic virus. The only fungus known to attack armyworms during conditions of high humidity and temperature is *Normuraea rileyi*. Armyworms infected by this fungi typically climb to the top of grass blades where they die amidst masses of mycelia.

Armyworm larvae are also subject to parasitism by some 28 species of tachnid flies (Diptera: Tachinidae). In cases of parasitism from wasps (Hymenoptera), some 25 parasitoids have been isolated from eggs, larvae and pupae of *S. exempta*. Apart from attack by parasitoids, there are several arthropod predators that prey on armyworms, including ants (Hymenoptera: Formicidae) and beetles (Coleoptera), which often prey on eggs and early larval stages of *S. exempta*. To date, there has been no effort to study the potential of some of these natural enemies for commercialization. Armyworm outbreaks also attract flocks of avian predators, notably storks such as Marabou storks, white (European) storks and Abdim's storks. Occasionally, such assemblages of predators help to eliminate small primary or secondary outbreaks of *S. exempta*.

For the more foreseeable future, it is evident that preventive control of armyworms will continue to rely on diligent surveillance during recessions and, as outbreaks occur, intensified scouting will be necessary to locate and then eliminate pockets of solitary morphs before outbreaks.

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African Honey Bee, Africanized Honey Bee, or Killer Bee, *Apis mellifera scutellata* Lepeletier (Hymenoptera: Apidae)

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The African honey bee (*Apis mellifera scutellata* Lepeletier) is a subspecies (or race) of western honey bee (*A. mellifera* L.) that occurs naturally in sub-Saharan Africa but has been introduced into the Americas. More than 10 subspecies of western honey bees exist in Africa and all justifiably are called "African" honey bees. However, the term "African (Africanized) honey bee" refers exclusively to *A.m. scutellata* in the bee's introduced range (Fig. 22).

Subspecies of western honey bees are native to Europe and Africa but have been spread widely outside their native range due to their economic importance as pollinators and producers of honey. Initially, only European subspecies of honey bees (hereafter referred to as European bees) were introduced into the Americas, where they were found to be productive in temperate North America but less so in Central and South America where tropical/subtropical climates dominate. In response to the poor performance of European bees in Brazil, Warwick Kerr, a Brazilian scientist, traveled to southern Africa to screen African honey bee subspecies for productivity and viability. His visit resulted in the importation of *A.m. scutellata* into Brazil in the late 1950s.

Dr. Kerr hoped that through experimentation and selective breeding, the African bee could be made manageable and available for use by Brazilian beekeepers. As such, he initiated efforts to breed gentleness into the African stock while amplifying its many positive traits. The breeding effort was not carried to completion because the African bees swarmed accidentally, ending their initial quarantine. Following this, the bees began to spread throughout Brazil and into other parts of South America.

All subspecies of *Apis mellifera* can interbreed or hybridize. Consequently, African bee hybridization with European bees became frequent as African bees moved into areas previously occupied by European bees. It is this hybridization with

African Honey Bee, Africanized Honey Bee, or Killer Bee, *Apis mellifera scutellata* Lepeletier (Hymenoptera: Apidae), Figure 22 **The natural distribution of *Apis mellifera scutellata* in Africa (modified from Hepburn HR, Radloff SE (1998) Honeybees of Africa. Springer-Verlag, Berlin, 370 pp), and its distribution in the Americas.**

European honey bees that earned them the name "Africanized" honey bees. Traditionally, "African" and "Africanized" have been used interchangeably although the former really refers to the pure race and the latter to the hybrid.

The spread of African bees throughout South and Central America, fueled by rapid hybridization with European subspecies and the dominance of African alleles over European ones, occurred at a rate of 200–300 miles per year. Because their movement through South and Central America was rapid and largely unassisted by humans, African bees earned the reputation of being the most successful biologically invasive species of all time. In 1990, populations of African honey bees had saturated South and Central America and begun to move into the USA. As of 2006, African honey bees were established in the southernmost USA: Texas, California, New Mexico, Arizona, Oklahoma, Louisiana, Arkansas, Alabama, and Florida.

The spread of African bees in the U.S. continues, albeit at a much slower rate than what occurred throughout South and Central America. This slowed rate of territory expansion appears due to climatic limitations. African bees do not survive in temperate climates as well as European bees do. Therefore, they have failed to establish populations below about 32° latitude in the southern hemisphere. Although they have expanded beyond this parallel in the northern hemisphere, African bee expansion northward also appears limited climatically, being found only below about 34° latitude currently.

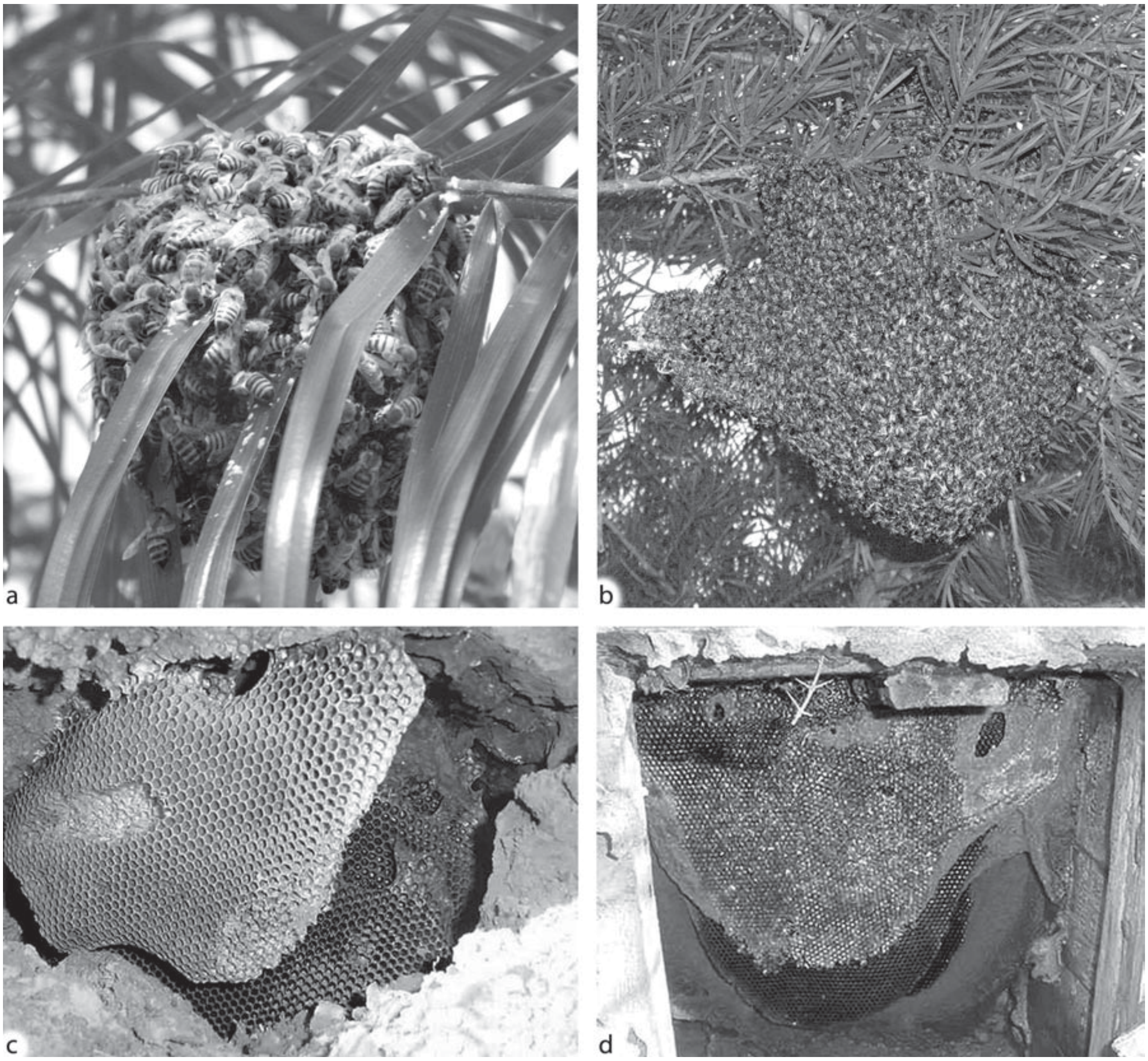
Description and Behavior

African honey bees cannot be distinguished from European honey bees easily, although they are slightly smaller than the various European races. Laboratory personnel use morphometric analyses to determine the likelihood that a given colony is Africanized or fully African. With honey bees, the measurement of wing venation patterns and the size and coloration of various body parts (morphometry) are important determinants of identification at the subspecific level. Morphometry has been used to differentiate honey bee races since the 1960s and remains the first round of identification when suspect colonies are discovered. Morphometric analyses were first used to differentiate Africanized and European honey bees in South America in 1978. A more rigorous identification is achieved by genetic analysis and often is necessary when the suspect bees are a hybrid between African bees and the European subspecies.

Other differences between African and European bees manifest themselves behaviorally. To the casual bystander, the primary identifying behavioral characteristic of Africanized bees is their heightened defensiveness compared to that of European subspecies. Selection pressures induced by man are, in part, responsible for this increased defensiveness. "Beekeeping" (management of honey bee colonies by humans) is more common in Europe, where the native honey bees have been bred for gentleness and ease of management. In contrast, "honey hunting" (near-complete destruction of hive to harvest contents) is more common in Africa, resulting in a bee that is more defensive of its nest. Other selection pressures that led to a heightened defensiveness in African bees include climatic stresses, resource availability, and predation by birds, mammals, and various reptiles. These selection pressures resulted in an African race of bee that can be 10 + times more defensive than any of the various European races of bee.

All honey bees readily defend their nests, and an attack usually means that the victim is too close to the nest. While European races of bees may attack a nest intruder with >10 bees, African bees may attack the same intruder with >1,000 bees. Further, African bees defend a larger radius around their nest and require lower levels of stimuli to initiate an attack. Because of these characteristics, African bees are capable of killing large mammals, including man. This defensiveness has earned them the nickname "killer" bee. It is important to note that their ability to kill humans has nothing to do with their size or the potency of their venom. African bees are smaller than European bees and probably deliver a comparatively smaller dose of venom to their victim than do European bees. Because both bees use the same type of venom, human deaths are a result of the number of stings they receive rather than an increased potency of African bee venom.

Another behavioral difference between African and European bees concerns colony level reproduction and nest abandonment. African honey bees swarm and abscond in greater frequencies than their European counterparts. Swarming, bee reproduction at the colony level, occurs when a single colony splits into two colonies, thus ensuring survival of the species. European colonies commonly swarm 1–3 times per year. African colonies may swarm >10 times per year. African swarms tend to be smaller than European ones, but the



African Honey Bee, Africanized Honey Bee, or Killer Bee, *Apis mellifera scutellata* Lepeletier (Hymenoptera: Apidae), Figure 23 (a) African bees swarm readily and nest in unusual locations, including (b) exposed on tree limbs, (c) within cavities in the soil, (d) within discarded furniture.

swarming bees are docile in both races. Regardless, African colonies reproduce in greater numbers than European colonies, quickly saturating an area with African bees. Further, African bees abscond frequently (completely abandon the nest) during times of dearth or repeated nest disturbance, while this behavior is atypical in European bees.

Another common difference between African and European honey bees is their choice of nest locations. African honey bees are less selective when considering a potential nesting site than are European bees. They will nest in a much smaller volume than European honey bees and have been found in water meter boxes, cement blocks, old tires, house eaves, barbecue grills, cavities in the ground, and hanging exposed from tree limbs, just to name a few places. One rarely finds European colonies in any of these locations because they prefer to nest in larger cavities like those provided by tree hollows, chimneys, etc. As one can imagine, humans inadvertently provide multiple nesting sites for African bees. Therein lies the primary reason African bees are encountered frequently by humans (Fig. 23).

A final behavioral curiosity of African bees concerns nest usurpation (or colony takeover) of European colonies. Small African swarms containing a queen often land on the outside infrastructure of a European colony (a wall, beekeeper-managed hive, etc.). As time passes, the worker bees in the African swarm begin to exchange food/pheromones with the European workers from the colony. This gradually ensures the adoption of the African bees into the European colony. Somewhere during this process, the European queen is lost (perhaps killed by the African bees – her fate remains uncertain at this point) and the African queen is introduced into the colony, thus becoming the reigning matriarch. European bees do not display this behavior but often fall victim to it, thus creating an African colony from a preexisting European one.

Other behavioral differences between African and European races exist and are worth discussing briefly. For example, African bees are more “flighty” than European bees, meaning that when a colony is disturbed, more of the bees leave the nest rather than remain in the hive. African bees use more propolis (a derivative of saps and resins collected from various trees/plants) than do European bees. Propolis is used to weather-proof the nest and has various antibiotic properties. African colonies produce proportionally more drones (male bees) than European bees. Their colonies grow faster and tend to be smaller than European colonies. Finally, they tend to store proportionately less food (honey) than European bees, likely a remnant of being native to an environment where food resources are available throughout the year.

Life Cycle and Genetic Dominance

Mating biology and developmental time play an important role in the success of African bee colonies in replacing European colonies in an area. For the most part, mating and developmental biology are similar for African and European bees, but key differences confer adaptive benefits to the former.

Virgin queens of all western honey bees emerge from peanut hull-shaped waxen cells. After a short time of further maturation, a virgin queen will leave the colony to mate with drones. All mating occurs in the air, with the fastest drones being the most successful suitors. Queens will mate multiple times over the course of 7–10 days and during this time they will mate with an average of 12–20 drones. Queen bees store semen in an organ called a spermatheca. African colonies produce more drones/colony so drone populations in an area tend to favor African bees. As such, virgin European queens are more likely to mate with African drones rather than European ones. Further, flight time and distances of mating flight from the colony tend to result in European queens encountering African drones more often than European drones, thus setting the stage for hybridization.

All honey bees undergo complete metamorphosis but the time from egg to adult varies by subspecies. The newly-mated queen bee oviposits in wax cells constructed by worker bees. Fertilized eggs result in female offspring, either workers or queens. If fed a diet rich in royal jelly, the female larva will develop into a queen, with the reciprocal true for the development of workers. Drones result from unfertilized eggs and consequently only inherit genetic material from their mother (they have no father).

Developmental time varies by caste member (see Table 4) and favor African honey bees because they generally develop faster than European bees. When bee colonies decide to make a new queen, newly emerged female larvae are fed royal jelly constantly. Because Africanized offspring, including queens, develop faster than European offspring, a queen having an African genotype is more likely to emerge earlier than a queen with a European genotype. The first queen to emerge kills all of her queen sisters that have not yet emerged from their cells. The Africanized virgin proceeds to mate in an area having higher densities of African drones. Over time, this results in the colony becoming more African with the European phenotype being replaced almost altogether. This process is exacerbated further due to the dominance of African genetic traits over European ones.

Finally, African bees are more resistant to many honey bee pests/pathogens than are European bees. Western honey bees face a myriad of pests and diseases, the most severe of which include varroa mites (*Varroa destructor*), tracheal mites (*Acarapis woodi*), small hive beetles (*Aethina tumida*), and American foulbrood (*Paenabacilis larvae*). These bee pests almost eliminated all wild colonies of European honey bees in North America. Because African bees are resistant to many of these pests/diseases, their survivorship in the wild is favored over that of European bees.

Public Risks

Due to their heightened defensive behavior, African honey bees can be a risk to humans. Children, the elderly, and handicapped individuals are at the highest risk of a deadly attack due to their inability or hampered ability to escape an attack. African honey bees are agitated by vibrations like those caused by power equipment, tractors, lawn mowers, etc. Further, their nesting habits often put them in close proximity to humans. Because of this, precautions should be taken in an area where Africanized honey bees have been established. These precautions are not suggested to make people fearful of honey bees but only to encourage caution and respect of honey bees. The precautions include remaining alert for honey bees flying into or out of an area (suggesting they are nesting nearby), staying away from a swarm or nest, and having wild colonies removed from places that humans frequent. The latter is perhaps the most important advice one can heed when dealing with African bees. In the USA, a large percentage of African bee attacks occur on people who know a nest is present but elect not to have it removed (or try to do it themselves).

If an attack occurs, remembering a few simple recommendations will increase one's chances of minimizing the effects and severity of the attack. If attacked, a victim should run away from the area using his shirt to cover his head and especially airways. Running through tall grass or small trees will help to disrupt the attacking bees. The victim should not stand and swat at the bees. The bees are defending their nest, and the victim needs to get away from that nest as quickly as possible. It is important that the victim get cover in a bee-proof vehicle or structure if either is available. One should not jump into the water or hide in bushes. The bees can remain defensive and in the area for some period of time, thus increasing the risk to the victim. If stung, the victim should remove the stinger quickly by scraping it rather than by pulling it. One should see a doctor immediately if breathing is affected.

Many African bee attacks can be prevented by limiting the number of nesting sites that are available to the bees. A homeowner, school worker, etc. can "bee proof" his or her property by eliminating possible nesting sites. This can be accomplished by removing any unnecessary debris from an area and closing off wall, chimney, electrical and plumbing-related gaps that are >30 mm using a small-mesh hardware cloth or caulking. This will limit bee access to potential nesting sites. Finally, one should check walls and eaves of structures regularly, looking for bee activity.

African Honey Bee, Africanized Honey Bee, or Killer Bee, *Apis mellifera scutellata* Lepeletier (Hymenoptera: Apidae), Table 4 The developmental time in days (from egg to adult) of European and African honey bees

	European honey bees	African honey bees
Queen	16	14
Worker	21	19–20
Drone	24	24

Managing African Bee Colonies

It is important to remember that African honey bees pollinate crops and produce honey just like other races of honey bees. Beekeepers in South Africa use African honey bees as the bee of choice in their operations. So, African bees can be managed efficiently and safely but the skills required to manage African bee colonies differ from those required to manage European bee colonies.

In general, the management of African bee colonies has been discouraged in the US while accepted in Central and South America. This may have to do with the public perception of honey bees, particularly African bees, in the USA and the robust legal system in place in the USA. On the other hand, beekeepers in Central and South America routinely use African bees in their operations with slight management modifications. In fact, some South American countries are among the leading honey producers in the world, due largely to the presence of African bees in the country.

Beekeepers in South and Central America utilize a number of management practices in order to keep African bees. First, they keep single bee colonies on individual hive stands rather than using one hive stand for multiple colonies. This limits the management activity to one colony at a time rather than aggravating other colonies while working only one.

Secondly, beekeepers in South and Central America use ample amounts of smoke when working African bee colonies. It is believed that smoke masks the alarm pheromone of the bees, thus lessening the defensive response of the colony. Most South and Central American beekeepers agree that copious amounts of smoke should be used when working African bee colonies. It is important to smoke the colonies well before any work is done, for once bees from a colony are agitated, smoke may fail to calm them down.

Beekeepers managing African bees wear appropriate protective gear. A typical beekeeper working an African colony would wear a full bee suit, boots, gloves, and a bee veil. Bee veils (protective headgear) are worn by almost all beekeepers worldwide. Traditionally, the veil mesh protecting the face is colored black to keep down the sun's glare. African bees (and most honey bees) attack dark colors so black-faced veils often get covered with bees. Consequently, beekeepers can use white-faced veils to keep the bees off of their veils. Beekeepers managing African colonies often tape their bee suits to their boots and gloves to limit the possibility of bee access.

Finally, some beekeepers in areas with African bees try to requeen African bee colonies with European queens. This is not a common practice in sub-Saharan Africa. Most African beekeepers in areas having African bees gladly use the bee in their operations, paying little attention to the bees' defensiveness.

Conclusion

The economic impact of African bees in an area can be substantial. Keepers of European bees often notice a decrease in resource availability for their bees because of the density of African bee colonies in an area, and thus the demand on the available resources is high. Furthermore, cities, municipalities, etc., often initiate eradication programs, with much futility. Finally, the loss of animal and human lives is a tragic occurrence, being beyond measurable cost.

African bees also may affect the environment negatively. Colony densities as high as 300 African bee colonies per square mile have been suggested. If true, African bees may have a substantial impact on the native flora and fauna in an area. While this impact often is not reported and largely is not understood, it could be significant considering the potential number of colonies and their need for resources. Thus, the world's most infamous honey bee is among nature's most enigmatic creatures.

► Apiculture (Beekeeping)
► Honey Bee

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African Horse Sickness Viruses

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African horse sickness is a highly fatal, noncontagious disease of equines, particularly horses. The African horse sickness virus group consists of nine serotypes, in the genus *Orbivirus*, family Reoviridae. It is closely related to the bluetongue viruses, which cause disease in cattle and sheep. Infection with any of the serotypes of African horse sickness virus usually results in severe disease and high mortality in horses. Donkeys and mules generally exhibit less severe disease and lower mortality, while wild equids such as zebra generally show no signs of disease or mortality after infection. The serotypes are differentiated based on the host immune response, and there is some cross reaction between serotypes.

All nine serotypes are endemic to sub-Saharan Africa, and have caused serious epidemics when introduced outside this area. African horse sickness has had a significant impact on the history of some parts of Africa, as horses could not be used in exploration and farming. Outbreaks of African horse sickness have a significant economic impact, resulting from the direct loss of animals, the costs of control programs, and trade regulations and quarantines restricting movement of equines from infected areas.

The virus is transmitted by biting midges in the genus *Culicoides*. *Culicoides imicola* has been implicated in most outbreaks, while in endemic areas there may be several species of *Culicoides* midge involved in the transmission cycle. Most species of equines can develop viremias sufficiently high to infect midges. Some tick species have been shown to be able to become infected and transmit the virus in the laboratory, but the importance of this transmission route in nature is unknown.

In endemic areas, African horse sickness viruses circulate primarily between midges and zebra, and frequently multiple serotypes are present. Transmission rates can be very high. For example, in the Kruger National Park, South Africa, zebra foals typically are exposed to all nine serotypes by the time they are 1 year old.

The first outbreak outside the sub-Saharan zone began in 1959 in Saudi Arabia and Iran, spreading to involve Afghanistan, Pakistan, Syria, Lebanon, Jordan, Iraq, Turkey, Cyprus and parts of India before being controlled by vaccination campaigns and the loss of most susceptible horses by the end of 1961. Another outbreak occurred in North Africa in 1965, crossing into Spain in 1966. An outbreak of African horse sickness serotype 4 virus began in central Spain in 1987 and ultimately encompassed a large part of Spain, along with parts of Portugal and Morocco. This outbreak was the first recorded instance of an African horse sickness virus overwintering outside of Africa. African horse sickness cases occurred for four subsequent years in Spain, and it was not eradicated until 1990. The most likely route of introduction was via zebra imported from Namibia. Control and eradication of the virus was achieved only by extensive vaccination campaigns and slaughter of infected or exposed equines. It is estimated that 2,000 horses died and over 350,000 were vaccinated during this outbreak. In 1989, an outbreak of serotype 9 occurred in Saudi Arabia.

Spain was divided into African horse sickness-free and infected regions, in order to allow movement of horses for the 1992 Olympics held in Barcelona. No vaccination was allowed in the African horse sickness-free region, so that any transmission activity would be observed. Equine movement out of the infected region was prohibited.

A similar strategy is used in South Africa, with an African horse sickness-free zone in the Western Cape Province, based on historically low incidence of African horse sickness, and that *C. imicola* is rare. Surrounding this zone is a surveillance zone and a protection zone. No vaccination is allowed in the free and surveillance zones, and strict movement controls are in place for equines moving from other areas of the country. The zoning creates an area where animals can be held prior to exportation. In 1999, there was an outbreak of African horse sickness in the surveillance zone, opening debate about the effectiveness of the movement restrictions and the vector species involved. Currently, the zoning is still in place and there have not been further outbreaks in the African horse sickness-free zone.

Clinical signs of African horse sickness in horses generally begin with fever. There are three forms of African horse sickness disease in horses: pulmonary, cardiac, and febrile. The febrile form, often referred to as horse sickness fever, does not progress beyond fever and generally resolves. The pulmonary form begins with fever and progresses to respiratory difficulty, coughing and nasal discharge. Death is due to pulmonary edema and cardiac failure. The cardiac form also begins with fever, and subsequently edemas develop around the head, neck and chest. Death results from cardiac insufficiency and progressive pulmonary edema. Mortality rates can be as high as 95% in horses, although donkeys and mules are much less susceptible and mortality rates are much lower. Movement of donkeys may be important in the spread of these viruses outside the endemic area, as they are rarely clinically ill and so infected animals are not noticed. There is variation in virulence between the nine African horse sickness serotypes, along with differences between breeds of horse and individual immune responses to the virus.

Vaccines have been developed against these viruses, but due to the immunological differentiation between the serotypes, cross protection is not complete and full protection requires vaccination against each serotype. Routine vaccination of horses, against all serotypes, is practiced in endemic areas. Elsewhere, vaccination generally is not used routinely or is not allowed. In outbreak situations, the virus is first typed to determine the serotype involved, then vaccination is targeted against that serotype only.

Most countries restrict importation of equids from endemic countries. An extended quarantine period usually is imposed, thus restricting the movement of horses for competition. Because it is difficult to differentiate between vaccinated and infected animals, generally there are restrictions on importing vaccinated animals.

Antibodies to African horse sickness viruses have been found in other animals such as elephants, camels, and bovines, but there is no apparent illness and their impact on the transmission cycle is not known. Dogs can become infected and die by eating meat from the carcass of an infected animal. Antibodies to African horse sickness have been found in wild canids and other carnivores, most likely also via feeding on infected carcasses. Humans have been infected only rarely, generally through laboratory accidents with vaccine strains.

African horse sickness has never been found in the New World. However, there are species of *Culicoides*, particularly the *C. variipennis* complex, present throughout the U.S. Some members of this complex are competent vectors of African horse sickness viruses in the laboratory, and will be competent vectors in the field should an African horse sickness virus be introduced. Vector competence for the *C. variipennis* complex varies considerably for the closely related bluetongue viruses, but we lack information on similar variation for African horse sickness viruses. The implications of this for an introduction of any of the African horse sickness viruses is unknown, but requires further study.

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Africanized Bees

Honeybees in the Western Hemisphere that are derived from hybridization of African and European subspecies of *Apis mellifera*. The degree of hybridization is unresolved.

► Bees
► Honeybee
► African Honey Bee

African Mahogany-Feeding Caterpillar, Heteronygmia dissimilis aurivillius (Lepidoptera: Lymantriidae)

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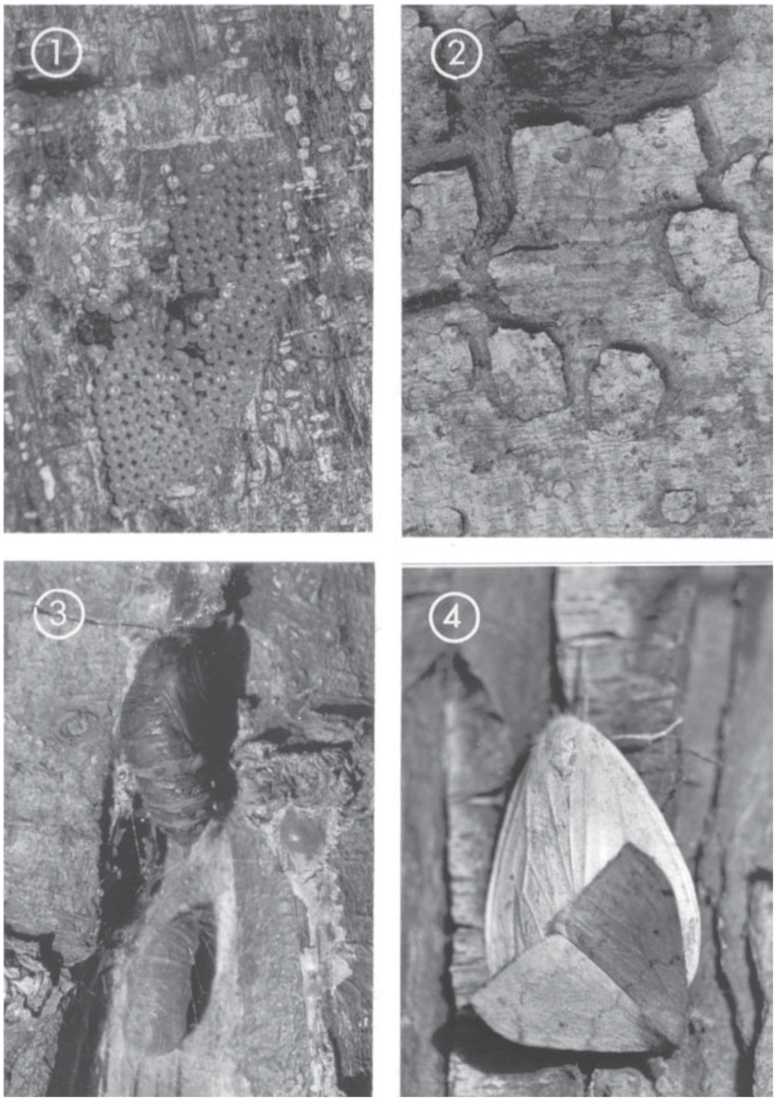
Several genera and species of mahoganies in various parts of the tropics are highly valuable timber species, among them African mahogany (*Khaya* spp.). Relatively few defoliators are known to target this genus, among them caterpillars of several silkmoths, the nymphalid Charaxes and the lymantriid *Heteronygmia*. Only the latter, presumably monophagous on *Khaya*, appears to have pest potential as indicated by small-scale outbreaks observed in Morogoro, Tanzania, in the 1980s.

A succession of four generations per year allow *Heteronygmia dissimilis* to be active most of the year, except for a period of estivation during the hottest season, i.e., from November to February. Eggs are found from early March to late October with peaks from May to August, i.e., during the cool, dry season. Egg clusters are located mostly on the lower trunks of trees and consist of 24–130 glossy, globular or dimpled spheres, each about 1 mm in diameter. They hatch 6–10 days after oviposition, depending on the season (Fig. 24).

Caterpillars of various instars are found anytime between early March to the end of November, with periods of greatest abundance from June to September. All larval instars are hairy and last instars occur in two color phases. One of them is milky-green; the other, more common one, a highly camouflaged, brown to greyish-white mottled bark pattern including up to three, more or less distinct dorsal saddles. Caterpillars feed solitarily, and move with great speed and agility when disturbed, including a hopping and ballooning response during the first four instars. Early instars skeletonize *Khaya* leaflets at night and spend the day motionless on or underneath leaflets. Older instars are free feeders and rest on the lower trunk during the day. All instars shun the foliage of just-expanding shoots. There are five instars in males and six in females, each of them lasting from 5–6 days.

Pupae are found from late February to early December, abundantly so from June to September. They often are cradled in loose leaf shelters tied together by sparse strands of silk or in other hiding places, such as under bark scales.

The moths are present from February to mid-November, most abundantly so from May to September. They rest during the day and are attracted to lights at night. Slender male moths are light to dark or reddish brown with substantial plumose antennae, whereas the white to cream-colored females are bigger and more robust with smaller antennae. Males have wingspans of about 40 mm and are able fliers, while females with wingspans of about 50 mm, are reluctant to take to the air and then only as poor fliers. Both sexes have faint to more pronounced grey line markings and a small black dot on each front wing. Before oviposition, the greatly distended abdomen of the female is greenish. Male moths reach adulthood after an average of 41 days (September/October), females after about 45



African Mahogany-Feeding Caterpillar, Heteronygmia Dissimilis aurivillius (Lepidoptera: Lymantriidae), Figure 24 **Egg (top left) (2x), last instar larva (top right) (1x), pupa (bottom left) (1.7x) and (mating) adult stages (bottom right) (2x) of *Heteronygmia dissimilis*, respectively. Both sexes are represented in the bottom figures, the larger females being above in each picture. (Photo: H. Schabel et al. 1988; reprinted with permission from ICIPE, the International Centre of Insect Physiology and Ecology.)**

days of development. On the average, each female produces about 200 eggs, laid in several batches.

While no field control of *Heteronygmia* has been undertaken to date, a laboratory study documented full protection of *Khaya* leaves from defoliation by *H. dissimilis*, following application of 1% crude, aqueous seed extracts of the neem tree (*Azadirachta indica*).

Numerous arthropod predators of the caterpillars and pupae are believed to be generalists with little impact. On the other hand, four hymenopterous and two dipterous parasites affecting various stages of *H. dissimilis* seem more specific. Seasonally, egg parasites in particular had significant impacts on this insect and in conjunction with the fungus *Paecilomyces farinosus*, which severely decimated pupae during the rainy season, were responsible for serious setbacks in the annual buildup of *H. dissimilis*. As a result, natural controls seem to be quite effective with this insect.

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African Maiden Moths (Lepidoptera: Thyretidae)

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African maiden moths, family Thyretidae, include 212 species, all African. The classification remains controversial and various specialists also place the group within Arctiidae. The family is in the superfamily Noctuoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium-size (23–57 mm wingspan). Haustellum usually reduced or vestigial; antennae pectinate; wings very elongated, with reduced hindwings (some with greatly reduced hindwings). Maculation typically dark with white or hyaline patches, or more colorful. Adults perhaps mostly diurnal; often wasp mimics. Larvae are thought to be leaf feeders, but most species remain unknown biologically. Host plant records include Thymelaeaceae and Ulmaceae, for the few species known biologically.

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African Pine-Feeding Grasshoppers, *Plagiotriptus pinivorus* (Descamps) and P. Hippiscus (Gerst.) (Orthoptera: Eumastacidae)

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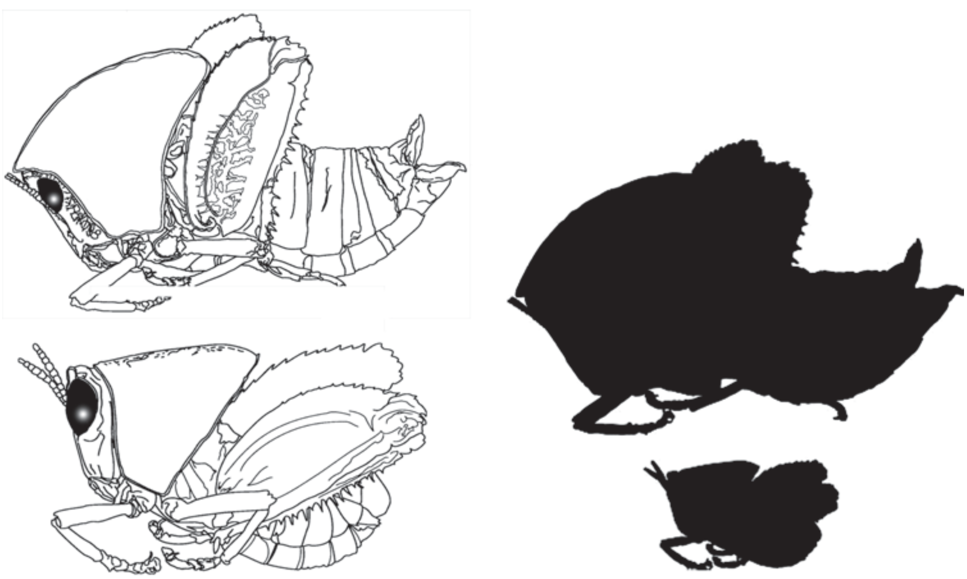
These grasshoppers are excellent examples of indigenous insects that developed a preference for an exotic plantation-grown crop, in this case pines. *Plagiotriptus pinivorus* attained some prominence after causing persistently severe defoliation of exotic pines, especially *Pinus patula*, in Malawi in the 1960s, resulting in significant tree mortality. A smaller scale defoliation of *P. patula* was observed at Morogoro in Tanzania in the mid-1980s, which was attributable to another, very closely related species, *Plagiotriptus hippiscus*. Both of these grasshoppers are highly polyphagous, including herbaceous hosts, shrubs and both angiosperm and gymnosperm trees. The prime requirement for *P. pinivorus* seems to be access to evergreen or semi-evergreen vegetation in areas of moderate to heavy rainfall, i.e., mostly at altitudes between 1,525–2,135 m, but occasionally as low as 490 m.

Plagiotriptus pinivorus in Malawi exhibits three generations every 2 years, and the complete life cycle takes about 1 year. Nymphs and adults have been observed on pines throughout the year, except from December to late January. Copulation occurs anytime, but peaks from October to January and May to June. During copulation, the small male assumes a characteristic dorso-lateral position by clinging to one of the hind femurs of the female. Both males and females are promiscuous. About 7–20 days after the last mating, females seek bare soil and dig a shallow pit to lay a batch of up to six eggs. They then resume voracious feeding in the trees, before laying other batches of eggs at 17–35 day intervals.

Eggs incubate from 49–248 days, with an average of 115 days. The winter population hatches from April to May, maturing in November, while the summer population hatches from December to January and matures from May to July. Within the same batch, an average of 34 days and a maximum of 88 days may elapse between first and last hatch.

Nymphal peak emergence and rainfall are strongly correlated in February, allowing prediction of emergence two weeks in advance. Another smaller peak in emergence in August, however, cannot be explained by rainfall. The first instar nymph is ephemeral (about 12 h), and will molt immediately when reaching the soil surface, before feeding on ground vegetation for the next 2–3 weeks. Advanced instars complete their life cycle on trees, each instar lasting about one and a half to over two months. Young instars are wasteful feeders. There are generally six instars for males and seven for females. Despite the extra instar, females develop more rapidly and reach adulthood at about the same time as do males.

Adult males (Fig. 25) are about 1.5–2 cm long, moderately robust grasshoppers. Their abdomen, shield-like pronotum and greatly enlarged hind femora are strongly compressed. A minute set of non-functional wings, not found on nymphs, is hidden under the pronotum. The thread-like antennae are about one third the length of the head. The abdomen is strongly reflexed over the back in the male. The insect is largely leaf-green, but sports inconspicuous, small areas of blue, pink, red and white on various parts of the legs, wings, antennae and the pronotal



African Pine-Feeding Grasshoppers, *Plagiotriptus pinivorus* (Descamps) and *P. hippiscus* (Gest.) (Orhthoptera: Eumastacidae), Figure 25 ***Plagiotriptus hippiscus*** **female (above) and male (below) with size comparison (shaded) (drawing, Paul Schroud).**

ridge. Eyes are golden yellow. Females are about twice the size of males, more robust and generally less compressed. They are uniformly leaf-green, except for the golden yellow eyes and valves of the ovipositor. Their wings are also minute and hidden under the pronotal shield.

Numerous invertebrate and vertebrate predators, including skinks, birds and blue monkeys, as well as parasites were documented, but ultimately they were deemed insufficient by themselves to reduce populations of the grasshopper to non-damaging levels. As a result, sticky bands and chemical controls were relied on for monitoring and control purposes, respectively. In the 1960s in Malawi, gamma-BHC at 0.5% proved the most effective insecticide for ground and aerial applications at ultra-low volume formulations. Spraying of road banks was particularly recommended, as insects clustered there for oviposition in the bare ground.

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African Primitive Ghost Moths (Lepidoptera: Prototheoridae)

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African primitive ghost moths, family Prototheoridae, comprise 12 species of small moths from South Africa. The family is in the superfamily Hepialoidea, in the infraorder Exoporia. Adults small (18–mm wingspan), with head rough-scaled; haustellum reduced and vestigial mandibles present; labial palpi long and porrect, 3-segmented; maxillary palpi short and 3-segmented; antennae short. Maculation is brown or gray, with various darker spots. Biologies and larvae remain unknown.

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African Red Tick, *Rhipicephalus evertsi*, (Acarina: Ixodidae)

This important tick, known as African red tick, affects ungulates in Africa.

► Ticks

African Skipper Moths (Lepidoptera: Apoprogonidae)

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African skipper moths, family Apoprogonidae, includes only a single species from South Africa. The family is in the superfamily Uranioidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (46–56 mm wingspan), with head rough scaled and eyes large; haustellum naked; labial palpi porrect; maxillary palpi minute, 1-segmented; antennae clubbed (hooked at tip). Wings triangular and

African Skipper Moths (Lepidoptera: Apoprogonidae), Figure 26 Example of African skipper moths (Apoprogonidae), *Apoprogones hesperidis* Hampson from South Africa.

short; body robust. Maculation dark gray with some pale markings, plus pale discal spot on fore- and hindwings. Adults presumed diurnal, but nothing is known of the biology or larvae (Fig. 26).

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African Sleeping Sickness

A disease of humans caused by protozoans in the genus *Trypanosoma*. It is also known as human sleeping sickness or human trypanosomiasis. The same disease, when infecting other vertebrate animals, is called nagana. It is transmitted by tsetse flies in Africa.

► Sleeping Sickness or African Trypanosomiasis
► Trypanosomes
► Tsetse Flies
► Nagana

African Slug Caterpillar Moths (Lepidoptera: Chrysopolomidae)

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African slug caterpillar moths, family Chrysopolomidae, are a small African family of about 30 known species. Two subfamilies are known: Ectropinae and Chrysopolominae. The family is in the superfamily Cossoidea (series Limacodiformes) in the section Cossina, subsection Cossina, of the division Ditrysia. Adults medium size (24–52 mm wingspan), with head scaling smooth; haustellum and maxillary palpi absent; antennae short and bipectinate in males. Body robust. Wings rounded and broad (some with irregular distal margins). Maculation mostly pale brown, often with subapical wing line and light discal spot; hindwing with forewing line and coloration continued (Fig. 27). Adults nocturnal as far as is known. Larvae leaf-feeding and slug-like, with small spines; often colorful. Host plants include Celastraceae. No economic species are known.

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African Swine Fever

A viral disease of hogs, this tick-transmitted disease is found on several continents.

► Ticks

African Slug Caterpillar Moths (Lepidoptera: Chrysopolomidae), Figure 27 Example of African slug caterpillar moths (Chrysopolomidae), *Chrysopoloma similis* Aurivillius from South Africa.

Agaonidae (Hymenoptera)

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A tropical family of about 750 species of miniscule wasps (order Hymenoptera) that are mutualistically associated with fig plants (*Ficus* spp.). The associations are usually between a unique pair of fig and wasp species and are crucial for the reproduction of both. The winged female wasp enters a young floral receptacle, the flask-like syconium, and lays single eggs in many of the tiny female flowers lining its inner surface. Carrying pollen from her natal fig, she deposits it onto the stigmas during oviposition, ensuring seed production for the fig and food for her own offspring. The syconium will generally not ripen without pollination. The female is trapped inside the syconium and dies there. After the larvae develop and pupate in seed-galls, the wingless adult males emerge first and chew holes into galls to mate with the quiescent females inside, and then cooperatively chew an opening through the syconial wall. The changed atmosphere inside the syconium wakes the females, which chew out of their galls, actively or passively pick up pollen, and leave through the opening. The females of some species actively gather and carry pollen in thoracic pockets or specialized leg structures. The cultivated fig, *Ficus carica*, has many varieties that no longer rely on pollination to produce edible ripe syconia. However, a few varieties still require the pollination service provided by the agaonid partner, *Blastophaga psenes*.

► Wasps, Ants, Bees and Sawflies
► Fig Wasps

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Agathiphagidae

A family of moths (order Lepidoptera). They commonly are known as Kauri moths.

► Kauri Moths
► Butterflies and Moths

Agassiz, Jean Louis Rodolphe

Louis Agassiz was born at Môtier-en-Vuly, Switzerland, on May 28, 1807. He displayed an early interest in natural history. In 1824 he entered Universität Zürich for medical training, then moved to Universität Heidelberg in Germany. In Heidelberg his interest in natural history increased. His next move was to Universität München and, while there in 1829 and still only 21 years old, he published a work on Brazilian fishes, using the collected materials of von Martius and von Spix. His next zoological endeavor was to begin research on fossil fishes. In 1831, he moved to Paris still with the ambition of completing his medical training. However, he spent part of each day studying fossil fishes and he came under the influence of Cuvier and adopted the latter's views of creation. Thus, according to Agassiz, each species was the result of separate creation, not of evolution. In 1832–1846 he was a professor at Université de Neuchâtel, Switzerland. In 1836, Louis began to study glaciers and their effects, on which he published works in 1840, 1846 and 1847. In Switzerland, he also published a large catalog "Nomenclator zoologici" of the names of animals, of which some fascicles were on insects. In 1846 he moved to the USA, was welcomed as a famous scientist, and in 1848 was appointed professor of zoology and geology at Harvard University. At Harvard, he clashed with Asa Gray, professor of botany, about evolution, because Gray supported Darwin's theory. However, it was Louis' efforts and influence that led to the foundation of the Museum of Comparative Zoology at Harvard University, an institution that became very influential in research on insect systematics. He also was a co-founder of the U.S. National Science Foundation. He died in Cambridge, Massachusetts, on December 14, 1873. His son Alexander and two daughters of his first marriage accompanied him to the USA (his first wife having died in Switzerland). Alexander Agassiz (1835–1910) likewise became a zoologist. Louis Agassiz remarried in 1850 in the USA.

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Age Polythism

This refers to the division of labor within a colony of social insects wherein the responsibilities of the individuals change as they mature.

Aggregation

A group of individuals consisting of more than just family members; a coming together of individuals to form a group. (contrast with colony)

► Cycloalexy
► Allelochemicals

Aggregation Pheromone

A pheromone that causes insects to aggregate. This type of pheromone is used by insects for mating, feeding, or oviposition.

► Pheromones

Aggregative Response

The response of predators in which they increase their time spent in areas with more prey, leading to higher predator density, and fewer prey.

► Learning in Insects
► Predation: The Role of Generalist Predators in Biodiversity and Biological Control

Agnathous

This term is used to refer to insects that lack mandibles, which essentially means that they lack mouth structures.

► Mouthparts of Hexapods

Aggressive Mimicry

This is a type of mimicry in which a predator mimics their prey, allowing ready capture and consumption of the victim.

► Mimicry
► Myrmecomorphy
► Myrmecophiles

Agonoxenidae

A family of moths (order Lepidoptera). They commonly are known as palm moths.

► Palm Moths
► Butterflies and Moths

Agricolous

This refers to species that dwell in agricultural habitats.

Agricultural Chemicals

Pesticides, adjuvants, and other chemicals, other than fertilizers, that are used to enhance crop production.

► Insecticides
► Acaricides or Miticides

Agricultural Consultant

Someone trained in the agricultural and management sciences who provides plant and animal production and protection services for a fee. Independent crop consultants sell the advising service only, deriving no income from sale of products, whereas other crop consultants usually derive some income from product sales such as pesticides or fertilizer.

► Careers in Entomology

Agricultural Crop Pests in Southeast Asia Including Southern China

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Southeast Asia is often called the Oriental faunal region and includes the provinces of southern China south of the Yangtse river (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hubei, Hunan, Jiangshu, Jiangxi, Sichuan, Yunnan and Zhejiang) as well as the island of Taiwan, islands and peninsular area of Hong Kong, Macao and those countries to the south including Vietnam, Malaysia, Singapore, Myanmar (Burma), Cambodia and Laos, as well as portions of Pakistan and India. The northern provinces of India share similar faunal elements as southern China as both are at a similar latitude. The insect fauna of northern China is more Palearctic in nature and many of the northern species will differ from those in the southern provinces or elsewhere in Southeast Asia.

Insects of Rice

What are believed to be key pests, or those of major importance as opposed to minor can vary from country to country. In Vietnam and southern China, the rice stemborer complex of lepidopterous insects includes the yellow or small rice borer, *Scirpophaga incertulas* (Wlk), the striped rice-stalk borer, *Chilo suppressalis* (Wlk), the dark-headed rice borer, *C. polychrysus* (Meyr) (all Pyralidae) and the noctuid pink borer, *Sesamia inferens* (Wlk). Although they are considered minor pests in some regions, because the rice plants are able to tolerate some damage and can compensate for light infestations, these insects have been ranked as major pests in the countries of Malaysia and Thailand. The yellow or small rice borer, *Sc. incertulas*, has a wide distribution in Southeast Asia and is found in India, Pakistan, Sri Lanka, Bangladesh, Myanmar (Burma), Vietnam, Singapore, Taiwan and Hong Kong.

The common names of these insects generally refer to the color of the larval stage such as the pink borer, *S. inferens*, with pinkish-colored larvae, or the yellow larvae of the small rice borer. The head capsule in larvae of *C. suppressalis* is brown in color while larvae of *Sc. incertulas* are yellow with brown heads and the pink borer caterpillar, *Sc. inferens*, is pink in color and larger when mature than the other species. The larvae tunnel as caterpillars into the stems of the rice plants. There they feed on the plant tissues and destroy the growing points of the plant causing wilting of new shoots, eventually producing a condition known as "dead heart."' In mature plants, empty panicles appear white in color, and the condition is known as "white-head." Masses of eggs are generally laid on the leaves in the case of the female dark-headed borer or striped rice borer. Pupation generally occurs in the stem with these species. The female pyralid moths in the genus *Scirpophaga* have a scale tuft at the tip of their abdomens, while female moths in the genus *Chilo* have no scale tuft at the end of the abdomen. The female *Sc. incertulas* has a yellow forewing, which is whitish in *Sc. nivella*.

The eggs of stemborers are often attacked by the parasitoid wasps *Trichogramma* sp. (Trichogrammatidae) and *Telenomus rowani* (Scelionidae). In Malaysia, granular insecticides have been used to control rice stem borers when the incidence in stems (tillers) exceeds l0%, but this practice is not recommended in southern China or in northern Vietnam where the plants are able to tolerate some damage and compensate for injury.

Rice Leafhopper and Planthopper Complex

The rice leafhopper and planthopper complex includes *Nephotettix virescens* (Dist) and *N. nigropictus* (Stål), the green rice leafhoppers (Hemiptera: Cicadellidae) and *Nilaparvata lugens* (Stål) and the brown plant-hopper (Hemiptera: Delphacidae). These leafhoppers are important in Thailand and Malaysia as well as in India and Pakistan, while the planthopper is more widely distributed and is found in southern China, India, Taiwan, Japan and some of the Pacific Islands. The planthopper is unusual in that it is able to migrate between land masses and migrates from East China to Japan annually. This insect also has migrated to Macao (where rice is no longer grown due to urbanization) from mainland China.

Nephotettix virescens is an important vector of two viral diseases in Malaysia. The first disease is similar to yellow dwarf disease and the second is called Tungro disease. Both cause a stunting of plant growth, the first disease a general yellowing and profusion of tillers, while the second causes a reddening of the leaves. Both diseases decrease crop yield.

The eggs of the rice leafhoppers are laid in rows within leaf-sheaths. The five nymphal stages are completed in l7 days in Malaysia. Leafhoppers generally feed on the upper parts of the plant, while the planthopper, *Nilaparvata*, feeds at the base of the plants near the water line. The brown planthopper is sometimes considered the most serious pest of rice in Asia. They cause a "scorching" of the plants, or a condition known locally as "hopper-burn," when the number of nymphs and adults per clump of rice exceeds 900 or more. The eggs are generally laid in plant tissue. The young resemble the parents except for their smaller size and absence of wings. Five nymphal stages generally require two weeks to develop. Predators can include the staphylinid beetle *Paederus fuscipes* and the coccinellid beetle *Harmonia octomaculata*.

In Thailand and Malaysia, another important pest of rice is the rice gall midge, *Orseolia oryzae* (W.-M.) (Diptera: Cecidomyiidae), which is also found in Pakistan, India, Bangladesh, Sri Lanka and parts of Indonesia as well as in southern China, where it is considered of minor importance. The larvae of the fly feed between the leaf sheaths and, when reaching the apical buds, can lacerate tissue and can cause the formation of a gall known locally as a "silver" or onion shoot. The adults are delicate looking midges, long and brown in color with long legs. Upon hatching, the pale, 1 mm long larva grows to 3 mm and becomes reddish in color. The pupa, when formed, is pinkish and turns red with age. Grassy vegetation near the rice fields is often associated with the presence of the midge.

The rice leaf folder, *Cnaphalocrocis medinalis* (Gn), (Lepidoptera: Pyralidae), is considered one of the more important pests of rice in southern China as well as in Malaysia and Thailand. It is also found in India, Pakistan, Sri Lanka and Bangladesh. The larvae fold the leaf while feeding and transparent patches form so that the rice plant appears ragged. The adult moths lay eggs on young, 4 to 6-week-old plants or in nursery stock in Malaysia. Early instar caterpillars feed by scraping the epidermis from rice leaves, while later instar caterpillars fold them. The opposite edges of the leaf, or one edge of the leaf, is attached to the midrib by silken threads produced by the larvae. Pupation occurs inside a silken cocoon within the folded leaf. Parasitoid wasps, such as *Apanteles opacus* (Braconidae) or *Temelucha philippinensis* (Ichneumonidae), often keep populations in check in Malaysia.

The lepidopterous armyworm and cutworm complex, including the rice armyworm, *Mythimna loreyi* (Duponchel), and the rice ear-cutting caterpillar or paddy armyworm, *Mythimna separata* (Wlk), are important pests in Thailand and southern China. The paddy armyworm affects rice in Pakistan, Sri Lanka, India and Bangladesh. The larvae feed on leaves and stems and can defoliate the plants.

The rice skipper, *Parnara guttata* (Bremer & Grey) (Lepidoptera: Hesperiidae), was formerly considered a major pest in southern China, but recent mass production and release of parasitic wasps has probably lowered its status to a minor pest. The larvae roll the apical portion of the leaves, web the sides and cut off the apex, forming long, conspicuous tubes.

Sugar Cane Insects

The lepidopterous sugar cane borer complex in Thailand includes several pyralids including the yellow top or early shoot borer, *Chilo infuscatellus* (Snellen), the sugar cane stem borer, *Chilo sacchariphagus* (Bojer), the white top borer, *Scirpophaga excerptalis* (Walker) and the noctuid sugar cane stalk borer, *Sesamia inferens* (Wlk).

The larvae of these insects bore into the shoots of sugarcane. As the common name suggests, the larvae of the yellow top or early shoot borer tunnel into the growing shoots of the plant, while the larvae of *C. sacchariphagus* bore into the stems. The noctuid moth larvae of purple stalk borer, *Sesamia inferens*, previously discussed as a pest of rice, also affects sugar cane, but sugar cane is not preferred for oviposition as are rice and grasses. The larvae are colored purple to pink dorsally and white ventrally and have a reddish-orange head capsule. The adult moth is fawn-colored with dark brown streaks on its forewings and whitish hindwings.

In Malaysia, the white sugar cane aphid, *Ceratovacuna lanigera* Zehntner, a mealybug-like insect (Hemiptera), causes injury. The non-winged females and nymphs are covered by a waxy layer, while the winged adults are bluish-green in color and are not covered with a layer of wax.

Fruit Tree Insects: Mango-Citrus-Banana-Litchi

One of the most important fruit tree insects is considered to be the Oriental fruit fly, *Batrocera dorsalis* Hendel (Tephritidae). It is found in Hawaii as well as in other Pacific islands and the southeast Asian countries of Thailand and Malaysia where it is a serious mango pest. In southern China, where there are fewer mangoes grown, it is considered a minor pest. In addition to mangoes, the guava and carambola are affected in Malaysia. The larvae or fly maggots feeding inside the skin of the fruit cause it to decay. Female flies puncture the skin of the fruit with their ovipositors, laying several eggs inside. The larvae can hatch in one day and develop through three instars in about a week. When mature, they are able to leave the fruit by "flipping" themselves in the air and dispersing to enter the ground to pupate. Fruits can be protected from these flies by bagging them using paper bags. The use of traps treated with methyl eugenol as an attractant has met with some success, but as only the males are attracted, it is not totally effective as a control.

In Malaysia, a longhorn beetle known as the mango shoot borer, *Rhytidodera stimulans* (White), tunnels into the young growing shoots of the tree. Eventually it kills the outer branches, which often break off during subsequent wind storms. In southern China, the citrus long-horn beetle, *Anoplophora chinensis* (Forst.) (Cerambycidae), is considered one of the most important pests of citrus trees. The larvae of these beetles tunnel under the bark of young trees and sometimes into the heartwood, which can cause the death of the plants. The adult beetles have striking black and white body coloration. Parasitoid wasps have difficulty reaching the larvae that bore into young healthy trees.

Butterflies (Lepidoptera) are not considered to be serious pests of agricultural crops in the northern hemisphere with the exception of the small white, *Pieris rapae*. However, in the semi and tropical regions of the world, cold climatic conditions are not as severe and the insects often do not have to enter diapause (hibernation), so there can be continuous generations in some regions almost throughout the year. Papilionid butterflies, as well as several species of skippers (Hesperiidae), cause injury to plants because they are able to oviposit in both the spring and the fall.

In Southeast Asia, the lemon or lime butterfly, *Papilio demoleus* (L.), and another species known by the common names of the common Mormon swallowtail or the white-banded swallowtail, *Papilio polytes* L., lay their eggs on the undersides of leaves of citrus plants and are considered important in southern China as pests of citrus. Another species, *Papilio xuthus* L., is also becoming increasingly important, particularly in the Pacific island area. The first instar in these Papilionid butterflies are colored differently than older larvae, which may be an adaptation that protects them from predators such as birds or lizards. The early stage larva resembles a bird or lizard dropping as it is dark brown in color with white markings that may appear to be unappetizing to the predator. When the caterpillar is older, its color changes to green with grey and white markings. Hand picking the larvae is probably an adequate control in young plants.

The orange spiny whitefly, *Aleurocanthus spinifera* (Quaintance) (Hemiptera: Aleyrodidae), is an important insect in southern China as well as India, Sri Lanka, Bangladesh, Malaysia and Thailand. The adults are 1 mm in length and lay eggs on the undersides of leaves. There are three nymphal stages and the third-stage nymph appears blackish in color with waxy secretions on the outer edge of the body so it looks superficially like an insect pupa. Both the nymphs and the adults remove plant nutrients when feeding, and the honeydew produced by the nymphs encourages a sooty mold to grow on the upper surfaces of the leaves and the fruits. Heavy infestations of this insect cause fruit production to fall off. A parasitic wasp, *Eretmocerus serius* (Aphelinidae), has been effective in regulating the orange spiny whitefly in Malaysia.

Aphids, such as the black citrus aphid, *Toxoptera aurantii* (Bayer de Fonscolombe), and the brown citrus aphid, *Toxoptera citricida* (Kirkaldy), are important in southern China and also range into India, Sri Lanka and Bangladesh.

Fruit-piercing moths, such as *Othreis fullonia* (Cl.) (Noctuidae), pierce the ripening fruits of citrus, mango, papaya and guava or banana in order to obtain sap. A short, stout proboscis with a barbed tip enables the moth to puncture the skin of the fruit and can permit the entry of plant pathogens such as viruses or secondary rots that can cause premature fruit drop. Fruit-piercing moths are considered of major importance today in southern China. Management of their populations is difficult as the immature of *O. fullonia* do not feed on citrus trees. Instead, the caterpillars feed on the foliage of the *Erythrina* species of shade trees. On the Pacific island of Guam, the eggs can be laid on the foliage all year round and the insects are considered to be major pests as they feed on ripe banana, mango, papaya, pomegranate and guava as well as tough-skinned citrus fruits.

On banana plants, there are two species of leaf rollers or banana skippers in Southeast Asia, one of which is *Erionota thrax* (Hesperiidae), which rolls the banana leaves in Malaysia, Thailand and in southern China. The caterpillars cut and roll strips of banana leaf, then hide in the roll that is held together by silken threads. They emerge at night to feed and are often covered with a white powdery secretion.

Litchi and Longan Fruit Insects

The litchie stink bug, *Tessaratoma papillosa* (Drury) (Hemiptera: Tessaratomidae), has been considered the most important pest of litchi (*Litchi chinensis*) and longan (*Euphoria longan*) fruit trees in the Guangdong region of southern China, including Hong Kong and Macao as well as Vietnam and Thailand. The adults are mostly brown dorsally and whitish underneath. Immature bugs, more brightly colored than the adults, have red markings dorsally often with a white waxy secretion underneath. Plant sap is taken from the stems of fruit trees. The saliva of the bug can stain the clothing of fruit tree workers. Also, the fluid is extremely irritable if it gets in the eyes. An effective biological control of the litchie stink bug has been developed in southern China by the Guangdong Entomological Institute in which the egg parasitic wasp, *Anastatus japonicus* (Eupelmidae), has been mass-reared and released to achieve control in the Fujian, Guangdong and Guangzi provinces. Biological control of the litchie stink bug has also been reported from the northern highlands of Thailand.

Vegetable Insects

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is currently considered among the top 25 most important arthropod pests in southern China. It was the first agricultural pest in Malaysia to be reported resistant to pesticides, and it is also an important pest in Thailand as well as in India. Its distribution has been considered cosmopolitan. Cruciferous plants, such as the cabbages, are affected. The caterpillars penetrate the epidermis of leaves, mining the tissue and making windows or holes in it. The adult is recognized by the pale triangular or diamond-shaped marks seen on the midline of the back when the wings are closed.

The caterpillar is pale green in color, and it wriggles violently when disturbed, sometimes falling off the edge of the leaf. A microbial insecticide, *Bacillus thuringiensis*, is effective in the control of the diamondback moth, but farmers in some areas of Malaysia have not accepted it because this method takes longer to kill the caterpillars than other insecticides.

The green stink bug, *Nezara viridula* (L.) (Hemiptera: Pentatomidae), is a cosmopolitan insect in Southeast Asia that damages developing vegetables, such as potato, sweet potato, tomato and cotton, by their feeding punctures. Three color varieties or subspecies of this insect are recognized in southern China. An all-green form, known as *N. viridula smaragdula*, is the most common, accounting for 75–80% of vegetable bugs observed in Macao in l996. A second form with yellow on the head and pronotum, *N. viridula torquata*, makes up about 10% of the stink bug population, while the least common form is mostly all yellow with green spotting on the hemelytra and abdomen, and is called *N. viridula aurantiaca* (1.0%).

The small white butterfly, *Pieris rapae* (L.) (Lepidoptera: Pieridae), along with two other species, is still considered important in southern China and Southeast Asia. The small cabbage butterfly, *Pieris canidia* (Sparrman), also damages nasturtium. In both species, larvae feed singly in the cabbage heart, make holes in the leaves and cause frass accumulation. The insects are also found in India, Taiwan and the

Philippines, and breeding can be continuous with up to eight generations annually, which is not the case in northerly regions, where overwintering occurs in the pupal stage.

The Asian corn borer, *Ostrinia furnacalis* (Guenee) (Lepidoptera: Pyralidae, Pyraustinae), is more important in the northern countries of Southeast Asia including southern China where corn is grown. The Guangdong Entomological Institute rates it as a highly important pest there. The larvae bore into the stalks and the ears of corn, and can also survive on foxtail millet, *Setaria italica*, and on *Panicum* grasses. The eggs are laid in clusters of 10–40 underneath leaves about a week before the plant forms its inflorescence. The young larvae can scarify the leaves and later, bore into the stem. Pupation generally occurs within the stalk, but can occur within the ear. The Asian corn borer's range includes India, Sri Lanka, Korea, China, Hong Kong, Taiwan, Vietnam, Japan, Malaysia, Thailand, Singapore and Indonesia.

► Tropical Fruit Pests and Their Management
► Sugarcane Pests and Their Management
► Vegetable Pests and Their Management

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Agroecology

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Agroecology is the application of ecological principles to agricultural production systems and the resources needed to sustain them. A convenient unit of study is the agroecosystem, often a single agricultural field. A major difference between an agroecosystem and a natural ecosystem is in the level of human intervention and management involved. Like natural ecosystems, agroecosystems consist of living (biological) and nonliving (chemical, physical) portions. The science of agroecology examines the living organisms (collectively called the community) in the system, their interactions with one another, and the environmental factors that influence them.

Nutrient Cycling

The organisms within an ecological community depend on one another for energy and materials. Green plants are referred to as producers since they are at the base of the food chain in ecosystems. Initially, carbon and energy are stored in plant tissues through the process of photosynthesis. Consumers must obtain their carbon and energy by eating plants or other organisms. Therefore carbon and other materials move from green plants to herbivores to carnivores, including predators and parasites. The different levels of energy production and consumption (producers, herbivores, predators) are called trophic levels, although in reality many organisms do not restrict their feeding to one level. For instance, some Hymenoptera that are parasitoids as larvae may feed on pollen or nectar as adults. As a result, the paths along which materials move through the organisms in the community can be quite complicated, and collectively they make up the food web within the community.

Many nutrients, including nitrogen, phosphorus, potassium, and other elements, are essential components of plant and animal tissues. These nutrients have distinct cycles in ecosystems, and they cycle in food webs along with carbon and other materials. Nutrients are released into the soil during decomposition of organic molecules, where they are converted into forms that can be taken up by plant roots, completing the nutrient cycle. Microarthropods such as mites and springtails are particularly important in the decomposition process.

Cropping Systems

Crop performance depends on a range of key resources including nutrients, water, soils, and other environmental factors, and many agricultural management practices are aimed at optimizing and conserving these resources. Various types of cropping systems may be selected to address specific goals or conservation issues. Conservation tillage and other reduced tillage practices are important for soil conservation and reduction of erosion. The crop residues that remain on the soil surface in uncultivated sites can also aid in conservation of water and organic matter, and may provide some nutrients when they decompose (Fig. 28). Monoculture allows a grower to specialize by growing only one crop, while polyculture permits a grower to diversify by growing multiple crops on the same land. Multiple cropping on the same site may occur at the same time or over time. In the United States, the most common form of multiple cropping is crop rotation, in which different crops are grown on the same site in different seasons or years. Cover crops are crops with limited market value that are grown on the site during seasons that are unfavorable for growing the main economic crops for the region. In the southeastern United States for example, a winter cover crop of rye (*Secale cereale*) or crimson clover (*Trifolium incarnatum*) may be grown in a field reserved for cotton or peanut production during the summer. Cover crops can provide various advantages, including erosion reduction, increased supply of nitrogen, competition with weeds, or hay for animals. Green manures, which are usually legume cover crops, are grown specifically for their nitrogen-rich residues and soil fertility benefits. Intercropping, or mixed cropping (Fig. 29), refers to the growing of two or more crops at the same time on the same land. The practice is quite common in some regions, and many variations exist. Some tropical subsistence intercropping systems are especially diverse and complicated.

Pest Management

The cropping system used has a direct effect on pest management, which is an important aspect of agroecology. For example, monoculture may encourage buildup of some pests, such as corn rootworms (*Diabrotica* spp.) or wireworms (Elateridae), that can be managed by appropriate crop rotation. In many cases, the use of intercropping has resulted in less severe pest outbreaks and increased diversity of natural enemies compared to monocultured systems.

Tritrophic (plant-herbivore-predator) interactions and the structure of the food web may be affected by changes in the cropping system, such as use of an intercrop, or changes in crop variety or fertility level. The development and use of biologically based pest management tactics such as use of natural enemies or resistant varieties require a detailed knowledge of pest biology and ecology, including life cycle, population dynamics, and interactions with the physical and biological environment, including potential competitors, predators, and parasites. Such tactics may be directed toward preventing pest buildup rather than reacting to high pest numbers already present in crisis situations. However, the design of a system in which pest numbers are less likely to reach crisis levels, due to the presence of effective natural enemies for example, requires advanced planning based on sound ecological data.

Landscape Ecology

An individual agroecosystem does not stand alone, since organisms, materials, and energy move freely in and out of the system. Landscape ecology examines the agroecosystem in the context of the surrounding region or landscape, an essential

Agroecology, Figure 28 **Residues from a previous rye crop cover the soil surface between plant rows in this conservation tillage system.**

approach in dealing with migrating insects or regulated pests. The condition of field borders, hedgerows, and adjacent fields critically affects pest management within a specific field. Movement of pesticides, fertilizers, and other potential pollutants from the agroecosystem to natural ecosystems is a major environmental concern.

Many natural ecosystems are highly dependent on recycling, since cycles of nutrients, water, and other materials tend to be relatively closed. In contrast, an agroecosystem is not a closed system, because its purpose is to produce harvest for export to other ecosystems. This process depletes essential resources from the agroecosystem

Agroecology, Figure 29 **One of the simplest forms of intercropping is to use one crop as a windbreak, like the sugarcane planted along with the eggplant crop shown here.**

which must be restored if the system is to remain productive. The movement of essential resources into the agroecosystem and the recycling of existing resources are therefore critical concerns, to anticipate and ensure that supplies of critical resources for agricultural production will be conserved over time to sustain future agricultural production.

► Organic Agriculture
► Integrated Pest Management (IPM)
► Conservation Biological Control
► Flower Strips as Conservation Areas for Pest Management
► Plant Resistance to Insects
► Cultural Control of Insect Pests

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Agromyzidae

A family of flies (order Diptera). They commonly are known as leaf-miner flies.

► Flies
► Leaf-miner Flies (Agromyzidae)

Agyrtidae

A family of beetles (order Coleoptera). They commonly are known as primitive carrion beetles.

► Beetles

A.I.

An abbreviation for "active ingredient," the active component of an insecticide, or the toxicant.

► Insecticides
► Insecticide Formulation
► Insecticide Toxicity

Alarm-Defense System

Defensive behavior that also serves as an alarm signaling mechanism.

Air Sacs

The trachea of insects are sometimes dilated or expanded to form pouch-like structures called air sacs. Their occurrence varies among taxa, but their presence lowers specific gravity and enhances air exchange, thus enhancing flight.

► Active Ventilation
► Abdominal Pumping

Alarm Pheromone

A pheromone released to trigger alertness, dispersion or group defense by insects.

► Alarm Pheromones of Insects
► Chemical Ecology

Alarm Pheromones of Insects

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Alarm pheromones are defined as chemical substances, produced and released by an organism, that warn or alert another of the same species of impending danger. This is exemplified by many species of aphids (Hemiptera: Aphididae) in which the pheromone is caused to be released by attack, for example, by predators, with ensuing dispersal by which individual aphids may avoid a subsequent attack. However, the term alarm pheromone also is employed when the responding individuals are stimulated to show aggression towards the attacking agent. This is common in the social Hymenoptera; for example, the honeybee, *Apis mellifera* (Hymenoptera: Apidae), and many ant species respond aggressively to their alarm pheromones.

As alarm pheromones can benefit the survival of members of the species involved, it is common for insects that employ alarm pheromones to live in congregations for some or all of their life cycle. In the case of social Hymenoptera, the colony is genetically related, and in asexually reproducing aphids, the colony is clonal. Although the survival of siblings or clones by alarm pheromone response at the cost of the attacked individual appears altruistic, in genetically related colonies, genes from the individual will predominate in the survivors and be passed on to their kin.

Hemipteran Alarm Pheromones

Alarm Pheromones of Aphids (Hemiptera: Aphididae)

When disturbed or attacked, many aphid species release alarm pheromone from droplets secreted from tube-like structures called cornicles on their dorsal posterior. This phenomenon has been studied exclusively in the asexual forms and most often in asexually reproducing wingless females. Aphids nearby exhibit a variety of behaviors ranging from stopping feeding and moving away, to running or dropping off the plant and even attacking the predator. However, not all aphids in a group respond. The relative risks of predation and costs of escape, for example, cessation of feeding and risk of desiccation, affect the likelihood of any particular response. In studies of the peach-potato aphid, *Myzus persicae*, the pea aphid, *Acyrthosiphon pisum*, and the rose-grain aphid, *Metopolophium dirhodum*, early stages were found to be less sensitive to alarm pheromone than later ones.

However, older wingless *M. persicae* require the greatest stimulation of alarm pheromone before responding, while winged *M. persicae*, particularly those not feeding, are extremely sensitive to alarm pheromone. The lack of response from the early stages suggests that the risk of predation to these nymphs is lower than the risk involved in ceasing to feed and dropping from the plant. When young *M. dirhodum* respond to alarm pheromone, they do so by moving to another part of the plant rather than by dropping. Winged adults, on the other hand, are more responsive to alarm pheromone, perhaps because they can more readily move off the host. The sugarcane woolly aphid, *Ceratovacuna lanigera*, also shows different reactions to alarm pheromones at different life stages; it shows attack behavior until adult, when the normal aphid dispersal response takes over.

Considerable variation is seen between aphid species in their sensitivity to alarm pheromones and in both the speed and the form of the response. This variation often can be explained by differences in the ecology of the species. Some aphids, particularly those tended by ants, stay on the plant and respond by walking or "waggling" their abdomens rather than falling off the plant. These aphids appear to depend more on the protection afforded by their ant attendants than their own defensive mechanisms. Aphids that walk away from a source of alarm pheromone tend to form new clusters a short distance from the original site, thus ensuring continued ant attendance.

Susceptibility to insecticide also has been found to correlate with responses to alarm pheromone. Susceptible strains produce more pheromone and respond more quickly and in higher numbers than insecticide-resistant strains. In addition, clones collected from around the world showing knockdown resistance to pyrethroid insecticides, and esterase-based insecticide resistance, showed lower levels of disturbance to the synthetic alarm pheromone. These aphids may therefore suffer increased predation or parasitism in the absence of insecticides, affecting the evolutionary fitness of insecticide resistant clones. This may be due to physiological effects associated with resistance, which could affect mobility or sensitivity of the nervous system to stimuli.

Aphids that have dropped from a plant may re-colonize or may move to another host plant further away. The turnip aphid, *Lipaphis erysimi*, and *M. persicae* dislodged by alarm pheromone are less likely to return to the original host plant than when mechanically dislodged. Similar patterns of behavior are found in *A. pisum*. Aphids dislodged by a predator or experimentally with synthetic alarm pheromone spend longer "running" before the "search" for a host plant began, whereas aphids dislodged mechanically are more likely to begin to search for a host plant immediately.

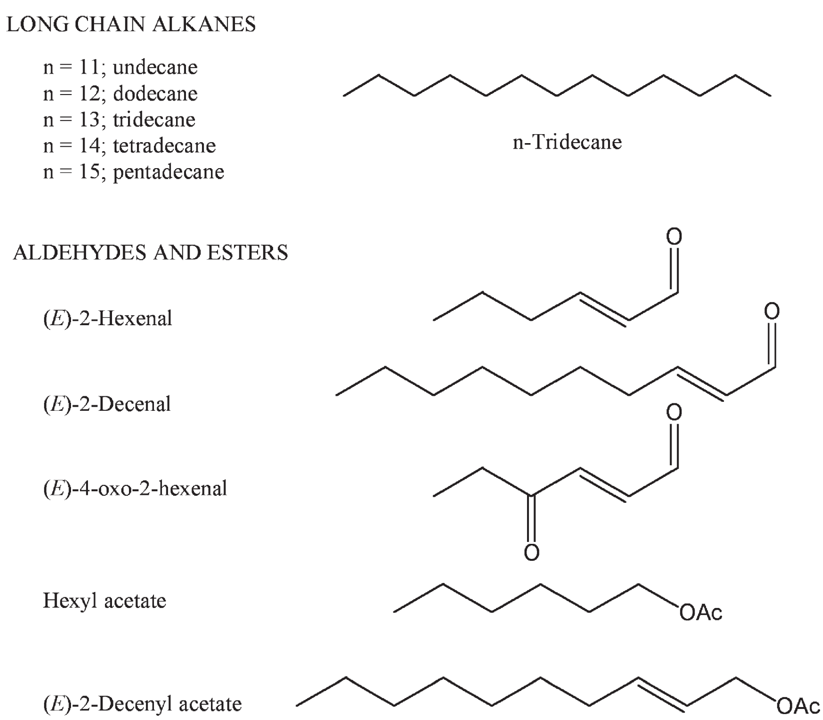
Droplets secreted from the cornicles comprise two types of material: a volatile, rapidly vaporizing fraction which is the alarm pheromone, and a waxy fraction, consisting mainly of triglycerides, that crystallizes on contact with foreign particles outside of the aphid's body. The waxy component appears to function as a sticky or quick-setting irritant to predators and parasitoids and a releasing substrate for the alarm pheromone component.

The main component of the alarm pheromone (Fig. 30) of many aphids is the sesquiterpene hydrocarbon (E)-β -farnesene (**1**). Other components may also be present as found in the alarm pheromone blend of the vetch aphid, *Megoura viciae*, which contains the monoterpenes (-)-α -pinene, (-)-β -pinene, (Z,E)-α -farnesene and (E,E)-α -farnesene, in addition to (E)-β -farnesene. There is a high degree of cross-activity of both natural alarm pheromone and (E)-β -farnesene among species within the aphid subfamilies, Aphidinae and Chaitophorinae. This is typical of insect alarm pheromones in general, since such cross-activity does not reduce their evolutionary value. However, the main component of the alarm pheromone of the spotted alfalfa aphid, *Therioaphis maculata*, and the sweet clover aphid, *T. riehmi*, in the Drepanosiphinae, is the cyclic sesquiterpene (-)-germacrene-A (**2**).

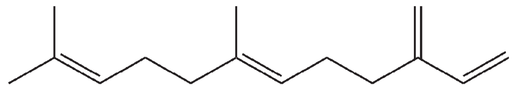
In the turnip aphid, *L. erysimi*, it has been demonstrated that isothiocyanates, acquired from chemicals in the host plants, synergize the effect of the alarm pheromone. These isothiocyanates are likely to be released from aphid honeydew so that, when there is a high number of other aphids in the immediate vicinity, the percentage of aphids responding to alarm pheromone increases.

Alarm Pheromones of True Bugs (Hemiptera, Heteroptera)

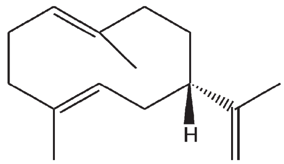
The Pentatomidae is the dominant family of stinkbugs, or shield bugs. The family comprises many species that are pests of economic importance, especially in warmer climates. These insects secrete a complex mixture of chemicals when strongly molested. The energetic cost of the defense response, especially production of defense chemicals, is significant and considerable provocation usually is required to cause release. In adults, the source of the defense compounds is the metathoracic gland, while in nymphs it is the dorsal abdominal glands. These are precursors to the metathoracic gland in adults and perform the same defense function. The chemical content of these secretions is similar throughout the order; for example, the components of the secretion of the stinkbug *Cosmopepla bimaculata* are a complex mixture of hydrocarbons, aldehydes and esters. The secretion, which can be ejected from either or both metathoracic glands in controlled amounts or even resorbed, displays a defensive function as a predator repellent. In one case, researchers have shown uncommon dedication in describing the repellency by squeezing adults in their mouths and chewing nymphs. The effects were a burning sensation and numbness of the tongue for up to two hours. In addition to repelling predators, the secretions possess alarm pheromone activity and cause adults to drop off plants. In the field, *C. bimaculata* are found highly clumped and the occurrence of large



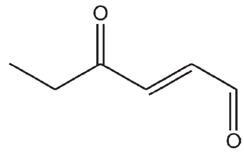
Alarm Pheromones of Insects , Figure 30 **Defense secretion of *Cosmopepla bimaculata* showing a typical range of compounds produced by stinkbugs. Chemical structures of alarm pheromones are referenced in the text by bold numbers.**



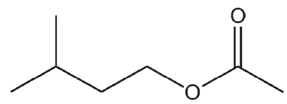
(*E*)-β-Farnesene **1**



(-)-Germacrene-A **2**

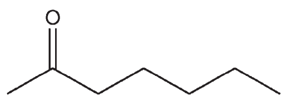


(*E*)-4-Oxo-2-hexenal **3**

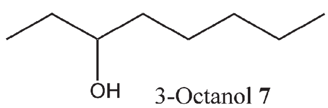


Isopentyl acetate **4**

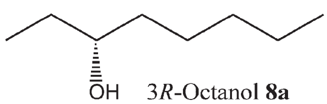
(*Z*)-11-Eicosan-1-ol **5**



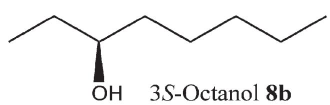
2-Heptanone **6**



3-Octanol **7**



3*R*-Octanol **8a**

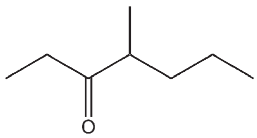


3*S*-Octanol **8b**

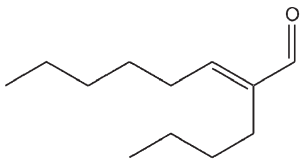
Alarm Pheromones of Insects, Figure 30 (Continued)

numbers living together gives an evolutionary advantage to possessing an alarm pheromone.

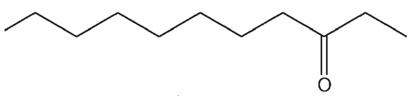
Six-carbon-long aldehydes, in particular (E)-2-hexenal, are common components of defensive secretions and are found in many families of heteropterous insects, including the Pentatomidae, Coreidae, Pyrrhocoridae, Cimicidae, Cynidae and Alydidae. it is thought that the general irritant properties of aldehydes provide a repellent effect to predators with hydrocarbons such as n-tridecane, another ubiquitous component, acting to spread the oily secretion so that the aldehydic components can exert full irritant effect. (E)-2-Hexenal has been reported to have the added dual functions of both alarm and aggregation pheromone, depending on the stimulus concentration, as well as use as a defense chemical. In the case of the bed bug, *Cimex lectularius*, and *Eurydema rugosa*, low concentration of (E)-2-hexenal acts as an aggregation pheromone while high concentration produces an alarm response. Alternatively, it has been reported that n-tridecane, the other



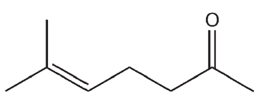
4-Methyl-3-heptanone **9**



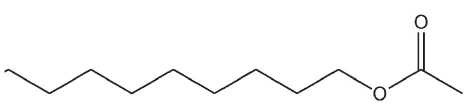
(*E*)-2-Butyl-2-octenal **10**



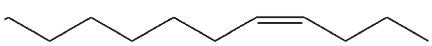
3-Undecanone **11**



6-Methyl-5-heptene-2-one **12**



Dodecyl acetate **13**



(*Z*)-4-Tridecene **14**

Alarm Pheromones of Insects, Figure 30 (Continued)

ubiquitous component of defense secretions, is a bifunctional pheromone for the southern green stinkbug, *Nezara viridula* (Heteroptera: Pentatomidae), which causes dispersal at high concentration (one individual equivalent) and aggregation at low concentrations. The multifunctional aspect of these compounds has important repercussions for their practical use as dispersal agents for pest species in the field, as the low concentration response of aggregation may dominate once the applied high concentration of compounds has diminished.

The pentatomid bug *Erthesina fullo* is a major pest of pine and hardwood trees. Both sexes produce a secretion from the metathoracic gland causing conspecific adults to drop from plants, fly or move away. The secretion comprises nine identified compounds, esters and aldehydes (about 35%) including (E)-2-hexenal and (E)-4-oxo-2-hexenal (**3**) and long chain alkanes, including 50% n-tridecane. Likewise, adult and nymph secretions from *Dysdercus cingulatus* (Heteroptera: Pyrrhocoridae) revealed 55 identified compounds, although the major components are again aldehydes and n-tridecane, features common with several more species of pentatomids from the genus *Chlorochroa* and *Piezodorus guildinii*.

The leaf-footed bug, *Leptoglossus zonatus* (Heteroptera: Coreidae), is an economically important pest of Brazilian corn. An extract obtained from the metathoracic gland by immersion in hexane showed that the major compounds were all of six-carbon length: hexanal, hexanol, hexyl acetate, hexanoic acid, and (E)-**4**-oxo-2-hexenal (**3**). (E)-2-Hexenal was found in the nymph extracts but not in the adult, an example of the general rule that exocrine chemistry of heteropterous nymphs is distinct from that of the adult. In this case, different life-stages possess different alarm pheromone systems. When tested individually, all components produced varying degrees of alarm response in adults and nymphs and even mating insects would stop and disperse, over-riding the sex pheromone response. These compounds are not species specific and are, for instance, found in *L. oppositus* and *L. clypealis*, a situation that mirrors the cross-activity of (E)-β-farnesene in many aphid species (see above), providing more evidence that this non-specific activity does not reduce alarm pheromone value in evolutionary terms.

Adults of the bean bug, *Riptortus clavatus* (Heteroptera: Alydidae), a pest of Japanese soybean, secrete (*E*)-2-hexenyl acetate in its defensive response. This causes an alarm response in adults and nymphs. Interestingly, adults also produce (E)-2-hexenal, and although some response was found when tested at high concentration, there was no response at physiological concentration, suggesting that this compound is not an alarm pheromone.

The examples shown above demonstrate that alarm pheromones of heteropteran families are based on a chemical selection general to insects of a wide taxonomy and show little species specificity. The alarm behavior caused by high concentrations of n-tridecane or (E)-2-hexenal is rationalized easily but the aggregation due to low concentrations is more difficult to explain. Perhaps these substances are constantly emitted in very small quantities due to their volatility and act so as to direct individuals to a region where conspecifics can be found and therefore where food most probably is located, as well as the defensive advantage in being part of a large group.

Triatomine bugs (Heteroptera: Reduviidae) are blood-sucking insects that live throughout the Americas and cause public health problems by transmitting the protozoa *Trypanosoma cruzi*, the causative agent of Chagas disease, to humans. Secretions from Brindley's gland (a simple sac, metathoracic in origin) of several species all revealed isobutyric acid as the major component. Subsequently, other short-chain and branched-chain fatty acids have been identified, and together with isobutyric acid, they act as a powerful defensive secretion. Pure isobutyric acid vapor, however, also caused an alarm response in *Rhodnius prolixus* while another report revealed that low concentrations of isobutyric acid attracted *R. prolixus* adults. This defense compound therefore shows the same multifunctional alarm and aggregation properties as described for components of the stinkbug secretions (see above). Triatomine bugs are inactive and hide during the day, congregating in protective sites. This aspect of group living can help explain the evolutionary advantage in possessing aggregation and alarm responses.

Alarm Pheromones of Social Insects (Hymenoptera)

The Honeybee (Hymenoptera: Apidae)

When the honeybee (*Apis mellifera*) is attacked, alarm pheromones released serve to muster help and to direct the attack. Specialized guard bees present at the nest entrance carry out attacks. Although these guards are relatively few compared to the colony population, release of alarm pheromone can result in synchronized attacks by more than 100 workers against an intruder. Guard bees initiate attacks by raising their abdomens, protruding their stings and releasing alarm pheromone from the sting chamber. The workers then alert the rest of the hive by wing beating, aiding dispersal of the pheromone, and by running into the hive. After a few seconds, many excited bees may rush out of the hive entrance and search, or stop and assume a characteristic tense and aggressive posture with a slightly raised body, wings extended, mandibles agape and antennae waving. In this highly activated state, they will fly to attack at the slightest further provocation. These two stages of alarm response are called alerting and activation and are characteristic of alarm pheromones.

Alerted workers need to search for and discover the enemy to prevent any further threat. To do this, they rely on other cues to direct the attack such as odor, jerky movement and hairy body covering. Once the threat is located, it is stung, injecting a dose of venom. However, the shaft of a sting is barbed and a bee is unable to withdraw it from the skin of vertebrates, so the sting, together with associated motor apparatus and glands, are severed from the bee as it attempts to fly away and are left attached to the enemy. The severed sting apparatus continues to pump venom into the victim and alarm pheromone is dispersed from the exposed under-surface of the sting shaft membrane to mark an enemy and make it a more obvious target.

The main alarm pheromone component of the sting gland was identified in 1962 as isopentyl acetate (**4**). Although a number of other compounds are known to be present, isopentyl acetate and (Z)-11-eicosen-1-ol (**5**) account fully for the activity of the sting pheromone. The roles of the two compounds in the pheromone appear to differ, with (Z)-11-eicosen-1-ol responsible for prolonging the activity of isopentyl acetate. Other compounds such as 1-hexanol and 1-butanol increase the number of bees responding.

Stinging bees often grip an enemy with their mandibles and deposit an alarm substance. At the hive entrance, more bees examine mandibular gland extracts of worker honeybees applied to filter paper than examined unscented filter paper. 2-Heptanone (**6**) has been identified from the mandibular gland secretion, and when filter papers or small corks carrying 2-heptanone were placed at the hive entrance, the guard bees were alerted and attacked them. As the mandibles are used for grasping an intruder, it seems likely that the main function of 2-heptanone is to label the intruder to be attacked.

Under certain circumstances, honeybee alarm pheromones are repellent. The presence of alarm pheromone deters honeybees from foraging at dishes of sugar syrup and from exposing their Nasonov glands and fanning which normally attracts other bees. Furthermore, a high concentration of alarm pheromone repelled foraging bees from crops including oilseed rape, normally highly attractive to bees, in an area that had many honeybee colonies.

Alarm Pheromones of Ants (Hymenoptera: Formicidae)

The Formicidae is a huge family comprising thousands of ant species, all of which are social insects, living in colonies that vary hugely in size. Members of an ant colony may be differentiated into castes that specialize in carrying out particular tasks and vary in their response to alarm pheromone. Soldiers show a more aggressive response, are more likely to respond when the threat is closer to the nest and may be specialized to deal with vertebrate predators. Also, workers of the Texas leaf-cutting ant, *Atta texana* (Formicidae: Myrmicinae), have a lower threshold for alarm pheromone response than the queen and males. Other factors governing the type and intensity of alarm response are the age and size of ant colony. When alarm pheromone is present in sufficient concentration to excite the workers, other stimuli are needed to direct an attack. Workers often will touch everything they encounter and the full-scale alarm response may rely on additional cues, such as the presence of an alien object. Alarm pheromones also may function with acoustic alarm signals. Ant species in the sub-family Dolichoderinae produce vibration signals using their mandibles to scratch the ground or the abdomen to hit the ground, increasing alarm behavior in other workers. Vibrations are produced also by leaf-cutting ants which act as warning signals. Alarm pheromones also are used by ants to attract attention if they are trapped, and may be released by reproductive ants just before mating flights to ensure that aggressive workers protect them from potential predators.

The context in which a worker encounters an alarm pheromone also influences the response. Workers of the grass-cutting ant *Atta capiguara* (Formicidae: Myrmicinae) are less likely to show alarm behavior if already engaged in a task. Foragers carrying leaves do not respond to alarm pheromone, whereas minor workers and foragers that are not carrying leaves do respond.

Ant alarm pheromones may be produced from one or several sources. The army ants or Eciton ants (Formicidae: Ecitoninae) and the rare *Leptanilla* sp. (Formicidae: Leptanillinae) of Indonesia have large mandibular glands, which are believed to be the sole source of the alarm pheromone. However, other species rely on a combination of secretions from several glands. *Formica* and *Myrmica* species use products from the poison and Dufour's gland (both opening near the base of the sting), as well as the mandibular gland. Ponerine ants (Formicidae: Ponerinae) use secretions from the pygidial gland as alarm components, whereas the poison gland is the most important gland of several other species, including the harvester ant, *Messor barbarus* (Formicidae: Myrmicinae).

Ants are able to detect and respond to specific isomers of their alarm pheromone. *Myrmica rubra* and *M. scabrinodis* use 3-octanol (**7**) as the alarm pheromone produced from mandibular glands. Experiments carried out using the two optical isomers (**8a, b**) of this compound showed that *M. rubra* workers only responded to one of the isomers, (*R*)-3-octanol (**8a**), while *M. scabrinodis* workers reacted more strongly to the natural 9:1 mixture of R and S isomers. This work suggests that there may not only be specific chemicals but also species-specific mixtures of isomers. Many other *Myrmica* species have 3-octanol and 3-octanone as alarm pheromones but may have species-specific ratios of the two, which allow ant species to only show a full alarm reaction to their specific alarm pheromone blend.

Myrmica species of grass-cutting ants share the main component of alarm pheromone, 4-methyl-3-heptanone (**9**), but they have species-specific modifying components. The response to 4-methyl-3- heptanone was compared to that elicited by the bodies of workers that had their heads crushed to release the natural alarm pheromone. 4-Methyl-3-heptanone and bodies caused the same level of attraction but the full range of alarm behavior was seen only with the bodies. In contrast, workers of the giant tropical ant, *Paraponara clavata* (Formicidae: Paraponera), produce two components, 4-methyl-3-heptanone and 4-methyl-3-heptanol.

Atta capiguara is a grass-cutting ant species that lives in colonies with hundreds of thousands of workers. Workers are polymorphic, varying in size from small minors and medias to the larger foragers and soldiers. Minors and medias do most of the nest tasks whereas foragers collect the grass; however, minors often are found on foraging trails despite the fact they do not carry grass. They are believed to be patrollers as they have a stronger response to alarm pheromone than foragers and soldiers. Minors of other *Atta* species are also more efficient at recognizing intruding ants than other castes.

As is the case with honeybees described above, the complete alarm response can be described by a number of behaviors. These behaviors and their elicitors have been dissected in an elegant piece of research on the African weaver ant, *Oecophylla longinoda*. The major workers produce a secretion from the mandibular gland comprising four active components: hexanal, hexanol, (*E*)-2-butyl-2-octenal (**10**), a dimer of hexanal produced chemically by self-condensation, and 3-undecanone (**11**). Hexanal, a highly volatile component with an active space of 5–10 cm (the area around an emission where the concentration is at or above that required for a behavioral response), causes the ants to be alerted, making quick runs in random and changing direction with mandibles open and antennae waving. Hexanol attracts directly to the source at a range of 1–5 cm; it is repellent at very close range and also causes further excitement. As the hexanol disperses, 3-undecanone is attractive over this close range and, along with (*E*)-2-butyl-2-octenal, acts as a marker for attack and biting to hold the source occurs. This process is called a local attack. In addition, *O. longinoda* also has a mass attack alarm response. The poison gland of the major and minor workers contains venom that is ejected by raising the gasters above vertical when an attacked object is held in the jaws. The venom contains a blend of straight chain hydrocarbons and formic acid. Formic acid initiates approach and attack while n-undecane causes mandible opening, gaster raising and also short-range approach to the source. The combination of these behaviors allows location and initial attack of still and moving objects followed by recruitment of workers to continue attack.

The properties that make alarm pheromone cues for conspecifics also enable them to act as cues for parasites and predators of ants to find their prey. *Apocephalus paraponerae* is a parasitic fly that attacks the ant *Paraponera clavata*. Females and males of *A. paraponerae* are attracted to injured, fighting or freshly killed workers. After finding a worker, the female lays a few eggs, which will hatch and then feed on the victim for 3–7 days. Both male and female *A. paraponerae* also feed on the wounds of the injured workers and gather near their victims to mate. The heads of *P. clavata* workers contain two chemicals, 4-methyl-3-heptanone and 4-methyl-3-heptanol, which are particularly attractive to *A. paraponerae*. These compounds are common alarm pheromone components of ants and are released when the workers are stressed. However, it has been suggested that because these parasites use alarm pheromone for finding their host, *P. clavata* may be under pressure to reduce the amount of alarm pheromone released and that this ant may even have lost alarm behavior response as a result of this pressure. Similarly, the zodariid spider, *Habronestes bradleyi* (Zodariidae), a predator of the meat ant, *Iridomyrmex purpureus*, detects the alarm pheromone, in this case 6-methyl-5-hepten-2-one (**12**), given out by fighting workers and uses it to locate its prey.

Alarm Pheromones of Thrips (Thysanoptera: Thripidae)

Thrips are small, economically important pest insects, often known as thunderflies. The defensive behavior of thrips includes raising and lowering the abdomen and secretion of a droplet of anal fluid highly repellent to predatory ants. Western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), are not social but tend to be found in clumped distributions. Adults and nymphs of western flower thrips produce an anal droplet containing decyl acetate and dodecyl acetate (**13**) in a molar ratio of 1.5:1. Each component, at levels of 1 ng, produces the alarm response of walking away from the source or dropping from leaves. The response, however, is only over short distances and limits the potential for pheromone use in pest management.

Cockroach Alarm Pheromones (Blattodea: Blattidae)

Defensive secretions are well known in cockroaches. They are produced from ventral inter-segmental glands and comprise an organic and an aqueous phase. In the case of the Florida woods cockroach, *Eurycotis floridana* (Dictyoptera: Blattidae), 90% of the organic phase (which comprises 85% of the total secretion) is (E)-2-hexenal, a compound found in many heteropteran bugs and discussed above. The rest of the organic secretion comprises approximately 40 other components, including mainly aldehydes, alcohols and carboxylic acids, while the aqueous phase contains gluconic acid, glucose and gluconolactone. The secretion acts as a conspecific alarm pheromone in these gregarious insects with nymphs responding at lower concentrations than adults do. Ethanolic extracts of the American cockroach, *Periplaneta americana*, also repel conspecifics from aggregations in daytime shelters. However, there was no evidence that this repellent is released by living insects as an alarm pheromone but is instead endogenously produced from dead insects and is effective against other cockroaches with diverse phylogenetic relationships. The effect, therefore, is not pheromonal, as the authors explain the activity in terms of unsaturated fatty acids (oleic, linoleic and linolenic acids) which emerge as signals of death and injury among organisms from a wide phylogenetic background. Both of the reports described above provide evidence that the use of alarm pheromones to increase dispersal for pest management purposes will be of limited value. Due to the aggregation effect at low concentration, treated areas could become attractive. Also, if low concentrations were used as attractants in a lure and kill approach, dead insects would repel others before they become ensnared.

Alarm Pheromones of Beetles (Coleoptera)

Despite the vast numbers of species in the order Coleoptera, inhabiting a wide range of ecological niches, little is known of the existence of behavioral responses to alarm pheromones they may possess. Species of beetles that are group-living are most likely to demonstrate alarm responses. Gyrinid beetles (Coleoptera: Gyrinidae), known as whirligig beetles, live in open habitats on fresh water surfaces and typically aggregate in groups containing hundreds of individuals, dispersing in the evening to forage. Although easy to detect by fish, they are seldom preyed upon due to a repellent secretion released as a last resort to physical attack. The secretion also acts as an alarm pheromone over short distances, increasing locomotory activity and defensive movement, such as diving and active underwater swimming. Although alarm dispersal after attack can occur, the aggregations of beetles themselves indicate to experienced predators to avoid the group and confer an aposematic effect acting at the group level rather than the individual level.

Lacewing Alarm Pheromones (Neuroptera: Chrysopidae)

The green lacewing, *Chrysoperla carnea* (Neuroptera: Chrysopidae), is an important predator of pest aphids and, as such, is a beneficial insect. It discharges a malodorous secretion from glands at the anterior of the prothorax. The major component of this secretion has been identified by gas chromatography, mass spectroscopy and chemical synthesis as (Z)-4-tridecene (**14**) and gas chromatography coupled electroantennagrams revealed that it is detected by the lacewing antennae. Predatory ants displayed avoidance behavior in response to it, suggesting a defensive function, and in laboratory experiments, adult lacewings avoid entering areas where it is present. In the field, it acts as an antagonist to trap catches using known attractants and, as such, could be described as an alarm pheromone. Another species of lacewing, *Peyerimhoffina gracilis*, also produces the identical compound. As lacewings are not known to be gregarious, the exact ecological purpose of this compound is being investigated.

Conclusions

It can be seen that alarm pheromones are used widely by a broad taxonomic diversity of insects and elicit equally varied behavioral responses, including escape or aggressive behavior. Alarm pheromones are generally low molecular weight, organic compounds and so are volatile, dispersing quickly, and do not persist in the environment. In addition, the chemical nature of the alarm pheromone often is unstable, increasing the lack of persistence. This allows conspecifics to be alerted very quickly over a fairly large area and yet not cause false alarm after the danger has passed. Alarm pheromones are often produced in glands responsible for biosynthesis, storage or release of defense secretions. This association between alarm pheromones and defense glands, including those near the sting or mandibles, has led to the hypothesis that alarm pheromones have evolved from chemicals that originally had a defensive role, or are themselves defense compounds that have taken on an additional alarm pheromonal role. The fact that known defense components have additional multifunctional pheromonal roles of alarm (high concentration) and aggregation (low concentration) also points to the possibility that these pheromonal roles have evolved from compounds originally used for defense. Of particular interest is the common lack of species specificity found in alarm pheromones, which is in contrast to that of other pheromones. Sex pheromones, for example, are so specific that they can be the sole identifiable trait in defining morphologically identical populations, such as within the species complex of the sandfly, *Lutzomyia longipalpis* (Diptera: Psychodidae). However, the alarm pheromone of different aphid species is (E)-β-farnesene and different species of *Atta* grass-cutting ant use 4-methyl-3-heptanone. In addition, production of (E)-2-hexenal and n-tridecane is ubiquitous as multifunctional pheromone components in terrestrial true bugs, and it is possible that (E)-4-tridecene may reveal itself to be common in green lacewings. Discrimination between these behavioral signal compounds, therefore, is not essential to their function as alarm pheromones, and there may even be evolutionary benefits in being able to respond to alarm pheromones of related species of insects.

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Alarm-Recruitment System

Recruitment of nest members to a particular location to aid in colony defense.

► Sociality of Insects

Alary Muscles

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The alary muscles, so named because of their general wing or delta shape in many insects, lie immediately on top of the dorsal diaphragm. The muscles probably aid the dorsal diaphragm in providing support for the heart, the part of the dorsal vessel in the abdomen. The muscle fibers fan out from a small point of origin on the lateral wall of the dorsum to a broad insertion on the heart in many insects, presenting the typical delta appearance. In some insects, however, the delta shape is not so evident. Some alary muscle fibers pass beneath the heart and extend laterally from side to side, and thus help to support the heart. In places, the fibers may also run parallel to the long axis of the heart for a short distance. The pairs of alary muscles tend to agree with the number of pairs of ostia, the (usually) lateral openings in the dorsal vessel that allow hemolymph to flow into the heart in the abdomen. Alary muscles generally do not occur in the thorax, but in some insects, a few ostia open outward in the thorax, allowing hemolymph to flow outward.

In addition to support, the alary muscle may assist in the expansion (diastole) of the heart after each contractile wave passes a given point, and thus aid in pulling hemolymph into the incurrent ostia. They are not necessary for diastole, however, as evidenced by severing them with little or no apparent effect on the heart beat.

Alate (pl., Alatae or Alates)

The winged forms of insects, particularly aphids.

Alderflies

Members of the family Sialidae (order Megaloptera).

► Alderflies and Dobsonflies

Alderflies and Dobsonflies (Megaloptera)

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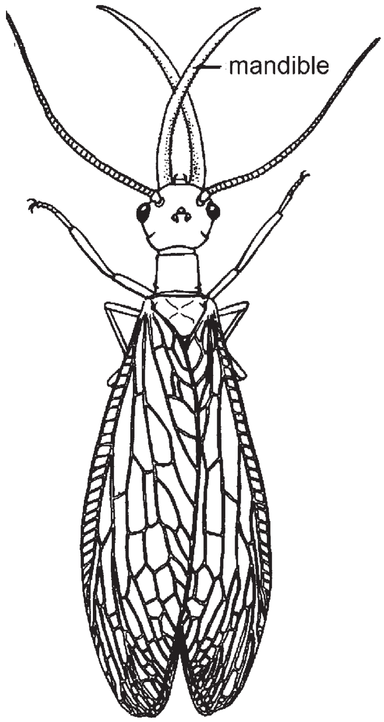
The order Megaloptera comprises about 190 species in 60 genera in two families. All the larvae are aquatic. The larvae, especially of Corydalinae, are among the most primitive of the Holometabola. The metamorphosis from larva to adult is relatively simple.

The family Sialidae, commonly called alderflies, is a small group of about 70 species in about eight genera. They are worldwide. Most of the adults have a similar appearance and are usually dark brown to black in coloration. They lack ocelli and have the fourth tarsomere bilobed. They are an ancient group known from the Permian, about 200 million years ago, and evidently have not evolved much since then. In fact, the wing venation has many features in common with the Protoperlaria, a fossil order considered by some as ancestral to the Plecoptera. The adult life span is probably short since the reduced mouthparts do not seem adapted for extensive feeding. The eggs are laid in rows, forming large masses situated on branches, bridges, and other objects overhanging the water. The larvae hatch and fall into the water where they are predacious on other aquatic insects, especially caddisflies. There are as many as 10 larval instars which may last up to two or more years until pupation. The larva crawls out of the water and digs into the bank to form an earthen cell several feet from the edge of the water. The genera are restricted geographically. The genus *Sialis* Latreille is Holarctic, *Protosialis* Van der Weele is South American, *Austrosialis* Tillyard and *Stenostialis* are Australian, *Haplosialis* Navas is from Madagascar, *Leptosialis* is African, *Indosialis* Lestage is Oriental and *Nipponsialis* Kuwayama is Japanese. The larva has seven lateral processes and the abdomen terminates in an elongate process. The only world compilation is by Van der Weele (1910) but is greatly out of date.

The family Corydalidae, or dobsonflies, is characterized by having three ocelli and the anal region of the hindwing is very wide, folded fanlike at rest (Fig. 31). The fourth tarsomere is not modified. There are several hundred species in about 20 genera and two subfamilies.



Alderflies and Dobsonflies (Megaloptera), Figure 31 **Adult dobsonfly (Corydalidae).**

The Corydalinae with about 60 species, is distributed in the New World (three genera), South Africa (one genus) and Asia (five genera). This subfamily does not have pectinate antennae and the head is usually quadrate, often with a postocular spine. Often there are more than four crossveins between the radius and radial sector. The male terminalia are distinctive with a well developed ninth gonostylus. Many of the species are very large. *Corydalis* Latreille is the largest genus in the New World with about 30 species. The males of this genus often have the mandibles greatly extended which is similar to *Acanthacorydalis* Van der Weele from Asia. *Platyneuromus christil* (Navás) from Central America, has a tremendously expanded postocular flange. The larva has eight lateral processes and the abdomen ends in a pair of claw-like structures. In America, the larvae are called hellgrammites and are used for fishing. In one case, a larva was found inside a fish stomach many hours after ingestion. Glorioso (1982) has provided a good reference.

The Chauliodini was reviewed by Kimmins (1954) who recognized 12 genera. The genera are restricted in distribution similar to the Corydalinae and are found in the Cape region of South Africa (two genera), North America (four genera), Chile (three genera), Australia (one genus), Madagascar (one genus), and Asia (four genera). Males and rarely females have pectinate antennae in some genera.

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Aldrovandi, Ulisse (Ulysse, Ulysses)

Ulisse Aldrovandi was born in Bologna, Italy, in 1522. He studied law in Bologna, and then philosophy and medicine in Padua and Rome, earning a doctorate in medicine in 1552. In 1560, he was appointed professor in Bologna, a position that he held for 40 years. He lectured mainly on pharmacology, but he collected natural history objects and employed artists to draw them. He published four large volumes during his lifetime, but his friends and pupils used his voluminous manuscripts to publish 10 more volumes after his death. His (1602) "De animalibus insectis libri VII" was the first book to be published on insects, although the "insects" included various other kinds of invertebrates. A chapter was devoted to the structure of the insect body. Insect reproduction and metamorphosis were described; respiration and the senses of touch, taste, and smell are discussed, and the life of honey bees is described. He died in 1605.

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Aldyidae

A family of bugs (order Hemiptera). They sometimes are called broad-headed bugs.

► Bugs

Aleyrodidae

A family of insects in the order Hemiptera. They sometimes are called whiteflies.

► Whiteflies
► Bugs

Alexander, Charles Paul

Charles Alexander was born in New York state on September 25, 1889. He entered Cornell University in 1909, receiving B.Sc. and Ph.D. degrees in 1913 and 1918, respectively. He was employed as systematic entomologist in the Snow Entomological Museum at the University of Kansas in 1917–1919 and then by Illinois Natural History Survey in 1919–1922. Next he moved to Massachusetts Agricultural College and was placed in charge of teaching entomology. He served as chairman of the Department of Entomology and Zoology for 10 years, for the last three of which he was dean of the School of Science (of what had by then become the University of Massachusetts). He was president of the Entomological Society of America in 1941–1943 (two terms). His almost exclusive subject of research was the family Tipulidae (crane flies) about which he published over 1,000 papers and described over 10,000 species, an enormous production. After retirement from teaching, he moved his insect collection to his house and continued working on it until the death of his wife, Mabel, in 1979. Two years later he transferred his collection to the National Museum of Natural History in Washington, DC. He died at home in Massachusetts on December 12, 1981.

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Alfalfa Leafcutting Bee, *Megachile rotundata* (Hymenoptera: Megachilidae)

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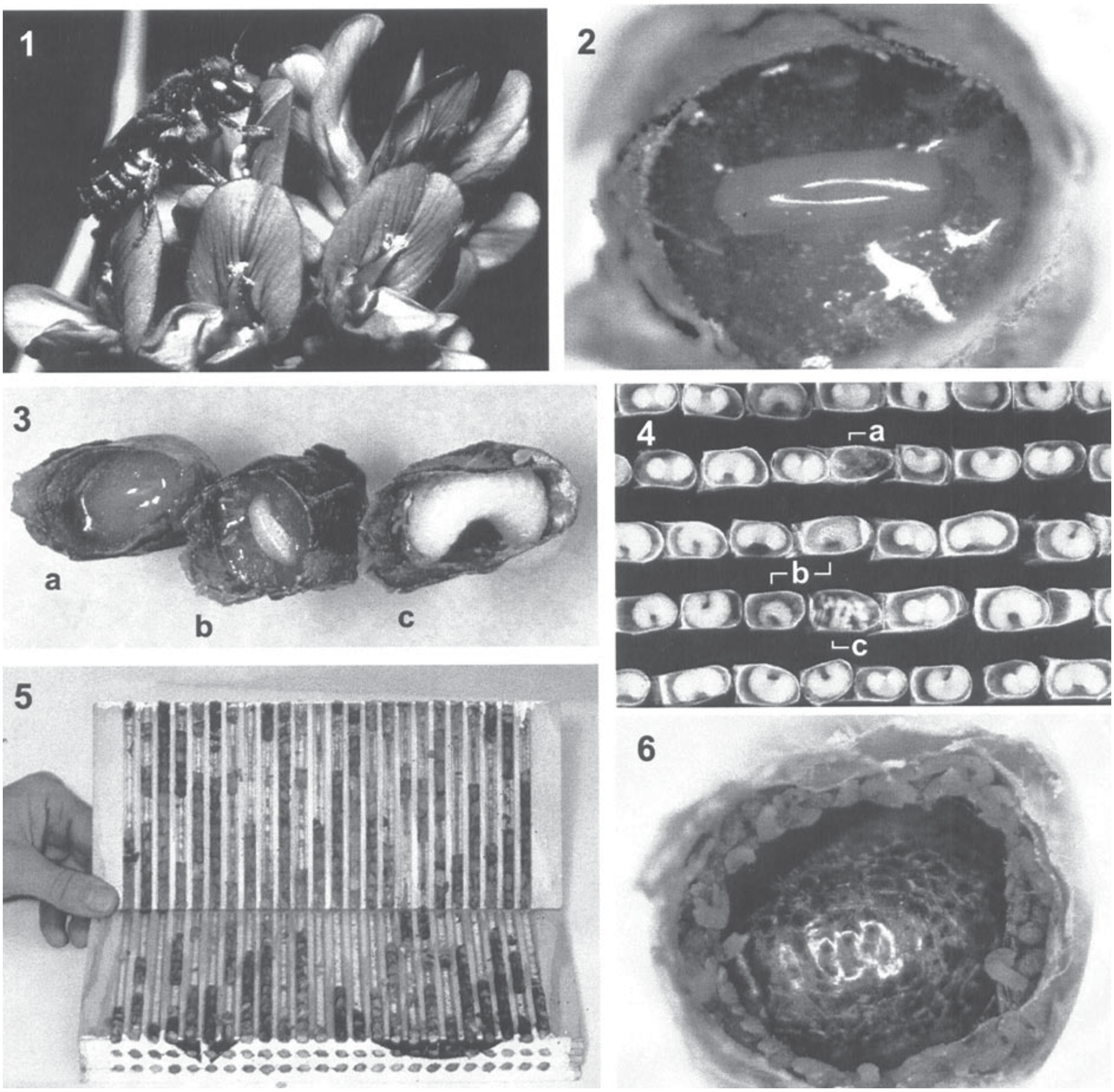
The alfalfa leafcutting bee, *Megachile rotundata* Fabricius (Hymenoptera: Megachilidae), has been successfully semi-domesticated within the last 50 years to pollinate alfalfa for seed production in North America. Honey bees are inefficient pollinators of alfalfa and, although bumbles bees and some other wild bees are efficient pollinators, they have proved difficult to manage. The use of the alfalfa leafcutting bee has succeeded in greatly increasing the seed yield of alfalfa. In western Canada, the average alfalfa seed yield using this bee exceeds 300 kg/ha, whereas without it is usually less than 50 kg/ha. The genus *Megachile* contains many species that nest in tunnels in dead trees or fallen logs. Most are solitary, but *M. rotundata* is gregarious and, although each female constructs and provisions her own tunnel, she will tolerate close neighbors. This behavioral characteristic is one of the main reasons why this species has been amenable to management on a commercial scale. *M. rotundata* is of eastern Mediterranean origin and was first found in North America in the 1940s near seaports. It probably gained entry as diapausing pre-pupae within tunnels in the wood used to make shipping crates or pallets.

Life History

Once a suitable tunnel has been found, the female uses her mandibles to neatly cut oblong pieces of leaves or flower petals which she uses to build cells end to end in the tunnel, starting at the far end and finishing near the entrance (Fig. 32). About 15 leaf pieces are arranged in overlapping layers and cemented together to form a thimble-shaped cell with a concave bottom. The cell is then provisioned with nectar and pollen. During this process, the female enters the tunnel head first, regurgitates the nectar, then turns around to remove the pollen from the scopa (the pollen-collecting hairs on the underside of her abdomen) and tamps the pollen into the nectar with the tip of her abdomen. The provisions for each cell consist of about two-thirds nectar and one-third pollen, requiring 15–25 provisioning trips. It is while collecting the nectar and pollen that the bees pollinate the flowers that they visit. When the cell has been adequately provisioned, the female lays a single egg directly on the surface of the provisions and then caps the cell with several circular leaf pieces. She then proceeds to construct the next cell, repeating this process until the tunnel is filled. She then plugs the end of the tunnel with 10–15 leaf pieces cemented together to form a plug. Females continue filling tunnels with cells until pollen and nectar sources are no longer available. Upon hatching, the larva immediately begins feeding on the provisions within its cell, undergoing four instars before reaching maturity. It then deposits a ring of fecal pellets within the cell and spins a tough silken cocoon within which it overwinters as a diapausing pre-pupa. During the feeding period, the waste



Alfalfa Leafcutting Bee, *Megachile Rotundata* (Hymenoptera: Megachilidae), Figure 32 **Alfalfa leafcutting bee, *Megachile rotundata*. (1) Adult on alfalfa flower. Flowers are pollinated while the bees visit the flowers to collect nectar and pollen for provisioning their cells. (2) A single egg is deposited on the surface of pollen/nectar provisions within a cell which the female constructs within tunnels using oblong pieces of leaves or flower petals. (3) The egg placed into the cell hatches within 2 to 3 days and the larva immediately begins to consume the provisions. The larva pupates after undergoing 4 instars. (a) single egg, (b) 3rd instar, and (c) 4th instar larvae within the cell. Cell caps have been removed. (4) X-ray of leafcutting bee cells used to determine quality of commercial bees. (a) empty cell, (b) chalkbrood cadavers, (c) *Pteromalus venustus* parasitoid cocoons. (5) Nesting boards separated to show arrangement of bee cells constructed within the tunnels. In the fall, the boards are removed from the field and the cells are stripped from the boards using specialized automated equipment. (6) Chalkbrood cadaver within the cell. Note the ring of frass deposited on the outside edge of the cell. Normally, the larva would spin a tough silken cocoon within which it overwinters as a diapausing pre-pupa. Larvae infected with chalkbrood usually succumb just after defecating and just prior to cocoon spinning.**

products of digestion are accumulated internally until the larva defecates just before forming the cocoon. In the spring, the pre-pupa pupates. After a pupal period of 3–4 weeks, the adult emerges and chews its way out of the cocoon. Mating takes place soon after emergence of the adults. Females store enough sperm from a single mating to fertilize all of their eggs. Soon after mating, the females seek out suitable sites in which to excavate tunnels or select suitable preexisting ones, either natural or man-made.

Domestication

The gregarious nature of *M. rotundata* and its willingness to accept artificial domiciles has permitted the commercial scale management of this species for crop pollination. Initially, observant alfalfa seed producers in the northwestern U.S.A. noticed that this species, which had undergone a population increase following natural establishment, would nest in man-made structures such as shingled roofs and they started to provide artificial tunnels by drilling holes in logs positioned around the edges of the seed fields. The next step was to provide nests consisting of wooden blocks drilled with closely spaced tunnels. Although reasonably successful on a small scale, this method was not suitable for the management of the large numbers of bees (50,000–75,000/ha) required for commercial alfalfa seed production. Consequently a "loose-cell" system was developed. This system uses 10 mm thick boards of wood or polystyrene which are grooved on both sides and stacked together to form hives of closely packed tunnels about 7 mm in diameter and 150 mm in length. At the end of the season, the boards are separated and the cells removed using specialized automated equipment. After being stripped from the boards the cells are tumbled and screened to remove loose leaf pieces, molds and some parasites and predators. The clean cells are then placed in containers for overwintering storage at about 50% R.H. and 5°C. In the spring, the cells are placed in trays for incubation at 70% R.H. and 30°C. A few days before the bees are due to emerge, the trays are moved to especially designed shelters spaced throughout the alfalfa seed fields. By selecting the date when incubation begins, and if necessary manipulating the incubation temperature, the emergence of the bees can be adjusted to coincide with the start of alfalfa bloom.

An advantage of the loose cell system of management is that it facilitates the control of parasitoids, predators and disease, and assessment of the quality of the progeny. Leafcutting beekeepers routinely send samples of cells to specialized leafcutting bee "cocoon" testing centers, where they are x-rayed and incubated to provide estimates of numbers of intact cells, incidence of parasites and pathogens, and sex ratio. These data are used to determine stocking rates and to set a price if bees are to be marketed. The proportion of females, which is usually only about a third, is of particular interest because they are the primary pollinators.

Natural Enemies

About 20 species of insects are known to parasitize or prey on the immature stages of the alfalfa leafcutting bee. The most important of these are several species of chalcid wasps, including *Pteromalus venustus* Walker, *Monodontomerus obscurus* Westwood, *Melittobia chalbii* Ashmead and *Diachys confusus* (Girault). The most widespread and damaging is *P. venustus*, which probably arrived in North America with its host. The female parasitoid pierces the host cocoon with her ovipositor, stings the larva or pupa to paralyze it, and then lays some eggs on its surface. The parasitoid larvae then feed upon the bee larva eventually killing it. Normally 15–20 adult *P. venustus* emerge from each host cocoon.

Two other enemies, which are more of biological interest than economic significance, are several species of cuckoo bees, *Coelioxys* (Megachilidae) and the brown blister beetle, *Nemognatha lutea* LeConte. Cuckoo bees are very similar to leafcutting bees, but lack the structures required for collecting pollen. The female cuckoo bee lays her egg in the partially provisioned cell of the leafcutting bee while the rightful owner is out foraging. When partly grown, the cuckoo bee larva kills the leafcutting bee larva and usurps the provisions. Brown blister beetle females lay their eggs on flowers and the first instar larvae (triungulins) attach themselves to any bee that visits the flower. When the bee returns to its nest, the triungulin detaches and begins feeding on the cell contents, destroying 2 or 3 cells before reaching maturity.

Several stored-product insects including the driedfruit moth, *Vitula edmandsae serratilinnella* Ragonot, and stored-product beetles such as the sawtoothed grain beetle, *Oryzaephilus surinamensis* (Linnaeus), the red flour beetle, *Tribolium castaneum* (Herbst) and the confused flour beetle, *Tribolium confusum* (Jacquelin du Val) can cause serious damage during overwintering storage, especially if sanitation practices are lax.

Most of the parasitoids and predators can be largely controlled by proper construction of hives and nesting materials, physical removal during the loose-cell processing and strict hygiene during storage. However, successful control of the major pest, the chalcid *P. venustus*, often requires carefully controlled fumigation using dichlorvos (2, 2-dichloro-vinyl dimethyl phosphate) resin strips.

The only disease causing significant losses to the leafcutting bee industry is chalkbrood, caused by the fungus *Ascosphaera aggregata* Skou. The disease was first reported in leafcutting bees in 1973, and remains most severe in the western U.S. states, where losses of more than 65% of bees are not uncommon. Bee larvae become infected after consuming pollen provisions contaminated with the fungal spores which germinate within the midgut and penetrate into the hemocoel. Larvae soon die and turn a chalk white color as the mycelium fills the body. Sporogenesis occurs beneath the host cuticle resulting in the formation of ascospores which are bound in "spore balls" within ascomata. At this stage, the cadaver turns black. Spores are spread by adults that must chew their way through infected cadavers in order to exit their nesting tunnels. Chalkbrood can be adequately managed through strict hygiene and decontamination of the bee cells, nest materials and shelters. Initially, decontamination was performed by dipping in household bleach. However, fumigation with paraformaldehyde has become the method of choice, and is highly effective for the control of both *A. aggregata* and foliar molds, which can sometimes pose a health risk to the beekeeper.

► Bees

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Alfalfa (Lucerne) Pests and their Management

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Alfalfa (lucerne), *Medicago sativae*, is one of the most important legumes used in agriculture. It is the principal roughage for ruminants, as well as being an important source of protein in animal diets. It is surpassed only by grass, corn, and soybean as an animal feed, and is especially important to the dairy industry. The USA is the world's largest producer of alfalfa, but it also is an important crop in Australia, Europe, Argentina, China, South Africa, and the Middle East.

There are other uses for alfalfa, though they are minor. Alfalfa sprouts are a salad ingredient, alfalfa shoots are sometimes consumed as a leafy vegetable, and dehydrated alfalfa is sometimes formulated as a tablet to be consumed as a dietary supplement. Alfalfa is a cross-pollinated species. It relies on insects, often domesticated leafcutting bees, honey bees, alkali bees, and various wild bees, for pollination. Wind pollination does not occur because the blossom is structured in a way that physical "tripping" to expose the stigma to the anthers is required. Bees manipulate the blossom when foraging for nectar and pollen and thereby "trip" the blossom, an action that results in the bee being struck in the head. An interesting aspect of pollination is that some bees learn to avoid the tripping process to avoid being struck, thereby robbing the flower without pollination occurring. Older honey bees are good at avoiding tripping, but naïve young honey bees trip the blossom and provide pollination.

Alfalfa is normally harvested before, or at, the initiation of flowering, which maximizes protein content of the harvested hay. Because pollinators are often present in alfalfa fields during the bloom period, care must be taken when using insecticides for pest suppression to avoid products that are highly toxic to pollinators, at least if seed production is a concern. However, most alfalfa is grown only for forage, and without regard for seed production. Thus, insecticide use may include the bloom period, though if pollinator populations are reduced, other crops that require pollination may be inadvertently affected.

Alfalfa is unusual as a field crop in that it is a short-lived perennial, living 3–12 years. It may be harvested from once to 12 times per year, depending on climate and growing conditions. It has deep roots, and is resistant to drought, though in arid climates it is irrigated. It is tolerant of cold, growing well in cool and cold climates. It does not tolerate hot, humid climates, however.

Alfalfa often is cut and dried before it is baled and stored. To speed up the process of drying, alfalfa is commonly flailed or passed through a set of rollers to break or crush the stems, facilitating the drying process. The crushing process is called crimping and sometimes can cause problems for horses because blister beetles (Coleoptera: Meloidae) are incorporated into the hay (see below, blister beetles). Dried alfalfa is tied into bales of various sizes, including large cylindrical bales, and stored under shelter, or packaged in plastic, to avoid moisture. If the alfalfa is to be fed to cattle, however, it is not dried, and instead it is finely chopped and stored in trenches, silos, or bags where it can ferment and maintain high nutrient levels. Cattle are not very susceptible to poisoning by blister beetles.

Alfalfa has undergone considerable breeding to produce strains that have not only suitable agronomic conditions, but also are disease and pest resistant. Nevertheless, insects can damage alfalfa nearly everywhere it is grown. Some of the important pests are listed in the table, and the most important are discussed below.

Alfalfa Weevil, *Hypera postica* (Gyllenhal) (Coleoptera: Curculionidae)

In many regions, this is the most important pest of alfalfa. It is found in Europe, the Middle East, Central Asia, and North America. Alfalfa weevils overwinter as adults in the soil of weedy, brushy areas near alfalfa fields. They disperse to alfalfa in the spring and oviposit within the stems. The eggs are oval and yellow. Early instars developing from these eggs are slate colored, but develop a bright green color and a white stripe down the middle of the back as they mature. Larvae have a black head capsule. They display four instars and will grow to about 8–10 mm in length. After feeding for 3–4 weeks, larvae spin loosely constructed cocoons on

Alfalfa (Lucerne) Pests and their Management, Table 5 **Some pests of alfalfa (lucerne), and locations where they are considered to be damaging**

Feeding behavior	Primary taxon	Common name	Scientific name	Location
Above-ground, chewing	Coleoptera	Sitona weevil	*Sitona discoides*	Australia
		Small lucerne weevil	*Atrichonotus taeniatulus*	Australia
		Vegetable weevil	*Listroderes obliquus*	Australia
		Alfalfa weevil	*Hypera postica*	Europe, Asia, N. America
		Clover leaf weevil	*Hypera punctata*	Europe, Asia, N. America
		Clover head weevil	*Hypera meles*	Europe, N. America
		Blister beetles	*Epicauta* spp.	N. America
		Flea beetles	*Epitrix, Systena, Disonycha* spp.	N. America
	Orthoptera	Grasshoppers	*Melanoplus* spp.	N. America
		Wingless grasshopper	*Phaulacridium* spp.	Australia
	Lepidoptera	Armyworm	*Mythimna* spp.,	Australia
		Armyworm	*Persectania* spp.	Australia
		Armyworm	*Pseudaletia unipuncta*	N. America
		Variegated cutworm	*Peridroma saucia*	Europe, Asia, Africa, N. America
		Army cutworm	*Euxoa auxiliaris*	N. America
		Granulate cutworm	*Agrotis subterranean*	N. America, S. America
		Black cutworm	*Agrotis ipsilon*	N. America, Europe, Africa
		Beet armyworm	*Spodoptera exigua*	Asia, N. America
		Fall armyworm	*Spodoptera frugiperda*	N. America, S. America
		Budworm	*Helicoverpa punctigera*	Australia
		Corn earworm	*Helicoverpa zea*	N. America, S. America
		Alfalfa looper	*Autographa californica*	N. America

Alfalfa (Lucerne) Pests and their Management, Table 5 Some pests of alfalfa (lucerne), and locations where they are considered to be damaging (Continued)

Feeding behavior	Primary taxon	Common name	Scientific name	Location
		Lucerne leafroller	*Merophyas divulsana*	Australia
		Alfalfa caterpillar	*Colias eurytheme*	N. America
		Webworms	*Loxostege* spp.	N. America, Europe, Asia
	Collembola	Lucerne flea	*Sminthurus viridis*	Australia, Europe, Africa
	Diptera	Alfalfa blotch leafminer	*Agromyza frontella*	Europe, N. America
Above-ground, sucking	Acari	Redlegged earth mite	*Halotydeus destructor*	Australia
		Clover mite	*Bryobia* spp.	Australia
		Twospotted spider mite	*Tetranychus urticae*	No. America
	Collembola	Lucerne flea	*Sminthurus viridis*	Europe, N. Africa, Australia
	Hemiptera	Pea aphid	*Acythosiphum pisum*	Europe, Asia, Australia, N. & S. America
		Blue alfalfa aphid	*Acythosiphum kondoi*	Mediterranean, Australia, N. & S. America
		Spotted alfalfa aphid	*Therioaphis maculata*	Mediterranean, Australia, N. America, Asia
		Potato leafhopper	*Empoasca fabae*	N. America
		Lucerne leafhopper	*Austroasca alfalfae*	Australia
		3-cornered alfalfa hopper	*Spissistilus festinus*	N. America
		Meadow spittlebug	*Philaneus spumarius*	N. America
		Tarnished plant bugs	*Lygus* spp.	Europe, N. America
		Alfalfa plant bug	*Adelphocoris* spp.	Europe, N. America
	Thysanoptera	Flower thrips	*Frankliniella* spp.	Europe, Asia, N. America
Below-ground	Coleoptera	Clover root curculio	*Sitona hispidula*	Europe, N. & C. America

Alfalfa (Lucerne) Pests and their Management, Table 5 Some pests of alfalfa (lucerne), and locations where they are considered to be damaging (Continued)

Feeding behavior	Primary taxon	Common name	Scientific name	Location
		Alfalfa snout beetle	*Otiorhynchus ligustici*	N. America
		African black beetle	*Heteronychus arator*	Africa, Australia
		Whitefringed beetle	*Naupactus leucoloma*	Australia, S. America
		Small lucerne weevil	*Atrichonotus taeniatulus*	Australia

plants or in litter on the soil, pupate, and emerge as adults in 1–2 weeks. Adults are 5–6 mm long, have a long snout, and have a dark stripe down the back. They are light brown at emergence and darken in several days. The number of generations varies according to climate, but eventually they leave fields for grassy, brushy, weedy areas where they become inactive until the onset of winter.

Damage is caused by the larval stage which feeds on leaves; damage ranges from pinholes to skeletonization of leaves. Adults generally cause minor damage. Peak damage is usually just prior to the first cutting or after the first cutting, as both larvae and adults feed on new growth; this can seriously affect regrowth of the stand. Also, cool, cloudy weather exacerbates damage done by the alfalfa weevil. Cool and cloudy weather conditions slow the regrowth rate of alfalfa, and also increase the daily feeding period of the weevil because both larvae and adults tend to hide under crop residue during bright sunlight and will not actively feed during such periods.

Weevil larvae can be found early in the Spring. It is important to scout for live larvae and injured terminals on the first crop, but also subsequent crops. Sweep net sampling can be used to detect weevil presence. Several species of wasps can be effective in maintaining weevil populations below economic threshold levels. Among the effective parasitoids are *Bathyplectes curculionis* (Thomson), *B. anurus* (Thomson) and *B. stenostigma* (Thomson) (Hymenoptera: Ichneumonidae); *Microctonus aethiopoides* Loan and *M. colesi* Drea (Hymenoptera: Braconidae) *Oomyzus incertus* (Ratzenberg) (Hymenoptera: Eulophidae); *Dibrachoides dynastes* (Forester) and *Peridesmia discus* (Walker) (Hymenoptera: Pteromalidae); and *Anaphes luna* (Girault) (Hymenoptera: Mymaridae). A fungal pathogen, *Zoophthora phytonomi* Arthur (Phycomycetes: Entomophthoraceae), attacks weevil larvae and can control populations in several days, though it is most effective under moist conditions. These biological control agents are extremely effective control measures in all but major outbreak periods. However, when fields show damage on 35–40% of plant tips more than 7–10 days prior to harvest, chemical suppression is often initiated.

Early harvest (first crop) is very effective in killing larvae, and is preferred to chemical control if the planned harvest is less than 7–10 days away. If harvesting is used to control alfalfa weevil, the stubble and debris should be examined closely for adults and larvae, and stems should be examined for feeding signs. It may be necessary to spray stubble, though in many areas producers can avoid insecticide use consistently through timing of harvest.

Root Weevils, *Sitona* spp., *Atrichonotus taeniatulus* (Berg), Others (Coleoptera: Curculionidae)

Root weevils such as clover root curculio, *Sitona hispidula* (Fabricius), in North America; and sitona weevil, *Sitona discoideus* Gyllenhal, small lucerne weevil, *Atrichonotus taeniatulus* (Berg), in Australia, and whitefringed beetle, *Naupactus leucoloma* Boheman in Australia and South America, can be significant pests of alfalfa. Although the adults commonly feed on the foliage, the principal damage is due to larval feeding on the roots of the alfalfa plant.

Eggs are laid in fall or spring, on the soil surface or lower parts of plants. Eggs hatch in the winter or spring. White, legless larvae move into the soil and feed on roots until they pupate. Pupae are found just below the soil surface. Adults emerge in the summer months and live up to a year. The adults are brown or black, blunt-snouted weevils up to about 10 mm long. There is one generation per year. Adults migrate by crawling, and thus infest new areas rather slowly.

The adults feed on alfalfa leaf margins, leaving crescent-shaped notches, and chew on stems and leaf buds of seedlings, but this tends to cause minor loss. Most damage is caused by the larvae. First larval instars feed on root nodules and lateral roots; later instars feed on the taproot. Feeding on the taproot can girdle the plant, resulting in plant death. Such damage also weakens the overall vigor of a stand, perhaps contributing to winter-kill and increased susceptibility to disease.

It is difficult to control larvae because they are in the soil and largely protected from insecticide. Suppression aimed at adults usually requires multiple applications. It is inadvisable to plant alfalfa into a field which has previous ly been infested, to plant into fields previously supporting legume crops, or to seed alfalfa next to established stands.

Blister Beetles (*Epicauta* spp.) (Coleoptera: Meloidae)

There are several species of North American blister beetles that can be of concern in alfalfa. They are a problem not because of their food habits (they tend to feed mostly on blossoms) but because they contain the toxin cantharidin within their bodies. When alfalfa is harvested, if the hay is crimped it may contain crushed blister beetles that may prove toxic to horses that ingest the hay. The most abundant blister beetle in alfalfa fields generally is the black blister beetle, *E. pensylvanica* (De Geer). However, the species that is most toxic is *E. vittata* (Fabricius).

Most blister beetles are recognized by the shape of their body. They are narrow, cylindrical, and soft. The region between the head and wings is distinctly narrower than the wings, and is usually narrower than the head. Most species have one generation per year, although some have two. Blister beetles overwinter as larvae. The adults begin to emerge in the Spring and adults deposit their eggs where grasshopper egg pods may occur, as larvae feed on the grasshopper eggs.

If grasshoppers are not abundant, then blister beetles are unlikely to be abundant. When both are numerous, it is advisable to harvest alfalfa early, before bloom, as this is the only time that beetles are attracted to the crop. There is some yield loss associated with this approach, of course, and an alternative it to treat the crop with insecticides. If insecticide is used, alfalfa should be harvested as soon as possible after the pre-harvest interval expires, to get hay out of the field before it is re-infested. A principal problem with blister beetle management is that the beetles tend to aggregate. Thus, there may be relatively few beetles in field, but a large number in one location, and these may be crushed together and concentrated into one or a few bales of hay. Thus, they are hard to detect by standard sampling methods. When alfalfa hay is purchased for horses, it is advisable to acquire early-crop hay, or hay from areas free of high grasshopper populations. Alternatively, inspection of the hay as it is fed to horses can reveal the presence or absence of beetles.

Potato Leafhopper, *Empoasca fabae* (Harris) (Hemiptera: Cicadellidae)

Potato leafhopper is indigenous to eastern North America. Adults are about 3.5 mm long, wedge-shaped, winged, and green. Nymphs are similar in appearance, but are smaller, yellowish-green to fluorescent green, and wingless. Each Spring, potato leafhoppers migrate north from southern states where they overwinter. Timing of the first and subsequent arrivals in the north is heavily dependent on weather patterns. Adults lay eggs in stems and leaf veins; eggs hatch in 6–9 days in mid-summer. Each generation takes approximately 30–35 days to mature, resulting in several generations.

Adults and nymphs both feed on alfalfa with piercing-sucking mouthparts, sucking plant sap and injecting a toxin into the plant. Damage is called "hopperburn," and is a yellow wedge-shape area beginning at the tips of leaves. The leaves may eventually turn entirely yellow or reddish. Plants may become stunted. Leaf hoppers cause yield loss, reduced nutritional quality of alfalfa, and reduced plant vigor that results in increased winter-kill and slower regrowth of the crop the next spring.

In some regions of the USA, the potato leaf hopper is the worst insect pest of alfalfa, and can cause losses of 80% or more if not controlled. Leaf hoppers are not generally a problem in the first crop in an established stand, but as the population increases, all subsequent crops will need to be monitored for infestation. The characteristic hopperburn will not appear until some yield and quality loss has occurred, so it is important to scout for leaf hoppers weekly on the second and subsequent crops. Scouting may be concluded 7–10 days prior to harvest.

Potato leaf hopper economic thresholds are based on plant height. Scouting is accomplished by sweep net sampling. As an example, following are treatment thresholds recommended for Minnesota, USA.

Average plant height	# adult leafhoppers/ sweep
< 3 inches	0.3
3–7 inches	0.5
8–12 inches	1.0
> 12 inches	2.0

Although the potato leaf hopper has natural enemies, they often get left behind when the adults disperse. Thus, a combination of crop monitoring and insecticide suppression is often the principal management strategy. Chemical control of potato leafhopper is effective, but should not be used if harvest is within seven days of harvest. Cutting will kill a large percentage of nymphs, and will force adults out of the field. Cutting is the control of choice if thresholds are reached within seven days of harvest. Additionally, early harvest may be an alternative to insecticides when thresholds are reached late in the year.

Aphids (Hemiptera: Aphididae)

Several aphids are pests of alfalfa, including pea aphid, *Acyrthosiphon pisum* (Harris); blue alfalfa aphid or bluegreen aphid, *Acyrthosiphon kondoi* Shinji, cowpea aphid, *Aphis craccivora* Koch; green peach aphid, *Myzus persicae* Sulzer; and spotted alfalfa aphid, *Therioaphis maculata* Buckton.

All these aphids are small, measuring 3 mm or less. Their color varies, depending on species. They may or may not be winged. In most climates, in early Spring nymphs hatch from eggs that were laid in the fall; these aphids are all female. Females can reproduce without mating when conditions are favorable, and they do so in Spring and Summer. In the Summer, the entire life cycle takes only a few days. Males appear in late Summer, and mate with females to produce eggs capable of overwintering.

Aphids use piercing-sucking mouthparts to remove plant sap, and prefer to feed on young growth. Aphid feeding can result in stunted or wilted plants. The plants may also turn yellow.

Aphids commonly attain high densities in alfalfa, but in most years natural enemies keep aphid populations at levels that are not economically important. Many natural enemies of pea aphids exist, including green lacewing larvae (Neuroptera: Chrysopidae), damsel bugs (Hemiptera: Nabidae), and parasitic wasps

(Hymenoptera, various families), lady beetles (Coleoptera: Coccinellidae), and disease (fungi).

Plant Bugs (Hemiptera: Miridae)

Several species of plant bugs affect alfalfa, but the most common are tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), and alfalfa plant bug, *Adelphocoris lineolatus* (Goeze). Adult tarnished plant bugs are brown, winged, and 4–6 mm long; nymphs are green, wingless, and the third and subsequent instars have black spots. Adult alfalfa plant bugs are light green, winged, and 7.5–10 mm long; nymphs are green, wingless, and have red eyes. Tarnished plant bugs overwinter as adults; alfalfa plant bugs overwinter as eggs in plant tissue. During the growing season, the entire life cycle takes 20–50 days, depending on temperature. There are two to five generations per year.

Plant bugs suck sap from plants and inject toxic saliva into the plant. They cause leaves to crinkle, plants to be stunted, and flower buds to abort. They are abundant in all but the earliest portions of the season. Although traditionally considered mostly a seed pest, plant bugs also contribute to forage yield reductions. If bugs are abundant more than seven days prior harvest, chemical control may be warranted.

Grasshoppers (*Melanoplus* spp. and *Phaulacridium* spp.) (Orthoptera: Acrididae)

Everywhere alfalfa is grown, grasshoppers and locusts will feed on the crop. However, they are only casually associated with alfalfa, attacking the crop only when abundant. None feed preferentially on alfalfa. In North America, the principal pests are *Melanoplus* spp., and in Australia *Phaulacridium* spp. is the major grasshopper pest. These economically important grasshoppers overwinter as eggs. Populations disperse into cultivated fields or pastures as their populations build through the season. Most egg laying occurs in late summer and fall in production areas; most species prefer uncultivated, grassy or weedy areas, and lay eggs 1–3 cm below the soil surface.

Grasshoppers are generally considered a minor pest except during periods of great abundance, and then they can do great damage. An exception is Australia, where wingless grasshopper has become an increasingly severe pest of alfalfa. Damage has increased in Australia due to widespread cultivation of alfalfa, which is more suitable than grasses for nymphal growth and survival. Grasshopper nymphs and adults damage alfalfa by chewing on leaves from the margin inward in an irregular pattern. Attacks are often on new growth, but will occur on any stage. The margins of fields are most likely to be damaged.

In North America, grasshopper infestations are more severe in warm and dry years. Warm, dry weather immediately following egg hatch favors survival of nymphs, because nymphal growth rates and survival are lower in cool, wet weather. Long, warm autumns prolong the egg-laying season, and result in larger populations in the next growing season. It can take 3–5 years for populations to build to economically important levels. In Australia, drought also is implicated, but mermithid nematodes are a critical element in grasshopper biology. Absence of rainfall, and clearing of drier, higher elevation pasture impedes the ability of the nematodes to parasitize the grasshoppers.

Grasshoppers are naturally suppressed by numerous natural enemies, but when weather conditions favor the grasshoppers their populations increase quickly. The natural enemy population increases as their food supply becomes more available, but the lag in natural enemy abundance can result in crop damage by the grasshoppers. Weedy fence rows, irrigation ditches, and fallow fields are important sources of grasshoppers. Weed populations should be managed, which may require tillage or burning to make these habitats less productive for grasshoppers.

Cutworms, Armyworms and Budworms (Lepidoptera: Noctuidae)

The caterpillars of several moths can become abundant enough to cause significant loss to alfalfa. Among these are the armyworms *Mythimna* spp., *Persectania* spp., and *Pseudaletia unipuncta* Haworth; variegated cutworm, *Peridroma saucia* (Hübner); army cutworm, *Euxoa auxiliaris* (Grote); granulate cutworm, *Agrotis subterranea* (Fabricius); beet armyworm, *Spodoptera exigua* (Hübner); budworm, *Helicoverpa punctigera* (Wallengren), and many others. The important species vary among regions, though they are similar ecologically.

The larvae of cutworms, armyworms, and budworms range in color from greenish-yellow to brownish-black. Larvae are 2–5 cm long at maturity. The wings of the adults vary from tan to dark brown with mottling or stripes. Pupae are 1–3 cm long and are reddish-brown to black in color. There are one to six generations per year. Larvae overwinter in the larval or pupal stage, depending on species.

Larvae feed on stems and leaves of plants, and can limit regrowth after harvest. Larvae will also cut the stems of seedlings. Their occurrence as economic pests is sporadic. Although these insects have many natural enemies, when they are abundant insecticides are the preferred approach to population reduction.

Lucerne Flea, *Sminthurus viridis* (Collembola)

Sminthurus viridis, the lucerne flea or clover springtail, is an insect relative (hexapod) belonging to the order Collembola (the springtails). It is bright green with a roughly spherical body and may swarms in large numbers on living plants, including alfalfa or lucerne, thus the first part of the common name. The second part of the common name was given for its jumping ability and its minute size, not because it is a flea or related to fleas. This species has a patchy distribution in Europe and North Africa, and has been accidentally introduced to Australia, where it is most injurious. It also affects lupine flowers, lentils, beans, and field peas. Immature lucerne fleas consume small patches of foliage, whereas adults consume the entire leaf except for the veins. Early season spraying of insecticide is the most common recommendation to curb their damage.

Mites (Acari)

Mites generally are not major pests of alfalfa, but under arid conditions or along the margins of fields they can be quite damaging. The most important are clover mites, *Bryobia* spp. (Acari: Tetranychidae), and redlegged earth mite, *Halotydeus destructor* Tucker (Acari: Penthaleidae), in Australia, and twospotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae) in North America. They rupture the cells of leaf tissue, imparting a silver or yellow appearance, and reducing yield.

Pest Management in Alfalfa

Alfalfa is an excellent crop for the practice of modern pest management tactics because (i) it is quite tolerant of damage; cosmetic injury is not important; (ii) it is a perennial crop, providing harborage throughout the year for an immense assemblage of insects, including predators and parasitoids; (iii) it is an important crop, so extensive research on the pests have been conducted; (iv) it is amenable to various cultural manipulations, and produces multiple crops over a large portion of the year; and (v) it is a favorite crop for rotations, so there is ample opportunity to integrate its culture with the culture of other crops.

The principal tactics used for alfalfa production include scouting and use of an economic threshold for decision making, natural and classical biological control, cultural control, and chemical control. The economic threshold varies among insect species, geographic locations, crop management practices and economic conditions, but most locations have established such benchmarks for initiating chemical control. A large number of insecticides are registered for this crop, so growers have ample opportunity to select products according to their need and budget. A modest level of host plant resistance apparently exists in alfalfa, and although resistance is effective mostly against aphids, there is also some success with alfalfa weevil and leaf hoppers.

A large number of beneficial arthropods have been moved around the world in an effort to attain biological suppression of invading alfalfa-feeding insects. In some cases this has met with success. For example, alfalfa blotch leafminer, *Agromyza frontella* (Diptera: Agromyzidae), was considered a serious pest when it first invaded the eastern USA, but following release of wasp parasitoids it fell to minor pest status. Similarly, the status of spotted alfalfa aphid, pea aphid and blue alfalfa aphid was affected by importation of beneficial insects. A native entomopathogenic fungus, *Zoophthora phytonomi*, has adapted to the invasive alfalfa weevil and sometimes provides good suppression. Pea aphid is affected by the fungus *Erynia neoaphidis* under favorable weather conditions. Generalist predators such as lacewings, lady bird beetles, nabids, soft-winged flower beetles, big-eyed bugs, and minute pirate bugs are often active in alfalfa, and provide good suppression of aphids, thrips, and also consume eggs and young larvae of caterpillars.

Cultural manipulations are the most important tactics for management of alfalfa pests. In particular, early harvesting can provide acceptable or even nearly complete control of alfalfa weevil, alfalfa blotch leafminer, several caterpillars, aphids, and leaf hoppers because when the crop is cut the insects are exposed to lethal levels of heat and dryness, or the environment becomes so unsuitable that the insects move elsewhere. Crop rotation is most important for root feeding pests, many of which take several years to develop damaging populations. Strip cropping is commonly recommended because the uncut areas retain populations of natural enemies, allowing the beneficial insect to move into newly harvested alfalfa as it regrows and becomes infested with pests. Farmers rarely embrace this approach, however, opting for operational efficiency over economic pest control.

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Alfalfa Weevil, *Hypera postica* (Gyllenhal) (Coleoptera: Curculionidae)

An important defoliator of alfalfa (lucerne).

► Alfalfa (Lucerne) Pests and their Management

Alga (pl., Algae)

An aquatic non vascular plant, often very small in size. Algae can reach pest status when weather and nutrient levels favor its growth, and pesticides may be needed to suppress it.

Alien

An organism that is native elsewhere. These are also referred to as exotic or foreign.

► Invasive Species

Alienicolae

In heteroecious aphids, viviparous parthenogenetic females developing on herbaceous (secondary) host plants.

► Aphids

Alimentary Canal and Digestion

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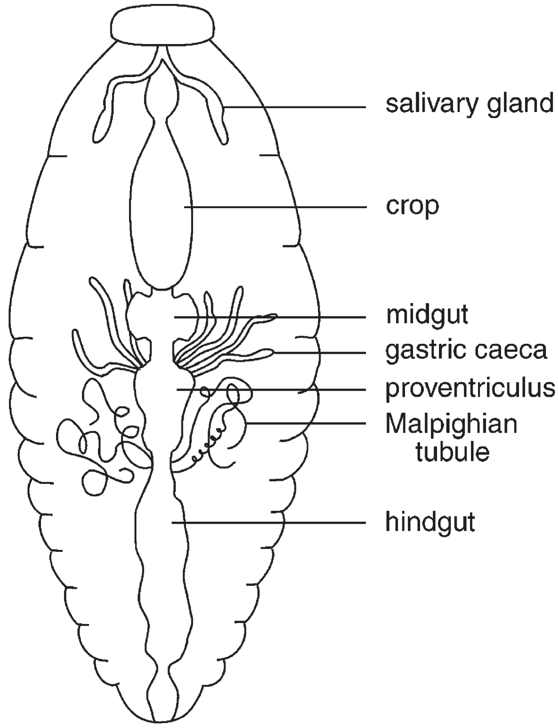
Insects feed upon many different kinds of food, including paper, wood, plant phloem and xylem sap, plant leaves, roots and stems, animal tissues, hair, wool, and vertebrate blood. The alimentary canal (often simply called the gut in much of the literature) evolved to accommodate such diverse foods in a variety of morphological and physiological ways. Thus, there is no “typical” insect alimentary canal just as there is no typical insect. Nevertheless, there are similarities in the structure of the alimentary canal in all insects and nearly all must digest some of the same complex molecules, such as proteins, lipids, and carbohydrates.

In every insect alimentary canal three regions can be identified morphologically and physiologically: the foregut or stomadeum, the midgut or mesenteron, and the hindgut or proctodeum (Fig. 33). One or more of these regions may be greatly reduced in size, or expanded in size, depending upon the feeding behavior of the insect. A cuticular layer, the intima, attached to the epithelial cells, lines the fore- and hindgut regions. The old intima is partially digested and the residue sloughed off into the gut and excreted at each molt, and a new intima is secreted. The midgut does not have an attached cuticular lining, but may have a non-attached peritrophic membrane that separates the food enclosed within from the delicate surface of the midgut cells. If a peritrophic membrane is present, it is often secreted several times each day.

The Foregut

The buccal cavity (mouth), pharynx, esophagus, crop, proventriculus and attached salivary glands comprise the foregut. Secretions from the salivary glands attached near the mouth are swallowed with the food, lubricate the food, and may begin some carbohydrate digestion. In some insects the crop is not a noticeably modified part of the foregut, but often the crop comes off the foregut as a diverticulum. In other insects it is an enlarged portion of the foregut. In opportunistic and possibly irregular feeders such as praying mantids, the crop composes more than half of the alimentary canal, apparently an evolutionary development to store a large amount of food when available and tide the mantid over periods when prey is scarce. Some insects (for example, many orthopterans) regurgitate enzymes from the midgut into the crop, and these enzymes, along with salivary secretions, digest food in the crop. The digested food components still enter the midgut to be absorbed, and there is no evidence that the crop ever secretes



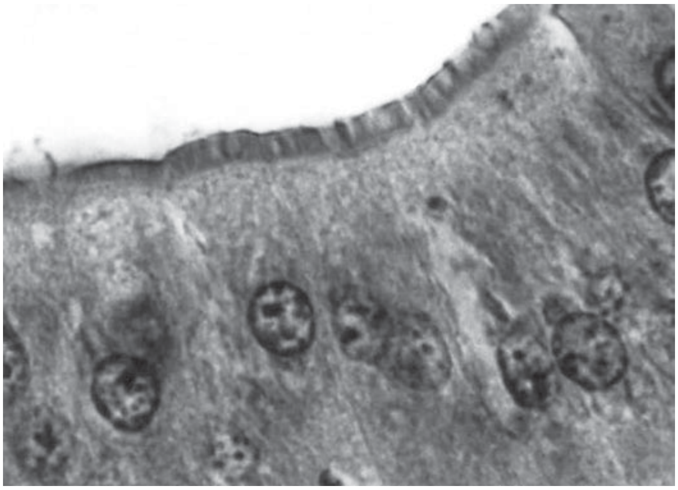
Alimentary Canal and Digestion, Figure 33 A generalized drawing of the alimentary canal in a cockroach to show the major divisions of the canal. Many variations occur in the overall structure of the alimentary canal in insects, and this is not intended to suggest that the cockroach alimentary canal is typical of insects.

enzymes itself. The cuticular intima creates a barrier even against the absorption of water from the crop. The proventriculus controls the entry of food into the midgut in liquid feeders, but in many insects it is modified into a grinding apparatus with hard, sclerotized ridges and spines, and heavy musculature for breaking and tearing the food into smaller particles.

The Midgut

The midgut in most, but not all, insects is the main site for digestion, absorption, and secretion of digestive enzymes. The epithelium is a single layer of cells, but several types of cells occur in some insects. The most common cells are tall, relatively narrow ones called columnar or primary cells by various authors. They have extensive microscopic microvilli on the apical or lumen surface (Fig. 34) and extensive invaginations of the basal cell membrane, features that greatly increase the surface area on both sides of the cell over which secretion and absorption occur. The columnar cells are the primary cells that secrete digestive enzymes and absorb digested products. In all insects that feed as adults and live for days or weeks, there are small regenerative cells distributed at the base of the columnar cells, or sometimes clustered together in nidi (nests). The regenerative cells grow into mature epithelial cells to replace cells worn out or those that disintegrate to release digestive enzymes. Midgut cells may be completely replaced every few days in insects that live longer lives. Gastric caeca, small finger or sac-like diverticula from the midgut, often arise at or near the origin of the midgut, but may be located at various points along the midgut. The caeca appear to secrete digestive enzymes and may be important in absorption of digested products.

The midgut does not have an attached cuticular lining on the surface of the cells, but midgut cells in the majority of insects secrete a thin membrane composed of chitin and protein, the peritrophic membrane, that surrounds the food and shields the delicate microvilli of the midgut cells from contact with potentially rough and abrasive food particles. Although the peritrophic membrane is thin, varying from 0.13 μm to about 0.4 μm thick, it also is thought to make it more difficult for viruses, fungi, bacteria, and protozoans to get to the surface of the midgut cells where they might be able to enter the cells and create an infection. Some insects produce several peritrophic membranes per day, each encasing the one before it, perhaps increasing protection from random breaks or punctures by larger food particles, and thus affording more protection for the midgut



Alimentary Canal and Digestion, Figure 34 **A brush border of microvilli on the lumen surface of midgut cells in a mole cricket.**

cells from possible fungi, parasites, viruses, and bacteria ingested with the food. A peritrophic membrane occurs in living representatives of some of the earliest insects to evolve, and it is believed to have evolved very early in a generalist scavenger feeder in which protection of midgut microvillar surfaces from food particles, sand, or other hard substances coincidentally ingested was likely to be important. A peritrophic membrane is present in many insects that do not feed upon rough or solid food, such as some blood feeders (but not all blood feeders), and in adult lepidopterans that take flower and plant nectars. Although the peritrophic membrane is not present in all groups of insects, like other gut features, it has been conserved over long evolutionary time, lending support to views that it has multiple functions, especially protection from disease invaders and may even have properties that could bind toxicants and limit their access to cells.

Absorption of digested food substances has not been studied in most insects, but one mechanism has been partially elucidated for absorption of amino acids derived from protein digestion in larvae of Lepidoptera. Interspersed among the tall columnar cells lining the midgut in larvae of Lepidoptera (and some other groups of insects as well) are cells shaped much like a goblet and called, appropriately enough, goblet cells. The apical cell membrane of the goblet cavity has metabolic machinery that uses energy derived from splitting ATP to push or pump protons (H^+) into the goblet cavity. A different set of machinery in the goblet cell membrane, an antiporter mechanism, reabsorbs the protons and simultaneously secretes potassium ions into the goblet cavity. The net result of the secretion of potassium ions is that a strongly alkaline midgut (a midgut pH as high as pH 8 to about 11) is produced, and a high voltage (up to 240 mV in some reports) is created between the gut lumen (positive) and the interior of cells lining the gut. The voltage created by the pump enables an absorptive mechanism in membranes of columnar cells to reabsorb K^+ and amino acids from protein digestion. Thus, potassium ions are recycled between the epithelium cells and the gut lumen and seem to play a major role in amino acid absorption. The high midgut pH may provide plant feeding insects some protection against tannins that are common in the food plants of phytophagous insects. Tannins can complex with an insect's own enzymes and proteins in the food, and may result in reduced digestion and absorption. Many details and the precise metabolic components in the cell membrane that support and enable these secretory and absorptive mechanisms remain to be elucidated, but what is already known emphasizes the complexity of insect digestive functions.

The Hindgut

The hindgut is not only a posterior extension of the alimentary canal, but it also plays a major role in excretion through secretion of some substance into the lumen, and reabsorption of useful substances such as ions, water and some nutrients from the Malpighian tubule effluent. The Malpighian tubules typically arise at the origin of the hindgut (but exceptions do occur) and pass relatively large volumes of an ultrafiltrate of hemolymph components minus proteins into the beginning of the hindgut. The cuticular lining on hindgut cells is thinner and has larger pores than the lining in the foregut, permitting reabsorption of water, some ions, and useful metabolites that are returned to the hemolymph. In most terrestrial insects, water conservation is vital to life, and the hindgut must conserve the water that the Malpighian tubules flush into the hindgut. Waste products such as undigested food material (cellulose, for example, which most plant-feeding insects cannot digest and use), uric acid, and other allelochemicals picked up from the food are concentrated in the rectum and eventually excreted. The hindgut secretes some molecules into the lumen for excretion. Experimental evidence indicates that secretion and selective reabsorption helps regulate pH of the hemolymph in some insects. Specialized cells, the rectal papillae and rectal pad cells, in the rectum of many insects have characteristic ultrastructure and physiological mechanisms typical of highly reabsorptive cells. Water conservation by the rectum results in the relatively dry frass or fecal pellets characteristic of many terrestrial insects.

The highest degree of specialization in the hindgut occurs in those insects that digest cellulose, such as termites. In termites, the hindgut is usually divided into several chambers harboring either bacteria or protozoa that secrete all or part of the cocktail of enzymes needed to digest cellulose. Glucose, liberated from cellulose digestion, may be fermented by the resident microorganisms, with the end products being short chain fatty acids (principally acetic acid) that can be absorbed by the termite and used as an energy source. Some termites release methane, a greenhouse gas, from the metabolic activities of their microorganisms, but whether this is a significant natural source of methane is a topic of debate by various scientists.

Digestive Enzyme Secretion

Midgut cells secrete and release digestive enzymes in several ways. They may enclose digestive enzymes in small vesicles surrounded by a membrane and then release the enzymes into the alimentary canal by fusing the vesicle membrane with the cell membrane. In some insects, parts of the cell (some of the microvilli) or the entire midgut cell may disintegrate and release enzymes into the gut lumen. Of course, when the entire cell breaks down, the cell must be repaired or replaced. Replacement occurs through the growth of the regenerative cells.

Extraoral digestion (digestion outside the insect body) occurs in some insects, including seed feeders and some predatory insects. By injecting enzymes from the salivary glands and midgut into the food source (animal or plant material) and then sucking back the liquefied digestion products, insects can utilize very high percentages of the nutrient value of the food source. Some insects reflux enzyme secretions and partially digested products by repeatedly sucking up and reinjecting the liquefied juices into the food. Refluxing mixes the secretions and fluids and extends the effective life of the digestive enzymes, and is particularly effective when the food contains a limiting boundary, such as the shell of a seed or the cuticle of an insect that acts as a container for the liquefying body contents.

Carbohydrate Digestion

Starch and sucrose are the typical carbohydrates that insects digest from plant food, and glycogen and various sugars are present in animal tissue eaten by carnivorous insects. Cellulose, the major complex polysaccharide present in plant tissue, cannot be digested by most insects. Carbohydrate digestion begins with the action of α-amylase, an enzyme present in the salivary gland secretions of many insects. Amylase works best at slightly acid pH, and hydrolyzes interior glucosidic linkages of starch and glycogen, resulting in a mixture of shorter dextrins. In the midgut α-glucosidase and oligo-1, 6-glucosidase (isomaltase) digest smaller dextrins, releasing glucose. Many insects also have one or more α- or β-glycosidases that digest a broad range of small carbohydrates, such as maltose, sucrose, trehalose, melezitose, raffinose, stachyose, melibiose, raffinose, and stachyose. Some insects can secrete trehalase in the gut to digest trehalose, the principal blood sugar typically in high concentration in insects. β-glucosidase, β-galactosidase, and β-fructofuranosidase act upon various substrates to release simple sugars in the gut. An insect usually has only a few of these carbohydrate digesting enzymes, depending upon the food it eats. For example, *Apis mellifera* honeybees have several α-glucosidases or sucrases that act rapidly upon sucrose, usually the principal carbohydrate in the nectar taken by honeybees. They utilize the resulting glucose and fructose for an immediate energy source and for making honey. Termites, some beetles, a few cockroaches, and woodwasps in the family Siricidae digest cellulose with aid (usually) from fungi, bacteria, or protozoa, which produce some or all of the complement of three enzymes necessary for cellulose digestion.

Lipid Digestion

The major storage forms of lipids (fats) in both plants and insects are triacylglycerols, esters of fatty acids with glycerol. Midgut cells, and in some cases symbionts, secrete lipases, which are enzymes that hydrolyze triacylglycerols and release fatty acids and glycerol. Amino acids, proteins, and fatty acylamino complexes act as emulsifiers in the midgut of some insects facilitating the digestion of fats. The glycocalyx layer, a viscous protein and carbohydrate complex that often lies on the surface of the microvilli, probably aid in emulsifying fats and in promoting contact between lipases and triacylglycerols. Fatty acids released from triacylglycerols are resynthesized into the insect's own triacylglycerols and stored in fat body cells. Immature insects typically store relatively large amounts of triacylglycerols, and use some of the released fatty acids during pupation and for egg development. Some insects, for example Orthoptera, Lepidoptera, and some aphids, mobilized fatty acids rapidly enough to use fatty acid metabolism to support flight, but other groups such as Diptera and Hymenoptera cannot release fatty acids from the fat body and transport them to the flight muscles rapidly, and so they only use carbohydrates for flight energy. They still can use lipids during pupation, and for other metabolic processes that occur more slowly.

Protein Digestion

All animals must have a pool of amino acids available for synthesis into proteins, and for repair of tissues and organs. Most animals, including insects, get their amino acids from digestion of dietary proteins. Within insects as a group, there are several different types of protein digesting enzymes, some of which act at acid pH, others at slightly alkaline pH, and some at highly alkaline pH. Usually a particular species will have several different proteinases, but no insect is known to have both an acid-effective proteinase and an alkaline-effective proteinase. The pH of the alimentary canal is important to the action of any digestive enzyme, and no insect is known to have an alimentary canal that is strongly acid in one part and strongly alkaline in another part.

Proteinases are classified broadly as serine, cysteine, aspartic acid, and metallo-proteinases depending upon the amino acid or metal at the active site of the enzyme. Trypsin and chymotrypsin are two endoproteinases with alkaline pH optima (about pH 8) that are common in many insects and which attack large proteins internally at the linkage between certain amino acid, thus breaking the protein into smaller polypeptides. Most insects appear to have several types of exopeptidases that remove the terminal amino acid from a protein or peptide chain. Thus, through the concerted action of both types of digestive enzymes, a protein can be completely digested with release of its component amino acids. Cysteine- and aspartic acid-proteinases have mildly acid pH optima, and are called cathepsins by some authors. All members of a taxonomic group may not have the same type of proteinases. Many beetles have cysteine proteinases most active at slightly acid pH, while some scarabeid beetles secrete serine-proteinases that act at the high midgut pH typical of these insects, and they have no detectable cysteine-proteinases. Lepidoptera typically secrete trypsin-like enzymes active at alkaline pH.

One defense mechanism that has evolved against herbivory in many plants is the presence of proteinase inhibitors, some of which inhibit serine proteinases while others act upon cysteine proteinases. Experimentally, it has been shown that some insects secrete multiple trypsin enzymes (isozymes of trypsin) and others just secrete larger amounts of the same few isozymes after consuming a trypsin inhibitor. This counter action by the insect probably allows some protein digestion to escape ingested inhibitors, but transgenic plants designed to have proteinase inhibitors have been tested and proven to have adverse effects upon the growth of some insects.

Absorption of Digested Products

Few details are known about the absorption of digested products by insects. In many vertebrates, glucose absorption from the alimentary canal requires an active mechanism involving ATP to supply the energy. In those insect that have been studied, glucose from digestion of carbohydrates is rapidly absorbed passively by a process known as facilitated diffusion, and involvement of ATP is not necessary. Fat body cells on the hemolymph side of the gut rapidly synthesize absorbed glucose into the disaccharide trehalose, keeping the hemolymph concentration of glucose low in most insects. Consequently, even low concentrations of glucose in the gut have a favorable diffusion pathway to the hemolymph and continue to be absorbed passively. In larvae of a few lepidopterans that have been carefully studied (*Manduca sexta*, *Philosamia cynthia*, *Bombyx mori*), amino acids are actively absorbed by transport proteins in the apical membranes of midgut columnar cells. Energy for absorption comes from the high K^+ concentration in the gut lumen and high transepithelial potential created by the proton-ATPase pump active in midgut goblet cells. The transport proteins in these membranes show strong specificity for particular amino acids, and transport systems for at least six different amino acids are known, and transport systems for other amino acids probably will be discovered. In the Colorado potato beetle, *Leptinotarsa decemlineata*, transport proteins for leucine and tyrosine have been demonstrated in midgut tissue.

Gut pH

The pH of the alimentary canal is highly variable in different species of insects. The pH of a gut segment influences the action of enzymes secreted into or carried with the food into the gut, influences solubility and toxicity of toxins and plant allelochemicals, and may alter the population of gut microorganisms. In most insects, the crop has little or no presence of buffering agents and tends to be slightly acidic, a factor favoring carbohydrate digesting enzymes. Larvae of Lepidoptera and Trichoptera tend to have a very high midgut pH, varying from about 8 to 10, promoted by goblet cells that secrete potassium and bicarbonate into the lumen of the midgut. They have protein digesting enzymes that are favored by the high pH, and the high pH may afford some protection from tannins and other allelochemicals that they ingest with their plant food.

Illustrative Examples of Diversity in Food, Form and Function of the Alimentary Canal

The following examples are not intended to be a comprehensive review of foods, and alimentary canal structure and physiology, but will merely highlight interesting diversity.

Opportunistic feeders may have evolved modifications to capture and store food when available, and thus survive lean periods when food is not available. For example, the foregut of the praying mantis, *Tenodora sinensis*, is long and wide, and occupies nearly the entire length of the body, apparently an adaptation for storage of prey when it can be captured. The midgut, eight gastric caeca, and hindgut are compressed into the last three abdominal segments. Probably much of the digestion occurs in the posterior part of the crop with enzymes passed forward from the small midgut.

Considering the universal presence of cellulose in plant tissues, relatively few insects evolved the ability to use cellulose as a source of nutrients.

Termites, some beetles, a few hymenopterans, and a few cockroaches do use cellulose as a carbohydrate source. The hindgut of termites is highly specialized for housing gut microbiota that provide the cellulase enzymes needed to digest cellulose, although there is some evidence that certain termites may be able to produce some or all of the several enzymes necessary to completely digest cellulose. Gut variation exists among the castes in a colony; for example, soldiers in the family Rhinotermitidae are fed liquid food by the worker caste, and do not have to digest cellulose so they have reduced gut structure. The workers are responsible for colony construction and nutrition, and they have highly evolved hindgut chambers to hold various types of microbiota. Termites hatch without their gut microbiota, and lose most of their gut symbionts at each molt, but they become reinfested by feeding upon fluid and excreta from older nymphs. Termites in the family Termitidae have symbiotic bacteria in the hindgut, while termites in some other families have flagellate protozoans as well as bacteria in a multi-compartmented hindgut, and they get some or all of their cellulase(s) from their symbionts. Some termites, the Macrotermitinae, cultivate fungus gardens in their underground nests and get their cellulases from the conidiophores of the fungus. Symbionts in the hindgut of some termites can capture atmospheric nitrogen in an organic form, which is probably quite important to many termites because their diet of wood is relatively low in proteins. Some fungus-growing termites convert some of the protons (H^+) and carbon dioxide from the initial fermentation of glucose into methane (CH_4), and some investigators have suggested that termites are a significant environmental source of methane, a greenhouse gas.

Larvae of the woodwasp (Hymenoptera, Symphyta, Siricidae, genus *Sirex*) acquire cellulase and xylanase from fungi ingested with the wood on which they feed. Larvae of cerambycid beetles and of some other beetles feed upon wood in down or dying trees; they generally have long life cycles because wood is so nutrient poor, especially protein poor. Fungi growing in the dead wood and ingested by the larvae may provide additional nutrients and/or enzymes for digesting the wood.

Hemiptera take xylem or phloem sap, both of which are poor in amino acids and protein, but usually rich in sucrose (150 to more than 700 mM). They typically excrete a copious, dilute fluid, and in some, such as aphids, the fluid contains so much sugar that it is called honeydew. They have to ingest large volumes of fluid to get the amino acids, and then they have to get rid of the excess water and sucrose. A characteristic evolutionary feature of the gut in Hemiptera is the filter chamber in which a loop of the hindgut is in direct contact with part of the foregut and a great deal of the ingested fluid diffuses directly into the hindgut from the foregut without passing through the midgut. This, of course, causes loss of some amino acids and other components that may be needed, but water and sucrose, both of which are in excess of needs, are the major components lost. The filter chamber is able to concentrate gut fluid up to 10-fold in some xylem feeders (Cicadoidea and Cercopoidea), but only about 2.5-fold in members of the Cicadelloidea, which are phloem feeders. Xylem feeders probably need to concentrate xylem fluids more because of the lower amino acid content (3–10 mM amino acids per liter in xylem fluid) than do phloem feeders (15–65 mM amino acids per liter in phloem fluid).

Pre-oral digestion with enzymes secreted into the prey occurs in many of the predacious beetles. Seed feeders also employ pre-oral digestion by injecting salivary secretions and possibly regurgitated midgut enzymes into the seed, allowing these to liquefy part of the seed, and then sucking the nutrients and enzymes back. Pre-oral digesters often reflux the liquefied contents by repeatedly imbibing and then reinjecting the mixture of enzymes and digested nutrients into the seed. Refluxing likely conserves enzymes longer, gives them more opportunity to function, and allows the insects to use more of their potential food.

In honeybees and some other related hymenopterans, the midgut is closed off from the hindgut by a plug of cellular tissue during larval development, and any food that cannot be digested and absorbed into the body must remain in the midgut. Just before pupation the connection between midgut and hindgut is opened, and accumulated undigested residue, such as the shells of pollen grains, is excreted into the cell. Adult honeybees clean the cell and the larva pupates inside the cell.

Nectar taken by male and female mosquitoes is stored in a large, sac-like crop that is a diverticulum from the foregut, but blood meals taken by the females are passed directly into the midgut for the beginning of digestion. The midgut is differentiated functionally into an anterior and a posterior region. The anterior part secretes carbohydrate digesting enzymes, and nectar components are digested as fluid from the crop and is passed into the anterior midgut. This arrangement keeps possible trypsin inhibitors that may be present in nectar away from the site of protein digestion, which occurs in the posterior midgut. Simple sugars resulting from digestion, or those already in the nectar, are absorbed in the anterior midgut. The posterior midgut cells secrete trypsin-like enzymes and protein (blood) digestion and absorption occur in the posterior midgut. The posterior midgut cells, more so than anterior midgut cells, have extensive microvilli and basal infoldings characteristic of secretion and absorptive processes. The midgut cells in this region get stretched by the large volume of blood that a mosquito takes if it is allowed to feed to repletion. Consequently, the cells have several types of connecting structures (desmosomes) between cells to help hold them together and prevent excessive leaking of materials in or out between cells while they are stretched.

Larvae of Lepidoptera have a very short foregut, a large, long, relatively straight midgut, and a short hindgut. There is no storage or digestion in the short, nearly vestigial foregut. Nearly all lepidopterous larvae are phytophagous feeders, and the gut modifications appear to be an adaptation to pass food quickly into the long midgut so that digestion can begin. Feeding is nearly continuous when plenty of food is available, and larvae may ingest more than their body weight in food daily. Food moves rapidly through the relatively straight gut and frass droppings are frequent in phytophagous caterpillars. Because the larval and adult forms of Lepidoptera have very different life histories and food habits, the adult gut is quite different from that of the larva. Many adult Lepidoptera feed only upon nectar, which is stored in the crop and slowly released into the midgut for digestion to simple sugars. Some adult Lepidoptera have vestigial mouthparts and do not feed at all; they survive and (females) produce eggs at the expense of body substance, and they generally live only a few days. An unusual food utilized by *Tineola bisselliella* larvae (clothes moth) is wool, and larvae have a very strong reducing action in the midgut that breaks disulfide bonds between adjacent loops of the proteins, causing the wool proteins to lose their three-dimensional shape and unfold. This allows more access for protein digesting enzymes.

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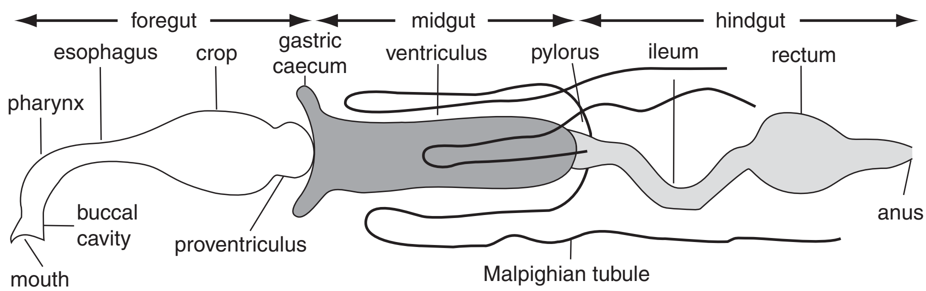
Alimentary System

The alimentary system (canal) is a system of tubular structures that takes in food at the mouth, stores the food, fosters digestion and absorption of nutrients, and allows excretion of waste materials from the rectum. It is conveniently divided into the foregut, midgut, and hindgut (Fig. 35).

► Alimentary Canal and Digestion

► Foregut



Alimentary System , Figure 35 Generalized insect alimentary system (adapted from Chapman, The insects: structure and function).

► Midgut
► Hindgut

Alinotum

The notal plate of the meso- or metathorax in a pterygote insect.
► Thorax of Hexapods

Alitrunk

The portion of the thorax to which the wings are attached.
► Thorax of Hexapods

Allatostatins

These are neuropeptides from neural and non-neural tissues that affect the corpora allata, inhibiting production of juvenile hormone. They likely have other effects as well, but they are still relatively unknown (contrast with allatotropins).
► Juvenile Hormone

Allatotropins

These are neuropeptides from neural and non-neural tissues that stimulate the corpora allata, resulting in synthesis of juvenile hormone. They likely have other effects as well, but they are still relatively unknown (contrast with allatostatins).
► Juvenile Hormone

Alleculidae

A family of beetles (order Coleoptera). They commonly are known as comb-clawed beetles.
► Beetles

Allegheny Mound Ant, *Formica exsectoides* (Hymenoptera: Formicidae)

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The Allegheny mound ant, *Formica exsectoides* Forel, is a common mound-building ant of the northeastern and central United States. Workers are approximately 3/8 inch long (1 cm) with a reddish-tan head and thorax, and a dark brown abdomen. In suitable habitat, *F. exsectoides* will form dense populations, their presence easily discernible due to conspicuous mound-type nests which can be as large as 15 feet (4.6 m) in diameter and 4 feet (1.2 m) high. At one site near Altoona, Pennsylvania, researchers counted more than 30 large mounds per acre. Despite the conspicuous nature of *F. exsectoides* nests and its wide geographic range, relatively few papers concerning this species have been published since H.C. McCook's first paper in 1877.

Nests tend to be clustered in the habitat (Fig. 36). Nests in each cluster often will share foraging trails and resources. Although there is little aggression between workers from different nests or nest clusters, the workers still show fidelity to a home nest. Nests of *F. exsectoides* have multiple queens (polygynous) although there is tremendous variation in the number of queens per mound. Over 1,400 queens were reported in one mound, but that is probably an anomaly. Most mounds probably contain fewer than 20 queens. Due to the large number of queens, the reproductive output of a nest can be prodigious resulting in large numbers of workers in a colony. More than 250,000 workers have been found in some nests. Reproductive forms (alates) are present in the nests from mid-summer until early fall. Activity of the ants is related to ambient conditions but, in general, workers are active from late March until November. *Formica exsectoides* are generalist predators, scavengers and collect honeydew from symbiotic hemipterans.

Habitat has a significant effect on physical characteristics of *F. exsectoides* nests. Forest nests tend to be significantly larger in height, width, length, nest footprint and volume than nests in meadows. In general, the nests are round, but it is not uncommon to find elongated nests that are orientated to the sun. The shape of a nest and its orientation may help the ants to maintain a relatively constant internal temperature and relative humidity.

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Allele

One of two or more alternative forms of a gene at a particular locus. If more than two alleles exist, the locus is said to exhibit multiple allelism.

Allelochemic

A non-nutritional chemical produced by one species (often a plant) that affects the growth, health, or behavior of another species (often an herbivore).

► Allelochemicals

Allelochemicals

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For thousands of years insects and plants have been locked in a battle for which survival is the ultimate prize. For insects, plants constitute food sources for growth and development, and in some cases, sites for reproduction. On the other hand, plants attempt to counter insects feeding on their tissues (herbivory) so that their own vigorous growth and development will occur and lead to reproductive success. The consequences of this warfare are great and for humankind the outcomes of these battles may be of major economic significance in terms of the production of various foods. The welfare of various human populations can be threatened if hordes of ravenous insects consume specific crops that are the mainstays of these populations. But plants do not take this "lying down." Over thousands of years, plants have done everything possible to make life miserable for insects. On the other hand, insects have returned the favor many times over. In recent geological time, plants and insects have changed their "spots" (plant-feeding strategies), resulting in an incredible point-counterpoint relationship of these organisms that is characterized by some remarkable developments.

As far as nutrients are concerned, different kinds of plants (species) are fairly similar and can provide an insect herbivore with the basic nutrients required for growth and development. These compounds (chemicals) are called primary compounds because they are required for the insect's growth, development, and reproduction. All insects require these compounds and in theory they should be readily available from a wide variety of plant species. But most species of insects, rather than feeding on many different kinds of plants, limit their plant menu to a relatively small number of plant species (monophagy), most of which are related. Significantly, the limited preferences that insects have for their food plant species are due to non-nutritive compounds that usually vary from one plant group to another. These compounds are not related to the primary compounds identified with growth and development, and it is apparent that these plant-derived compounds (allelochemicals) generally have functions related to other species of organisms. These compounds are obviously not primary compounds but rather secondary compounds (non-nutritive) whose manufacture has been described as secondary metabolism. Indeed, these allelochemicals appear to be responsible for both the associations and non-associations that insects have with specific groups of plant species. In essence, it would be no exaggeration to state that the host-plant preferences of insects really reflect the ability of an insect species to either tolerate, or be repelled by, an allelochemical. Allelochemicals are not mysterious compounds but rather are a very important part of the everyday world, especially in terms of human food preferences. In a sense, the strong food preferences exhibited by insects are not so different from those of humans, with one striking exception. Many insect species are "locked in" to specific food plants, and these insects will reject a foreign plant species and die in the absence of their normal food plant. On the other hand, there is little evidence that human beings will subject themselves to starvation if their favorite foods are not readily available.

A World of Allelochemicals

Fruits and vegetables possess characteristic odors and tastes that create desire (preference) for these foods. Significantly, these tastes and smells are not identified with the primary compounds responsible for plant growth and development, such as sugars, fats, and proteins. Therefore, the plant has invested in producing a variety of chemicals that will not help it grow or reproduce. While an onion may possess a distinctive odor and taste for both insects and humans (not necessarily the same odor and taste for both), this fact hardly justifies the onion spending its energy and resources to produce an onion fragrance. On the other hand, if the taste and odor of onions combine to make this vegetable distasteful and repellent to most plant-feeding insects, then these allelochemicals perform a very vital function. In essence, it is generally believed that these secondary compounds are responsible for protecting plants from herbivores and possibly pathogens as well. A brief examination of some well-characterized allelochemicals offers a means of examining these compounds as agents of defense both as toxins and as repellents.

Oleander, which has a very limited number of herbivores, is extremely toxic because of the presence of allelochemicals that are somewhat related to cholesterol. The odor of the plant probably constitutes an early-warning system that makes potential herbivores aware of the danger of feeding on this plant. The same can be said for the tobacco plant which, like oleander, does not have too many insect herbivores. Leaves of the tobacco plant are quite toxic, but in some South American populations young children become addicted to the nicotine in the leaves before they are ten years old. Nitrogen-containing compounds (alkaloids) produced by opium poppies are powerful repellents for a wide range of insect species, and there is no doubt that compounds such as morphine and heroin, which are powerful human narcotics, were evolved to deter herbivores rather than to function as narcotics for humans.

Alkaloids such as nicotine have been adapted to function as insecticides, and a variety of plant products such as derris, rotenone, ryania, and sabadilla are also used as insecticides in different cultures. In some cases, allelochemicals such as prunasin in cherry leaves cause poisoning in livestock. Not to be outdone, humans have frequently utilized the alkaloid strychnine to murder people. However, it would be a mistake to lose track of the fact that, human abuses notwithstanding, these allelochemicals were evolved as plant protectants long before humans appeared. Obviously, allelochemicals do not provide plants with absolute protection against herbivores. Indeed, probably all plants containing allelochemicals are fed upon by insects, and in many cases these herbivores are only found on a limited number of host plant species. For example, monarch butterfly caterpillars are limited to the milkweed species. Bark beetles limit their attacks to pines and related conifers, developing in environments that are rich in toxic turpentines. These insects have breached the chemical defenses of their hosts, and in so doing, they have "captured" specific kinds of food plants that are either repellent or highly toxic to most other species of insects. Guaranteed these "forbidden fruits," these herbivores should have to share their food resources with very limited numbers of competitors. Barring an ecological disaster does not devastate the populations of their host plant species, this specialization should have much to recommend it. On the other hand, many insect species choose a lifestyle which is characterized by feeding on a variety of unrelated plant species.

Insects like the monarch butterfly and bark beetles that are restricted to a limited number of related plant species are referred to as specialists.

These herbivores have become resistant to the toxic effects of their host plant allelochemicals, and in many cases they appear to be completely immune to the plant toxins they ingest. In the case of monarch caterpillars feeding on milkweeds, it has been demonstrated that these larvae actually grow more rapidly on milkweed plants containing the highest concentration of toxins.

Indeed, allelochemical concentrations may be generally quite high, often averaging 5–10% of the dry weight of the plant. By contrast, plant-feeding generalists feed on a wide range of plant species, often unrelated. However, in general, these herbivores select plant species in which the concentrations of allelochemicals are not too high, enabling them to process low levels of a wide variety of plant toxins.

The immunity of specialists to the toxic effects of the allelochemicals in their diets demonstrates that for these insects these compounds can no longer be considered poisons. Surprisingly, the basis for this important allelochemical resistance, which has great economic significance, was only understood about thirty years ago.

Sequestration and its Consequences

Insects such as the monarch butterfly store compounds in their tissues that render them unpalatable to predators. These compounds, the cardenolides, were ingested by the larvae from their milkweed food plants, and retained in their bodies into the adult stage. The storage of these milkweed compounds is called sequestration, and constitutes a widespread phenomenon among specialists feeding on allelochemical-rich plants. In a sense, sequestration represents the insect's success in utilizing the plant's chemical defenses for its own purposes. Indeed, sequestration can be regarded as a form of detoxication since potentially toxic compounds are removed from the circulation and stored in the tissues.

Sequestration has been detected in at least seven orders of insects including species of toxic grasshoppers, aphids, lacewings, beetles, wasps, butterflies and moths. In general, these insects are brightly (= warningly) colored, a characteristic described as aposematic. Armed with the toxins from their food plants, large insects such as brilliantly colored grasshoppers move very slowly, as if to advertise their poisonous qualities to the world. Obviously the term toxic is relative, since these insects routinely sequester these allelochemicals during normal feeding. However, since these specialists are physiologically adapted for ingesting these compounds, their ability to tolerate these allelochemicals is really not surprising. On the other hand, non-adapted species (e.g., predators) would certainly encounter toxic reactions if they ingested these toxic plant products.

The fates of allelochemicals, which are usually present in mixtures, are not at all predictable after ingestion by an adapted herbivore. Although many compounds are sequestered immediately after ingestion, others may be metabolized before being stored, or even eliminated after being metabolized. In other cases selected allelochemicals in a mixture may be absorbed and sequestered whereas other compounds in the mixture may be eliminated immediately. An examination of the options for initially processing ingested allelochemicals emphasizes the versatility of specialists in treating the toxic compounds produced by their food plants.

Sequestration of Insect Toxins by Vertebrates: A Significant "Allelochemical" Phenomenon

It has become evident that the allelochemical relationship of insects and plants is paralleled by a similar relationship of amphibians and insects. It is now recognized that the sequestration of ingested toxic insect compounds by vertebrates differs little from this phenomenon in insect herbivores and plants. In essence, a variety of insect toxins is sequestered by amphibians and these compounds have similar protective functions for frogs and insects (see *Allelochemicals as phagostimulants*). Frogs exploit insect allomones (defensive compounds) as if they were animal "allelochemicals," and it seems worthwhile to emphasize this congruency in examining the scope of allelochemistry.

Frogs in the genus *Dendrobates* contain mono-, di-, and tricyclic alkaloids which are clearly of ant origin. The alkaloids, termed pumiliotoxins, appear to be products of ant species in the genera *Brachymyrmex* and *Paretrechina* and constitute the only known dietary source of alkaloids of these frogs, not unlike the specialist insects feeding on narrow plant diets enriched with allelochemicals. The same phenomenon has been described for the myrmicine ant *Myrmicaria melanogaster* which synthesizes ten alkaloids. Some of these alkaloids have previously been identified in a dendrobatid frog and a toad.

Neurotoxic steroidal alkaloids, the batrachotoxins, have been isolated from New Guinea birds in the genera *Pitohui* and *Ifrita*. These compounds are among the most toxic natural substances known, and they are not produced by captive birds, suggesting a dietary source. Recently, the batrachotoxins were identified in beetles in the genus *Chloresine* (Melyridae) which are normally fed on by the bird species. Since the genus *Chloresine* is cosmopolitan, it is the possible source of some of the avian alkaloids found in birds in different areas.

Vertebrate sequestration of alkaloids from insects has only recently been explored. Clearly this chemical storage has a common denominator with sequestration of alkaloids by insects (see *Allelochemicals as pheromonal precursors*) and should be examined as a paradigm of comparative physiology. Clearly, insects are pivotal to both systems, either as food for vertebrates or food for insects, with sequestration the major common feature.

Initial Processing of Allelochemicals by Specialists

Once an adapted insect has ingested an allelochemical, a menu of options is available for processing it. An insect species may utilize a variety of adaptive strategies for processing a single compound that is characteristic of the host plant defense.

Immediate Allelochemical Excretion

Some insects essentially fail to absorb ingested allelochemicals from the gut. These compounds are excreted directly and are concentrated in the feces. A lymantriid moth larva that is a specialist on the coca plant, which is the source of the alkaloid cocaine, rapidly excretes this compound with only traces being found in the blood. However, cocaine may still have defensive value for the larva as part of an oral regurgitate that is externalized when the larva is disturbed.

Three different species of moth larvae that feed on tobacco plants rapidly excrete nicotine, a very toxic and reactive alkaloid. There is no evidence that nicotine is absorbed from the gut of any tobacco feeder, but as is the case for the moth larva excreting cocaine, nicotine in oral or anal exudates constitutes an excellent defensive compound.

Allelochemical Metabolism

Many insect specialists rapidly metabolize ingested allelochemicals which are then sequestered, or in some cases excreted. Nicotine, which is both highly reactive and very toxic, is converted to a non-toxic metabolite called cotinine by both tobacco-feeding insects and those that are not tobacco feeders. Since cotinine has virtually no toxicity to insects, it is probable that its production from nicotine constitutes true detoxication.

Cabbage-feeding insects feed on plants that are rich in sinigrin, a compound that yields a highly toxic mustard oil when metabolized.

Although sinigrin can be sequestered without generating the reactive mustard oil in a variety of cabbage-feeding species, cabbage butterflies (whites) actually break down sinigrin and sequester the highly reactive mustard oil. For these butterflies, the mustard oil is more suitable for storage than sinigrin.

Larvae of the tiger moth *Seirarctia* have evolved a novel strategy for coping with the toxic effects of MAM, a compound derived from cycasin which is a constituent in the cycad leaves upon which they feed. When larvae encounter MAM, they convert it to cycasin which is absorbed through the gut wall before being sequestered. Since the enzyme that produces cycasin or MAM is only found in the gut, once cycasin crosses the gut wall into the blood prior to sequestration there is no chance of MAM being generated from cycasin.

Many species of moths, butterflies, and grasshoppers feed on plant species that produce extremely toxic compounds known as pyrrolizidine alkaloids. These alkaloids, present as mixtures, are frequently sequestered by these specialist insects and, in some cases, metabolized plant compounds are the preferred storage forms. For example, larvae of the tiger moth (*Tyria* species) feed on ragwort and primarily sequester the alkaloid seneciphylline, although this compound is present in the plant as the N-oxide. Conversely, the grasshoppers of the *Zonocerus* species convert the ingested alkaloid monocrotaline to its N-oxide before sequestering the compound.

Insects feeding on milkweed metabolize the toxic cardenolides (steroids) produced by these plants, converting them into compounds that can be readily sequestered. The milkweed bug (*Oncopeltus* species) oxidizes cardenolides as a mechanism for converting these steroids into compounds that can be efficiently sequestered. Similarly, larvae of the monarch butterfly store metabolized cardenolides in tissues after oxidizing these compounds into suitable chemical forms for sequestration.

Selective Biomagnification of Allelochemicals in Tissues

There is little indication that the profiles of insect-stored allelochemicals in any way mirror those of their host plant. In a sense, each insect species treats ingested allelochemicals distinctively, so that a compound totally excreted by one species may constitute the main sequestration product of another.

The very toxic grasshopper *Poekilocerus bufonius* sequesters only two of the cardenolides that it ingests from its milkweed food plant. Similar selectivity is shown by moth larvae (*Syntomeida* species) which sequester oleandrin, the main steroid found in the leaves of oleander. On the other hand, a variety of other insects feeding on oleander leaves do not sequester oleandrin.

Similar unpredictability characterizes the sequestration of pyrrolizidine alkaloids by moth larvae. Tiger moths (*Amphicallia* species) sequester the alkaloids crispatine and trichodesmine, whereas the main alkaloid present is crosemperine. Another tiger moth (*Tyria* species) concentrates senecionine in its tissues in spite of the fact that this compound is a trace constituent in the leaves. *Tyria* is no less curious as a sequestrator because it stores jacobine, jacozine, and jacoline as minor constituents in adults, yet these three compounds are major alkaloids in the leaves.

The Diverse Functions of "Captured" Allelochemicals

While highly concentrated allelochemicals may constitute a major deterrent to non-adapted insects, these compounds can represent a real treasure trove for species for which these plant products are non-toxic. Indeed, in the course of exploiting for their own protection compounds that are repellent or toxic to most insect species, specialists have gone beyond the point of simply being resistant to allelochemicals. In many cases, a variety of specialist species have utilized the rich allelochemical pool that is available in order to develop a menu of remarkable functions.

Insect Sequestration of Bacterial Compounds and their Glandular Secretion

Prokaryotes (bacterial types) are almost everywhere and their widespread association with insects is certainly well established. But the bases for these diverse bacteria-insect relationships are, for the most part, *terra incognita*. However, very recent research suggests one very surprising function for bacteria in insect glands.

All major types of metabolism evolved in prokaryotes and the success of these organisms was both cause and effect of changing environments on earth. If these bacteria are sequestered in insect secretory glands, their great metabolic abilities could be utilized to biosynthesize bacterial allelochemicals which could be used as potent defensive compounds. This possibility appears to have been realized as a product of the virtual ubiquity of both insects and their biosynthetically versatile prokaryotes.

Predaceous diving beetles (*Dytiscus* species) are distinguished by their ability to produce defensive steroids, some of which are novel animal products that are limited to species of diving beetles. Furthermore, insects do not synthesize cholesterol which in insects must be obtained from exogenous sterols. However, it now appears that the surprising steroidal versatility of dytiscids may reflect the biosynthetic elegance of bacteria rather than insects.

Adult diving beetles may contain concentrations of at least 10 bacterial species, mostly detected in a variety of organs. Culturing individual bacterial species resulted in the identification of diverse steroids that had previously been characterized in the prothoracic defensive glands of the adults. The steroid-rich secretions of these glands function as vertebrate deterrents that can cause emesis of fish that swallow these beetles. If the dytiscid-bacterial association is typical of a variety of insect species and their bacterial symbiotes, then a multitude of insect-bacterial relationships may require reevaluation of possible examples of insect sequestration of bacterial allelochemists.

Non-pathogenic bacteria are commonly housed in insects and, in a sense, these prokaryotes are sequestered by their insect hosts. Furthermore, if the bacteria synthesize toxic compounds which may be externalized from a defensive gland (prothoracic glands of dytiscids), then the bacterial products may be regarded as bacterial allelochemicals that have been sequestered. Indeed, bacterial compounds of symbiotic bacteria of insects clearly constitute an unrecognized group of allelochemicals.

Additives in Defensive Glands

Milkweed bugs (*Oncopeltus* species) add cardenolides, derived from their milkweed host plants, to their thoracic defensive gland secretion which considerably enhances the deterrency of their secretion. Similarly, a warningly colored generalist, the lubber grasshopper (*Romalea guttata*) incorporates a large number of allelochemicals derived from a variety of plant species into its thoracic gland secretion. This grasshopper generally feeds on plants with low concentrations of allelochemicals, but if it is fed high concentrations of plants with known repellents (e.g., onion), the odorous secretion can be highly deterrent.

Another toxic grasshopper, *Poekilocerus bufonius*, utilizes allelochemicals as the mainstay of its defensive secretion. This aposematic (very warningly colored) insect sequesters two of six cardenolides from its milkweed diet which are the major irritants in the secretion when it is sprayed at adversaries. Utilization of allelochemicals as defensive gland constituents is particularly pronounced in the swallowtail larvae of *Atrophaneura alcinous*, which feed on leaves that are rich in toxic aristolochic acids. Seven aristolochic acids are sequestered by the larvae and all are transferred to the defensive gland in the head. The acids are concentrated in the gland and are the major deterrents for birds.

Regurgitation and Defecation of Allelochemicals

The intestines of stimulated grasshoppers can discharge ingested plant products which may serve as repellents for predators. Regurgitated allelochemicals can effectively repel ants, as is the case for anal discharges from the hind gut. When tactually stimulated, the milkweed bug, *Oncopeltus fasciatus*, also defecates a solution containing repellent allelochemicals. In this case, they are cardenolides ingested from their milkweed food plant.

Allelochemicals as Tissue Colorants

The cuticular (skin) coloration of many insects is diet-dependent and is highly adaptive since it enables the insect to respond in a positive way to its background color. Diet-induced changes may result in the insect being cryptic (background matching), whereas aposematic species can be background contrasting. Background quality, which is of great survival value, appears to be controlled by allelochemicals that are widespread in the diets of moths, butterflies and true bugs. These insects are particularly sensitive to the carotenoids (e.g., tomato red) that fortify their host plants.

If the large white butterfly, *Pieris brassicae*, is reared on its normal diet of cabbage leaves, the pupae are green and contrast with their background. This toxic insect contains high concentrations of carotenoids, and the carotenoid lutein is concentrated in the cuticle. On the other hand, if these insects are reared on an artificial diet lacking carotenoids, they possess a turquoise-blue coloration and exhibit no response to background. In the absence of carotenoids, these insects are quite conspicuous on their background and could be readily detected by predators.

Allelochemicals as Inhibitors of Toxin Production

Some plant toxins are present in plants in an inactive form only to be converted to toxic compounds after ingestion by herbivores. This is particularly true for many cyanogens (cyanide-containing toxins) that generate cyanide when the leaf surface is broken as would occur with a plant feeder. It now appears that cyanogenesis (producing cyanide) in damaged leaves may be inhibited by allelochemicals that are compartmentally isolated from the cyanogens in the intact leaves.

Leaves of papaya, *Carica papaya*, contain two cyanogens that yield hydrogen cyanide after enzymatic attack. However, tannins, which are widely distributed in plants, inhibit the release of cyanide caused by the action of enzymes that attack the cyanogens. Insects attacking plants containing cyanogens may have adapted tannins to prevent cyanide release, a strategy that may be suitable for other plant groups that yield toxic products after leaf damage.

Allelochemicals as Pheromonal Precursors

Bark beetles (Scolytidae) in the genera *Dendroctonus* and *Ips* convert the hydrocarbons produced by their pine hosts into alcohols that are utilized as either aggregation or sex pheromones (communication compounds) by the attacking beetles. Similarly, butterflies in the family Nymphalidae and moths in the family Arctiidae convert pyrrolizidine alkaloids (PAs) into sex pheromones that are especially critical during courtship. The PAs may be collected from damaged plants by males to be transformed into sexual pheromones that constitute the key to reproductive success. For these males, the allelochemicals (PAs) are identified with reproductive fitness.

Allelochemicals as Structural Paint

Some insects actually "paint" structures with ingested compounds possessing considerable biological activity. Larvae of the parsnip webworm, *Depressaria pastinacella*, apply ingested allelochemicals to silk-webbed flowers that serve as housing units. The applied compounds are derived from wild parsnip, a food plant that is rich in highly toxic furanocoumarins. These compounds are sequestered in the silk glands before being applied to the flowers in which the larvae reside. Since the larvae are quite sensitive to ultraviolet light, the presence of UV-absorbing furanocoumarins on their silken housing is highly adaptive. In addition, because these allelochemicals possess pronounced antimicrobial activity against bacteria and fungi, their presence on the silk can act as a major barrier to pathogens.

Allelochemicals as Metabolites in Primary Metabolic Pathways

Some specialist herbivores metabolize the characteristic allelochemicals in their host plants into compounds that are of major significance in growth and development. In essence, these specialists exploit their food plants by utilizing not only their primary nutrients for growth and development, but their allelochemicals as well.

Larvae of the bruchid beetle, *Carydes brasiliensis*, develop exclusively on seeds of a legume (pea family) that contains canavanine, a foreign amino acid related to arginine. Canavanine is highly toxic when incorporated into proteins by non-adapted herbivores. On the other hand, larvae of *C. brasiliensis* metabolize canavanine into products of great metabolic significance. Large amounts of ammonia are generated for fixation into organic compounds, and an amino acid is produced from canavanine for ready metabolism. Thus, the very toxic allelochemical of the legume has been thoroughly exploited by the beetle larvae as a source for key nutrients.

Beetle larvae in the genus *Chrysomela* also convert a toxic allelochemical into a metabolite with considerable importance in growth and development. These larvae feed on leaves of willow (*Salix*), a rich source of salicin, a toxic metabolite. Metabolism of salicin yields a very effective defensive compound that is sequestered by the larvae in defensive glands. In addition, this metabolism generates enough glucose to account for about one-third of the daily caloric requirements of the larvae. Salicin should be regarded as an allelochemical nutrient.

Allelochemicals as Agents of Sexual Development

Tiger moths in the genus *Creatonotus* feed on plant species that produce high concentrations of pyrrolizidine alkaloids (PAs). These compounds are converted to sex pheromones by the males. Additionally, these allelochemicals control the development of important secondary sexual characters called coremata. The coremata are eversible andraconial (male) organs that are the source of the volatile sex pheromones of the males, and their degree of development is controlled by the amount of PAs ingested by the developing larvae. In effect, PAs are functioning as male hormones that regulate both sex pheromone production and development of the coremata.

Allelochemical Discharge from Non-glandular Reservoirs

Some insects sequester ingested allelochemicals in non-glandular reservoirs that can be evacuated upon demand. Gregarious larvae of the European pine sawfly, *Neodiprion sertifer*, sequester toxic turpentine terpenes in foregut pouches. These pine-derived compounds can be discharged upon demand to function as highly effective predator deterrents. Similarly, lygaeids such as the milkweed bug, *Oncopeltus fasciatus*, sequester cardenolides from their milkweed hosts in dorsolateral spaces on the thorax and abdomen. Significantly, high concentrations of cardenolides are stored in these spaces, resulting in a concentrated deterrent discharge which repels potential predators.

Allelochemicals as Defensive Agents of Eggs

Insects ingesting allelochemicals often utilize these compounds as protectants for the next generation of insects. These plant compounds may be sequestered in the eggs in order to provide a formidable defense against predators and pathogens. The insect embryo must be resistant to the toxic effects of the allelochemicals that have been sequestered in the reproductive system. For example, chrysomelid beetle adults feeding on willow and poplar sequester the toxic allelochemical salicin which is used to fortify the eggs. Salicin has different functions in the embryo and the larvae. For the embryo, salicin is a deterrent toxin which can kill ants. For the young larvae, salicin is converted to salicylaldehyde, a powerful repellent that is not frequently encountered in insects. A wide variety of allelochemicals are sequestered in insect eggs which includes pyrrolizidine alkaloids, aristolochic acids, cannabinoids, quinones, cardenolides and mustard oils. It is evident that the females of a large number of species have appropriated their host-plant defenses (allelochemicals) for protection of their eggs.

Allelochemicals as a Copulatory Bonus

Females may obtain allelochemicals suitable for their own protection and that of their eggs from the seminal ejaculate. For example, males of ithomiine butterflies gather pyrrolizidine alkaloids (PAs) from flowers and decomposing foliage and about half of the PAs are channeled to the spermatophore (sperm packet) that is transferred to the female during copulation. Since the females are rarely found feeding on alkaloid sources, the copulatory bonus ensures that these toxic allelochemicals will be available to protect both the female and her eggs. It is also very significant that the resistance of the spermatozoa to the known toxic effects of the pyrrolizine alkaloids enables the copulatory bonus strategy to be highly adaptive.

Allelochemicals as Synergists for Pheromones

The intimate relationship of specialist insects and their food plants is exemplified by the turnip aphid, *Lipaphis erysimi*, and its alarm pheromone. This aphid is typical of many aphid species. Paired glands near the tip of the abdomen secrete an alarm pheromone that causes both adults and larvae to disperse and drop off of the food plant. The alarm pheromones synthesized by the aphids are key communications chemicals that enable these insects to "abandon ship" when threatened by a predator. Surprisingly, (*E*)-*B*-farnesene, the major alarm agent for a large variety of aphid species, is only weakly active when secreted by the turnip aphid. However, the activity of this pheromonal secretion is increased appreciably by allelochemicals that act as powerful synergists for the major alarm pheromone. These synergists are derived from typical food plant compounds that have been modified by the aphids.

Allelochemicals as Phagostimulants

The close relationship of insect specialists and their allelochemicals is further demonstrated by some species of sawflies and chrysomelid beetles which feed on very bitter food plants. Adults of the turnip sawfly, *Athalia rosae*, feed on the surface of a plant that is not a larval food plant. Compounds in the leaf surface that are responsible for their bitter taste are powerful phagostimulants for *A. rosae*. In addition, these bitter compounds are incorporated into the cuticle, thus providing these sawflies with a cuticular set of "armor" to protect against aggressive predators.

Similarly, species in three genera of chrysomelid beetles utilize cucurbitacins, compounds found in their squash and pumpkin hosts, as phagostimulants that are biomagnified in their bodies. The beetles are rendered distasteful and, as is the case for the sawflies, the allelochemicals possess dual roles that both induce ingestion and promote sequestration of highly distasteful compounds.

Allelochemicals as Inducers of Detoxifying Enzymes

Both generalist and specialist insects can encounter a diversity of allelochemicals with varying degrees of toxicity. For generalists this is particularly true since a generalist diet can sample a wide variety of plant species containing a large diversity of allelochemicals. On the other hand, specialists may encounter fewer allelochemicals but it is likely that these compounds will be at high concentrations. In the case of both feeding modes, it is obviously necessary to possess mechanisms for blunting the toxic properties of the ingested allelochemicals. Detoxication would appear to constitute the key process for neutralizing the toxicities of ingested allelochemicals. The enzymes chiefly identified with converting allelochemicals into less toxic compounds are the mixed-function oxidases, particularly cytochrome P-450.

Mixed-function oxidases metabolize fat-soluble toxins into water-soluble ones that can be excreted. The level of these enzymes may determine the tolerance of an insect for a particular allelochemical. For a generalist ingesting a large diversity of allelochemicals derived from many plant species, the induction of a variety of these oxidases would promote the possibility of detoxifying many kinds of plant compounds. For a specialist, fewer oxidases at very high levels would enable the herbivore to detoxify the very high concentrations of allelochemicals in its restricted food plants.

Mixed-function oxidases play a key role in protecting the southern armyworm, *Spodoptera eridania*, from a host of allelochemicals. Unrelated plant compounds rapidly induce enzymatic increases of 2 to 3-fold in larvae. Significantly, the rise in P-450 activity is immediate and proceeds rapidly over much of its course during the first few hours. These results strongly suggest that P-450 induction is critical to allelochemical tolerance.

Allelochemicals as Allomonal Precursors

In some cases, insects have produced powerful repellents from allelochemicals in their food plants and have thus exploited the plant's defensive chemistry in a very efficient way. Such a strategy is particularly adaptive because the insect has benefited both nutritionally and defensively from feeding on its host.

Host plant exploitation is particularly pronounced in some chrysomelid beetle larvae in the genera *Chrysomela* and *Phratora*. The larvae feed on willow and poplar leaves, both of which contain salicin, a well known feeding deterrent for non-adapted species. The beetle larvae convert salicin to salicylaldehyde and glucose, utilizing the former for defense and the latter for growth. For these chrysomelid larvae, the conversion of salicin to salicylaldehyde is doubly beneficial. Very little energy is used to synthesize salicylaldehyde, compared to what is required to produce other defensive compounds that must be totally synthesized. Because salicylaldehyde is a far more effective repellent than salicin, the beetle larvae receive a very important double bonus by converting the allelochemical into a compound that can be readily stored and secreted from the defensive glands.

Allelochemicals as Communicative "Jamming" Agents

In theory, plant species could reduce or eliminate herbivory if the plants generated volatile compounds identical to or similar to the pheromones utilized by herbivores as signals. If these signals were behaviorally disruptive, feeding could be appreciably diminished, to say the least.

The wild potato, *Solanum berthaultii*, has effectively "jammed" the pheromonal alarm signal of its potential aphid herbivore. (*E*)-*B*-farnesene, an alarm pheromone of the aphid *Myzus persicae*, is also produced by wild potatoes, resulting in repellency and dispersion of the aphids. In effect, the potato has exploited the aphid's herbivory by utilizing a highly disruptive compound that has been evolved by aphids as a warning signal.

Quenchers of Phototoxic Allelochemicals

Diverse plant species produce photo-activated compounds that are highly toxic to insects after digestion. In essence, these compounds generate highly toxic species of oxygen that attack key biochemicals such as nucleic acids. On the other hand, if the herbivore simultaneously ingests allelochemicals that are effective quenchers of toxic oxygen species along with the phototoxins, then survival and prosperity are possible. The availability of these allelochemical antioxidants has enabled some insect species to utilize food plants that are "forbidden fruits" for most herbivores.

Larvae of the tobacco hornworm feed on a variety of plant species that contain the phototoxin α-terthienyl, a constituent of many species of asters (Asteraceae). However, the additional ingestion of β-carotene reduces mortality from 55% (controls) to 3% (+carotene) during 48 h. β-carotene, an effective quencher of toxic oxygen species, is concentrated in the tissues of the larvae where it can serve as a potent antioxidant for photoactivated toxins found in its food plant.

Antibiotic Functions of Allelochemicals

The demonstrated range of allelochemicals against insect-associated viruses, fungi and bacteria makes it probable that these arthropods have commonly exploited plant compounds as key elements in their phytochemical defenses.

A compound commonly produced by conifers is *a*-pinene, which inhibits diverse microorganisms including the insect pathogen *Bacillus thuringiensis*. Along with several related compounds, α-pinene reduces the infectivity of *B. thuringiensis* for larvae of the Douglas fir tussock moth, *Orgyia pseudotsugata*. At concentrations approximating those found in fir needles, *a*-pinene increases the 50% lethal dose for *B. thuringiensis* by 700-fold.

A pathogenic fungus, *Nomuraea rileyi*, frequently attacks lepidopterous (moth) larvae such as the corn earworm, *Helicoverpa zea*. However, the pathogenicity to this larva can be reduced if the moth ingests a tomato alkaloid, α-tomatine. If the larvae ingest α-tomatine prior to exposure to fungal conidia, it increases larval survivorship considerably. The alkaloid is a further asset to *H. zea* because it is quite toxic to larval parasites of the corn earworm.

The pathogenicity of viral pathogens of *H. zea* can also be compromised by host plant allelochemicals. Chlorogenic acid, a common plant compound, is oxidized to chlorogenoquinone by plant enzymes, and this oxidation product binds to a nuclear polyhedrosis virus. Binding to this baculovirus results in a reduction in digestibility and a decrease in infectivity. Furthermore, it appears that the liberation of infective virons in the midgut, which is a requirement for successful infection, is impaired by the binding of chlorogenoquinone to the baculovirus.

Specialists and Generalists: Two Selected Case Studies

Although specialists and generalists may be highly efficient sequestrators, the storage characteristics of both groups differ considerably. Some insights into how these insects manipulate the allelochemicals in their diets have been provided by recent studies of the fates of a variety of ingested plant chemicals. An analysis of these studies demonstrates that the particulars of sequestration are, if nothing else, very unpredictable.

The Monarch Butterfly, *Danaus plexippus*

The monarch is a specialist that feeds exclusively on different species of milkweeds. Milkweeds contain steroids called cardenolides, which are somewhat related to vertebrate hormones such as testosterone. These compounds are toxic and highly emetic, vomiting often following their ingestion by non-adapted species.

Polar (water soluble) cardenolides are sequestered in the large volume of gut fluid possessed by the larvae. Sequestration is much more efficient from plants with low level cardenolide concentrations than with high concentrations. Significantly for the monarch, and not necessarily for other milkweed feeders, it is the large volume of gut fluid that makes it possible to feed and develop on these plants.

The cardenolide-rich gut fluid, which may exceed one-third of the larva's total liquid volume, is withdrawn at pupation to become part of the hemolymph (blood) pool, stored primarily under the wings. Subsequently, the wing scales (bird predators beware), along with the hemolymph, become the richest sources of cardenolides in the body after being withdrawn from the gut fluid. The volume of gut fluid decreases before pupation only to increase again before pupal molting. Again, gut fluid diminishes during pupal development only to increase again in the new adult. The cardenolide-rich gut fluid is again converted to hemolymph during adult development so that very little remains to be lost when the newly developed adult evacuates accumulated waste products from its gut.

The polar cardenolides in the gut fluid clearly are the source of the defensive compounds manipulated by the monarch at all stages. The larval and pupal exuviate (cast skins) eliminated after molting are an excretory form for the cardenolides, as is the case for these compounds in the wing scales. Excretion notwithstanding, the ability of all life stages to manipulate the cardenolide pool is quite pronounced. This is evident in 2-day-old pupae that contain low concentrations of cardenolides in the gut fluid but high concentrations in the hemolymph. However, before wing expansion in the newly developed adult, the cardenolide level in the hemolymph is at its lowest, only to increase to the highest level in any life stage.

The presence of high levels of cardenolides in the blood of the adult demonstrates that these compounds are not locked in tissues but rather are circulating freely, possibly to be utilized upon demand. The warningly colored (aposematic) adult monarch utilizes a defensive system based on compounds that it did not ingest as an adult. Although the complexities of cardenolide sequestration in this species are evident, it is highly significant to understand these ingested steroids are an extraordinarily dynamic state.

The Lubber Grasshopper, *Romalea microptera* (also known as *R. guttata*)

This large grasshopper found in the southeastern United States is quite conspicuous because of it red, black and yellow coloration. It is one of the most aposematic (warningly colored) species in its habitat. This brightly colored grasshopper is especially distinctive because it is a generalist that feeds on a very wide range of plants belonging to a variety of species. Lubber grasshopper is known to feed on 104 plant species belonging to 38 families, many of which produce toxic allelochemicals. Both immature and mature grasshoppers are capable of causing emesis in predators such as lizards, demonstrating that all stages of these insects are protected from at least some predatory vertebrates.

Immature individuals of *R. microptera* produce defensive compounds that cause emesis in both lizard and bird predators. Additionally, mature and adult grasshoppers secrete defensive compounds from paired tracheal (respiratory) glands in the metathorax. These glands only become active near the adult period and their secretion can be extremely repellent to small predatory insects such as ants. At least 50 compounds are produced by the defensive glands, the secretions varying intraspecifically, so that components of females of the same age and population sometimes differ by 70-fold, with some compounds being absent in certain individuals. However, in addition to the compounds synthesized in the metathoracic glands, a number of allelochemicals are sequestered in these glands as a reflection of an individual grasshopper's diet. Indeed, the composition of the metathoracic gland secretion of each grasshopper appears to be unlike that of any other grasshopper, since no two of these generalist grasshoppers have identical diets from which to sequester allelochemicals. For a predator, each lubber secretion may be sufficiently distinctive to make it impossible to learn an olfactory pattern that clearly identifies the prey as lubber grasshopper.

Lubber grasshopper is unusual in being a polyphagous (eating many plant species) insect species that sequesters allelochemicals. In general, monophagous (feeding on one group of plant species) and stenophagous (feeding on a limited range of plant species) insect herbivores characteristically sequester plant compounds, but not generalist feeders. Furthermore, if *R. microptera* is presented with a restricted diet (specialist feeding mode), the number of compounds in the secretions and their concentrations are reduced, and the relative composition of the secretion is markedly different from that of field-collected grasshoppers. Significantly, if grasshoppers are presented with only a single-host plant as a food source, they frequently feed readily, sequestering host-plant volatiles, and exhibit no immediate ill effects. Lubbers feeding only on wild onion sequester a large number of onion volatiles which impart a strong onion odor to the secretion. The secretion is a powerful repellent to hungry ants and is considerably more active than the secretions of field-collected grasshoppers. Compounds in other single-plant diets (e.g., catnip) produce secretions that are similarly active.

The secretion of lubber grasshopper clearly has both a dietary and an individual origin that correlates with great variations in secretory components. The possibility that these grasshoppers can temporarily switch to a monophagous feeding mode in the presence of a preferred host plant is not unreasonable, and can result in a secretion with a high a concentration of sequestered allelochemicals as is characteristic of some specialist insects.

Lubber grasshopper is quite unpalatable and emetic to a variety of vertebrates, especially birds. Diverse bird species have been demonstrated to vomit after ingestion of these grasshoppers, presumably as a consequence of *Romalea*-synthesized toxins that fortify their bodies. While *Romalea* would appear to be completely defended against birds, as is often the case, the best defense has been overcome by a better offense. Shrikes, predatory birds that impale their insect prey on spines or even barbed wire, capture lubber grasshoppers and impale them. However, the birds wait for about 48 h before they remove and eat the grasshoppers. Though shrikes "store" all their food in this manner, in all likelihood the emetic toxin(s) produced by *Romalea* decomposes during the time the grasshopper is impaled.

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Allelopathy

The ability of a plant species to produce substances that are toxic to certain other plants. Allelopathic chemicals may affect germination, growth or reproduction of plants.

Allen's Rule

Among mammals and birds, individuals of a species occurring in colder climates tend to have shorter appendages, and a correspondingly lower surface to volume ratio, than members of the same species living in warmer climates. This trend results from the need to conserve heat in cold climates but to eliminate excess heat in hot climates. A variant of this is Bergmann's rule. These rules do not apply to ectothermic animals such as insects.

► Bergmann's Rule
► Thermoregulation

Allochronic Speciation

A mechanism of speciation wherein new species develop in the same place but are separated due to their tendency to occur at different times.

► Speciation Processes Among Insects

Allogenic Succession

A temporal succession of species that is driven by processes from outside the community (contrast with autogenic succession).

Allometric Growth

A growth pattern in which different parts of an organism grow at defined rates. In some cases, the body parts remain proportional (isometric growth), in other cases they do not. Departure from isometric growth is used to explain castes of social insects, which may have disproportionately large heads, mandibles, etc.

Allomone

A chemical that is released by one species that influences the behavior or physiology of a different species. The organism releasing the substance usually benefits. Allomones are a type of semiochemical used in warning.

► Chemical Ecology

Allopatric

Having separate and mutually exclusive areas of distribution (contrast with sympatric).

Allopatric Speciation

A mechanism of speciation resulting from geographic separation of populations, particularly physical barriers such as mountains and oceans.

► Speciation Processes Among Insects

Allophagic Speciation

A mechanism of speciation wherein new species develop in the same place, but are separated by their preference for different food.

► Speciation Processes Among Insects

Allozyme

Allozymes are a subset of isozymes. Allozymes are variants of enzymes representing different allelic alternatives of the same locus.

Almond Seed Wasp, *Eurytoma amygdali* Enderlein (Hymenoptera: Eurytomidae)

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The almond seed wasp is a serious pest of almonds, *Prunus amygdalus* Batch, in several countries of southeastern Europe and the Middle East, and also in Armenia, Azerbaijan, and Georgia. The adult female is 6–8 mm long and has a black head with dark brown eyes. The thorax and the spindle-shaped abdomen are shiny black. The tibiae and tarsi are light brown while the remaining parts of the leg are black. The male is usually smaller than the female (4–6 mm long). The larva is whitish, legless, tapering in both ends, curved and clearly segmented. Its head is light brown and very small. Its length when fully grown is about 6 mm.

Almond seed wasp is a univoltine species, with a small part of the population completing its life cycle in two or more years because of prolonged diapause. The diapause terminates during the winter. Pupation takes place inside the fruit in late winter to early spring. Adults emerge after boring a circular exit hole through the hard pericarp with their mandibles. Shortly after adult emergence, virgin females release a volatile sex pheromone to attract males for mating. Within a few days they mate and the females start ovipositing (Fig. 37) into unripe, green almonds. Using her long ovipositor, the female drills through the pericarp of unripe, green almonds and the integument of the seed, and deposits a stalked egg within the translucent nucellar tissue. After oviposition, the female deposits onto the fruit surface a host-marking pheromone. This pheromone enables females to discriminate between the infested and uninfested fruit, and to select the latter for oviposition. Thus, a uniform distribution of eggs among available fruits is achieved, and an optimal use of the available fruit for larval development. The newly hatched larva bores through the nucellus and the embryo sac to feed on the developing seed embryo. The larva attains full size in midsummer, and enters diapause within the seed integument of the destroyed almond, which usually remains on the tree in a mummified condition.

Owing to oviposition by the wasp certain varieties suffer a heavy premature drop. In most varieties though, the main damage consists in the consumption of the seed by the larvae. This damage varies depending on the variety. Certain soft-shelled varieties may lose up to 90% of their crop. Others are nearly immune because by the time females emerge in spring their pericarp has become too thick and endocarp too hard for the ovipositor to penetrate. Though not a common practice, planting of resistant varieties might be an effective strategy against this pest.

The pest can be controlled by collection and destruction of mummified fruits before adult

Almond Seed Wasp, *Eurytoma Amygdali Enderlein* (Hymenoptera: Eurytomidae), Figure 37 Female *Eurytoma amygdali* ovipositing into an almond.

emergence in spring, which is an effective measure if applied in large areas by multiple growers. However, the method most commonly used is the application of systemic insecticides against the neonate larvae within the oviposited almonds. This strategy is meant for varieties that do not suffer fruit drop because of oviposition. Recent studies have indicated that a single spraying can be effective if applied when 10–50% of the eggs have hatched. This percentage can be determined by dissecting sampled almonds under a binocular microscope. Estimates of egg hatch can be obtained by knowing the time the first adults emerge from infested almonds in spring. This can be determined by following the exit of adult wasps from infested almonds kept in cages in the orchard, or by following the population of males with the use of sex pheromone traps containing live virgin females as lures.

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Alpha Taxonomy

The identification of organisms, and particularly the description and naming of organisms (species) new to science.

► Beta Taxonomy
► Gamma Taxonomy

Alternate Host

One of the hosts of a pathogen or insect where a portion of the life cycle occurs. Often this term is used to refer to a weed host of a crop pest or disease.

Alternation of Generations

Some insects undergo reproduction that involves alternation of sexual and asexual generations. Typically, females produce both males and females but at some point females cease producing males and produce only females parthenogenetically. Later generations then commence production of males again, allowing sexual reproduction to occur before the parthenogenetic cycle begins again. This occurs most often in Hymenoptera and Hemiptera.

► Aphids (Hemiptera: Aphididae)
► Gall Wasps (Hymenoptera: Cynipidae)

Altruism

Self destructive behavior that is performed for the benefit of others; sacrifice.

Alucitidae

A family of moths (order Lepidoptera). They commonly are known as many-plumed moths.

► Many-Plumed Moths
► Butterflies and Moths

Alula

The expanded membrane at the base of the trailing edge of the front wing.

► Wings Of Insects

Amazonian Primitive Ghost Moths (Lepidoptera: Neotheoridae)

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Amazonian primitive ghost moths, family Neotheoridae, are defined on the basis of a single species from the Amazonian area of southern Brazil, although two additional species have been discovered for the family recently. The family is part of the superfamily Hepialoidea, in the infraorder Exoporia. Adults medium size (38 mm wingspan), with head roughened; haustellum short and vestigial mandibles present; labial palpi long, porrect and 3-segmented; maxillary palpi very small and 2-segmented. Wing maculation is dark and unicolorous. Biologies and larvae remain unknown.

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Amber Insects: DNA Preserved?

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Amber is a polymerized form of tree resin that was produced by trees as a protection against disease agents and insect pests. The resin hardened and, sometimes, captured insects, seeds, feathers, microorganisms, plants, spiders, and even small vertebrates that got stuck in the sticky exudate. The hardened resin was preserved in the earth for millions of years, especially in regions where it was deposited in dense, wet sediments such as clay or sand that formed in the bottom of an ancient lagoon or river delta. For thousands of years, people have collected amber. Many people use amber as a gem, but scientists find amber a magnificent way to identify ancient organisms.

Amber can be found in a variety of sites around the world. The composition, color, clarity, and other properties of amber vary according to age, conditions of burial and type of tree that produced the resin. The oldest amber is from the Carboniferous (360–285 million years ago, mya) and can be found in the United Kingdom and in Montana in the USA. Permian amber is 185–145 million years old and found most often in Russia. Triassic amber (245–215 mya) can be found in Austria, and Jurassic amber (215–145 mya) is found in Denmark. Cretaceous amber (65–140 mya) is found in many locations around the world and represents the time when dinosaurs reigned and flowering plants evolved along with a variety of insects. For example, the rich amber deposits in central New Jersey in the USA are from the Turonion period of the Upper Cretaceous, about 92 mya. Other Cretaceous-period amber is found in North Russia and Japan. Baltic amber is found in the Baltic sea where amber has been collected and made into decorative objects for at least 13,000 years. In the Dominican Republic, amber deposits 23–30 million years old are found in rock layers. Dominican amber is particularly rich in insect inclusions. This amber was formed from the resin of an extinct tree in the legume family. Tertiary amber deposits are found in several locations around the world and are from 1.6 to 65 million years old. Tertiary deposits in the USA are found in Arkansas. Some websites with photographs showing amber inclusions can be viewed at:

- Amber Inclusions at: http://www-user.uni-bremen.de/~18m/amber.html;

– Amber on-line at: www.ambericawest.com/amberpics.html;
– American Museum of Natural History at: www.amnh.org/exhibitions/amber/; or
– The Amber Room at: http://home.earthlink.net/-skurth/AMBER.HTM.

Insect DNA in Amber?

The ability to amplify dinosaur DNA from insects preserved in amber in the film *Jurassic Park* captured the imagination of the public. Subsequently, the PCR was used to amplify DNA fragments from insects preserved in ancient amber, but these results have been controversial, as have been the results from amplifying dinosaur DNA.

Why the controversy? Is amber a special form of preservative that allows DNA to persist for unusually long periods of time (millions of years)? Amber entombs insect specimens completely, after which they completely dehydrate so the tissue is effectively mummified. Terpenoids, which are major constituents of amber, could inhibit microbial decay. Certainly, preservation of amber-embedded insects seems to be exceptional and insect tissues in amber appear comparable in quality to the tissues of the frozen wooly mammoth (which is "only" 50,000 years old). But is the DNA in these tissues preserved?

DNA has been extracted from a variety of insects in amber, including a fossil termite *Mastotermes electrodominicus* estimated to be 25–30 million years old, a 120- to 130-million year old conifer-feeding weevil (Coleoptera: Nemonychidae) and a 25- to 40-million year old bee. These are extraordinary ages for DNA!

The DNA sequences obtained from all amber-preserved insects meet several, but not all, criteria of authenticity; the fossil DNA sequences "make phylogenetic sense" and DNA has been isolated from a number of specimens in several cases (although the weevil example was derived from a single specimen). However, the extraction and amplification of fossil DNA sequences from amber-preserved insects has yet to be reproduced in independent laboratories, despite multiple attempts to do so, which has cast doubt on the authenticity of the reports.

One of the most controversial claims involved the isolation of a "living" bacterium from the abdomen of amber-entombed bee. Bacterial DNA from a 25-million-year-old bee was obtained and sequenced and a bacterial spore was reported to be revived, cultured, and identified. The classification of the bacterium is controversial because the bacterium could have come from a currently undescribed species of the *Bacillus sphaericus* complex. The modern *B. sphaericus* complex is incompletely known, so the "new" sequence obtained could be that of a modern, but previously unidentified, bacterium because this group of bacteria often is isolated from the soil.

Other claims of amplifying ancient DNA have been disproved. For example, the mitochondrial cytochrome b sequence of an 80-million-year-old dinosaur from the Upper Cretaceous in Utah was later discovered to be, most probably, of human origin. Likewise, a 20-million-year-old magnolia leaf produced sequences that were similar to those of modern magnolias. The authenticity of the magnolia sequences were cast into doubt because they were exposed to water and oxygen during preservation and DNA is especially vulnerable to degradation under such conditions.

The most common ancient DNA analyzed is usually mitochondrial DNA because it is so abundant; however, this abundance makes it easy to contaminate the ancient sample with modern mtDNA. The amplification of ancient DNA remains highly controversial because the technical difficulties are great.

DNA is a chemically unstable molecule that decays spontaneously, mainly through hydrolysis and oxidation. Hydrolysis causes deamination of the nucleotide bases and cleavage of base-sugar bonds, creating baseless sites. Deamination of cytosine to uracil and depurination (loss of purines adenine and guanine) are two types of hydrolytic damage. Baseless sites weaken the DNA, causing breaks that fragment the DNA into smaller and smaller pieces. Oxidation leads to chemical modification of bases and destruction of the ring structure of base and sugar residues. As a result, it is almost always impossible to obtain long amplification products from ancient DNA.

PCR products from ancient DNA often are "scrambled." This is due to the phenomenon called "jumping PCR," which occurs when the DNA polymerase reaches a template position which carries either a lesion or a strand break that stops the polymerase. The partially extended primer can anneal to another template fragment in the next cycle and be extended up to another damaged site. Thus, in vitro recombination can take place until the whole stretch encompassed by the two primers is synthesized and the amplification enters the exponential part of the PCR. This phenomenon makes it essential that cloning and sequencing of multiple clones be carried out to eliminate this form of error in interpretation.

Most archeological and paleontological specimens contain DNA from exogenous sources such as bacteria and fungi, as well as contaminating DNA from contemporary humans. Aspects of burial conditions seem to be important in DNA preservation, especially low temperature during burial. The oldest DNA sequences reported, and confirmed in other laboratories, come from the remains of a wooly mammoth found in the Siberian permafrost; these sequences are "only" 50,000 years old rather than millions of years old.

Theoretical calculations and empirical observations suggest DNA should only be able to survive, in a highly fragmented and chemically modified form, for 50,000–100,000 years. Because only tiny amounts of DNA usually can be extracted from an archeological specimen, stringent precautions and multiple controls are required to avoid accidental contamination with modern DNA.

A methodology to deal with ancient specimens has been proposed that includes careful selection of well-preserved specimens, choice of tissue samples that are likely to have best DNA preservation, and surface sterilization to eliminate surface contamination. The operations should be carried out in a laboratory dedicated to work on ancient specimens and work on ancient DNA should be separated from that on modern DNA. Most importantly, multiple negative controls should be performed during DNA extraction and PCR set up, although a lack of positives in the negative controls is not definitive proof of authentic ancient DNA. Another crucial step is the authentication of the results. Putatively ancient DNA sequences should be obtained from different extractions of the same sample and from different tissue samples from different specimens. The ultimate test of authenticity should be independent replication in two separate laboratories. So far, this type of replication has not been achieved for DNA from amber-preserved arthropod specimens.

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Ambrosia Beetles

Some members of the subfamily Scolytinae (order Coleoptera, family Curculionidae).

► Beetles

Ambush Bugs

Members of the family Reduviidae (order Hemiptera).
► Bugs

Ameletopsidae

A family of mayflies (order Ephemeroptera).
► Mayflies

Amelitidae

A family of mayflies (order Ephemeroptera).
► Mayflies

Amerasinghe, Felix P

Felix Amerasinghe was a noted Sri Lankan medical entomologist. He was known for his work on the taxonomy and ecology of disease-transmitting arthropods. Amerasinghe graduated from the University of Peradeniya, Sri Lanka, and received his Ph.D. from the University of Bristol, United Kingdom, in 1977. He made important long-term studies in the effects of irrigation on mosquito populations and malaria transmission, and became an authority on Japanese encephalitis. The development of keys for the identification of South Asian mosquitoes was one of his important contributions, greatly enhancing disease surveillance programs.

Amerasinghe worked principally at the University of Peradeniya, but also at the University of Sri Lanka, and in later years joined the International Water Management Institute as research leader, initiating studies on the socioeconomic impact of malaria, malaria parasitology, and molecular biology. He died in Colombo, Sri Lanka, on June 7, 2005.

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American Butterfly Moths (Lepidoptera: Hedylidae)

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American butterfly moths, family Hedylidae, total only 40 known species, all Neotropical. The family is in the superfamily Geometroidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (35–65 mm wingspan), with head scaling normal; haustellum naked; labial palpi upcurved; maxillary palpi 1 to 2-segmented; antennae filiform. Wings triangular, with forewings somewhat elongated and often with apex emarginated (Fig. 38); hindwings usually more rounded. Body usually narrow. Maculation somber hues of brown and gray, often with apical dark patch and some speckling, plus pale or hyaline patches (rarely mostly pale or hyaline). Adults nocturnal. Larvae are leaf feeders. Host plants are recorded in Euphorbiaceae, Malvaceae, Sterculiaceae, and Tiliaceae.

American Butterfly Moths (Lepidoptera: Hedylidae), Figure 38 Example of American butterfly moths (Hedylidae), *Macrosoma lucivittata* (Walker), from Ecuador.

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American Dog Tick

► Ticks

American False Tiger Moths (Lepidoptera: Dioptidae)

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American false tiger moths, family Dioptidae, total 507 species, primarily Neotropical (505 sp.); actual fauna likely exceeds 800 species. Two subfamilies are known: Dioptinae and Doinae. Some specialists place the family within the Notodontidae. The family is in the superfamily Noctuoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (22–58 mm wingspan) (Fig. 39). Maculation mostly very colorful, with various patterns of large spotting, and some lustrous. Larvae and pupae often also colorful Adults are mostly nocturnal, but some are diurnal or crepuscular. Larvae are leaf feeders, particularly toxic plants in families like Aristolochiaceae, Euphorbiaceae, Passifloraceae, and Violaceae, but also on various others like Fagaceae. Very few are economic.

American False Tiger Moths (Lepidoptera: Dioptidae), Figure 39 Example of American false tiger moths (Dioptidae), *Josia gigantea* Druce, from Mexico.

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American Grasshopper, *Schistocerca americana* (Drury) (Orthoptera: Acrididae)

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This grasshopper is found widely in eastern North America, from southern Canada (where it is an occasional invader) south through Mexico to northern South America. In the midwestern states, where it is common, the resident population receives a regular infusion of dispersants from southern locations. In the southeast it is quite common, and one of the few species to reach epidemic densities. It is native to North America.

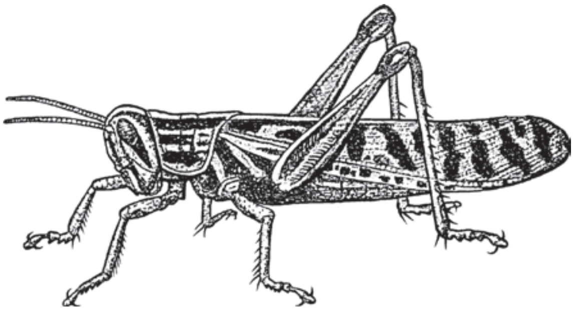
Life History

In warm climates, American grasshopper has two generations per year and overwinters in the adult stage. In Florida, eggs produced by overwintered adults begin to hatch in April-May, producing spring generation adults by May-June. This spring generation produces eggs that hatch in August-September. The adults from this autumn generation survive the winter.

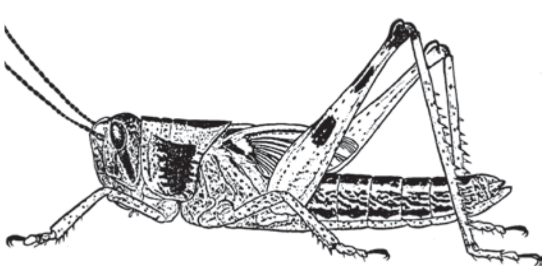
The eggs of *S. americana* initially are light orange in color, turning tan with maturity. They are elongate-spherical in shape, widest near the middle, and measure about 7.5 mm in length and 2.0 mm in width. The eggs are clustered together in a whorled arrangement, and number 75–100 eggs per pod, averaging 85 eggs. The eggs are inserted into the soil to a depth of about 4 cm and the upper portion of the oviposition hole is filled by the female with a frothy plug. Duration of the egg stage is about 14 days. The nymphs, upon hatching, dig through the froth to attain the soil surface.

Normally there are six instars in this grasshopper though sometimes only five. The young grasshoppers are light green in color. They are extremely gregarious during the early instars. At low densities the nymphs remain green throughout their development, but normally gain increasing amounts of black, yellow, and orange coloration commencing with the third instar. Instars can be distinguished by their antennal, pronotal, and wing development. The first and second instars display little wing development but have 13 and 17 antennal segments, respectively. In the third instar, the number of antennal segments increases to 20–22, the wings begin to display weak evidence of veins, and the dorsal length of the ventral lobe of the pronotum is about 1.5 times the length of the ventral surface. Instar four is quite similar to instar three, with 22–25 antennal segments, though the ratio of the length of the dorsal to ventral surfaces of the pronotal lateral lobe is 2:1. In instar five there are 24–25 antennal segments, and the wing tips assume a dorsal rather than ventral orientation but the wing tip does not exceed the first abdominal segment. In the sixth instar (Fig. 41) there are 24–26 antennal segments and the wing tips extend beyond the second abdominal segment. The overall body length is about 6–7, 12–13, 16–18, 22–25, 27–30, and 35–45 mm for instars 1–6, respectively. Development time is about 4–6, 4–6, 4–6, 4–8, 6–8, and 9–13 days for the corresponding instars when reared at about 32°C.

The adult (Fig. 40) is rather large, but slender bodied, measuring 39–52 and 48–68 mm in length in the male and female, respectively. A creamy white stripe normally occurs dorsally from the front of the head to the tips of the forewings. The forewings bear dark brown spots, the pronotum



American Grasshopper, *Schistocerca Americana* (Drury) (Orthoptera: Acrididae), Figure 40 Adult of American grasshopper, *Schistocerca americana* (Drury).



American Grasshopper, *Schistocerca Americana* (Drury) (Orthoptera: Acrididae), Figure 41 Sixth instar of American grasshopper, *Schistocerca americana* (Drury).

dark stripes. The hind wings are nearly colorless. The hind tibiae normally are reddish. Overall, the body color is yellowish brown or brownish with irregular lighter and darker areas, though for a week or so after assuming the adult stage a pinkish or reddish tint is evident.

Adults are active, flying freely and sometimes in swarms. They normally are found in sunny areas, but during the warmest portions of the day will move to shade. Adults are long lived, persisting for months in the laboratory and apparently in the field as well. This can lead to early-season situations where overwintered adults, all instars of nymphs, and new adults are present simultaneously. Mild winters favor survival of overwintering adults and apparently lead to population increase if summer weather and food supplies also are favorable.

Adults of American grasshopper tend to be arboreal in habit, and a great deal of the feeding by adults occurs on forest, shade, and fruit trees. The nymphs, however, feed on a large number of grasses and broadleaf plants, both wild and cultivated. During periods of abundance, almost no plants are immune to attack, and vegetables, grain crops, and ornamental plants are injured. American grasshopper consumes bean, corn, okra, and yellow squash over some other vegetables when provided with choices, but free-flying adults normally avoid low-growing crops such as vegetables, corn (maize) being a notable exception.

The natural enemies of *S. americana* are not well known. Birds such as mockingbirds, *Mimus polyglottos polyglottos* (Linnaeus), and crows, *Corvus brachyrhynchos brachyrhynchos* Brehm have been observed to feed on these grasshoppers. Fly larvae, *Sarcophaga* sp. (Diptera: Sarcophagidae) are sometimes parasitic on overwintering adults. Fungi have also been investigated for grasshopper suppression and *Metarhizium anisopliae* var. *acridum* kills American grasshopper quickly under laboratory conditions. This fungus is effective under adverse field conditions in Africa, so it may prove to be a useful suppression tool.

Damage

Grasshoppers are defoliators, eating irregular holes in leaf tissue. Under high density conditions they can strip vegetation of leaves, but more commonly leave plants with a ragged appearance. American grasshopper displays a tendency to swarm, and the high densities of grasshoppers can cause severe defoliation.

Because American grasshopper is a strong flier, it also sometimes becomes a contaminant of crops. When the late-season crop of collards in the Southeast is harvested mechanically, for example, American grasshopper may become incorporated into the processed vegetables. Although most grasshoppers can be kept from dispersing into crops near harvest by treating the periphery of the crop field, it is much more difficult to prevent invasion by American grasshopper because it may fly over any such barrier treatments.

Populations normally originate in weedy areas such as fence rows and abandoned fields. Thus, margins of fields are first affected and this is where monitoring should be concentrated. It is highly advisable to survey weedy areas in addition to crop margins if grasshoppers are found, as this gives an estimate of the potential impact if the grasshoppers disperse into the crop. Also, it is important to recognize that this species is highly dispersive in the adult stage, and will fly hundreds of meters or more to feed.

Management

Foliar applications of insecticides will suppress grasshoppers, but they are difficult to kill, particularly as they mature. Bait formulations are not usually recommended because these grasshoppers spend little time on the soil surface, preferring to climb high in vegetation.

Land management is an important element of *S. americana* population regulation. Grasshopper densities tend to increase in large patches of weedy vegetation that follow the cessation of agriculture or the initiation of pine tree plantations. In both cases, the mixture of annual and perennial forbs and grasses growing in fields that are untilled seems to favor grasshopper survival, with the grasshoppers then dispersing to adjacent fields as the most suitable plants are depleted. However, as abandoned fields convert to dense woods or the canopy of pine plantations shades the ground and suppresses weeds, the suitability of the habitat declines for grasshoppers.

Disturbance or maturation of crops may cause American grasshopper to disperse, sometimes over long distances, into crop fields. Therefore, care should be taken not to cut vegetation or till the soil of fields harboring grasshoppers if a susceptible crop is nearby. Planting crops in large blocks reduces the relative amount of crop edge, and the probability that a crop plant within the field will be attacked.

► Grasshopper Pests in North America
► Grasshoppers and Locusts as Agricultural Pests
► Grasshoppers, Katydids and Crickets (Orthoptera)

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American Foulbrood

Historically, this is the most virulent disease of honey bees throughout the world. The bacterium responsible for the disease, *Paenibacillus* (= *Bacillus*) *larvae*, form heat- and drought-resistant spores that persist for years and germinate under favorable conditions. It is expressed in older larvae and young pupae, though infection occurs earlier, and young larvae are more susceptible than older larvae. Infected individuals turn darker in color, then black, and eventually collapse into a hardened mass in the cell. Signs of infection include a sour odor, perforated or sunken caps on the cells, and the presence of black deposits in the cells. If foulbrood is present, insertion of a twig or probe into a suspect cell will result in a gummy, stretchy substance being drawn out of the cell, often forming a thread or rope and called "ropy." Field diagnosis is possible by experienced inspectors, but is best confirmed microscopically or by molecular techniques. There are several subspecies of *P. larvae*, and *P. larvae* ssp. *larvae* is considered responsible for American foulbrood, with other subspecies also affecting honey bees.

Transmission occurs by feeding infected honey or pollen, by using infected equipment, and sometimes by installing infected package bees or queens. Feeding bees sugar syrup therefore is preferable to feeding them honey, and disinfection of hive tools is always recommended. Natural transmission from hive to hive can occur through robbing behavior. Queens and workers can carry the disease. Bee colonies that are infected normally are eliminated by burning them. Antibiotics can be fed to colonies to prevent infection.

► Honey Bees
► Apiculture
► *Paenibacillus*

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American Serpentine Leafminer, *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae)

This leafminer has long been found in eastern North America, northern South America, and the Caribbean. However, in recent years it has been introduced into California, Europe, and elsewhere. Expanded traffic in flower crops appears to be the basis for the expanding range of this species. *Liriomyza trifolii* (Burgess), sometimes known as the American serpentine leafminer, readily infests greenhouses. As a vegetable pest, however, its occurrence is limited principally to tropical and subtropical regions.

Life Cycle and Description

Leafminers have a relatively short life cycle. The time required for a complete life cycle in warm environments is often 21–28 days, so numerous generations can occur annually in tropical climates. Growth at a constant 25°C requires about 19 days from egg deposition to emergence of the adult. Development rates increase with temperature up to about 30°C; temperatures above 30°C are usually unfavorable and larvae experience high mortality. At 25°C, the egg stage requires 2.7 days for development; the three active larval instars require an average of 1.4, 1.4, and 1.8 days, respectively; and the time spent in the puparium is 9.3 days. Also, there is an adult preovipostion period that averages 1.3 days. The temperature threshold for development of the various stages is 6–10°C, except that egg laying requires about 12 C.

Egg

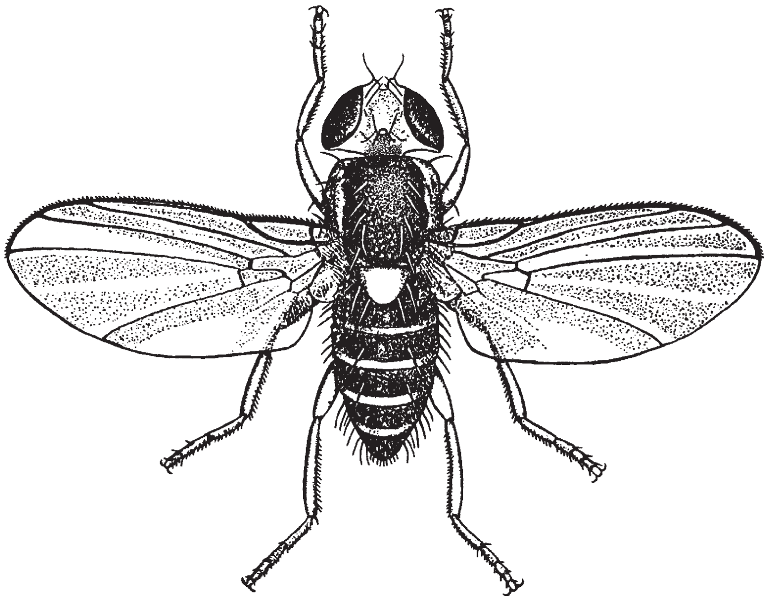
Eggs tend to be deposited in the middle of the plant; the adult seems to avoid immature leaves. The female deposits the eggs on the lower surface of the leaf, but they are inserted just below the epidermis. Eggs are oval in shape and small in size, measuring about 1.0 mm long and 0.2 mm wide. Initially they are clear, but soon become creamy white in color.

Larva

Body and mouth part size can be used to differentiate instars; the latter is particularly useful. For the first instar, the mean and range of body and mouth parts (cephalopharyngeal skeleton) lengths are 0.39 (0.33–0.53) mm and 0.10 (0.08–0.11) mm, respectively. For the second instar, the body and mouth parts measurements are 1.00 (0.55–1.21) mm and 0.17 (0.15–0.18) mm, respectively. For the third instar, the body and mouth parts measurements are 1.99 (1.26–2.62) mm and 0.25 (0.22–0.31) mm, respectively. A fourth instar occurs between puparium formation and pupation, but this is a nonfeeding stage and is usually ignored by authors. The puparium is initially golden brown in color, but turns darker brown with time.

Adult

Adults (Fig. 42) are small, measuring less than 2 mm in length, with a wing length of 1.25–1.9 mm. The head is yellow with red eyes. The thorax and abdomen are mostly gray and black although the ventral surface and legs are yellow. The wings are transparent. Key characters that serve to differentiate this species from the vegetable leafminer, *Liriomyza sativae* Blanchard, are the matte, grayish black mesonotum and the yellow hind margins of the eyes. In vegetable leafminer the mesonotum is shining black and the hind margin of the eyes is black. The small size of this species serves to distinguish it from pea leafminer, *Liriomyza huidobrensis* (Blanchard), which has a wing length of 1.7–2.25 mm. Also, the yellow femora of American serpentine leafminer help to separate it from pea leafminer, which has darker femora. Oviposition occurs at a rate of 35–39 eggs per day, for a total fecundity of 200–400 eggs. The female makes



American Serpentine Leafminer, *Liriomyza Trifolii* (Burgess) (Diptera: Agromyzidae), Figure 42 **Adult of American serpentine leafminer, *Liriomyza trifolii.***

numerous punctures of the leaf mesophyll with her ovipositor, and uses these punctures for feeding and egg laying. The proportion of punctures receiving an egg is about 25% in chrysanthemum and celery, both favored hosts, but only about 10% in tomato, which is less suitable for larval survival and adult longevity. Although the female apparently feeds on the exuding sap at all wounds, she spends less time feeding on unfavorable hosts. The males live only two to three days, possibly because they cannot puncture foliage and therefore feed less than females, whereas females usually survive for about a week. Typically they feed and oviposit during much of the daylight hours, but especially near mid-day.

Host Plants

Liriomyza trifolii is perhaps best known as a pest of chrysanthemums and celery, but it has a wide host range. For example, at least 55 hosts are known from Florida, including bean, beet, carrot, celery, cucumber, eggplant, lettuce, melon, onion, pea, pepper, potato, squash, and tomato. Flower crops that are readily infested and which are known to facilitate spread of this pest include chrysanthemum, gerbera, gypsophila, and marigold, but there are likely many other hosts, especially among the Compositae. Numerous broad-leaved weed species support larval growth. The nightshade *Solanum americanum*, Spanish needles, *Bidens alba*, and pilewort, *Erechtites hieracifolia*, were suitable weed hosts in Florida.

Damage

Punctures caused by females during the feeding and oviposition processes can result in a stippled appearance on foliage, especially at the leaf tip and along the leaf margins. However, the major form of damage is the mining of leaves by larvae, which results in destruction of leaf mesophyll. The mine becomes noticeable about three to four days after oviposition, and becomes larger in size as the larva matures. The pattern of mining is irregular. Both leaf mining and stippling can greatly depress the level of photosynthesis in the plant. Extensive mining also causes premature leaf drop, which can result in lack of shading and sun scalding of fruit. Wounding of the foliage also allows entry of bacterial and fungal diseases. Although leaf mining can reduce plant growth, crops such as tomato are quite resilient, and capable of withstanding considerable leaf damage. It is often necessary to have an average of one to three mines per tomato leaf before yield reductions occur. Leafminers are most damaging when they affect floricultural crops due to the low tolerance of such crops for any insect damage.

Natural Enemies

Parasitic wasps (parasitoids) of the families Braconidae, Eulophidae, and Pteromalidae are important in natural control, and in the absence of insecticides usually keep this insect at low levels of abundance. At least 14 parasitoid species are known from Florida alone. Species of Eulophidae such as *Diglyphus begina* (Ashmead), *D. intermedius* (Girault), *D. pulchripes*, and *Chrysocharis parksi* Crawford are generally found to be most important in studies conducted in North America, although their relative importance varies geographically and temporally. Predators and diseases are not considered to be important, relative to parasitoids. However, both larvae and adults are susceptible to predation by a wide variety of general predators, particularly ants.

Management

Sampling

There are many methods to assess leafminer abundance. Counting mines in leaves is a good index of past activity, but many mines may be vacant. Counting live larvae in mines is time consuming, but more indicative of future damage. Puparia can be collected by placing trays beneath foliage to capture larvae as they evacuate mines, and the captures are highly correlated with the number of active miners. Adults can be captured by using adhesive applied to yellow cards or stakes.

Insecticides

Chemical insecticides are commonly used to protect foliage from injury, but insecticide resistance is a major problem. Insecticide susceptibility varies widely among populations, and level of susceptibility is directly related to frequency of insecticide application. In Florida, longevity of insecticide effectiveness is often only two to four years, and then is usually followed by severe resistance among the treated populations. Rotation among classes of insecticides is recommended to delay development of resistance. Reduction in dose level and frequency of insecticide application, as well as preservation of susceptible populations through nontreatment of some areas, are suggested as means to preserve insecticide susceptibility among leafminer populations. Insect growth regulators have been more stable, but are not immune from the resistance problem. Insecticides also are highly disruptive to naturally occurring biological control agents, particularly parasitoids. Use of many chemical insecticides exacerbates leafminer problems by killing parasitoids of leafminers. This usually results when insecticides are applied for lepidopterous insects, and use of more selective pest control materials such as *Bacillus thuringiensis* is recommended as it allows survival of the leafminer parasitoids. Because parasitoids often provide effective suppression of leafminers in the field when disruptive insecticides are not used, there has been interest in release of parasitoids into crops. This occurs principally in greenhouse-grown crops, but is also applicable to field conditions. *Steinernema* nematodes have also been evaluated for suppression of leaf mining activity. High levels of relative humidity (at least 92%) are needed to attain even moderately high (greater than 65%) levels of parasitism. Adjuvants that enhance nematode survival increase levels of leafminer mortality, but thus far nematodes are not considered to be a practical solution to leafminer infestations.

Cultural Practices

Because broadleaf weeds and senescent crops may serve as sources of inoculum, destruction of weeds and deep plowing of crop residues are recommended. Adults experience difficulty in emerging if they are buried deeply in soil.

► Vegetable Pests and Their Management
► Flies

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American Silkworm Moths (Lepidoptera: Apatelodidae)

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American silkworm moths, family Apatelodidae, are exclusively New World, and total 252 species, mostly Neotropical (247 sp.). Three subfamilies are known: Apatelodinae, Epiinae, and Phiditiinae.

American Silkworm Moths (Lepidoptera: Apatelodidae), Figure 43 Example of American silkworm moths (Apatelodidae), *Apatelodes palma* Druce, from Ecuador.

Some researchers consider the family part of Bombycidae. The family is in the superfamily Bombycoidea (series Bombyciformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults (Fig. 43) small to medium size (20–74 mm wingspan), with head scaling roughened; haustellum absent (rarely vestigial); labial palpi small; maxillary palpi absent; antennae bipectinate; body robust. Wings broadly triangular; hindwings rounded. Maculation varied but mostly shades of brown or gray, rarely more colorful, with various markings. Adults are nocturnal. Larvae are leaf feeders. Host plants include various records in Aquifoliaceae, Betulaceae, Bignoniaceae, Lauraceae, Oleaceae, Rosaceae, among others.

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American Swallowtail Moths (Lepidoptera: Sematuridae)

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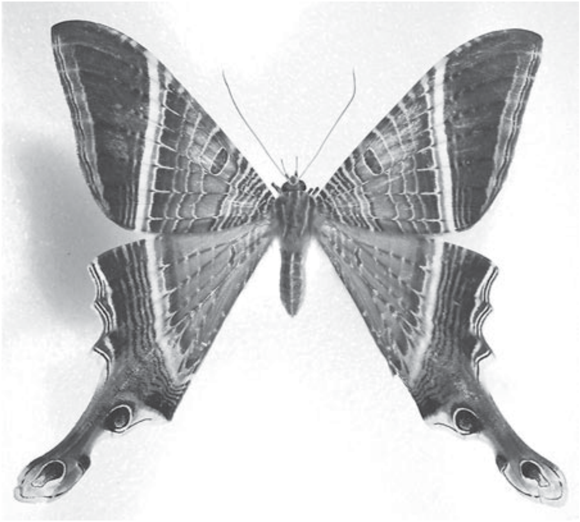
American swallowtail moths (Fig. 44), family Sematuridae, total 36 Neotropical species, one of which just reaches into the United States, in southern Arizona. The family is in the superfamily Uranioidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium to large (42–100 mm wingspan), with head roughened and eyes large; haustellum naked; labial palpi upcurved, with long second segment and correctly angled short, smooth apical segment; maxillary palpi minute, 1-segmented; antennae thickened, with elongated club (slightly hooked at tip). Wings triangular, with hindwings tailed (usually hindwings with some emarginations); body sometimes robust. Maculation various shades of darker brown, with vertical lines and bands, often brightly colored in the hindwings; often with eyespots on the tails. Adults are nocturnal but some may be crepuscular.



American Swallowtail Moths (Lepidoptera: Sematuridae), Figure 44 Example of American swallowtail moths Sematuridae), *Sematura lunus* (Linnaeus), from Costa Rica.

Larvae are leaf feeders, but few known biologically. Host plants are unrecorded.

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American Tropical Silkworm Moths (Lepidoptera: Oxytenidae)

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American tropical silkworm moths, family Oxytenidae, include 60 species, all Neotropical. Some specialists consider this family a subfamily of Saturniidae. The family is in the superfamily Bombycoidea (series Saturniiformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size to large (45–98 mm wingspan), with head vertex somewhat roughened; haustellum developed; labial palpi very large; maxillary palpi absent; antennae bipectinate; body somewhat slender or robust but with hair-like scales. Wings triangular with with falcate apex but sometimes rounded; hindwings somewhat angled and with short tails or sometimes rounded. Maculation mostly white with paired dark gray vertical striae and hindwings similar, but some species are dark brown with indistinct markings. Adults nocturnal. Larvae are leaf feeders; some mimic snakes. Host plants recorded in Rubiaceae.

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Ametabolous

Organisms that do not display the process of metamorphosis. In ametabolous organisms there is little change in body form during growth and molting.

► Metamorphosis

Ametropodidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Amino Acid

Chemical compounds that may occur free, or linked by peptide bonds into proteins.

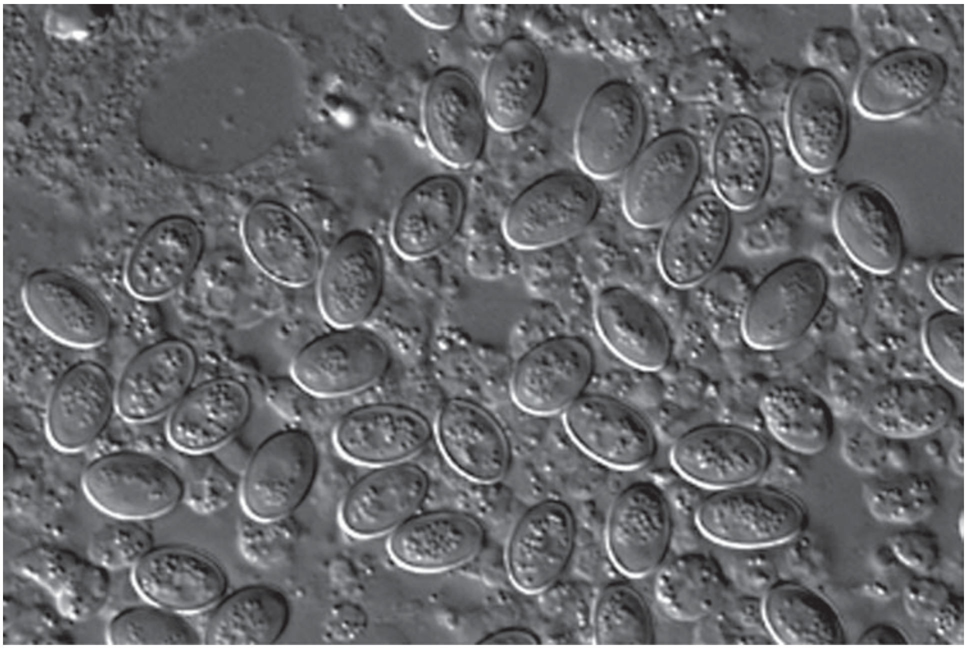
Ammophilous

Sand loving. Organisms inhabiting or preferring sandy habitats are called ammophilous (adjective) or ammophiles (noun).

Amoebae

The two best-studied insect amoebae are *Malpighamoeba mellificae* and *Malamoeba locustae*, which are associated with the honeybee, *Apis mellifera*, and the *Melanoplus* grasshoppers, respectively. The cysts of the honeybee amoeba are ingested and excyst, releasing slender primary trophozoites that penetrate and multiply in the midgut epithelium. Secondary trophozoites emerge from these cells and migrate to the lumen of the Malpighian tubules. These trophozoites, having pseudopodia, feed in the lumen and cause a flattening of the epithelial layer and a distension of the tubules. The brush border in contact with the amoeba swells in size and loses the associated secretory transport vesicles. Infected tubules contain a mix of secondary trophozoites, precysts, and cysts. The primary damage to the host bee is the malfunction of the Malpighian tubules. Both numbers of amoeba and the presence of other disease agents determine the severity of the amoebiasis in the bee. In general, this disease either induces stress or under appropriate conditions in the springtime can be debilitative, resulting in hive dwindling.

Malamoeba locustae, also known as *Malamoeba locusta*, has been detected in a wide range of grasshopper species and in a single *Thysanuran* species. Its life cycle is very similar to that observed with *M. mellificae*. The host grasshoppers ingest the resistant uninucleate cysts, and excysted primary trophozoites invade the midgut and caecal tissues. Within these tissues the trophozoites grow and divide, and within about 10 days release progeny secondary trophozoites into the lumen. These cells migrate to the lumen of the Malpighian tubules and undergo additional cell divisions (Fig. 45). The vegetative development of this amoeba damages the serosal membrane of the tubules, inhibiting their response to insect diuretic hormone. The infected tubules become packed with trophozoites and cysts. At high levels, *M. locustae* may inhibit the excretory function of the tubules and cause the grasshoppers to become lethargic prior to death. The distended, amoeba-infected tubules may rupture, releasing both trophozoites and cysts into the hemocoel. These amoebas are quickly recognized as non-self and are encapsulated by circulating phagocytic



Amoebae, Figure 45 **Light micrograph of the cysts of *Malamoeba locusta* released from infected Malpighian tubules.**

hemocytes. This disease, although a problem in laboratory cultured grasshoppers, is rarely detected in natural populations.

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Amoebiasis

Infection of an insect by amoebae.

Amorphoscelididae

A family of praying mantids (Mantodea).

► Praying Mantids

Amphienotomidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice, or Psocids

Amphiposocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice, or Psocids

Amphipterygidae

A family of damselflies (order Odonata).

► Dragonflies and Damselflies

Amphitheridae

A family of moths (order Lepidoptera) also known as double-eye moths.

► Double-Eye Moths
► Butterflies and Moths

Amphitoky

A type of parthenogenesis in which both females and males are produced.

Amphizoidae

A family of beetles (order Coleoptera). They commonly are known as trout stream beetles.

► Beetles
► Wasps, Ants, Bees and Sawflies

Amplification

In molecular biology, the production of additional copies of a chromosomal sequence, found as either intrachromosomal or extrachromosomal DNA. In medical entomology, the production of increased numbers of virus in a host. This is often a prerequisite to acquisition and transmission of the virus by a blood-feeding insect.

Amplification Hosts

Hosts of viruses that allow amplification of the virus, usually used in the context of arboviruses. Some hosts do not allow amplification, and so serve as an end-point in the virus cycle.

► Dead-end Hosts

Ampulicidae

A family of wasps (order Hymenoptera).

Anagrus Fairyflies (Hymenoptera: Mymaridae)

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Anagrus species (Mymaridae), among the smallest insects known, are endoparasitoids of eggs of Odonata and Hemiptera. The genus is worldwide and about 60 species is now recognized.

Taxonomy and Adult Morphology

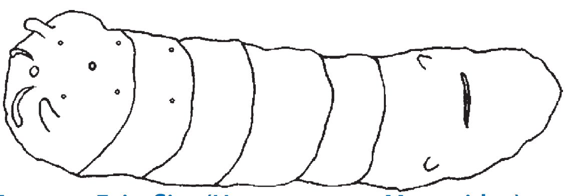
The metasoma of *Anagrus* is not constricted basally, so it appears broadly sessile, the hypochaeta in front of the marginal vein is basal to the first macrochaeta, the tarsi are 4-segmented, the posterior scutellum is longitudinally divided, and the foretibia has a comb-like spur. Adult males and females are similar, differing mainly in their antennae, with nine segments and clubbed in females (Fig. 46) and 13 segments and filiform in males. Body color is often darker in males. The genitalia, both in males (the aedeagus) and in females (the ovipositor), have features of taxonomic importance.

The genus is subdivided into three subgenera – *Anagrella*, *Anagrus*, and *Paranagrus*.

Biology

Like all holometabolous insects, *Anagrus* species have three distinct immature stages, egg, larva and pupa. The egg is stalked, with an ovoid body that swells during embryogenesis. There are two, apodous, larval instars (Fig. 47), which appear completely different from one another. The first instar is sacciform and usually attached to the egg chorion. It does not show any cuticular structure that could serve to feed, breathe or feel. It is completely immobile and probably obtains nourishment and breathes through its cuticle. The second instar is divided weakly into six body segments, has a mouth and a salivary gland opening, two mandibles and an anus, and various other, probably sensory, structures. No spiracle is present. Second instar larvae are very active and fight each other when in the same host egg. The mature larva (prepupa) develops inside the egg into an exarate pupa and does not spin a cocoon. When development is complete, adults are

Anagrus Fairyflies (Hymenoptera: Mymaridae), Figure 46 **Adult female of *Anagrus* sp.**



Anagrus Fairyflies (Hymenoptera: Mymaridae), Figure 47 **Larva of *Anagrus* sp.**

recognizable through the host egg chorion, through which they chew a hole to exit. After emergence the adults shed their waste products (meconium). Males are usually protandrous.

Behavior and Ecology

Reproduction is bisexual or parthenogenetic. The latter reproduction is usually arrhenotokous but, rarely, thelytokous parthenogenesis has been recorded. Females are ready to oviposit as soon as they emerge. Copulation, if it occurs, is usually very quick (some tens of seconds) and inseminated females generally do not copulate again. When fed with sugar water, honey or nectar, adults may live for up to 10 days. It is thought that adult host feeding may occur as in other parasitoids.

Anagrus species mainly parasitize leafhoppers (Cicadellidae), planthoppers, (Delphacidae) and damsel- or dragonfly (Odonata) eggs, all of which are embedded in plant tissue. To reach the eggs, females insert their ovipositor into the slit made by the host or through the plant tissue itself, depending on the species. Adults occur in various habitats, both natural and cultivated, depending on where their hosts occur. This includes dry habitats such as vineyards and beet fields to damp or aquatic ones (ponds) where host eggs are found in plants such as *Cyperus* or *Nuphar*.

Certain *Anagrus* species can develop both as solitary or gregarious parasitoids in eggs of different size, whereas others appear to be much more specialized on eggs of the same size, in which they always develop as solitary parasitoids.

Many *Anagrus* are extremely important because they provide control of potentially serious pests on many agricultural crops. The most important examples are against leafhoppers such as *Empoasca vitis* Goethe and *Zygina rhamni* (Ferrari) in vineyards in Europe and *Erythroneura* spp. in North America, against leaf- and planthoppers such as *Nilaparvata* spp. and *Sogatella* spp. on rice in eastern Asia, and against *Perkinsiella sacharicida* Kirkaldy on sugarcane in Hawaii.

Some biological supply companies mass produce and sell *Anagrus atomus* L. for biological control. Care must be taken to ensure the sanitary conditions of the product as the parasitoid is bred on the natural host eggs inserted into plant tissue, which could be a potential vehicle for other pests or diseases.

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Anajapygidae

A family of diplurans (order Diplura).

► Diplurans

Anal Angle

The hind angle of the forewings.

► Wings of Insects

Anal Cell

A cell in the anal area (anal lobe) of a wing.

► Wings of Insects

Anal Comb

This term is applied to a variety of structures that differ depending on the taxon. In flea (Siphonaptera) larvae, it refers to several rows of setae on the tenth abdominal segment; in caterpillars (Lepidoptera) it refers to a ventral projection at the tip of the abdomen that is used to eject frass; in some beetle (Coleoptera) larvae it refers to cerci-like projections near the tip of the abdomen.

Anal Gills

Gills found at the tip of the abdomen and usually consisting of three to five small clusters.

► Abdomen of Hexapods

Anal Hooks

In Lepidoptera, small hook or club-shaped structures at the tip of the abdomen that serve to anchor the pupa to the cocoon or silk pad.

Anal Furrow

The suture-like groove in the membrane of the wing.

► Wings of Insects

Anal Legs (Prolegs)

In holometabolous larvae, especially Lepidoptera larvae, the appendages of the tenth abdominal segment (the terminal prolegs).

Anal Lobe

The posterior region of the wing, occupied by the anal veins.

► Wings of Insects

Anal Loop

A cluster of cells between the anal wing veins, or between the cubitus and anal vein, in Odonata.

► Wings of Insects

Anal Plate

The shield-like plate or dorsal covering on the terminal segment in caterpillars, and some other larvae. It usually is dark in color, and is also called the anal shield.

Anal Tube

Eversible, tubular organs in the anal region of larval Coleoptera. These organs are armed with microspines and assist in attachment to the substrate.

Anal Vein

Longitudinal unbranched vein, or veins, extending from the base of the wing to the outer margin of the wing, below the cubitus vein.

► Wings of Insects

Anamorphosis

Postembryonic development in which additional abdominal body segments are added at the time of molting (the opposite of epimorphosis).

Anaxyelidae

A family of wood wasps (order Hymenoptera, suborder Symphyta). They commonly are known as incense-cedar wood wasps.

► Wasps, Ants, Bees and Sawflies

Ancistrosyllidae

A family of fleas (order Siphonaptera).

► Fleas

Andean Moon Moths (Lepidoptera: Cercophanidae)

JOHN B. HEPPNER
Florida State Collection of Arthropods, Gainesville, FL, USA

Andean moon moths, family Cercophanidae, include 30 species of mostly austral South American moths. There are two subfamilies: Cercophaninae (four sp.) and Janiodinae (26 sp.). Some specialists consider this family a subfamily of Saturniidae. The family is in the superfamily Bombycoidea (series Saturniiformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults (Fig. 48) medium size to large (24–105 mm wingspan), with head vertex roughened; haustellum absent; labial palpi very large; maxillary palpi absent; antennae bipectinate; body robust, with long hair-like scales. Wings broadly triangular, often with apex falcate, or more rounded; hindwings rounded or emarginated but sometimes with tails. Maculation various, but mostly shades of brown with diagonal line and fainter markings, but some with long tails and lighter tan, and with eyespots. Adults are nocturnal. Larvae are leaf feeders.

Andean Moon Moths (Lepidoptera: Cercophanidae), Figure 48 Example of Andean moon moths (Cercophanidae), *Cercophana venusta* (Walker) from Chile.

Host plants recorded in Celastraceae, Lauraceae, Saxifragaceae, and Tiliaceae.

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Andesianidae

A family of moths (order Lepidoptera) also known as valdivian forest moths.

► Butterflies and Moths
► Valdivian Forest Moths

Andrenidae

A family of bees (order Hymenoptera, superfamily Apoidae).

► Bees
► Wasps, Ants, Bees and Sawflies

Andrewartha, Herbert George

Herbert Andrewartha was born in Perth, Australia, on December 21, 1907. In 1924, he entered the University of Western Australia from which he obtained a bachelor's degree in agriculture. He was then appointed as assistant entomologist by the Western Australia Department of Agriculture. He began a study of a weevil pest of fruit trees, *Otiorhynchus cribricollis*, that required detailed autecological studies. In 1933, he moved to Melbourne, appointed by the CSIR as assistant research officer, to work on the autecology of *Thrips imaginis*, a pest of apple trees. He worked in the School of Agriculture and Forestry at the University of Melbourne. While working, he was able to complete a thesis for which he was awarded the degree of Master of Agricultural Sciences. He married, and in 1935 moved to the Waite Agricultural Research Institute in Adelaide. His main duties now turned to a study of *Austroicetes cruciata*, a plague grasshopper, and diapause of its eggs. However, his supervisor, who had been working on *Thrips imaginis*, died suddenly, leaving copious unanalyzed data, whose completion and publication fell to Herbert. The published work was criticized because it concluded that climatic factors were all-important in the population dynamics of the pest, without room for action of biotic factors. But it led to collaboration with L.C. Birch on a book (1954) "The distribution and abundance of animals." Then, after Herbert moved to the Zoology Department of the University of Adelaide, it led to a book designed as a textbook for students: (1961) "Introduction to the study of animal populations." In 1962, Herbert was appointed chairman of the Zoology Department. In the 1960s, with collaborators, he developed a program for control of *Dacus tryoni*, Queensland fruit fly, by release of sterile males. His next book, also co-authored with L.C. Birch was (1984) "The ecological web." He died on January 27, 1992, following his wife by some years, but survived by his son and daughter.

Reference

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Androconia

In Lepidoptera, glandular wing and body scales. Scent scales.

Androparae

In aphids, viviparous females that are produced on the secondary host in the autumn, and then fly to the primary host to produce males.

► Aphids

Anemometer

An instrument used for measuring wind speed, an important tool when considering use of pesticides because high wind speeds can result in pesticide drift.

Anemotaxis

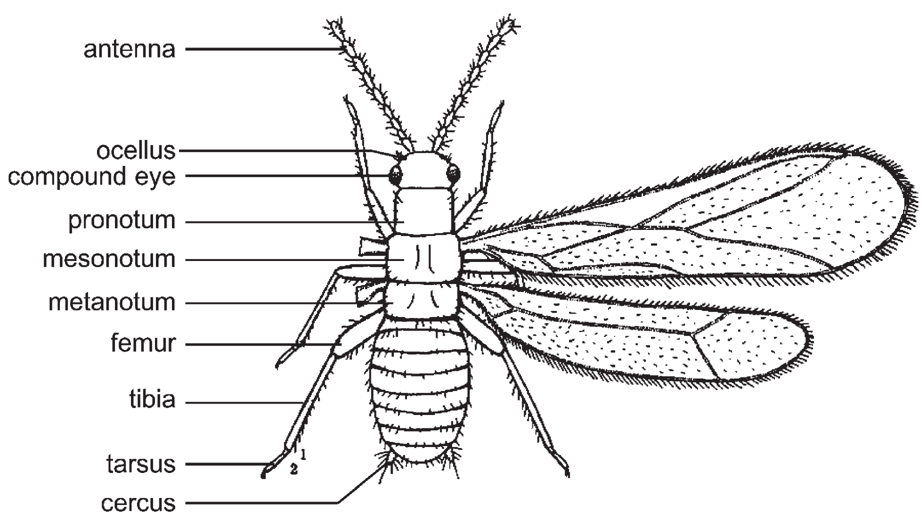
A movement in response to air movement or air currents.

Angel Insects (Zoraptera)

This is a small group of minute insects. They are infrequently encountered, and poorly known. The order name is based on the Greek words *zoros* (pure), *a* (without), and *pteron* (wing). There are only about 30 species described, all in the family Zorotypidae.

Characteristics

Angel insects are only about 3 mm long, with a wing span of 7 mm. They are dimorphic: a wingless form that lacks eyes, ocelli, and is only slightly pigmented, and a winged form (Fig. 49) that bears eyes, ocelli, and is darker in color. They have chewing mouthparts. The antennae are filiform, and consist of nine segments. The legs are unspecialized, the tarsi 2-segmented. The wings have simplified venation, and the wings can be shed, as is the case with termites. The abdomen is cylindrical and consists of 11 segments. Very short, 1-segmented cerci occur near the tip of the abdomen. Metamorphosis is not pronounced.



Angel Insects (Zoraptera), Figure 49 A diagram of an angel insect showing a dorsal view. The wings are removed from the left side of the body.

Biology

Angel insects are found beneath bark, in humus, decaying wood, and sometimes in association with termites. They are believed to feed on fungi. Apparently they swarm, and drop wings after swarming. They are gregarious, but there is no evidence of social organization.

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Angoumois Grain Moth, *Sitotroga cerealella* (Lepidoptera: Gelechiidae)

This is an important primary pest of stored grain.

► Stored Grain and Flour Insects

Angulate

Forming an angle.

Anholocyclic Life Cycle

A life cycle in which there is a complete lack of male insects (generally aphids). In this type of life cycle only viviparous parthenogenetic females are present throughout the year. (contrast with holocyclic life cycle)

► Aphids

Animal Sleeping Sickness

Also known as nagana, this is a disease of animals caused by protozoans in the genus *Trypanosoma*. In humans the same disease is known as African sleeping sickness or human trypanosomiasis. It is transmitted by tsetse flies in Africa.

► Trypanosomes

► Tsetse Flies

► Sleeping Sickness or African Trypanosomiasis

Anisembiidae

A family of web-spinners (order Embiidina).

► Web-spinners

Anisopodidae

A family of flies (order Diptera). They commonly are known as wood gnats.

► Flies

Anneal

The process by which the complementary base pairs in the strands of DNA combine.

Annual

A plant that normally completes its life cycle of seed germination, vegetative growth, reproduction, and death in a single growing season or year.

Anobiidae

A family of beetles (order Coleoptera). They commonly are known as death-watch beetles.

► Beetles

Anomosetidae

A family of moths (order Lepidoptera). They also are known as Australian primitive ghost moths.

► Australian Primitive Ghost Moths

► Butterflies and Moths

Anoplura

A suborder of wingless ectoparasitic insects commonly known as sucking lice (order Phthiraptera). It is sometimes treated as an order.

► Chewing and Sucking Lice

Anostostomatidae

A family of crickets (order Orthoptera). They commonly are known as wetas and king crickets.

► Grasshoppers, Katydids and Crickets

Anteclypeus

The lower of the two divisions of the clypeus.

► Mouthparts of Hexapods

Antagonist

An antagonist usually is an organism (usually a pathogen) that does no significant damage to the host, but its colonization of the host protects the host from significant subsequent damage by a pest.

Antecosta (pl., antecostae)

An internal ridge on the anterior portion of a tergum or sternum. It serves as a point of attachment for the longitudinal muscles.

Antenna (pl., antennae)

The paired segmented sensory organs, borne one on each side of the head. The antennae commonly protrude forward. Each antenna (Figs. 50 and 51) consists of three segments: the basal scape, a small pedicel, and an elongate flagellum. The flagellum is usually subdivided into many sections.

► Antennae of Hexapods

Antennae of Hexapods

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According to the known data on anatomy and embryology, the antennae are postoral structures of an appendicular nature that have been displaced, and now situated secondarily above the anterolateral regions of the cranium, in front of the mouth.

Taking into account their intrinsic musculature, two fundamental types of antennae can be distinguished:

Segmented Type

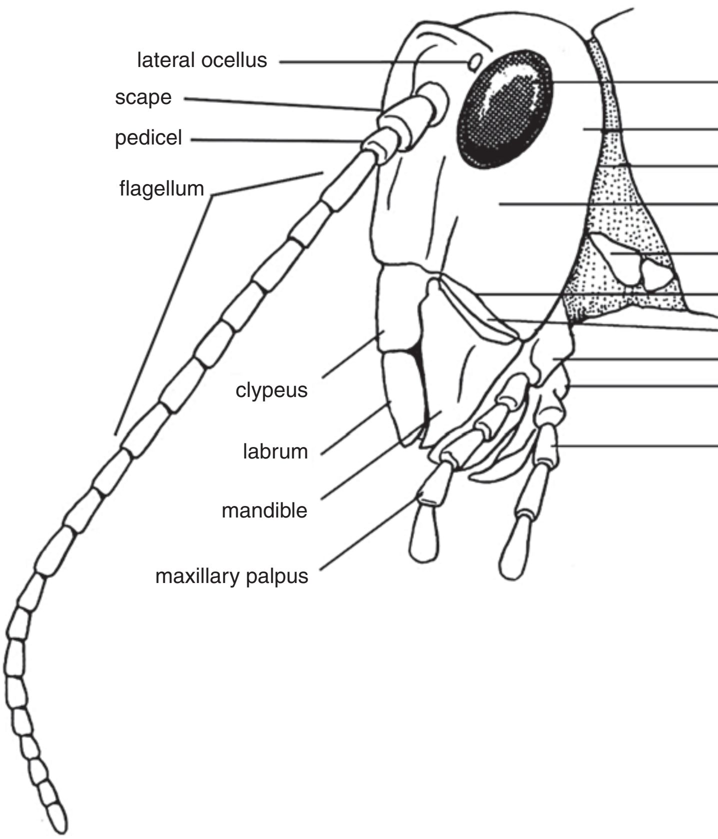
Each antennal division (antennomere) possesses intrinsic musculature (although the last segment generally lacks it). This type is found in Diplura and Collembola.

Annulated Type

Three segments are recognized that, from the basal to the apical zone of the antenna, are called scape, pedicel and antennal flagellum (Fig. 50).

The scape is a robust segment that unites the head capsule with a cuticular reinforcement (Fig. 51), the antennal socket (also called the torulus). In the antennal socket one or two condyles are distinguished, which serve to articulate the scape. The second segment is called the pedicel, and it usually varies in form and development, although it is generally small. Lastly, the flagellum is usually divided into several divisions called flagellomeres.

The movement of the antennae is carried out through extrinsic or motor muscles of the scape, generally forming three or four functional groups. Depending on the insect group, these muscles are inserted in the head capsule or in the tentorium.



Antennae of Hexapods, Figure 50 **Side view of the head of an adult grasshopper, showing some major elements.**

The antennae usually have bristles and sensilla of different types that act as chemoreceptor-, thermoreceptor- or hygroreceptor-type sensory organs. In addition, the antennae of males display modifications tending to increase their surface area, which permits harboring a great number of sensilla and acting as "detectors" that detect pheromones emitted by the females, and enable (usually) the males to locate the females for reproductive functions. Certain modifications in the antennae of the males can also be related to particular courtship behavior prior to mating.

In relation to the functions carried out by the antennae, it is necessary to highlight the presence, in the pedicel, of Johnston's organ, which is formed by cordotonal sensilla. It is fundamentally a proprioreceptor organ that provides information about the position of the antennae with respect to the head, the direction and force of the wind, or of the water currents in aquatic insects. In addition, it can act as an auditory organ in male mosquitoes and chirinomids, which perceive the sound produced by the females in flight.

The number of flagellomeres is a character that, in certain cases, is related to the sex, as occurs in some Aculeate Hymenoptera in which the males display 11 flagellomeres and the females 10. In others, it represents an important taxonomic character, emphasized in this sense the family Argidae (Hymenoptera: Symphyta) whose individuals display the flagellomere undivided.

Various types of antennae exist (Fig. 52), the appearance of which is owed fundamentally to the variation in form and development of the flagellomeres. The most important are:

Antennae of Hexapods, Figure 51 **Front view of the head of an adult grasshopper, showing some major elements.**

Filiform

The flagellomeres, normally numerous, are narrow, cylindrical, and of similar size. It is the most common type in the insects.

Moniliform

There exists a narrowing in the union of each flagellomere, which are more or less spherical, with the antenna acquiring a "rosaried" appearance (like the beads of a rosary). There are examples in various families of beetles.

Setaceous

The flagellomeres are extremely fine and diminish in diameter gradually toward the tip; the antenna thus acquires an appearance of seta or hair. The antennae of Odonata constitute a typical example.

Aristate

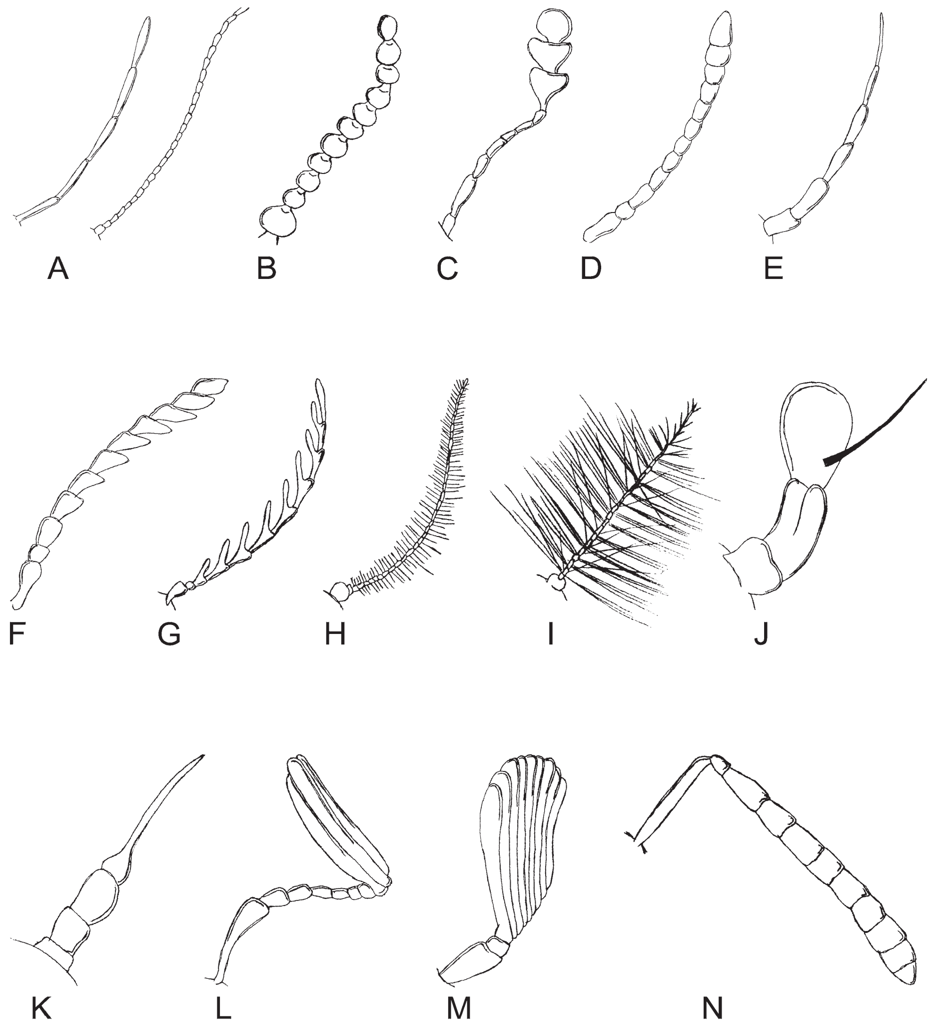
The last flagellomere is normally very wide and bears a conspicuous bristle named the arista. Examples are found in Diptera (Syrphidae and Muscidae).

Stylate

The last flagellomere is prolonged apically in a fine and elongated process named the style. Examples are found in Diptera (Rhagionidae and Asilidae).

Clavate

The flagellomeres increase in diameter gradually toward the apex. Examples are found in Coleoptera (Coccinellidae and Tenebrionidae).



Antennae of Hexapods, Figure 52 **Some common types of antennal forms: A, filiform; B, moniliform; C, capitate; D, clavate; E, setaceous; F, serrate; G, pectinate; H, bipectinate; I, plumose; J, aristate; K, stylate; L, lamellate; M, flabellate; N, geniculate.**

Capitate

In this case the last flagellomeres are of greater diameter, in contrast with the preceding, forming a "club" or "mace." Examples are found in Coleoptera (Nitidulidae and Silphidae).

Serrate

The flagellomeres display pointed, lateral prolongations, on one side or on both. Examples are found in Coleoptera (Elateridae).

Pectinate

The flagellomeres project laterally, forming a fine and more or less elongated projection. When it is produced over two sides of each flagellum, the antennae are called bipectinate. Examples are found in Coleoptera (Pyrochroidae).

Flabellate

The flagellum displays long, flattened or more or less cylindrical expansions. Examples are found in some species of Coleoptera (Scarabeidae).

Lamellate

Only the last flagellomeres display long, lateral expansions. Examples are found in Coleoptera (Scarabeidae, subfamily Melolonthinae).

Plumose

Flagellomeres with numerous long hairs are arranged in a feather-like or whorled form. Examples are found in male mosquitoes (Diptera).

Geniculate

The scape is relatively long, forming a clear angle with the rest of the antenna (pedicel plus flagellum). Examples are found in Hymenoptera (Formicidae and Chalcidoidea), and in Coleoptera (Lucanidae). Within this type of antenna, particular variations can exist, as in the case of the Ormyridae (Hymenoptera: Chalcidoidea), in which the first divisions of the flagellum are of a lenticular type (lens shaped, or double convex).

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Antennal Club

On a clubbed antenna, the enlarged distal segments.

► Antennae of Hexapods

Antennal Fossa

A groove or cavity in which the antennae are located or concealed. This is also called the antennal insertion.

► Antennae of Hexapods

Antennal Sclerite

A ring into which the basal joint of each antenna is inserted.

► Antennae of Hexapods

Antennation

Sensory or tactile movements with the antennae that result in contact of the antennae with an object.

Antennule

A small antennal or feeler-like process.

Anterior

This term usually is used to refer to the end of the body containing the head, or the direction of the head, or the front of the insect.

Anthelidae

A family of moths (order Lepidoptera) also known as Australian lappet moths.

► Australian Lappet Moths
► Butterflies and Moths

Anther Smut of Carnations

This is a fungal disease of carnations that is transmitted by insects.

► Transmission of Plant Diseases by Insects

Anthicidae

A family of beetles (order Coleoptera). They commonly are known as antlike flower beetles.

▶ Beetles

Anthocoridae

A family of bugs (order Hemiptera). They sometimes are called minute pirate bugs.

▶ Bugs

Anthomyiid Flies

Members of the family Anthomyiidae (order Diptera).

▶ Flies

Anthomyiidae

A family of flies (order Diptera). They commonly are known as anthomyiid flies or root maggots.

▶ Flies

Anthomyzid Flies

Members of the family Anthomyzidae (order Diptera).

▶ Flies

Anthomyzidae

A family of flies (order Diptera). They commonly are known as anthomyzid flies.

▶ Flies

Anthophilous

Flower loving. Most insects that feed on nectar or pollen are anthophilous, including many butterflies and moths (Lepidoptera), wasps, ants and bees (Hymenoptera), but also numerous flies (Diptera), beetles (Coleoptera) and thrips (Thysanoptera).

▶ Pollination and Flower Visitation

▶ Butterfly Gardening

▶ Night Blooming Plants and their Insect Pollinators

▶ Pollination by Yucca Moths

▶ Apiculture

▶ Plant Extrafloral Nectaries

Anthribidae

A family of beetles (order Coleoptera). They commonly are known as fungus beetles.

▶ Beetles

Anthrophagy

Feeding on humans by other organisms. The most common anthrophagous organisms are insects, particularly biting flies, followed by lice, fleas, and ticks.

▶ Mosquitoes

▶ Lice

▶ Fleas

▶ Ticks

▶ Pathogen Transmission by Arthropods

Anthrophoridae

A family of bees (order Hymenoptera, superfamily Apoidae). They commonly are called cuckoo bees, digger bees, and carpenter bees.

▶ Bees, Wasps, Ants and Sawflies

Anthropocentric

An interpretation based on the belief that humans are the central fact or element of the universe, and interpreting everything in relation to human values of interests.

Anthropomorphism

The attribution of human qualities or forms to animals or their behaviors.

Anthropophilic

An insect that prefers humans as a source of food. A blood-sucking insect that feeds on humans.

Antibiosis

A characteristic, often a chemical within a plant, that inhibits survival or reproduction when an insect feeds upon it.

► Plant Resistance to Insects

Antibiotic

A chemical produced by a microorganism that affects the ability of another microorganism to survive or grow.

Anticodon

The triplet of nucleotides in a transfer RNA molecule that is complementary to and base pairs with a codon in a messenger RNA.

Antidote

A treatment used to treat the effects of chemical (e.g., insecticidal) poisoning.

Antidiuretic Hormones

Hormones acting on the hindgut to promote water reabsorption and conservation.

Anti-Drift Agent

A compound that is added to pesticides to reduce the number of droplets produced at the spray nozzle, and therefore to reduce the possibility of the product drifting away from the target.

Antixenosis

An effect due to a characteristic, often a physical or chemical attribute of a plant, that deters feeding or oviposition. This is also called nonpreference.

► Plant Resistance to Insects

Antlike Flower Beetles

Members of the family Anthicidae (order Coleoptera).

► Beetles

Antlike Leaf Beetles

Members of the family Aderidae (order Coleoptera).

► Beetles

Antlike Stone Beetles

Members of the family Scydmaenidae (order Coleoptera).

► Beetles

Antlions

Members of the family Myrmeleontidae (order Neuroptera).

► Lacewings, Antlions and Mantidflies

Ant-plant Interactions

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Drop a spoon at a picnic and the ubiquity of ants (family Formicidae) is soon apparent. Ants are everywhere, lurking in leaf litter or brazenly scouring terrestrial and arboreal habitats for food in any form. Except in extreme climates that are inhospitable to insects, most terrestrial organisms have necessarily evolved ways to reduce the damage ants can cause, and many have managed even to extract benefits from them. Relationships between ants and humans provide examples: not only have we devised means of protecting our food stores from ants, but we have utilized ants to protect our food. Centuries ago, nests of Old World weaver ants (*Oecophylla smaragdina*) were cultivated in Asian orchards to control plant pests. Workers of this highly predatory species captured and devoured both the juvenile and adult stages of herbivorous (plant-eating) insects.

In some ways, early ants were better suited to serve plants than to injure them. Descended from predatory wasps, they were poorly adapted for herbivory (consumption of plant tissues), and no ant is truly folivorous (leaf-eating). Unable to digest cellulose themselves, ants also differ from termites in lacking gut microbes that can do this for them. Although much of the plant world is therefore not available to ants, plant sap, seeds, and fruit pulp are relatively easy to digest, and many (mostly arboreal) taxa feed on those resources. Such foods tend to be rich in carbohydrate (CHO) but poor in nitrogen (N) (amino acids, peptides and proteins), and dietary excesses of energy-rich CHOs may have subsidized colonization of the arboreal zone, where foragers must commute around a three-dimensional and poorly connected environment. Most ants also scavenge N-rich arthropod carrion, and many are active predators that can potentially benefit plants by attacking their herbivores. In some taxa, associations with intracellular and extracellular gut microbes contribute to the colony's N economy through N-recycling and possibly upgrading (conversion of non-essential to essential amino acids).

When disturbed by ants, many active insects and other animals can simply fly or walk to safety, but for plants and their seeds, as well as for comparatively immobile nesting animals and juvenile insects, there are no ready escape routes. It is in these organisms that we find some of the most unique or unusual adaptations for both defending against ants and exploiting their behaviors to advantage. Here, several categories of interactions between ants and plants are explored, together with some of the myriad ways in which plants have evolved to reduce or promote association with these ubiquitous insects. Included also are the influence of plant resources on ant ecology and evolution, and the effects of ants on the evolution of plant defenses.

Ants as Seed Predators

In warm deserts and other arid regions, ants are often both abundant and diverse, and annual and perennial plants are present more often as seeds than as adults. Here, seed-eating ants abound and may exert strong selection pressures on plant. Selection is mediated mainly by seed consumption, but also by ant effects on soil disturbance and nutrient availability. Seed-eating "harvester ants" typically return seeds individually to a central nest site where they husk and then cache them in underground granaries, often for long time periods. By storing foods that degrade slowly over time, ant colonies can persist in habitats where the production of seeds and other resources is sporadic and unpredictable. During periods of low food availability, many of these ants simply remain underground and forego the risks and poor rewards of external activity.

The small individual sizes and ectothermy of ants are correlated with low foraging costs, enabling these insects to forage economically even for tiny seeds with dispersed distributions. Ants can

Ant-plant Interactions, Figure 53 **An extensive nest of leaf-cutter ants in the genus *Atta* (above) and high rates of leaf removal from an unlucky tree (below).**

therefore reduce soil seed banks to lower levels than can large, endothermic (“warm-blooded”) vertebrate seed-eaters like rodents and birds. Those taxa have higher foraging costs and tend to specialize in feeding on seeds in high density “hotspots,” either in soils or on the plants themselves. Though reduced seed densities can potentially affect both plant densities and community composition, ants may commonly have less impact on plant communities than do vertebrate seed predators. This is so because seed predation by ants tends to fall most heavily on offspring of small-seeded plant species, whereas that by vertebrates often targets large seeds. Seedlings germinating from large seeds begin life with more resources than do those from small seeds and are therefore superior competitors within plant communities. Consequently, the removal of small seeds by ants has comparatively little effect on the densities of large-seeded species, while the removal of large seeds by rodents may lead to increases in the densities of small-seeded species.

In at least some localities, differences in seed size specialization by ants and rodents account for disparities in the short-term and long-term effects of these granivores on one another’s populations. When seed-eating rodents were removed experimentally in one study, densities of harvester ants first increased and then declined. The short-term increase was likely due to competition between the two types of granivores, as there was some overlap in the sizes and species of seeds used by the two groups. However, rodent removal eventually led to increases in the densities of large-seeded plants, which subsequently out-competed small-seeded species, to the long-term detriment of ants.

Coexisting species of harvester ants often differ in worker body sizes, and small ants cannot carry the largest seeds. To a degree, therefore, worker size differences may remove small and large ants from resource competition with one another, and also determine disparate effects on plant communities. When ant communities are disturbed, either directly or by the introduction of non-native ants, there can be consequences for plant communities. Pathways of interaction can be indirect and complex. For example, if an introduced ant species produces a decline in populations of a native harvester ant, plant species on which the native ants specialize may increase at the expense of other components of the plant community. Such changes in community composition are hard to predict, and often become apparent only over long time periods, especially in arid lands with variable climates.

On an evolutionary time scale, some plants have acquired adaptation that reduce depredation of their progeny by ants. An example of such an adaptation is the use of hygroscopic awns (e.g., that of *Erodium cicutarium*) that alternately extend and coil when wet and dry, respectively, pushing the attached seeds beneath the soil surface. Unlike seed-eating rodents, harvester ants have little access to individually buried seeds, so such awns do appear to proffer a refuge from predation by granivorous ants. Whether mechanical, chemical, or phenological (e.g., timing of seed production), mechanisms of seed escape from granivorous ants remain poorly explored.

Early "Farmers" (Attines)

To the uninitiated, the cutting and transport of leaf, flower and fruit fragments by New World ants in the tribe Attini looks a great deal like herbivory (Fig. 53). However, as was originally proposed by Thomas Belt, a nineteenth century British mining engineer and amateur naturalist, the ants themselves do not digest cut leaves. Rather, they cultivate fungi that degrade cellulose and other plant products otherwise inaccessible to the ants. In more recent members of this group (species of *Atta* and *Acromyrmex*), the workers themselves feed on plant sap released from cut leaves, whereas larvae are fed gonglydia, or swollen tips of fungal hyphae (arms). Together, fungal mycelia and gongylidia supply CHOs (simple sugars, as well as glycogen in *Acromyrmex*), lipids and N (amino acids and protein). On her nuptial flight, the queen carries fragments of fungal gardens in her infrabuccal chamber, adjacent to the anterior digestive tract in the head. After mating, she removes her wings, excavates a terrestrial nest, begins to cultivate her fungal garden, and feeds her first worker brood on trophic eggs composed of resources from her degraded wing muscles.

Workers eventually take over cultivation and maintenance of the fungal gardens. Larger castes cut, drop, and carry the leaf fragments, while their smaller nestmates "hitch-hike" rides on leaf fragments to defend larger workers against parasitic phorid flies, and care for brood inside the nest. There, they lick and shred leaf fragments into finer pieces, and then chew their edges, depositing fecal droppings with digestive enzymes to aid in decomposition. Protein-degrading enzymes are recycled from the fungi themselves through the ant's digestive system, which lacks enzymes to degrade them. New leaf fragments are then inoculated with mycelia of older parts of the garden and fertilized with plant material (recent attines) and/or feces and animal matter (early attines). Through application of growth hormones, enzymes, nutrients, and antibiotics, higher attines maintain their fungi almost in monocultures. Nevertheless, recent studies by M. Poulsen, C.R. Currie, and colleagues have identified a virulent fungal pathogen of the gardens, as well as a bacterium living in fovea (small depressions) in worker exoskeleton. These filamentous bacteria, or actinomycetes, produce antibiotics directed mainly toward the common pathogen.

Although most folivorous insects are limited to eating a narrow spectrum of plant species, use of fungi as agents of digestion may explain leafcutter tolerance of more varied diets. Nevertheless, different taxa of higher attines specialize on grasses or dicots, and specialization exists even within those categories. Like other herbivores, leafcutters are especially likely to harvest tender young leaves, which lack the fiber and lignin to make them tough. For *Atta cephalotes*, J.J. Howard and colleagues showed that, the diet is apparently not chosen in response to energy, nitrogen, or moisture content,

Ant-plant Interactions, Figure 54 **Ants tending Hemiptera outside and inside plant stems: (above) *Azteca* tending mealy bugs (Pseudococcidae) in the New World tropics, and (below) *Podomyrma* sp. tending scale insects (Coccidae, arrows) inside branches of *Chisocheton* (Meliaceae) near Madang, Papua New Guinea.**

but rather to avoid various terpenoids that could poison fungi.

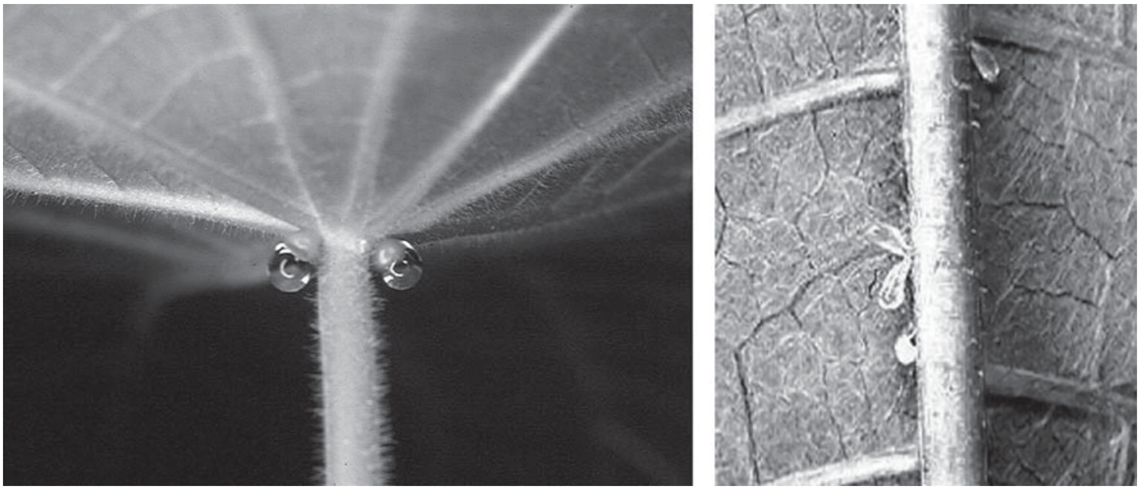
According to U.G. Mueller and colleagues, all attines appear to have descended from a common ancestor that forged relationships with fungi either growing on walls of leaf-litter nests or using ants to disperse their spores. Together, with gene sequence data, the fossil record, and confinement of this group to the New World, suggests that this ant-fungal partnership first formed between 45 and 65 million years ago. Direct transmission of fungi from queens to reproductive daughters provided opportunities for greater specialization and dependency to evolve in both partners. Nevertheless, new fungal species have also been domesticated by older, less specialized ant taxa in recent times.

The success of the attine-fungal partnership is measurable in its impact on the forest. Mature *Atta* nests can range over several hundreds of square meters, and worker columns can reach trees more than 100 m from the colony along trails cleared of vegetation. In tropical areas not regularly flooded, attines can be very abundant and exact a considerable toll on plants. Some accounts in the literature judge them to be responsible for 12–17% of all herbivory, but these figures may be too high because they fail to include the mostly invisible losses of plant resources to sap-feeding insects. Throughout much of the Neotropics, higher attines also thrive in disturbed areas dominated by poorly defended pioneer (weedy) plant species. They are similarly destructive to agriculture, and cause millions of dollars in losses annually to crop plants that have been selected by humans for low toxicity.

Pastoralists

Ants may also affect plants indirectly through the farming (or "tending") of insects in the order Hemiptera. With mouthparts highly modified as stylets, or "soda straws," these insects are phloem- or xylem-sucking consumers of plant sap (Fig. 54) and include aphids, leafhoppers, treehoppers, scale insects, and the like. Because plant sap is N-poor, sap-feeding hemipterans must process large quantities of these liquids to concentrate sufficient nitrogen for growth and reproduction. Moreover, while they feed, their relatively immobile immature or nymphal stages are exposed for long time periods to the risks of predation and parasitism. As a by-product of processing large quantities of sap for N, many Hemiptera release excess sugars as "honeydew" from their abdomens. When compensated by this attractive resource, ants forego predation of these insects and even protect them from other natural enemies. Relatively N-rich tissues like young leaves, and the pedicels of flowers and fruits, are particularly good sites for sap-feeders and the ants which herd them there. In Asian rain forests, where plant reproduction is highly sporadic, ants in the genus *Dolichoderus* have evolved as "migratory herdsmen," carrying their sap-feeding mealy bugs over long distances in search of optimal feeding sites.

Hemipteran tending, often compared to human tending of domestic livestock, is a mainstay for many arboreal ants. Still, to balance their diets, ants occasionally harvest some of the tender hemipteran nymphs and consume N-containing hemolymph of these and other arthropods. The relative strengths of positive and negative effects of the ants (herbivore reduction vs. hemipteran tending) determine the net effect of ants on a plant's well-being and reproduction (i.e., its fitness). This net outcome can be positive if herbivores are abundant and tending ants are effective in driving them away. However, as hemipteran populations thrive and grow under ant protection, removal of large quantities of sap can threaten the host plant's health. Living in intimate contact with hosts, Hemiptera also transmit viral and other plant pathogens. Not surprisingly then, plants appear to have fought back over evolutionary time. For example, hairs (trichomes) on leaves or stems prevent hemipteran stylets from reaching the plant surface. Other evolved responses are best understood in the context of the old adage that "the enemy of my enemy is my friend." Thus, many plants may have short-circuited the Hemiptera out of these tripartite interactions by paying the ants directly, i.e., by provisioning them with carbohydrate rewards in the form of sugar-rich extrafloral nectars (EFNs, Fig. 55) or lipid-rich pearl bodies (PBs). J.X. Beccera and D.L. Venable hypothesize that by increasing the CHO:protein ratio in the ants' own diets, plants induce ants to consume more of their Hemiptera. Arguing against this hypothesis for the origin of EFNs are observations of ants tending both sap-feeders and EFNs. Despite such observations, D.W. Davidson and colleagues have proposed that the hypothesis might help to



Ant-plant Interactions, Figure 55 Myrmecophyte-produced food rewards for ants: (left) Extrafloral nectaries (EFNs) at the junction of leaf blade and petiole of *Endospermum medullosum* (Euphorbiaceae) near Madang, Papua New Guinea; (right) pearl bodies (PBs) on lower leaf surface of *Cecropia engleriana* (Cecropiaceae) at Cocha Cashu, Peru. Both EFNs and PBs also occur in myrmecophilic plants.

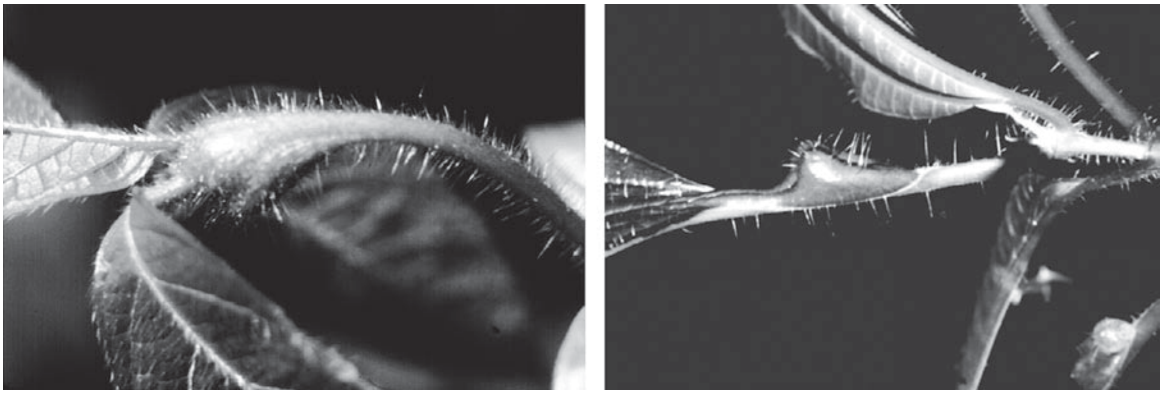
explain early divergence in foraging habits of major ant taxa that differ in their propensity to tend hemiptera versus EFNs.

Biotic Defenses of Plants

Even in relationships not (or no longer) involving Hemiptera, production of ant attractant foods should increase the presence of ants on vegetative and reproductive plant tissues and help to deter a variety of insect and other herbivores. Plant adaptations for defense by ants, wasps and other potential predators of insect herbivores are referred to as "biotic defenses," since they require the collaboration of other living things.

Some Definitions and Constructs

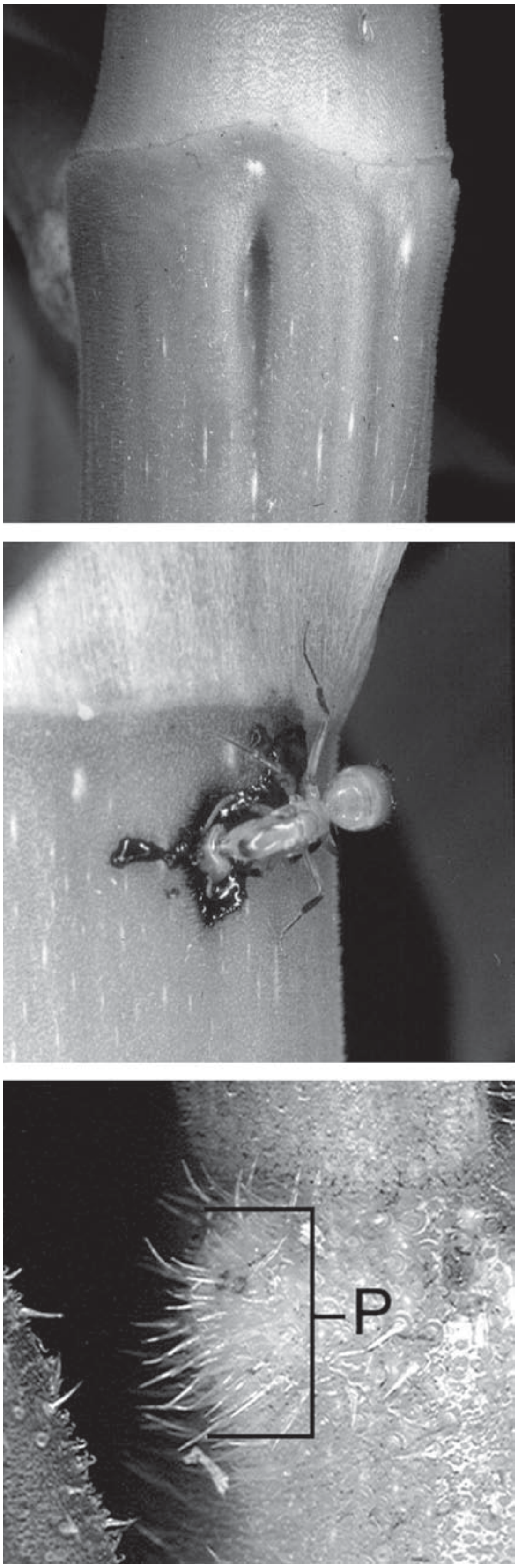
Whether the anti-herbivore protection of plants by ants is afforded through consumption of Hemiptera or deterrence of other herbivores, such protection completes the requirement for what are termed "mutualistic" interactions. Both parties in these relationships benefit, the ants directly from plant provisioning of resources, and the plants indirectly, usually through deterrence of damaging herbivores. Mostly, these interactions are opportunistic and unspecialized, depending on which ants, herbivores, and plants co-occur within a community. Plants with opportunistic ant associations based on production of food rewards alone are said to be "myrmecophilic" or "ant-loving." In contrast, at tropical latitudes, many ant-plant relationships have become more highly specialized and obligatory. That is, in the context of their natural communities, partners cannot survive and reproduce in the absence of their associates. In this case, resident "phytoecious" ants protect their host plants, (Fig. 56) and "myrmecophytes" (true "ant-plants") provide not only food but housing in stem or leaf structures termed "domatia." Individual ant colonies and myrmecophytes may live together over substantial portions of their life histories in relationships therefore termed "symbiotic mutualisms." (Although often used incorrectly in place of "mutualism," the term "symbiosis" - literally "living together" - is value neutral, including negative interactions like parasitism, as well as mutually beneficial interactions.) "Cheater" ants, which benefit plants less than the evolved partner, or otherwise negatively



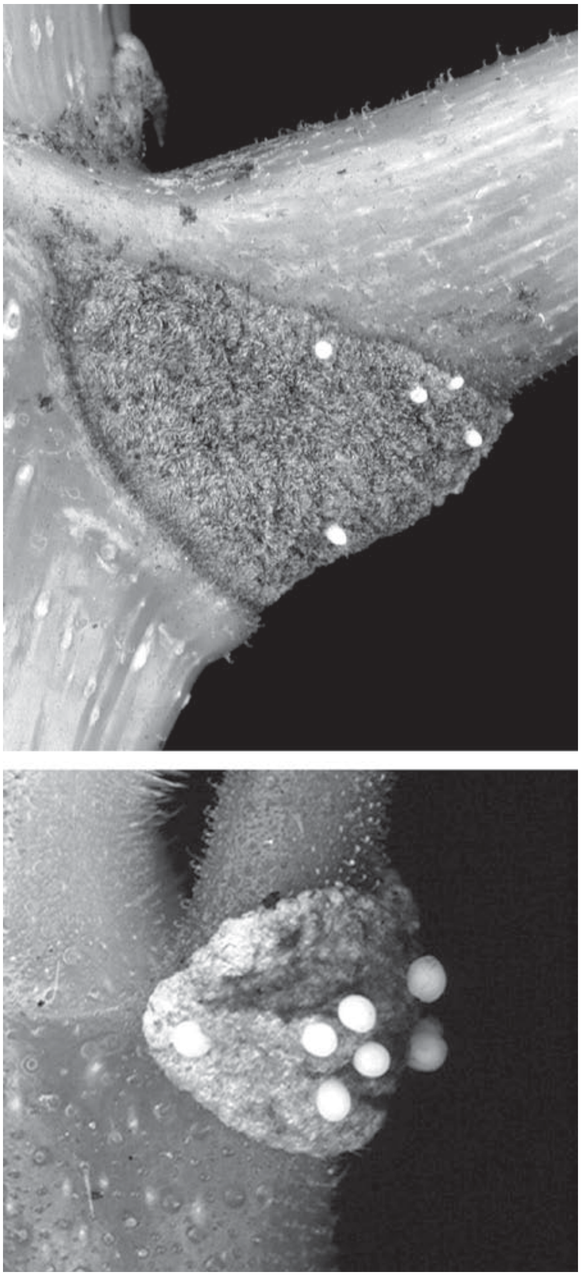
Ant-plant Interactions, Figure 56 **Caulinary (left) and foliar (right) domatia of ant-plants. Forming the domatia of many myrmecophytes are swollen stems or support structures, either naturally hollow or with weak pith, removed by ants. Shown here (left) is a branch of *Duroia hirsuta* (Rubiaceae, vic. Iquitos, Peru), swollen at attachment of large opposite leaves. Tiny ants in genus *Myrmelachista* inhabit these naturally hollow caulinary domatia. Foliar domatia, like that shown here for *Tococa* sp. (Melastomataceae, from Cocha Cashu, Peru) (right) are highly modified and more obviously evolved to accommodate ants.**

impact hosts, may occasionally prevail in symbioses because they are better colonists or competitors.

In symbiotic ant-plant relationships, partners are more likely to have undergone coevolution, i.e., reciprocal genetic (evolutionary) responses to selection pressures exerted by each partner on the other. Coevolution has two aspects: coadaptation and cospeciation, and only the former occurs frequently in symbiotic ant-plant partnerships. Illustrating coadaptation (reciprocal adaptation), many plants have evolved restrictive (Fig. 57) entrances to their domatia as a means of favoring colonization by certain ant taxa over others, while queens of phytoecious ants have responded by evolving traits enabling them to recognize and colonize such entrances expeditiously. Similarly, plants and ants may have coadapted with respect to the types or sizes of food rewards offered (Fig. 58) and their utilization or accessibility. In contrast, cospeciation (the co-radiation of ant and plant lineages to give congruent phylogenies) appears to be quite rare even in tropical symbiotic ant-plant relationships. Rarity likely results from the fact that ant and plant propagules (i.e., new queens and seeds) disperse independently, leaving much opportunity for new partnerships to form over evolutionary time. Seeds must germinate and produce seedlings of a threshold size before the next generation of hosts can support ant colonies. Environmental variation or randomness in the abundances of, and proximities

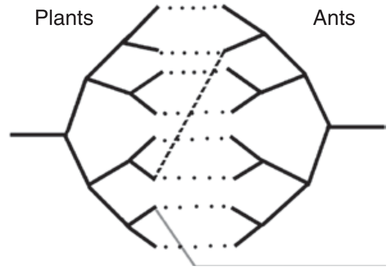


Ant-plant Interactions, Figure 57 **The prostomata (stem entrances) of *Cecropia* species come in various sizes and forms correlated with host use by different ant taxa: *Cecropia engleriana* (above) produces a narrow inverted prostoma, recognized and colonized by comparatively small queens of *Azteca australis* (Dolichoderinae) (center); in contrast (below), those of *Cecropia* sp. nov ("pungara") are convex and covered in urticating hairs; this host species attracts much larger queens of a ponerine ant, *Pachycondyla luteola*. Both photos are from Cocha Cashu, Peru.**



Ant-plant Interactions, Figure 58 **Food bodies of myrmecophytic *Cecropia* also come in different sizes, as shown here for *Cecropia membranacea* (above), usually associated with tiny *Azteca* ants, and closely related *Cecropia* sp. nov. ("pungara") (below), housing the much larger *Pachycondyla luteola*. Both are from at Cocha Cashu, Peru.**

to, sources of colonizing queens, provide ample opportunity for host-switching or *de novo* colonization by previously uninvolved ant taxa. This



Ant-plant Interactions, Figure 59 **A hypothetical case of cospeciation, illustrated by the congruent or mirror-image phylogenies (= genealogies, solid dark lines) of associated (dotted lines) ant and plant taxa. On each occasion when a plant species splits into two distinct taxa, the associated ant lineage also undergoes a speciation event. For cospeciation to have occurred, splits in plant and ant lineages must have occurred contemporaneously and be attributable to selection imposed by the partner. Otherwise, an ant lineage may have just radiated secondarily over a pre-existing plant lineage. The dotted and grey lines depict two kinds of evolutionary colonization events: respectively, host switching and *de novo* colonization by a previously unassociated ant lineage.**

picture contrasts sharply with that for, e.g., higher attines and their fungi; there, I.H. Chapela and colleagues have shown that queens transmit fungi between generations of colonies, and phylogenies of the two lineages are largely congruent (Fig. 59).

Despite little evidence for cospeciation in symbiotic ant-plant associations, contemporaneous diversification within partner lineages may occur through diffuse coevolution, defined by D.H. Janzen as reciprocal evolutionary responses to a suite of potential partners. Additionally, if host availability were often limiting, phytoecious ants may frequently have colonized non-myrmecophytic relatives of those plants, exerting new selection on these species to evolve ant-attractive traits. Based on multiple independent origins of myrmecophytism in older and more recent Asian *Macaranga*, S.-P. Quek and colleagues have proposed just such a scenario. A parallel argument is that, lacking their typical associates, habitat-switching hosts could have provided evolutionary opportunity for the origin of new phytoecious ant taxa.

These examples are relevant in the context of the different selection pressures driving diversification in myrmecophytes versus phytoecious ants. As noted by D.W. Davidson and D. McKey, proliferation of plant species has been driven principally by colonization of new habitats, accompanied by evolution of new defensive strategies and (correlated) growth rates, etc. In contrast, ants have diversified mainly in response to biogeographic factors and (especially) plant traits favoring certain associates over others (below). Why this asymmetry? Plants grow through seedling stages without their ants, and their success during this most vulnerable period depends on factors such as light and nutrient regimes, i.e., on habitat. Additionally, any of several ant taxa may provide acceptable protection against herbivores. In contrast, phytoecious ants are typically restricted to their hosts throughout the life history, and disparities in host characteristics (e.g., habitat-correlated growth rates and investment in biotic defense) should be highly consequential. This asymmetry in selection pressures is reflected in both the specificity of partnerships and evidence for coadaptation. Individual *Cecropia* species can house ants in different genera or even sub-families, while associated ants do not inhabit plants outside this genus. Similarly, phytoecious ants of bamboos have adapted to these hosts by evolving means of water evacuation from nest culms (active bailing or passive engineering), and they do not live elsewhere. In contrast, no bamboo has been determined to have evolved ant attractants.

Factors Driving Evolutionary Specialization

Factors driving evolutionary specialization in phytoecious ants are apparent from assessing both the taxonomic affiliations of these ants and traits of coadapted partners. Despite the frequent impression that such ants are ferociously aggressive against vertebrates (including many an unfortunate investigator), they appear often to include comparatively weakly competitive ant taxa that persist only in association with myrmecophytes. Several plant traits, separately or in combination, contribute to the capacity of these plants to serve as refugia from natural enemies. First, many myrmecophytes produce nutritionally complete food rewards that eliminate the need for resident ants to forage in more competitive environments off their hosts. *Acacia* and *Macaranga* are examples. Second, derived from taxa in which stem hairs are common, a number of myrmecophytes possess stems and domatia covered with long, dense hairs (trichomes, Fig. 55) that exclude larger-bodied enemy ants, competitors and perhaps predatory army ants, while permitting tiny resident taxa to commute among them. Such hosts include *Cordia nodosa*, *Duroia hirsuta*, and *Hirtella* spp., with tiny *Allomerus* and *Azteca* ants, as well as a variety of myrmecophytic Melastomataceae. Third, many myrmecophytes, e.g., *Macaranga* and *Cecropia*, grow as little-branched, pole-like plants with few points of contact over which enemy ants might invade from neighboring vegetation. Fourth, the mutualism between ants and *Macaranga* has been shown by S.-P. Quek, S.J. Davies, and colleagues to have originated on hosts with irregular "wax blooms" on stems. Many insects, including most ants, have difficulty walking on epicuticular waxes, but as W. Federle and colleagues have demonstrated, "wax-running" ants in at least two genera (*Crematogaster* and *Camponotus*) evolved to utilize the slippery hosts. During the co-radiation of plant and *Crematogaster* lineages, stem types (waxy or smooth) continued to constrain host shifts.

All of the previously described traits are attributes that likely preadapted plants to associate with competitively inferior ants searching for sanctuary. In addition, phytoecious ants themselves have often evolved to reduce interaction with enemies by pruning vines and other vegetation contacting their hosts. (This behavior may coincidentally enhance the host's light environment.) At least one such ant species (*Pseudomyrmex dendroicus* on

Triplaris americana) even prunes leaves of its own host when they bear invasions of enemy ants. In the Neotropics, a majority of pruning ants defend themselves using proteinaceous stings, which tend to be very effective against vertebrate enemies, but less effective than chemical sprays against social insect enemies, including many other arboreal ant taxa. Also suggesting that pruning evolved to limit invasions of competitors, Federle and colleagues find that ant taxa living on waxy-stemmed *Macaranga* hosts do not prune as intensively as do those inhabiting more recent non-waxy species. The latter ants are also more recent, and the evolution of pruning in ants may have benefited host plants by reducing the cost of epicuticular waxes. The advent of pruning coincides with a switch to more generalized host associations, as ant taxa from waxy stem hosts expanded their host ranges to non-waxy hosts. Finally, M. Frederickson has shown that phytoecious ants best at pruning are not always those that are best at protecting plants from herbivores. Therefore, a myrmecophyte's failure to filter out supposed "cheaters" that didn't prune may be due to alternative benefits provided by the ant species in question.

Conflicts of Interest between Partners

As for partners in virtually all interspecific interactions, the evolutionary interests of paired ants and plants are often in conflict. For example, although selection may favor ant colonies that extract the maximum resource possible from their hosts (e.g., by tending sap-feeders, as well as consuming plant-produced ant rewards), selection on plants should magnify cost-efficiency by producing the greatest protection for the least investment in resources devoted to housing and feeding of ants. The most striking examples of evolutionary conflicts of interest come from cases where ants modify plant architecture in ways that are beneficial to them but harmful to their hosts. Working in African savannahs, M.L. Stanton and colleagues have shown that *Crematogaster nigriceps* attacks the axillary buds of its host (*Acacia drepanolobium*), killing apical meristems (growing tips) and greatly curtailing host reproduction in the process. However, by reducing lateral spread, destruction of meristems may also diminish potential contacts between branches of hosts and those of neighboring acacias, some with competitively superior ants that threaten resident colonies. *Tetraponera penzigi*, a second, competitively subordinate occupant destroys EFNs of its host, perhaps making it less attractive to more dominant ants on neighboring hosts.

Similar conflicts of interest are apparent in neotropical ant-plant relationships. The most common inhabitant of *Cordia nodosa* in southeastern Peru is an *Allomerus* that destroys flowers and fruits of its host. D.W. Yu and N.E. Pierce have shown that ant fecundity is greater on plants with curtailed reproduction, because hosts produce more domatia and associated leaves, sites of food body production. *Cordia* populations might be expected to decline to local extinction under such "cheating" by *Allomerus*, but Yu and colleagues have also demonstrated that alternative and beneficial *Azteca* ants are better long-distance colonists, and that the frequency of association with these ants increases as plant density declines. Finally, T.J. Izzo and H.L. Vasconcelos report that selection on plants to fight back under similar circumstances is apparent in relationships between *Allomerus* and another Amazonian ant plant, *Hirtella myrmecophila*. Reproductive structures of this understory treelet are produced only on older branches from which leaf domatia have been aborted, and where worker ants are therefore few or absent.

Long-Term Evolutionary Histories of Ant-Plant Associations

Over long-term evolutionary history, one can expect "ownership" of host taxa to have changed hands in concert with changes in the fortunes of one-time ant partners and their competitors for the benefits of mutualistic association. Are there regularities in the trajectories that these relationships take over time? One might speculate that competition among ants for plants, together with filtering of ants by plants, could produce even greater specialization by the associated taxa, and that this might be a one-way and largely irreversible process. For ants, possible examples involve several closely related genera of tropical arboreal, stem-nesting ants in the formicine tribe Plagiolepidini. (Together, these genera are set apart from others in the tribe by workers possessing just 9 or 10 antennal segments.) Two Old World tropical genera, *Petalomyrmex* and *Aphomomyrmex*, are each represented by just a single West African species and are specialized to one and two host plant species, respectively. Because the probable closest relatives of these taxa (*Myrmelachista* and *Brachymyrmex*) occur as free-living species in the New World, it seems likely that ancestors of the African species were once free-living and more widely distributed, and that competition could have driven *Petalomyrmex* and *Aphomomyrmex* to extreme specialization. The genus *Myrmelachista* includes both free-living and plant-associated species. On average, the former (mainly with 10-segmented worker antennae) have generalized foraging and stem-nesting habits and reside mainly in high elevation cloud forests along the Andean and Central American mountain chains, normally above the elevational ranges of dominant free-living competitors in ant genera *Crematogaster* and *Azteca*. At intermediate and low elevations, and within the ranges of these dominants, J.T. Longino has found that congeneric species are mostly phytoecious ants, principally inhabiting hosts in plant families Lauraceae and Meliaceae. *Myrmelachista* hosts generally lack domatia and food rewards (i.e., are not true myrmecophytes), and associated ants tend sap-feeders inside stem nests. At least some phytoecious *Myrmelachista* occurring at intermediate elevations apparently do not attack encircling vines, though a congeneric species at lower elevations (likely *M. flavocotea* in a more competitive environment) does prune vegetation contacting its host.

Finally, in Central Amazonia, at least two different *Myrmelachista* species occupy and maintain "supay chacras," or "devil gardens." These are orchard-like stands where all but one or two myrmecophytes (and sometimes small, herbaceous resource plants) are killed by the tiny workers that cut major leaf veins and deposit formic acid in the wounds. Leaves necrose and die, and none but favored host and resource plants are able to recruit new individuals inside these bizarre areas. In summary, it is possible that basal *Myrmelachista* species persist only in the absence of strong competitors, or where competitively dominant ant taxa have driven lowland lineages toward increasing specialization that permits coexistence with strong competitors. However, this hypothesis will remain conjecture until tested rigorously after reconstructing phylogenetic histories of associated lineages.

Natural selection to magnify the colonizing and competitive abilities of particular ant associates, coupled with that to filter cheaters, may eventually reduce partnerships to relationships between single, highly specialized ant and plant species, whose persistence is balanced precariously on the premise that each partner will thrive despite changes in the abiotic (physical) and biotic environment. However, natural selection is short-sighted, capable only of enhancing short-term fitness. Over the long term, it can neither anticipate nor respond to the threat of loss of the sole partner. Therefore, it is reasonable to speculate that fewer than all of the ant-plant associations that have ever existed still exist today. Nevertheless, the most thoroughly studied evolutionary trajectories of phytoecious ants are those described by S.-P. Quek and colleagues for *Crematogaster* of *Macaranga*, and show wax runners breaking away from hosts with waxy stems to occupy plants that should constitute a more competitive environment.

Implications of Exudate-Feeding for the Evolutionary Ecology of Ants

The most conspicuous effects of plants on ant ecology and evolution involve phytoecious ants whose colonies are specialized to live their entire life histories on myrmecophytic plants. However, more generally, plants appear to have markedly influenced the biology of ant taxa feeding substantially as "herbivores," either directly on plant wound secretions and EFN, and/or indirectly, on insect honeydew. Such foods, collectively termed "exudates," consist principally of sugars (EFN) and water and are notoriously poor sources of essential amino acids and proteins. Though a certain amount of carbohydrate might be paired with available nitrogen sources as the "nutritionally complete food" needed to subsidize growth and reproduction, exudate-feeders should be left with an "excess" of CHOs. Natural selection may then favor colonies that are able to deploy excess CHO for acquisition of more limiting nutrient, N.

Across the spectrum of exudate-feeding ants, species appear to accomplish this in one or more of several ways. First, they may use excess CHOs to subsidize rapid locomotion, leading to what have been termed higher "dynamic densities." Faster locomotion enables workers to cover more area per unit time, and potentially, to encounter protein resources at a faster rate. Second, defense of true spatial territories is rare among ants generally, but appears to be commonest in species most apt to have excess CHOs to fund this costly behavior. Third, N-starved ants may also reduce percent body weight N, though there are competing explanations for this pattern. Thus, evolutionary transitions from predation and scavenging to substantial dependence on plant and insect exudates correlate with transitions in chemical weaponry. N-rich proteinaceous compounds, or N-containing alkaloidal compounds (both mediated by stings) are replaced by N-free compounds released as volatile sprays or sticky glues from the same or different glands. Whether such transitions are due to N-limitation, or the ineffective nature of C-based weaponry in killing or paralyzing prey, is currently unsettled.

By "paying" ants mainly in CHO-rich food rewards, myrmecophilic and myrmecophytic plants may encourage predatory behavior by attending ants seeking to balance their diets (above). Recently, D.W. Davidson and S.C. Cook found that rainforest plants supply EFN at sugar concentrations far exceeding those acceptable to most arboreal ants. They therefore suggest that high sugar concentrations may serve to manipulate communities of attending ants by favoring the most protein-limited taxa that would not forage for sugar at lower concentration.

Finally, widespread availability of CHO-rich plant foods in the arboreal zone undoubtedly selected for domination of these foods by placing nests near the food source. For ants already nesting in leaf-litter twigs, this transition may not have been difficult, but appropriate cavity space would not always have been available. Many arboreal ant taxa have therefore evolved the capacity to construct their own nests from carton, silk, or leaves cemented to one another to create cavity space.

Some Parallels Between Ants and Plants

A central theme running through this article has been that the balance of resources accessible to animals (Hemiptera and ants) affects the evolutionary ecology of these organisms by determining the types of resources available for various organismal functions. This argument is no less true for myrmecophytic plants and, in fact, was adopted by ant biologists based on its explanatory power in plants. In rainforest plants, for example, E.W. Schupp and D.H. Feener have shown that N-free but carbon-rich food rewards for ants (EFNs and PBs) are more typical of taxa growing in disturbed habitats under high light, than of groups typical of the dark forest understory. Apparently, high rates of carbon-gain in open habitats enable plants to divert some of that carbon to defense.

A second reason why biotic defenses may occur at high frequency in fast-growing, "pioneer" species of disturbed sites may relate to the shorter average leaf life spans of those species. D. McKey has argued persuasively that shorter leaf life spans should favor foliar defenses that are "reclaimable," i.e., can be diverted from aging leaves to more valuable young leaves as time passes. In contrast, much higher, but one-time, investment in non-reclaimable defenses (e.g., the lignin and fiber contributing to leaf toughness) are warranted only when the life expectancy of leaves is relatively long. One can speculate that the pattern in plants might also be applied to predict aspects of ant biology. For example, a substantial, one-time investment in producing thicker (N-rich) exoskeleton might only be warranted in ant species with long-lived workers. This interesting hypothesis has yet to be tested.

Two final patterns in defensive investment are apparent in at least some myrmecophytic plants, and may extend as well to ants and other social insects. Comparing closely-related pairs of *Cecropia* species from different microhabitats at the same rainforest site, it appears that relatively slow-growing taxa from shaded habitats invest in biotic defenses both earlier and more heavily than do their faster-growing relatives from sunny habitats. The latter pattern is understandable in the context of a cost-benefit analysis of defense. For species growing regularly at low light, leaf replacement is very slow due to resource limitation, so plants ought to defend existing leaves well. Moreover, any opportunity cost of defense (calculated in lost growth, survivorship, and reproduction) would be low in comparison to that for species capable of growing rapidly in high light. The combination of high replacement costs and low opportunity costs is thought to select for high defensive investment. (Applied to ants, this pattern suggests the currently untested hypothesis that mean colony growth rates are inversely related to defensive investment in individual workers.) C. Brouat and D. McKey have argued that, in myrmecophyte lineages with interspecific variation in developmental onset of biotic defense, precocious (early) onset should be the derived state; however, few data are available to test this prediction. Others have suggested that costly chemical defenses produced early in development should be abandoned after onset of biotic defense, but recent tests in genera *Acacia* and *Inga* contradict this theory, and suggest that chemical and biotic defenses may be targeted at different types of herbivores.

With respect to ants and other social insects, parallel reasoning might predict an inverse relationship between colony growth rate and investment in defense of incipient (young) colonies. One form of protection for young colonies is production of "nanitic" workers, scaled-down in size. This strategy enables young colonies to make more workers from a given resource base, and to spread the risks of foraging over more individuals. Are young workers smaller relative to normal workers in otherwise comparable species with intrinsically slow growth rates? Again, relevant data are lacking.

In summary, ant colonies and plants share some intriguing features that make models developed in one taxon potentially useful to investigators of the other taxon. Both types of organisms live anchored to a central place (not perfectly true for ants), grow to indeterminate size set by local resource availability, and add vegetative and reproductive parts in a modular way. These commonalities suggest that we might eventually discover additional models that are useful in explaining life history traits and other characters shared by the two groups.

Nutritional Benefits to Plants (Myrmecotrophy)

Among plants evolving associations with benevolent ants are certain epiphytic higher plants. Depending on trunks and branches of other plant species for structural support, epiphytes grow without directly parasitizing their hosts and obtain water and nutrients from rainfall and aerial deposition. Because high humidity and warm temperatures are conducive to this lifestyle, epiphytic higher plants are exceptionally diverse and abundant in tropical lowland wet forests, and (especially) in misty montane forests. (Tropical Africa is exceptional in this regard, due to frequent and severe droughts during the evolutionary histories of its plant life, and small expanses of montane forests in contemporary times.) By virtue of small size, these unrooted plants stand to benefit significantly from even small quantities of nutrients amassed as workers retrieve prey, discard refuse, and defecate within a confined area. From a mix of vegetable fiber, glandular secretions, refuse, and feces, many ants build "carton" shelters (for themselves and tended Hemiptera), and carton can potentially contribute to plant nutrition.

Two categories of plants, New World "ant-garden" epiphytes and Australasian "ant-house" epiphytes, have evolved a variety of traits that increase frequency and intimacy of relationships with beneficial ants. To encourage seed dispersal to nutrient hotspots in ant nests and carton, both sets of species produce seeds with attractive chemicals and/or food bodies. The common occurrence of methyl-6-methyl-salicylate on seeds of 11 unrelated ant-garden epiphytes, combined with the use of these same compounds as pheromones (within-species communication chemicals), suggests that this chemical could function as an ant attractant. Generations of seed dispersal by ants appears to have allowed ants to "capture" the evolution of their epiphytes, just as humans have captured and diverted the evolutionary histories of their crop species. (Alternatively, in both of these systems, plants may have captured and diverted the evolutionary histories of their gardeners!) The successes of ant-epiphyte partnerships are evident from their often remarkable abundances. Ant gardens can account for the majority of epiphytic higher plants in forests with a distinct dry season, and ant-house plants dominate the epiphytic floras of open kerangas forests in Asia. Whereas other epiphytes cannot survive extended periods of drought, ant-garden taxa benefit from moisture absorbed from the air and stored in the rich, organic ant cartons.

Ant-house epiphytes have evolved even more elaborate adaptations to procure benefits from their ant inhabitants. Those in the sub-family Hydnophytinae (Family, Rubiaceae) are descended from tuberous ancestors whose storage tissues were devoted principally to water storage. Ant-associated species in several different genera have reduced their investments in storage and allocated space within their tubers to two types of cavities used by the ants. Colonies of *Anonychomyrma* and *Philidris* nest in smooth- and dry-walled cavities, while placing feces and refuse in wet-walled cavities with "warts," actually modified roots. The epiphytes satisfy a significant fraction of their nitrogen requirements by tapping into these wastes. Epiphytic *Dischidia* species (Asclepiadaceae) frequently grow adjacent to the Hydnophytinae on the same hosts and are inhabited by the same ant colonies. In addition to their "normal" leaves, which grow appressed to tree trunks, these species produce highly modified leaves, involuted to form the cavities in which ants live. Stomata are concentrated on internal cavity walls formed by abaxial (lower) leaf surfaces. Through their stomata, plants take up the carbon dioxide (CO_2) needed for photosynthesis. When stomata (Fig. 60) open to perform this chore, they lose precious water, an especially limiting commodity for unrooted epiphytes of the hot, dry canopy. However, stomata of ant-house *Dischidia* open into a relatively moist, enclosed space where the partial pressure of CO_2 is enhanced by ant respiration, and this alleviates transpirational water losses. Using stable isotope technologies, K.K. Treseder and colleagues showed that *Dischidia major* from Bako National Park in Sabah, Malaysia, obtains about 39% of its carbon from ant-respired CO_2. Isotopic studies of N revealed that about 29% of the plant's N comes from ant feces, refuse and carton, into which plants insert adventitious roots from the bases of both normal leaves and leaf domatia.

Often growing with the Hydnophytinae and *Dischidia* are ant-occupied ferns in the genus *Lecanopteris*, and any of several ant taxa can occupy each of these epiphytes. Although associations between ants and epiphytes are not obligate for either party, it is rare to find one partner in the absence of the other. This is likely due to the combination of frequent nest site limitation in ants, and water and nutrient limitation in epiphytes.

Ant-plant Interactions, Figure 60 **Myrmecotrophic epiphytes: (upper left) At Cocha Cashu, Peru, 11 different epiphyte species from seven plant families can occur in carton "ant-gardens." This garden contains mainly seedling *Peperomia macrostachya*; (upper right) *Myrmecodia tuberosa* (Rubiaceae, Hydnophytinae) growing on a stunted tree in open "kerangas" forest at Bako National Park, Sarawak; (lower left) cross section of *Anthocephalus* sp., vic. Wau, Papua New Guinea, showing dry-walled cavities inhabited by ants, and wet-walled cavities with warts (modified roots) that extract nutrients deposited as ant refuse and feces; (lower right) Bornean *Dischidia major* (Asclepiadaceae, also from Bako): small, circular, flat leaves are typical of non-myrmecotrophic members of the genus, whereas much larger, involuted leaves have evolved in myrmecotrophic species and house associated ants.**

Myrmecotrophy is commonest in epiphytes, but as P. J. Solano and A. Dejean have shown, it can also occur where ants leave waste in abandoned domatia as colonies move to new growth. Thus, in *Maieta guianensis*, protrubances on domatia walls appear to take up N from waste of *Pheidole minutula*. By an as yet poorly defined mechanism, some rattan palms also benefit nutritionally from ants that build carton nests among spines on external stems. Another monocot (*Guadua* bamboo), apparently cannot take advantage of ant waste inside stems and actually loses N to scale insects tending by resident carpenter ants.

Ant-plant Interactions, Figure 61 **Seeds of *Acacia cana* (northwestern New South Wales, Australia) have white arils contrasting with black seeds and are "displayed" at the soil surface, where ants are most likely to find them.**

Ants as Seed Dispersers, Pollinators and Partners of Insectivorous Plants

Seed Dispersal

Tropical epiphytes are not the only group of plants to take advantage of the willingness of ants to transport seeds. In general, plants are thought to be selected for both "distance dispersal" and "directional dispersal," and the balance of selection for the two objectives almost certainly varies from species to species. Distance dispersal, or seed dispersal away from the maternal parent, is important for avoiding both asymmetrically strong competition from the mature plant against its seedlings, and transfer of pathogens and seed predators to these offspring. Because ants generally forage over relatively short distances from a central place, they are probably more important in directional dispersal, i.e., directing seeds to "safe sites" or favorable microhabitats. The importance of both forms of dispersal may explain why some "diplochorous" species accomplish both objectives, e.g., by first explosively propelling seeds away from the parent and then using ants to target seeds to a preferred location. The majority of ant-dispersed seeds are taken to or near the nest site, if not into the nest itself, and evolutionary advantages of "myrmecochory" (dispersal by ants) are usually discussed in relation to these sites.

Ant-dispersed plants, bearing small food rewards for ants, are common in habitats ranging from rain forests (e.g., herbs in the Marantaceae) to temperate deciduous forests (e.g., violets) and arid lands (North American jimson weed and some Australian acacias and saltbushes, Fig. 61), but the greatest diversity of myrmecochores may occur in areas with infertile soils, Mediterranean climates, and high fire frequency, e.g., especially African fynbos and Australian heath. Depending upon habitat characteristics, hypotheses for the adaptive value of myrmecochory have included giving seeds refuge from fire (chaparral), from competing plants (temperate deciduous forests, where ant nests may be the only vacant sites), or from seed predators (diverse habitats), as well as dispersal to nutrient hotspots on ant mounds (e.g., the nutrient-poor soils of arid Australia). While controversies continue about particular plants and sites, it is likely that each of these hypotheses holds for a subset of plant species.

The rewards that plants offer for seed dispersal fall mainly into the category of "elaiosomes," a kind of aril (= dry fruit) that is rich in oils. Both birds and mammals also feed on arillate fruits. When ant-dispersed species were compared with bird-dispersed (ornithochorous) species in the same sub-genus of Australian *Acacia*, fruits and seeds of the two types of species differed in size, aril composition, color, and presentation. Myrmecochorous seeds were somewhat smaller on average, with arils poorer in lipids (an energy source) and water, but marginally richer in N (amino acids or proteins). In contrast to the colorful arils that ornithochores display prominently on the host, arils targeting ants were white (contrasting readily with black seeds) and presented on the ground after dehiscing. A study by L. Hughes and colleagues compared the elemental composition of myrmecochore arils with that of fleshy fruits from diverse vertebrate-dispersed plant plants. A difference in potassium (K) levels suggested that vertebrate frugivores may require comparatively high levels of K in their fruits. Species growing in poor soils may simply have too little K to produce K-rich fruits, and so may be relegated to myrmecochory. Hughes and colleagues have also identified fatty acids (especially 1,2-diolein) as important components of elaiosomes, which may mimic the composition of insect prey (especially haemolymph) and therefore induce a variety of carnivorous and omnivorous ant species to transport seeds to the nest. Given the ubiquity of ants in most habitats, plants may have evolved to attract ant species that consume only the appendage and not the seed itself. Together, these studies point to syndromes of traits characterizing species with different dispersal agents.

Inconstancy in availability of elaiosomes probably prevents ants from specializing on fruits of a particular plant species. Moreover, aside from making a dispersal unit smaller or larger, it is difficult logistically to direct seeds to particular ant species. Not surprisingly then, relationships between ants and myrmecochorous plants tend to be diffuse rather than species-specific, with a variety of ants carrying seeds of a given plant, and often more than one type of elaiosome in an ant diet. Nevertheless, all ant species are not equal in their effects on plant reproductive success. Interspecific differences among carriers affect transport distances, frequency of dropping without retrieval, and rates of seed burial and escape from seed predators. Despite the opportunistic nature of interactions between myrmecochorous plants and ants, one or more ant species may often have a disproportionate effect on plant reproductive success. For example, at increasing frequency, disruption of ant communities by non-native species (e.g., Argentine ants, *Linepithema humile*) threatens populations of native plants, including rare and endemic (geographically restricted) species.

Ants as Pollinators

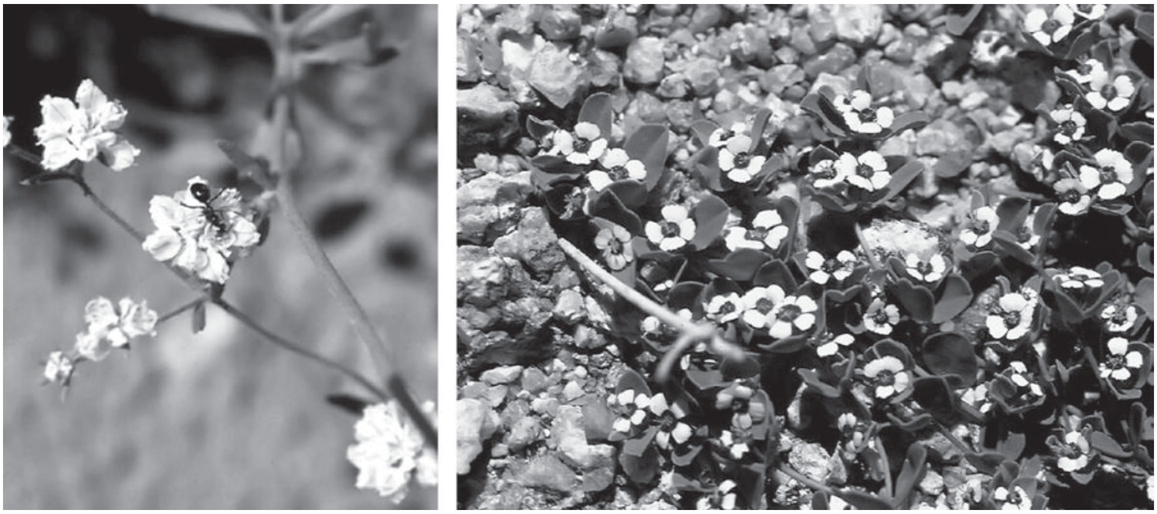
While we think most often of bees, flies and hummingbirds as agents of plant pollination, ants can also be effective pollinators under a restrictive set of circumstances. This is apparent despite observations by A.J. Beattie and colleagues that antibiotic compounds produced by the ants' metapleural and poison glands can suppress pollen germination and pollen-tube growth. (Unlike their wasp ancestors, ants often inhabit nests for multiple generations, and metapleural glands with hygienic function appeared early in ant evolution.) Nevertheless, M. Ramsey suggests that if ubiquitous ants were otherwise effective pollinators, some or even many plant species might be expected to have evolved pollen insensitive to metapleural secretions. The apparent rarity of such immunity suggests that ants may be inadequate as pollinators for some other reason(s). A signal attribute of ants is their tendency to revist food sources such as extrafloral nectaries and Hemiptera. Very likely, conservatism in ant movements detracts from their ability to transmit pollen effectively among individual plants, a requisite for reproduction by self-sterile taxa. Nonetheless, ants may play a role in pollination where smaller plants (e.g., epiphytes or annual herbs) occur at high densities, or by enhancing rates of self pollination when more effective pollinators are scarce.

Among the few plant taxa pollinated by ants, a suite of traits, or an "ant-pollination syndrome" (a term coined by J.C. Hickman) points to the circumstances under which ants can be induced to move among individual plants. Ant-pollinated plants (Fig. 62) tend to be small in stature and mostly prostrate in growth form, so as to preclude the need to compensate ants energetically for walking vertically rather than horizontally. As a consequence of paying little reward, plants encourage workers to keep moving in search of additional nectar or fuel. Other aspects of the ant-pollination syndrome are white color, and open structure, granting ants access to floral nectars, but just small amounts of pollen, and thereby diminishing the need for ants to groom pollen from their bodies. Ant-pollinated flowers also have relatively few ovules, which may all be pollinated even by small pollen deliveries.

Given their general ineffectiveness as pollinators, and their almost universal taste for sweet solutions, ants mostly interact with flowers as parasites of the relationships between plants and their real pollinators. Almost certainly for this reason, numerous plants have evolved barriers to exclude ants from floral rewards, e.g., with dense fields of hairs or sticky bands inside the corolla. It has even been suggested that nectars are made toxic or disagreeable to ants, though the taxonomic and geographic distributions of such nectars remain poorly known. J. Ghazoul presents some of the strongest evidence for floral ant repellents, demonstrating that a diversity of ants are repelled by something in floral tissues themselves. Still unresolved is the extent to which protection of nectar versus pollen has been the principal stimulus for the evolution of ant repellents. At least some pseudomyrmecine and myrmicine (*Cephalotes*) ants feed on pollen, but nectar feeding is more widespread in ants, probably because less specialization of the digestive system was required to use that resource. Nevertheless, early in their evolution, flowering plants must have found ways of protecting nutritious pollen from the ubiquitous and often protein-limited ants.

Relationships Between Ants and Insectivorous Plants

Carnivorous plants of diverse forms occur on infertile soils in various locations throughout the



Ant-plant Interactions, Figure 62 ***Mymecocystus*** **species pollinate flowers of at least two desert annuals:** ***Eriogonum abertianum*** **(Polygonaceae) (left) at Portal, AZ, and** ***Euphorbia*** **sp. (Euphorbiaceae) (right) from southern California. The latter is more typical of ant-pollinated plants because of its prostrate growth form. Individual flowers of both species produce minute quantities of nectar, so ants must walk back and forth among individual plants to fill their crops. However, on both species, workers can commute among individuals without energetically costly vertical movement.** ***E. abertianum*** **is rare except in years when winter rains continue through the spring; then it grows in almost monospecific stands with branches of adjacent individuals overlapping at the same level.**

world, and are united by their use of trapped insects as N sources. Pitcher plants are a particularly fascinating life form. They lure insects to the slippery edges of steep-walled pitchers into which fluids with digestive enzymes are secreted and protected from dilution by rainfall by a sort of "roof." Ants are among the most abundant prey of pitcher plants, being attracted to the pitcher edges by a form of extrafloral nectar. However, C.M. Clarke and R.L. Kitching show that one *Camponotus* species has evolved a more complicated relationship, perhaps a mutualism, with a carnivorous pitcher plant in Borneo. Thus, the hollow tendrils of *Nepenthes bicalcarata* house ants that feed on both large insects trapped by its pitchers and mosquito larvae therein. Unlike smaller prey, large insects apparently overwhelm the plant's digestive capacity and lead to accumulation of ammonia in the pitcher fluids. Removal of excess prey by *Camponotus* prevents putrefaction of the fluids. Therefore, although the ants do rob some prey from their host plants, the net effect of their presence may be positive.

Effects of Ant-Plant Interactions on the Diversification of Ants

Given the extraordinary diversity and widespread abundance of interactions between plants and ants, the two groups would be expected to have influenced one another's evolutionary histories. This conjecture is supported by recent molecular phylogenetic studies by C. Moreau and colleagues, who show that the diversification of ant "crown groups" (contemporary major taxa) occurred coincidentally with that of flowering plants (angiosperms) in the Late Cretaceous and early Eocene, and involved major taxa of litter ants, as well as the arboreal ants reviewed in the present article.

With respect to plants, relationships with ants likely contributed to recent and rapid diversification of species in the genus *Inga* (Fabaceae), defined in part by EFNs on leaf rhachis, and containing an estimated 300–450 species. Major radiations of ant inhabited plant taxa have also occurred in genera *Cecropia* (Cecropiaceae), *Macaranga* (Euphorbiaceae), Ocotea (Lauraceae), *Tachigali* (Fabaceae), *Triplaris* (Polygonaceae) *Tococa* and *Clidemia* (Melastomataceae), as well as in various genera of ant-house epiphytes in sub-family Hydnophytinae (Rubiacae).

► Ants
► Leaf-Cutting Ants
► Pollination
► Insectivorous Plants
► Carnivorous Plants

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Ants

Certain members of an order of insects (order Hymenoptera)

► Ants (Hymenoptera: Formicidae)
► Wasps, Ants, Bees and Sawflies

Ants (Hymenoptera: Formicidae)

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Ants are one of the most highly evolved and dominant insect groups. They are the largest family of insects in terms of the diversity of species and certainly sheer numbers of individuals. Currently there are well over 12,000 described species of ants, and some suggest that a similar number is yet to be discovered. Individual colonies of some species can contain over 20 million members. Ants belong to the family Formicidae, which consists of 23 subfamilies and 287 genera that are not extinct.

Order Hymeoptera
  Suborder Apocrita
    Superfamily Vespoidea
      Family Formicidae

They are found in all terrestrial regions of the world, including the cold subarctic tundra and dry deserts. About half of the world's precinctive genera are from the Neotropics and a third from the Afrotropical [sub-Saharan Africa] region. The subfamily with the greatest number of species is the Myrmicinae, and is followed by the Formicinae.

Ants are true social (eusocial) insects, which is defined by the following characteristics: (i) cooperative brood care, where immature ants are tended by groups of adults that are not their parents; (ii) overlapping generations, where at least two different generations of adults occur simultaneously in the same colony; and (iii) reproductive and non-reproductive castes, where only the reproductives are capable of producing fertile offspring. The non-reproductives, or workers, perform tasks necessary for colony survival, such as foraging for food, caring for immature ants and reproductives, and nest building. Eusocial insects have a competitive advantage over nonsocial insects because there is a better probability that groups of sterile workers will be able to complete a task necessary for the survival of the reproductive queen, and also complete a series of tasks simultaneously. If a task is not completed by one worker, another worker can finish the job. This is opposed to a solitary insect where the entire burden of completing tasks from start to finish rests with the individual.

Caste determination, or what causes an ant to develop into a reproductive or a worker, is thought to be due to differential genetic expression stimulated by environmental factors. Based on a limited number of species, at least six factors have been identified as being influential in reproductive and worker caste determination: (i) Egg size, where eggs with more yolk and hence larger in size will more likely become queens. (ii) Chilling, eggs and larvae that have been exposed to sufficiently cold winter temperatures tend develop into reproductives in the spring. (iii) Larval nutrition, where food quality and quantity affect larval size. Larvae that reach a threshold size by a critical developmental time become the reproductives. (iv) Temperature, larvae that grow in optimal developmental temperatures tend to become queens. (v) Caste inhibition, production of new queens is inhibited by the presence of a mother queen. (vi) Queen age, where younger queens generally produce more workers. Regulating the occurrence of some of these factors are titers of juvenile hormone. Depending on species and colony conditions, all or just some of these factors may be involved and the degree of the factors' influence also varies. A sequence of criteria may need to be met for an egg to more likely develop into a queen, otherwise it will be a worker. To illustrate, for an egg to develop into a queen the following criteria may need to be met more or less sequentially: (i) is the egg of sufficient size, (ii) did it receive enough winter chilling, (iii) was food sufficient and (iv) temperatures optimal for the larva to reach a critical size by the right time, (v) are mother queens young and preventing new queen development? Meeting criteria will bias or increase the probability of the development of a queen. Determination of major (soldiers) and minor workers in some species is under both environmental and genetic regulation, thus maintaining a characteristic major: minor ratio within a colony. Recently, genetic regulation of workers and queens was found to be absolute in a hybridization zone between two species, where workers were heterozygous and reproductives were homozygous at marker loci for caste determination.

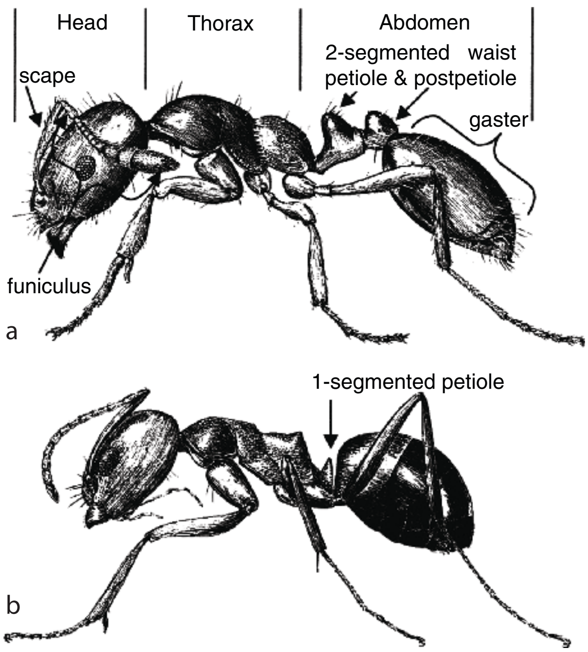
Communication needed to coordinate the activities within a colony is mediated by chemical signals called pheromones. Some of the pheromones that have been isolated include a queen pheromone that allows worker ants to recognize a queen, trail-following pheromone which workers use to mark paths between the nest and food, and alarm pheromones which cause ants to disperse and/or attack. Chemical cues also are used in the recognition of colony nest mates, and play a role in aggression and establishing territorial boundaries between colonies.

Ants are omnivorous and mobile, allowing them to exploit a wide range of habitats. This is in contrast to termites, another abundant eusocial insect, which are restricted to feeding on wood or other vegetation. Moist environments are conducive to microbial contamination. Secretions from the ant's metapleural gland contain antibiotics that disinfect moist environs. Having a portable means of sanitation allows ants to exploit areas that other organisms may not be able to live in. These attributes permitted ants to become a dominant terrestrial organism, especially in the tropics. With their large populations and adaptation to a plethora of ecological niches, ants play an important role in natural ecosystems. They are tremendous earth-movers because of their underground nest building, and thus contribute greatly to the cycling of nutrients. They disperse seeds, scavenge dead organisms, and are a major predator of other arthropods and small invertebrates. In some instances they are directly beneficial to man by being major predators of pests such as crop feeding caterpillars, and ticks of livestock.

Morphology

Ants are easy to distinguish from other insects mainly because of the combination of a thin-waist and the presence of elbowed antennae. The waist refers to a segmented constriction called the petiole, located between the thorax and the gaster. The gaster is composed of the broad 4 or 5 posterior segments of the abdomen. Morphologically ants are distinguishable by having a one or two-segmented waist (Fig. 63); always consisting of a petiole if one-segmented, and both a petiole and a postpetiole if two-segmented. The petiole and postpetiole are actually the second and third segments of the abdomen that are reduced or constricted in size. They often have a distinctive node-like form, however in some species it is scale-like or just a small cylindrical segment. Following (Table 6) is a list of four terms that describe sections of the ant abdomen and the corresponding abdominal segments for ants with one- and two-segmented waists.

The adult workers and queens have antennae that are geniculate, meaning bent or elbowed. The elbowed appearance arises from having a long first, or basal, antennal segment called the scape, followed by 3–11 short segments (collectively called the funiculus). The basal segments in male antennae are usually not long, and thus, the antennae will not appear to be elbowed. Another unique feature of ants is the small opening or orifice of the metapleural gland. This is located just above the basal segment of the third leg, but often requires magnification to be visible.



Ants (Hymenoptera: Formicidae) , Figure 63
Distinguishing morphological structures of ants: (a) two-segmented petiole or (b) one-segmented petiole. Elbowed antenna consisting of a long basal segment (scape) and 3–11 short segments (funiculus); posterior portion of abdomen beyond petiole (gaster) [drawings modified from M.R. Smith 1965, (a) *Monomorium minimum*, (b) *Dorymyrmex pyramicus*].

Ants (Hymenoptera: Formicidae), Table 6
Abdominal segments that compose sections of the abdomen for ants with one- and two-segmented waists

Abdominal Sections	One-segmented waist	Two-segmented waist
Propodeum	abdominal segment 1 fused to posterior of thorax	
Petiole	abdominal segment 2	abdominal segment 2
Postpetiole	None	abdominal segment 3
Gaster	abdominal segments 3–7	abdominal segments 4–7

Life/Colony Cycle

Ants are holometabolous, having a complete life cycle consisting of eggs, larvae, pupae, and adults. Thus, little adult ants do not grow into big adult ants. The eggs, larvae, and pupae are collectively called brood. In general, colony development is as follows: ant colonies originate after a mating flight when winged virgin queens mate with winged males. After mating, the males die, while the newly mated queen sheds her wings and finds a protected location or excavates a chamber in soil. Within this chamber she will lay a batch of eggs and care for the subsequent larvae and pupae until they become adults. These adults are usually sterile females, which are the worker caste, and they will assist the queen by caring for additional brood, foraging for food, and expanding the nest. An important aspect to the survivorship and growth of ant colonies is trophallaxis, or the exchange of regurgitated food among nestmates. Trophallaxis ensures that food is distributed to all members of the colony including the queen and brood. Once the colony is well established, winged virgin females and males (reproductives) will be produced and will proceed to have a mating flight when environmental conditions are suitable. The original colony will continue to be maintained and produce new reproductives as long as the queen is able to produce viable eggs. Depending on the species, queens have been reported to live from less than a year to as long as 29 years. A major variation to this cycle is the absence of a mating flight by the virgin queens in some species. Mating takes place within the nest with either their brothers or males that fly in from other colonies. New colonies are formed by budding, where a portion of the colony, containing adults, brood, and either or both mated or virgin queen(s), separate from the original colony and move to a new location.

In addition to the tremendous number of ant species, there is a broad range of interesting behaviors or life styles among species. Many species have mutualistic relationships with honeydew-producing insects such as aphids and mealybugs

(Hemipteran). Ants will transport and protect these insects in order to harvest the honeydew they produce. In essence, these ants tend and herd the honeydew producers as if they were cows. Some hemipterans carry plant pathogens, and disease spread is facilitated by ants moving the infected hemipterans to other plants.

Another agrarian life-style is that of the leaf-cutting ants that raise their food in fungal gardens within their nest. These ants use leaves and other fresh vegetation to provide a substrate on which to grow the fungus, and these ants can defoliate trees overnight. Leaf-cutting ants cut pieces of leaves or flowers with their jaws and then carry them back to their nest. Once in their nest, they further chew the vegetation and add feces to form a suitable medium for fungal growth. Finally, they plant and maintain a specific fungus species on the substrate. In Central and South America, leaf-cutting species in the genus *Atta* and *Acromyrmex* (subfamily Myrmicinae) can have colonies with an estimated 1–8 million individuals. They build nests consisting of an extensive network of subterranean galleries, and are the most significant pests of agriculture in South America, feeding on citrus, forage grasses, and other crops.

Symbiotic relationships with plants been reported for several ant species. One well-studied mutualistic relationship is that between *Acacia cornigera* trees and the ant *Pseudomyrmex ferruginea* (subfamily Pseudomyrmecinae). The acacia tree produces thorns, which serve as nesting sites for the ants and it produces structures, called Beltian bodies, that are eaten by the ants. The ants protect the plant from herbivorous arthropods and vertebrates, and destroy competing plants that sprout nearby.

Besides their symbiotic interactions with plants and other insects, ant species also have parasitic relationships among each other of which slavery, or dulosis, is one of the more interesting forms. The genus *Polyergus* (subfamily Formicinae) consists entirely of slave-making species. Workers of *Polyergus* colonies dash into the nests of ants in the genus *Formica* (subfamily Formicinae) and steal their larvae and pupae. The stolen immatures are allowed to develop into adult workers and carry out colony maintenance tasks for their abductors. In fact, the *Polyergus* workers are so specialized for raiding and killing other ants that their jaws are like sharp curved sabers, morphologically ill-suited for nest building, tending immatures, and food gathering.

More extreme extensions of this parasitism are species without a worker caste. These species contain only males and queens that are cared for by the workers of a host colony, which they have infiltrated. They are either fed by the workers or steal food from the host queen, which they often mount and hold onto. The eggs of the parasite are reared to adulthood by the host workers. Parasitized host colonies can be smaller in size, presumably because of the partial diversion of resources to the parasites. Examples of these parasitic ants include *Solenopsis daguerrei*, a parasite of imported fire ants (*Solenopsis invicta, S. richteri*), and *Teleutomyrmex schneideri*, a parasite of *Tetramorium caespitum* and *T. impurum* (all in the subfamily Myrmicinae).

In contrast to the symbiotic life-styles, many species of ants are extremely predatory and have gained the reputation of being an unrelenting scourge of the jungle. The subfamily Dorylinae consists of a single genus, *Dorylus*, which contains the African driver ants, also referred to as army ants or legionary ants. Most species are found in the Afrotropical region (sub-Saharan Africa), but a few species are also found in the southern Palearctic, Oriental, and Indo-Australian regions. The various species of African driver ants have colonies with millions of individuals, which regularly move nesting sites and forage for food in large swarming columns or groups. The columns can fan out to produce a large moving front that preys on anything that remains in its path, especially arthropods. At night the colony forms a bivouac, protecting their queens and brood within a mass of worker ants. Thus, there is no permanent nest structure for these nomadic ants. Besides the army ants in the Dorylinae, the subfamily Ecitoninae contain many species of army ants found in the Neotropics, and a few species in the Nearctic. These armies are smaller than the African species, with colonies of hundreds of thousands rather than millions.

The pillaging, nomadic life of the army ants requires a high level of organization and cooperation. Extraordinary cooperative behavior is further exhibited during nest construction by the weaver ants in the genus *Oecophylla* (subfamily Formicinae). These ants are dominant arboreal ants of the Afrotropical region. They link their bodies together to form chains by grasping the petiole of an adjacent worker with their jaws. The living chains are used to pull the edges of leaves together. Once leaves are held in a desired position, other workers bring forth silk-producing larvae and individually press larval heads to one leaf surface then another, resulting in thousands of sticky silk threads being drawn between the leaves to hold them together. Eventually leaves and stems are bound together to form a tent within which a nest of silken galleries is constructed. This communal nest construction is unique in that it involves the use of immature stages that secrete silk on command. It has allowed these ants to build expansive networks of nests across several trees, which can house a colony of over 500,000 individuals.

The adaptability and high reproductive output of many species of ants allow them to thrive in many environments, including that of humans. As such, ants that live in buildings or have high populations in areas used by man are often considered pests. Many pest ants have characteristics that typify the "tramp species". These ants generally (i) spread around the world via human commerce; (ii) can thrive in man-made environments; (iii) have colonies that are not territorial and thus can result in interconnected nest sites; (iv) have many queens per colony; and (v) have limited or no mating flights resulting in colony reproduction by budding. Ants that sting, such as red imported fire ants (*Solenopsis invicta*, subfamily: Myrmicinae), are of veterinary and medical importance. Newborn livestock can be blinded or killed by stings at birth. People who are stung usually develop itching pustules that last for several days, but some can have hypersensitive reactions, resulting in anaphylaxis and even death in rare instances. Non-stinging ants, such as the Pharoah ant (*Monomorium pharaonis*, subfamily: Myrmicinae) may be a nuisance to building occupants and are also known to contaminate sterile surgical units, supplies, and food items in hospitals. Invasive ant species, such as the red imported fire ant and the Argentine ant (*Linepithema humile* subfamily: Dolichoderinae), establish and thrive in non-native locations, invade surrounding areas, and eventually become the dominant faunal species. Invasive ants are a major concern in many areas, ranging from nature preserves to suburbia, because they displace native ants as well as other native organisms.

Control

Controlling pest ants can be a difficult task given their broad habitat range, large populations, and a social organization that protects the queen(s) from external influences such as insecticides. Because traditional control approaches of excluding ants from buildings by sealing cracks and crevices or applying insecticides directly to ants or nests generally do not target the queen, significant population reductions, if any, are temporary. Ant baits, however, were developed to use the foraging and nest mate feeding behaviors of ants to distribute a toxicant throughout a colony, including the queen(s). Ant baits typically contain a toxicant dissolved into a liquid food preferred by the pest ant species. This poisoned food can be mixed with an absorbent carrier such as corn grit or formulated into a gel to facilitate handling and application. Some baits are left in liquid form and must be dispensed in a container that serves as a feeding station.

Key to effective ant bait is a toxicant with the following three characteristics. First, the concentration of toxicant used should not deter feeding on the bait, because ideally enough bait should be readily foraged upon to be shared with adults and immature stages of all castes within a colony. Second, the toxicant should not immediately kill the ants foraging upon the bait. In general, a delay in death or sickness of a minimum of 8 hours from the time of ingestion is required to allow sufficient toxicant to be collected and fed to a significant portion of the colony. If the toxicant causes sickness or death too quickly, distribution of the bait to the rest of the colony stops before enough of the colony is affected, and control will not be obtained. Third, the toxicant should provide a delay in mortality over a wide range of concentrations (typically at least a 10 fold range) because the toxicant is diluted as it is shared among nest mates. Depending on the type of toxicant and colony size, ant baits may take from three days to several months to eliminate a colony. Some bait toxicants do not kill adults but instead disrupt reproduction by the queen, whereby worker caste ants are no longer produced. As the original adult worker population dies naturally, the lack of replacement workers dooms the colony to a slow death as functions that sustain a colony such as food gathering, defense, nest repair, and queen care cannot be carried out.

While ant bait development has been a major focus for ant control, other strategies have been developed for specific species. For example, planting forage grasses that are a non-conducive substrate for the growth of fungus needed by leaf-cutting ants can significantly reduce their populations. Natural enemies of ants are also used to suppress ant populations. In particular, tiny parasitic flies, in the genus *Pseudacteon*, that develop in the heads of ants, and a pathogen, *Thelohania solenopsae*, that debilitates queens are being used to suppress populations of imported fire ants. These natural enemies require development within fire ants and unlike chemical control measures, are self-sustaining and can spread naturally among fire ant populations. Effective control of pest ants, as with most insect pests, generally requires the use of several control tactics adapted for a particular species and circumstance.

► Myrmecophiles
► Myrmecomorphy
► Ant-plant Interactions
► Driver Ants
► Leaf-cutting Ants
► Carpenter Ants
► Castes

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Anus

The external opening of the digestive tract, through which the food remnants and metabolic waste products are passed.

► Alimentary Canal and Digestion
► Internal Anatomy of Insects

Aorta

A tube located dorsally in the insect's body that conducts blood from the heart forward to the head region.

Apatelodidae

A family of moths (order Lepidoptera). They commonly are known as American silkworm moths.

► American Silkworm Moths
► Butterflies and Moths

Aphelinidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Aphelocheiridae

A family of bugs (order Hemiptera).

► Bugs

Aphicide

An insecticide that is especially effective against aphids.

Aphididae

A family of insects in the order Hemiptera. They sometimes are called aphids, green flies, and plant lice.

► Aphids
► Bugs

Aphidivorous

Aphid loving. Many insects are associated with aphids because the feed on the honeydew produced by the aphids (e.g., many ants, some flies including mosquitoes) or on the aphids (e.g., many lady beetles and flower flies). Those that feed on the aphids are said to be "aphidophagous."

► Aphids
► Sugar Feeding in Blood-Sucking Flies
► Aphidophagous

Aphidophagous

Aphid feeding.

► Aphidivorous
► Predation: The Role of Generalist Predatory in Biodiversity and Biological Control
► Natural Enemies Important in Biological Control

Aphids (Hemiptera: Aphididae)

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Aphids are among the most interesting, unusual, and thoroughly studied of all insect groups. They are worldwide in distribution, and are also called plant lice, antcows, green flies, die Blattläuse, les aphides, los áfidos, etc. They have economic importance because many aphid species are pests of agricultural crops, forest and shade trees. Although small in size (1–10 mm) compared to many other insects, professional as well as amateur entomologists have always been intrigued by their specialized life cycles that are influenced by their host plant relationships. This results in both sexual and asexual reproduction, with a highly dependent, almost parasitic mode of sessile existence that can be parthenogenetic during lengthy periods with a telescoping of generations. Yet, when the photoperiod shortens and the temperature cools, offspring are produced that reproduce sexually. In addition, aphids have life cycles with a polymorphism in adults that have wingless (apterous) and winged (alate) forms or morphs, as well as polyphenism or different morphs even within clones. As alates, migration is enhanced, and this can be involved with overwintering behaviors because of host plant alternation. Hence, aphids are excellent animals for the study of multitrophic ecology, behavior, physiology, genetics, evolution, biological control, molecular biology, etc. Besides using field studies of aphids for population sampling and damage assessment, many species can be reared rather easily in the laboratory and greenhouse, thus making them ideal subjects for precise observation and experimentation.

Classification

Aphids are usually classified in the order Hemiptera, series Sternorryncha or sometimes suborder Homoptera along with the psyllids, whiteflies, scale insects, and mealybugs. Another approach is to put aphids in the order Homoptera and suborder Sternorryncha. Some taxonomists have increased the number of aphid families to as many as 20 with a corresponding realignment of the subfamilies. Further phylogenetic studies with molecular techniques are in progress, but in this overview summary the following composite scheme of the major taxa in aphid classification is given below such that there are 8 subfamilies in the family Aphididae:

Order Hemiptera
- Series Stemorrhyncha (= Suborder Homoptera)
  - Superfamily Aphidoidea
    - Family Aphididae (aphids)
      - Subfamily Aphidinae
        - Tribe Aphidini
        - Tribe Macrosiphini
      - Subfamily Calaphidinae (= Drepanosiphinae)
      - Subfamily Lachninae
      - Subfamily Chaitophorinae
      - Subfamily Greenideinae
      - Subfamily Eriosomatinae
      - Subfamily Hormaphidinae
      - Subfamily Anoeciinae
    - Family Adelgidae (adelgids)
    - Family Phylloxeridae (phylloxerans)

Although the number and organization of the subfamilies can vary, there is general agreement that within the family aphididae, the largest subfamily is the aphidinae, followed by the calaphidinae (=Drepanosiphinae), and the Lachninae. There are over 4,000 species of aphids which is a relatively small number compared to many other insect taxa. However, adult polymorphism as winged (alate) and wingless (apterous) morphs, as well as polyphenism within clones increases their overall diversity.

Distribution

Although aphids are found worldwide, their species are most abundant in the temperate latitudes, and less so in the tropics. This preferential distribution may have evolved in response to the selective pressures of the temperate regions having constantly changing, yet rather predictable, environmental conditions. As a result, unlike most other phytophagous (herbivorous) insects, aphids show an inverse relationship between the number of aphid species and the number of plant species in different parts of the world. Hence, there are many more aphid species in the temperate latitudes than in the tropics, although there are more plant species in the tropics than in the temperate regions, but with fewer species of aphids. Most aphids (70%) are in the subfamilies Aphidinae and Calaphidinae (=Drepanosiphinae), and many are pests of crops in these temperate zones. However, when some of these species are introduced (accidentally) into tropical and subtropical regions, they are still able to adapt and become pests in these new environments. In addition, although the tropics and subtropics are fairly constant in temperature and photoperiod, it is surprising that there are some endemic species in these regions that are holocyclic in their life cycles (female cyclical parthenogenesis, alternating with sexual reproduction by males and females) which is more common in the temperate zones. This is in addition to the expected anholocyclic life cycle (absence of males, only parthenogenesis by females) which would be normal in the tropics and subtropics. Aphids find their host plants by random search, and ecologists emphasize the importance of the concept of "plant apparency." Of the more numerous species of aphids in the temperate regions, many are monophagous (feed on one or only a few species of related host plants). However, in the tropics where there are more species of plants and relatively fewer aphid species, these aphids are more polyphagous (feeding on a variety of host plants). Hence, some suggest that aphids originated in the northern hemisphere, and that the tropics presented a barrier to a similar multiplication of species in the southern hemisphere.

Origin and Evolution

Based on the classification given above, in the hemipteran superfamily Aphidoidea are the families Aphididae (aphids), Adelgidae (adelgids), and Phylloxeridae (phylloxerans). Paleontology and phylogeny are two sources of information used by systematists to study the evolutionary history of this group. According to these experts, although paleontology should provide a time scale for their ages, unfortunately the fossil evidence is very limited. Only about 125 fossil species have been described, while the number of extant aphid species is over 4,000. Two kinds of fossils exist: (i) imprints from carbonized remnants in clay, limestone or other sediments, which provide only minimal information because aphids are soft-bodied and are not well preserved; and (ii) amber inclusions which have entire specimens that are often caught in a natural position, and so are much more important as fossils.

Probably aphids, along with the closely related adelgids and phylloxerans, evolved from a common ancestor about 280 million years ago in the late Carboniferous or early Permian Periods when there were seasonal climatic changes associated with the glacial period. They are now classified together in the superfamily Aphidoidea, and their host plants were primitive gymnosperms (Cordaitales, Cycadophyta). By utilizing their specialized piercing – sucking stylets on the phloem and parenchyma tissues of the gymnosperms, polyphagy was most likely the primitive feeding behavior of the superfamily Aphidoidea. As a result of their parasitic mode of life, individual size in these three families (Aphididae, Adelgidae, Phylloxeridae) was similar and rather small. Although their wings were delicate, their light body weight could take advantage of air currents for dispersal. Some consider monophagy as a recent development in aphid evolution, although others speculate that like parthenogenesis, it could have evolved early in the evolutionary history of the Aphidoidea. Another characteristic which aphids share with the adelgids and phylloxerids is the simple nymphal eye of three lenses (triommatidium).

From the Triassic Period (240–205 million years ago), only the front wing of one species of aphid (*Triassoaphis cubitus*) from Australia is known, and it is not easily placed in any superfamily of later periods. Cytogenetic evidence indicates that parthenogenetic reproduction by means of unfertilized eggs may have evolved over 200 million years ago, before these three families (Aphididae, Adelgidae, Phylloxeridae) became independent. This view is supported because a holocyclic life cycle (cyclical parthenogenesis by females, alternating with sexual reproduction by males and females) is now common to all three groups. However, viviparity (live birth) is a special characteristic of aphids, and must have evolved later because the modern adelgids and phylloxerans are only oviparous (lay eggs). By the Jurassic Period (205–138 million years ago), there had developed the recognizable shape of the body, wing venation, proboscis, and legs, while the siphunculi or cornicles and cauda evolved in the Cretaceous Period (138–65 million years ago).

A major botanical event also occurred during the Cretaceous with the evolution of angiosperms (flowering plants), which coincided with the radiation and species diversification of aphids. Within the family Aphididae, the Aphidinae (the largest subfamily of modern aphids) is not represented in the fossil record until the late Tertiary Period (65–1.65 million years ago). Tribes of the second largest subfamily, the Calaphidinae (=Drepanosiphinae), developed much earlier in the Upper Cretaceous and early Tertiary Periods. Concerning the third largest subfamily, the Lachninae, there is limited palaeontological evidence of its evolution. Hence, there is some debate as to the relative age of the lachnids. Because 80% of them live on conifers (which are older than the angiosperms), the lachnids have generally been regarded as ancient, although some genera may have a recent origin.

Metamorphosis

Regardless of whether aphids are born from an egg of oviparous sexual females or live from viviparous parthenogenetic females, their type of metamorphosis is called simple or incomplete: the developmental sequence is egg, to nymph(s), to adult. A nymph resembles the adult, and usually develops in four molts (four nymphal instars or stages) growing larger each time until the adult stage of sexual maturity is reached. This type of metamorphosis is to be distinguished from complex or complete metamorphosis wherein the developmental sequence is from egg, to larva (several molts and instars), to pupa, to adult.

External Morphology

Aphids are mostly soft-bodied insects and relatively small (only 1–10 mm in length), usually being plump and ovoid in shape. Because they are plant-sucking insects, they feed by inserting their slender mouthparts into the plant. These needle-like stylets consist of an outer pair of mandibles and an inner pair of maxillae. The inner faces of the maxillary stylets lock together to form two canals: a large central food-canal for the uptake of plant sap, and a fine duct down which saliva is injected into the plant. The tips of these mouthparts also have a chemosensory function. When the stylets penetrate the plant, they often go between the cells instead of passing through the cells, and in this way they reach the phloem sieve tubes within the veins of the host plant.

Most aphids have well-developed compound eyes (larger in the alates than in the apterous morphs) with a great many individual round lenses called facets or ommatidia. In addition, at the posterior margin of the eye protrudes an ocular tubercle or triommatidium composed of three lenses. Aphids without wings are called apterous, while alate aphids have wings with the hind wings being much smaller than the front wings. Alate aphids (but not apterous) bear three ocelli on the front of the head. The antennae are usually long and thin with five or six segments, and bear placoid sensilla called rhinaria which are the olfactory organs. Legs of aphids do not show much interspecific variation, although more active species tend to have longer legs. Both sets of wings are membranous with the fore wing having two longitudinal veins, one being prominent and the other a weak vein. Both veins run apically into the pterostigma which is a dark, thickened area near the leading edge of the fore wing. When flying, the two pairs of wings work as one, being held together by small hooklets or hamuli on the leading edge of the hind wings that fit into a groove on the trailing edge of the fore wings.

On the dorsal surface of both the thorax and the abdomen, many species have cuticular glands that secrete copious quantities of waxy exudates that are powdery or filamentous or rod-like. As a result, when these species are gregarious, the entire colony appears as a white, powdery or cottony mass. At the end and dorsal surface of the abdomen, there are usually a pair of tubular structures called siphunculi or cornicles. By contraction of a muscle, a droplet of a waxy exudate is discharged through the cornicles which rapidly solidifies in the air. When an aphid is touched or attacked by a predator, one or both cornicles may be raised and the sticky fluid released in a defensive role to gum-up the mouth parts and/or antennae of an attacking predator. This may also function as a pheromone either as an alarm to warn other aphids of a predator or for maintaining distance between aphids on a leaf. Above the anal opening, adult aphids usually have a distinct tail or cauda which varies in shape among species from being short and stubby or long and tapering. In the latter case, aphids can flick off a droplet of honeydew that emerges from the anus. Concerning the external genital organs in the adults, the female genital opening or vulva is only a small slit because there is no ovipositor. On the other hand, the male genitalia have prominent sclerotized claspers and an aedeagus or penis that can be retracted.

Internal Anatomy

Digestive System

Aphids have the usual regions: pharynx, foregut, midgut, hindgut, etc. with subdivisions and associated parts. However, some species have a filter chamber which is a special structure. With some variations, it consists of a concentric filter system in which the tubular anterior region of the midgut is enveloped by the anterior region of the ectodermal hindgut forming a filter chamber. Perhaps this permits selective filtering of the required nitrogen compounds while rejecting the sugars and conveying excessive amounts of water to the hindgut. The precise function is not clear, and since most aphids do not have a filter chamber, it is probably not essential to their method of feeding.

Bacteriocytes

Most aphids have specialized groups of cells called bacteriocytes (or mycetocytes) that usually contain the bacterium *Buchnera aphidicola*. This symbiotic association seems to be mutualistic, and it is not surprising because many insects that live on specialized and often unbalanced diets such as plant sap do indeed possess symbionts. Although their role in aphid biology is still not completely known, they may help the aphid with its nitrogen utilization, synthesis of vitamins, sterols, etc. Although numerous at birth, the bacteriocytes decrease in number during growth. By the end of the aphid's reproductive period, practically none remain, suggesting a contribution to embryonic development. These bacterial symbionts are transmitted transovarially to the embryos so that nymphs are born with them.

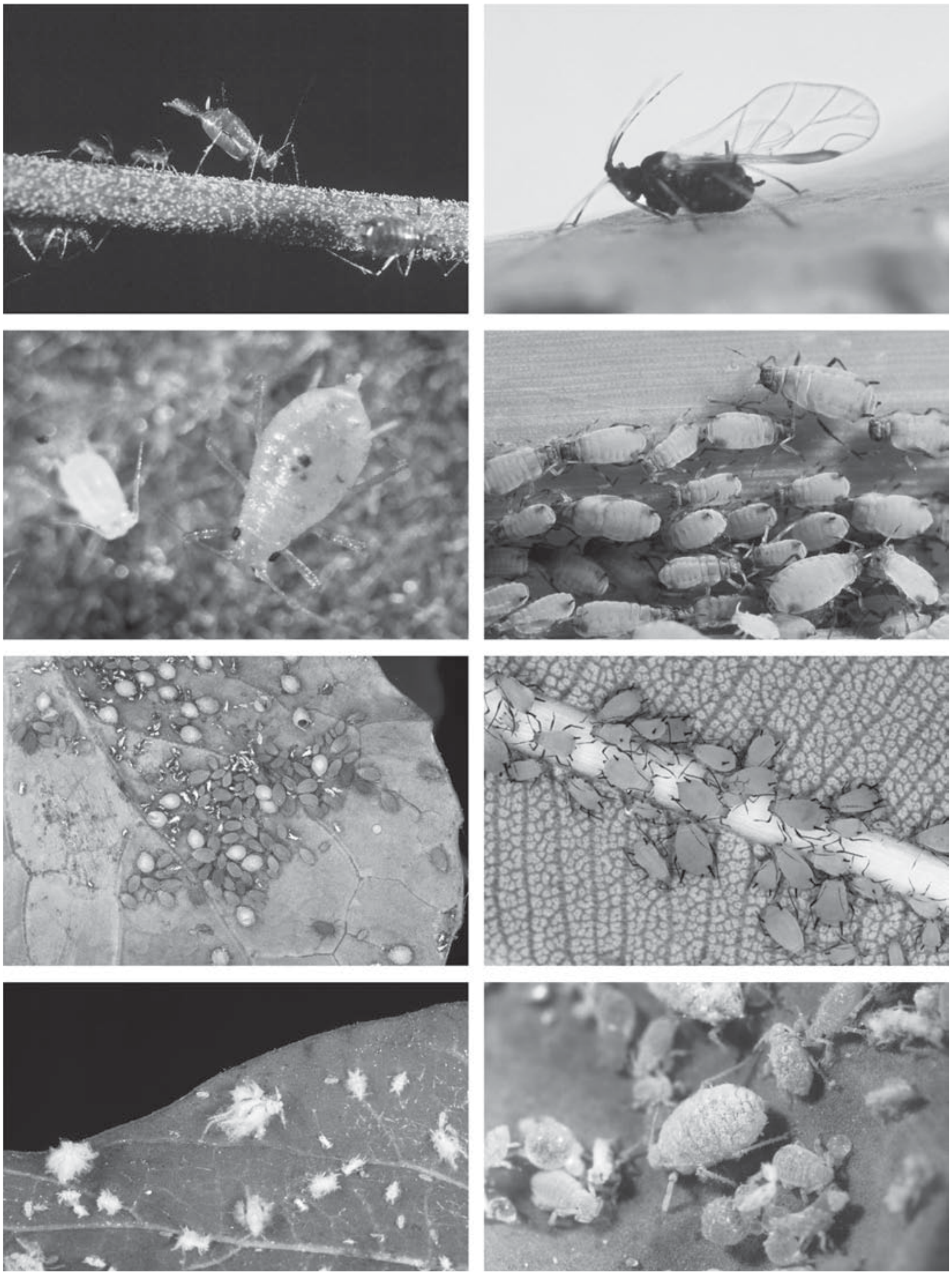
Nervous System

The nervous system comprises four structural parts: brain or supraoesophageal ganglion in the head, suboesophageal ganglion under the brain, thoracic ganglionic mass terminating in the ventral nerve cord, and ganglia plus nerves of the stomatogastric system.

Reproductive System

Female aphids have two ovaries composed of 4–6 ovarioles. They are remarkable because different female morphs can reproduce parthenogenetically (Fig. 64) and be virginopara/vivipara (give birth to live young by larviposition) without mating because males do not exist at this time. At other times, females can reproduce sexually and be ovipara (deposition of eggs that have been fertilized by males). Development of the female embryo depends on whether it is destined to become a vivipara (live birth) or an ovipara (lays eggs). Influences on the adult female can be genetic as well as environmental. Realizing exceptions depending on the aphid species and geographical location, in general when the environment is favorable (long photoperiod, moderate temperature), the viviparous mother will reproduce parthenogenetically. The embryonic female within her will be born alive as a female nymph, and in turn will give live birth to other viviparae also being all females (see below about anholocyclic life cycle). On the other hand, with less favorable conditions (shorter photoperiod, cooler temperature), the oviparous mother will reproduce sexually after mating with a male, and she will lay fertilized eggs (see holocyclic life cycle).

The viviparous parthenogenetic female does not require fertilization, and eggs begin development as soon as they are ovulated from the ovary. Even ovarioles of newly born parthenogenetic females contain developing embryos rather than just eggs. Hence, "telescoping of generations" refers to the fact that a mother can have in her ovarioles developing embryos which in turn also contain embryos or future granddaughters. In the modern family Aphididae, therefore, development may commence even before the mother is born, resulting in a consequent "telescoping of generations." As a result,



Aphids (Hemiptera: Aphididae), Figure 64 **Aphid diversity. Top left, aphid giving birth to a nymph (photo J.L. Capinera); top right, winged brown citrus aphid, *Toxoptera citricida* (photo Paul Choate); second row left, green peach aphid, *Myzus persicae* (photo Jim Castner); second row right, corn leaf aphid, *Rhopalosiphum maidis* (photo Paul Choate); third row left, turnip aphid, *Lipaphis erysimi* (photo Jim Castner); third row right, oleander aphid, *Aphis nereii* (photo Jim Castner); bottom row left, Asian woolly hackberry aphid, *Shivaphis celti* (photo Lyle Buss); bottom row right, cabbage aphid, *Brevicoryne brassicae* (photo Paul Choate). Note copious and moderate amounts of waxy exudate on woolly hackberry and cabbage aphids, respectively.**

postnatal development periods and generation times are short, and reproductive rates are potentially very high. Because aphids are born on the very host plant where they can feed, in many species it requires only 7–14 days for an immature aphid or nymph to metamorphose by several molts into a sexually mature adult when it can begin reproducing. When this is combined with a high fecundity (30 or more nymphs born to each aphid) in a short period of time, the rate of increase is very rapid not only for the individual, but even more so for the entire colony.

The offspring of viviparous parthenogenetic females are born rear first, and are fully active. A nymph is similar in shape to the adult, only much smaller. If destined to be a winged (alate) adult it is either born with wing buds or in some species during the early postnatal period the nymph itself will develop them. This can be triggered by unfavorable conditions due to aphid crowding and/or plant deterioration as well as by seasonal changes such as shorter photoperiod and cooler temperatures. However, colonies founded by alates usually produce only apterous offspring, and only later on might alates develop. Hence, there seems to be a "biological clock" mechanism so that there is a gradual switch to alates that depends on an interval of time.

In the superfamily Aphidoidea, this viviparity (live birth) characterizes the entire family Aphididae. But only females in this family do this, and not females in the families Adelgidae and Phylloxeridae. However, in all three of these families there are sexual females (oviparae) that mate and deposit eggs (see Life Cycles).

Male aphids usually have two to four follicles per testis, although the number, size, and shape varies between species. The vasa deferentia lead to the ejaculatory duct, and in some species there are paired accessory glands.

Excretion

Unlike most insects, aphids have no Malpighian tubules, and excrete nitrogenous waste in the form of ammonia instead of uric acid. The large amounts of water in the diet may dilute the ammonia, and in addition, symbionts in the mycetomes may detoxify it as well.

Ingestion and Digestion

Both as nymphs and as adults, aphids feed by sucking up the sap from the host plant. When the stylets penetrate the plant between the cells, they reach the phloem sieve tubes. In a healthy plant, the sap is under turgor pressure which forces the sap up the food canal between the stylets which reduces the energy needed by the aphid to suck the sap. Nevertheless, there is also a muscular cibarial food pump at the entrance to the pharynx which can be used when the plant wilts and the sap ceases to be under pressure.

Although this plant sap is rich in sugars, it is poor in amino acids that are essential for the growth of the aphid. Hence, aphids ingest large amounts of sap in order to acquire sufficient protein. Although there are less nitrogenous compounds in plant sap compared to leaf tissue (such as would be eaten by other phytophagous insects such as the larvae or caterpillars of lepidopterans), aphids make up for this deficiency by imbibing sap at a very fast rate. The unneeded portion of the sap is mainly sugars which can be stored temporarily in a dilated rectum. This sugary material can be eliminated by ejection from the anus in the form of a sugary droplet called honeydew (see section on Ant-Aphid Mutualism). When aphids are numerous, the leaves of their host plant can become coated with sticky honeydew on which sooty mold fungus can develop causing an economic problem on fruit, vegetables, and even cars parked under a tree.

Sex Determination

As expected, the number of chromosomes varies with aphid species, but all aphids have sex chromosomes for females designated as XX and males as XO. This system of sex determination is called the XX:XO type wherein females have the full diploid complement of autosomes plus one pair of sex chromosomes: XX.

Males also have a diploid set of autosomes, but they have only one sex chromosome (XO) rather than two (not the XY as in some other insects and even humans). As discussed below, in holocyclic life cycles (female cyclical parthenogenesis, alternating with sexual reproduction), sexual females and males are produced in response to cues/stimuli that could be external or internal. On the other hand, anholocyclic life cycles (absence of males, only parthenogenesis by unfertilized females) usually exists when the environment (photoperiod and temperature) is relatively constant.

Parthenogenesis

This is reproduction without mating, and therefore without a female's egg being fertilized. As mentioned above, all aphids have the normal diploid autosomes, but the sex chromosomes for females are XX and males are XO (lacking an X). Among insects in general (not just aphids), when a female's egg is not fertilized, there can be two types of parthenogenetic reproduction:

Arrhenotokous parthenogenesis by females produces only male offspring that are all haploid (n) from her unfertilized eggs (common in the order Hymenoptera – ants, bees, wasps). In aphids, some authors hold that the male's XO sex chromosome determination is only a "type of arrhenotoky" probably resulting from a mini-meiosis in the unfertilized female by which her two X-chromosomes pair and then separate. Males are then XO with the result that they could produce two types of sperm (X and O). However, during meiosis in the male, those sperm without an X-chromosome (designated O) degenerate. This leaves the X-chromosome as the only viable sperm which can fertilize an adult female's haploid egg (X) resulting in all of her offspring being female (XX). Hence, males are produced by the loss of an X chromosome during a meiotic division resulting in the sex determination of XO. Adult male aphids then produce haploid sperm all of which contain one X chromosome. However, this is not really "arrhenotoky" as traditionally used with other insects because although male aphids have the sex determination of XO, they do have two sets of autosomes, but only one X chromosome.

Thelytokous parthenogenesis by females produces only adult diploid (2n) females from unfertilized eggs, but no males. Female aphids seem to have "diploid parthenogenesis" because there is no reduction division, and development starts from a cell with a complete set of chromosomes including the XX sex chromosomes. Both the adult parthenogenetic females and the sexual females are diploid (2n) with XX sex chromosomes. In anholocyclic life cycles (absence of males, only parthenogenesis by unfertilized females), this reproductive method could continue almost indefinitely, if the environmental conditions permitted. However, in holocyclic life cycles (female cyclical parthenogenesis, alternating with sexual reproduction), sexual females and males are produced. The sexual female produces only haploid eggs (X), and requires mating and fertilization by a male (X) resulting in a diploid zygote with two XX sex chromosomes, such that all aphids hatching from these fertilized eggs are females.

Life Cycles

Life cycles in aphids are varied and complicated, but the essential terms are given below:

Holocyclic life cycle: A viviparous parthenogenetic female produces live nymphs without mating. But, this is cyclical because it is interrupted during the year with the production of males and females that mate, and this oviparous sexual female deposits eggs.

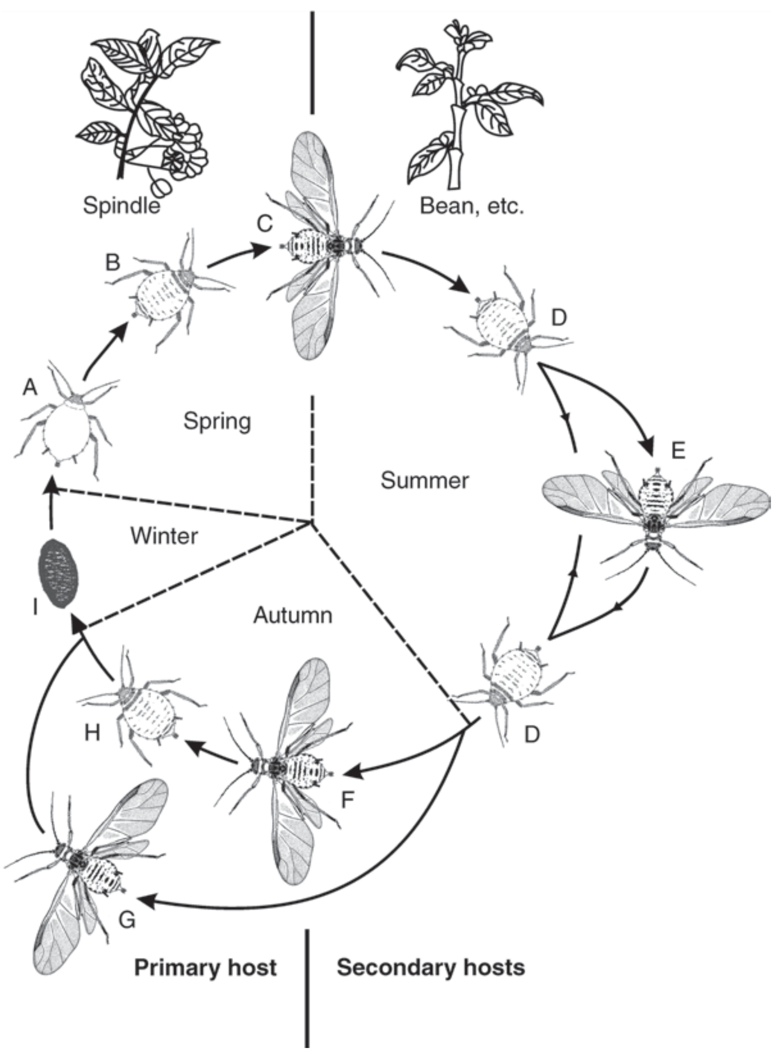
Anholocyclic life cycle: This is the complete absence of males, so that only viviparous parthenogenetic females exist with parthenogenetic reproduction continuing throughout the entire year with all the progeny being female.

Host Plant Alternation

Host plant alternation in aphids involves the two types of life cycles:

Autoecious (monoecious) in which aphids are host plant specific, and live on one or only a few species of closely related plants even within a particular genus during the entire year. Most aphid species (over 90%) are of this type, and as a result, there is usually no need for an annual alternation between primary and secondary hosts, so that the anholocyclic life cycle is common.

Heteroecious or host plant alternation life cycle (Fig. 65) by which about 10% of aphid species spend autumn, winter, and spring on a primary woody host, and the summer usually on secondary herbaceous plants. The primary and secondary host plants usually are unrelated and belong to different families of plants. Although such aphids may be classified as polyphagous, many species are really sequentially monophagous if they live on only one host plant species at a time. This alternation of host plants during the year is accomplished by the holocyclic life cycle described above. These aphids



Aphids (Hemiptera: Aphididae), Figure 65 **Life cycle of the heteroecious holocyclic black bean aphid, *Aphis fabae*. (a) Fundatrix or apterous stem mother, (b) her apterous viviparous parthenogenetic female progeny or fundatri-genia, (c) alate emigrant or spring migrant, (d) apterous virginopara, (e) alate virginopara or summer migrant, (f) alate autumn remigrant or gynopara, (g) alate male, (h) apterous ovipara or mating female, (i) egg (after Dixon 1998; Kluwer Academic Publishers).**

use a specialized reproductive strategy by which the sexual generation produces eggs on the primary (woody) host plant on which they overwinter. This is done because eggs are better able to survive the rigors of a cold winter, snow, etc. The cold period of winter is required before the embryo in the egg can complete its development, and this suspended physiological state is called diapause. The embryo will not hatch until the warmth of spring arrives, and when it does, all of the offspring will be female. This female fundatrix or stem mother on the primary (woody) plant is the first individual to begin the new parthenogenetic line which results in only female offspring all of which are genetic clones of herself. Spring not only provides nutrient availability, but also at this time natural enemies probably have not arrived in dangerous numbers. Again there is a trade-off such that all fundatrices are apterous, thus avoiding unnecessary expenditure of energy on developing wings that are not needed because they do not migrate. Instead, energy can be concentrated on embryological development resulting in very high fecundity of more and more females by viviparous parthenogenesis.

When the colonies of female progeny on the primary (woody) plant become crowded, morphs appear and become alate spring migrants that fly (often with the help of wind currents) to the secondary host plant. The summer secondary host plant is usually herbaceous, and since these alate migrants are all viviparous females, they will produce only females parthenogenetically for as long as this favorable summer weather continues. By dispensing with mating and egg-laying, their numbers can increase at an astonishing rate. These aphids are usually apterous and sessile, remaining on the host plant for long periods in a parasitic "plant lice" mode. But if there is crowding and/or the plant deteriorates, alates will develop in the next generation, thus permitting movement to a new location and even to a new herbaceous host plant. However, such relocation need not be far away if the agroecosystem consists of many acres planted to monoculture. In the autumn, environmental cues (shorter photoperiod and cooler temperature) will trigger the seasonal alternation back to a primary (woody) host plant, and a behavioral change into an alate autumn migrant or gynopara. This parthenogenetic female produces sexual females that will mate with males. Overwintering fertilized eggs are deposited, and the cycle is repeated.

Polymorphism and Polyphenism

Polymorphism means that there are two or more phenotypes or morphs in a population of the same species. Polyphenism means that there are two or more phenotypes or morphs in the same clone. In other words, genetically identical individuals derived from the same mother by parthenogenesis can differ even though they are all clones. This phenomenon is more common in aphids than in any other insect group, especially in aphids that have host plant alternation. In such a parthenogenetic system of genetic clones, females may have as many as eight different phenotypes that differ in such characteristics as morphology, color, physiology, timing of reproduction, developmental time, numbers and sizes of offspring, longevity, host plant preferences, and alternative host plant species. It is probable that some of this variation is not caused only by genetic differences, but also by variations in the host plant and/or the environment.

When environments are regularly cyclical, then seasonal changes and predictable weather patterns can influence the availability and quality of phloem sap that is the basis of aphid feeding. Because of this predictability and reliability, the evolution of aphid species occurred mainly in temperate zone habitats. With this in mind, it is understandable that there has been an environmentally induced morphological and behavioral trade-off so that because alate morphs have energy-costly wings, their developmental time should be slower/longer with a reduced lifetime fecundity compared to the apterous morphs that do not have to expend their energy on wings but rather on offspring production. Hence, there has evolved in aphids both polymorphism and polyphenism that is adapted to changing yet predictable environmental conditions, and resulting in the types of sexual and migrant morphs already mentioned above in earlier sections. No other group of insects can match this diversity.

Soldiers

In addition to the sexual and migrant morphs, there is still another of interest: soldiers. These are female nymphs in only a few (1%) of the more than 4,000 species of aphids, and are found in some but not all gall-forming aphids (see section on Galling). They exhibit a behavior of defending the colony against predators, but they do not molt into reproductive adult females and will never produce offspring. These soldiers aggressively attack invaders, sometimes being suicidal. In some, the fore legs and middle legs are thickened which they use to hold and even crush the intruder. If they have frontal horns, they will use these as well as their stylets as weapons in combat. Both soldiers and normal nymphs can be produced by the same mother aphid. In some species, soldiers (like males) do not have symbionts. Animal behaviorists note the evolutionary convergence of "altruism" in these aphid soldiers with the sterile soldier castes of ants, termites, and thrips.

Color Morphs

Coloration in aphids may be caused by: (i) brown or black pigmentation of the integument (mainly the tergum) or by sclerotization of the cuticle which can give a metallic shine; (ii) body contents show through the cuticle revealing pigments in internal organs, tissues, hemolymph (types of glycosides not found in any other group of animals or plants), bacteriocytes, etc. Colors can vary between and even within species, but the color is usually green, yellow, reddish, creamy, or almost black; (iii) waxy exudates that form a pattern from glands on the body and appear powdery white or grey.

Intraclonal color variation is usually induced by environmental factors, especially temperature, crowding, and poor nutrition. Therefore, it is reversible if these factors revert to the previous state. On the other hand, interclonal color variation is genetically fixed between different color morphs of males and females in some species or between the green and red-pink morphs in the pea aphid (*Acyrthosiphon pisum*), green peach aphid (*Myzus persicae*), and potato aphid (*Macrosiphum euphorbiae*). In the first two aphid species, the red-pink allele is dominant to the green allele, so there may be some biological differences influencing fecundity, reproductive rate, host plant preferences, selection of feeding sites, activity, high or low temperature tolerance, etc. For instance, it seems that thermal conditions may influence the pea aphid when the red-pink morph appears in the summer with the green morph doing better in cooler weather. Also crowding and/or reduced plant nutritional value may cause the red-pink morph of the pea aphid to become green. Any ecological significance such as defensive behavior using camouflage or cryptic coloration has not been demonstrated. However, colonies of some species may use color as aposematic warning behavior against birds or other predators as with the oleander or milkweed aphid, *Aphis nerii*, with its bright yellow color contrasted with black cornicles and cauda, and dark antennae and legs. In other species, some color or pigmented bands may absorb solar radiation that would be advantageous in cool weather.

Aphid Influence on Host Plants

Negative Effect

Aphids like many sucking insects can have a negative effect on the host plant in one or more of the following ways as will be discussed below: nutrient drain, pathogen transmission, salivary toxins, and honeydew excretion.

Nutrient Drain

When aphids are in sufficient numbers, they can drain the plant of its nutrient sap and cause a breakdown in its tissues. Ironically, it could be this less-healthy situation for the plant that satisfies the nutrient needs of this "parasite." As a result, the plant may have its leaf area reduced, growth slowed, early leaf fall, become stunted and/or die before its time.

Pathogen Transmission

The major danger to plants is probably the damage done only indirectly by aphids sucking sap. The greater harm is done when they are inadvertently the vectors of plant pathogens that cause disease. Most important of such plant pathogens are the viruses**.** There is a parallel here between aphids transmitting viruses to plants, and mosquitoes transmitting such pathogens as protozoa and viruses to humans resulting in malaria, yellow fever, etc. Like the mosquito, the aphid's mouthparts are ideally suited for such transmission because the stylets act like a hypodermic needle injecting the virus into the plant as it probes and then sucks the sap. Also, even if the aphid did not have the virus, it would pick it up when it feeds on an already virus-infected plant. A winged aphid (alate) is especially like the mosquito because by flying it can disperse the pathogen to many other host plants.

There are two ways in which an aphid vector can transmit a virus from one plant to another: (i) stylet-borne transmission, where the virus contaminates the mouthparts just by the aphid's probing the host plant. However, this virus is non-persistent on the stylets, lasting only an hour or so, and therefore will eventually disappear on the aphid vector. (ii) circulative transmission, when the aphid actually feeds on an infective plant already having the virus. As a result, the virus invades the body of the aphid. After a latent period, the virus multiplies in the aphid's tissues and enters the salivary glands, from where it can be injected into the next plant when it goes to feed. What is especially dangerous about this mode of transmission is that once infected, the aphid maintains the virus for life, and so continues as a vector being able to infect many other plants in succession.

In either case, more plant viruses are transmitted by aphids than by any other group of animals, and they probably do more damage this way than by merely sucking the sap from plants. Vegetatively propagated plants such as potatoes are especially susceptible because the disease is transferred with the seed tubers to the progeny causing further yield losses. Weeds sometimes act as host reservoirs for such viruses.

Salivary Toxins

Some aphids have toxins in their saliva that cause plant tissues to yellow around the feeding site, and sometimes develop deformities such as leaf-curl, galls, etc. This can negatively influence plant growth and reduce a productive yield of the crop.

Honeydew Excretion

This very natural aspect of aphid biology and behavior is discussed later in the section on "Ant–Aphid Mutualism." In the present context, however, the honeydew that is deposited not only becomes sticky to the touch, but can attract saprophytic sooty-mold fungi to the plant. This may cover the leaf surface and accelerate aging of the plant. It is economically damaging if the fruit or vegetable is blemished and rendered unattractive for sale in a market. Also, car owners are unhappy with this sticky goo on their automobiles if they unknowingly parked under a tree infested with aphids.

Beneficial Effect

Some researchers suggest that aphids may be beneficial to plants in a kind of symbiotic mutualism.

In this unproven scenario, plants benefit by having the aphids remove surplus sugars (especially tri-saccharide melezitose) which can be utilized by nitrogen fixing bacteria in the soil. As a result, these bacteria increase in the soil beneath aphid-infested plants and make more nitrogen available for the plant's growth, and hence are beneficial to the plant.

Galling

Some species are called gall aphids because they cause the plant to develop swollen tissues called "galls" that are usually on the leaf or petiole. This involves a combination of both inhibition and stimulation of the plant tissue at the feeding site that results from stylet probing and injection of saliva. Galls are hollow outgrowths on the plant and can appear as abnormalities or deformities. This cecidogenesis or gall-forming behavior is not limited to aphids, but is also produced by hymenopteran gall wasps and dipteran gall flies or midges. Although relatively few species of aphids induce galls, the shape of the galls is often characteristic for each species of aphid, so that the aphid seems to have the major role in forming the shape of the gall. Galls not only give protection to the aphid, but may also provide a better food source in the following way. A gall provides sheltered protection for the aphid from insect predators and parasitoids, and the aphid's feeding may influence the metabolism of the plant and cause physiological changes that could improve the aphid's food supply. Often, there can be intense competition and aggressive behavior among gall aphids for the best feeding sites on a leaf or petiole where a gall can be formed.

The formation of a gall by the plant probably is due to the plant tissue's reaction to aphid feeding when it probes with its stylets and injects large amounts of saliva into the host plant. It is known that a plant growth hormone called indole acetic acid (IAA) is present in aphid saliva, and so it may be that this chemical induces gall formation. However, this growth hormone normally is found in the plant itself which may account for its presence in the sap-feeding aphid. Gall aphids synchronize their development with their host plant, and may even modify the development of the host plant itself. Finally, some galling aphids are unusual in having soldiers (see section above on Soldiers), and these species tend to produce completely closed galls on their primary hosts. However, not all aphid galls are completely closed, but in those that are, a monoclonal colony of aphids can exist within the gall that was started by a fundatrix. Hence, there is probably a long evolutionary history between the plant as host and the aphid as parasite in this galling behavior. As is often true in similar host-parasite relationships among animals, the host plant may not suffer unduly in this parasitic type of symbiosis when both organisms have been in contact with each other over millions of years.

Ant-Aphid Mutualism

There is a symbiotic mutualism between these two major groups of insects by which the ants obtain a sugar-rich food (honeydew) from the aphids, while the ants protect aphids from predators and parasitoids (see section on Natural Enemies). This is the result of a long-term evolutionary history. An ant that imbibes this sugary honeydew can transport it to nestmates in its crop, and then transfer it to another ant by means called trophallaxis. However, not all species of aphids are ant-attended, nor do all species of ants attend aphids, and even myrmecophilous (ant-loving) aphids differ in their dependence on ants. Most myrmecophilous aphids live above-ground and are gregarious, rather large in size, and often conspicuously colored. But as a result of this mutualism with ants, these aphids do not have well-developed defensive structures on their bodies, and do not display escape behavior to avoid an approaching ant nor even a predator or parasitoid, perhaps because they feel "safe" in the company of their ant protectors.

This mutualistic behavior is all the more amazing when it is realized that most ant species are aggressive predators that would normally attack any available prey, especially rather helpless aphids. Yet, the ants that associate with aphids do so in an almost tender way, and "milk" them for their sugary honeydew which comes from the anus. The ant may antennate or stroke the rear of the aphid's abdomen to stimulate this release of honeydew droplets which the aphid does in an accommodating way without any interruption in its normal feeding behavior.

Aphids that are not attended by ants behave differently by raising and contracting the abdomen/rectum, thus ejecting the droplet of honeydew some distance from themselves. Some species even use their hind legs to flick the honeydew away, perhaps to avoid contaminating the colony with this sugary material that might develop sooty-mold fungus. As a general rule, aphids that are not ant attended have a long cauda and long siphunculi or cornicles, perhaps used for defensive purposes against predators and parasitoids, since there are no ants to protect them.

Studies have shown that ants can have a positive effect on the number of aphids, and even on the efficiency of feeding by increasing the ingestion of phloem sap with a resulting increase in the production of honeydew as a reward for the ants. Ant attended aphid colonies are usually larger, feed more heavily, and produce fewer winged (alate) offspring. There can also be a stabilizing effect on aphids, so that the size of the aphid colony may be dependent on the presence of ants. However, when an aphid colony becomes too large, the host plant will deteriorate more quickly and the aphids may move off it leaving the ants behind. To avoid this loss of honeydew source, it may be that ants control the aphid population size and keep it stable so that the host plant will not be excessively harmed. On the other hand, if the aphids become too few to produce an adequate supply of nutritious honeydew, the ants may switch to another and larger myrmecophilous aphid colony or even to a different aphid species that might be nearby.

Ants search plants for aphids, and when they are discovered, the ant returns to the nest laying down a recruitment chemical pheromone trail which worker ants from the nest follow to the aphids. Since many species of ants tend a variety of species of aphids, it has been suggested that at least some elements of the ants'behavior are learned rather than innate. Both ants and aphids make great use of intra-specific and perhaps even inter-specific pheromonal communication. Most ant colonies tend a number of aphid species simultaneously, and it seems likely that there is competition between the aphids for the ants'attention. Seasonal changes in ant availability and their demand for honeydew might be factors in this competition. In temperate regions, host plant availability for aphids and therefore honeydew production vary seasonally, as does the ants'ability to collect these sugars.

It is unclear to what extent there may be predation of aphids by their ant "protectors," but it seems that a significant amount of predation does indeed occur. Perhaps the ants need some protein as well as carbohydrates from honeydew, and in a coevolutionary way the aphids may find limited predation (especially in large colonies) a necessary price to pay for protection from natural enemies, and even for the removal of potentially contaminating sugary honeydew.

Natural Enemies of Aphids

This discussion will be limited to the natural enemies of aphids that are themselves insects, and not other animals such as birds, nor even pathogenic fungi, etc., that also can kill aphids. In entomology, insects that attack, feed on, and kill other insects are called entomophagous insects. However, in the present context, insects that kill aphids are more precisely called aphidophagous insects. As a general introduction, some definitions must be given. Insects that attack, feed on, and kill other insects (not just aphids) are divided into two major categories:

Predators

Predators are insects that attack, feed on, and kill the prey directly. Depending on the species of predator, both males and females as well as the immature stage and/or the adult can do this. Usually, more than one prey is required for the predator to reach adult sexual maturity.

Predators of aphids expend energy and time searching for prey, and so maximum efficiency is achieved when the predator finds an entire colony of aphids and not just an individual. Once in a colony, many predators proceed slowly and stealthily so as not to raise an alarm. An extreme example of such a predator would be the blind, legless larva of a syrphid hoverfly (mentioned below). Examples of major predators of aphids are given next:

Ladybird Beetles (Order Coleoptera, Family Coccinellidae)

These are the best known of aphid predators, and they feed both as immature larvae and also as adults. These are very familiar beneficial insects, but often incorrectly called "ladybugs" because "bug" should be limited to the true bugs in the order Hemiptera that have piercing-sucking mouthparts. They have a convex shape and usually colorful markings. Because they are very common wherever aphids are found around the world, they have been intensely studied for their use in biological control programs. The coccinellids that are brightly colored are demonstrating warning or aposematic behavior, i.e., they are distasteful to their own predators, such as birds. Even their eggs are often orange or yellow. The larvae that hatch from these eggs are notorious for their cannibalism on coccinellid eggs and other smaller sibling larvae because they have to feed almost immediately on some prey or die. As the larva molts and increases in size, it can sometimes consume more than 100 aphids per day. The larva has pointed jaws which it uses to pierce the aphid cuticle. Saliva is then injected into the aphid which digests the body contents into a semi-liquid which can be sucked up. Solid remains of the aphid may be eaten later if the larva is large enough. However, coccinellids have their own natural enemies especially in the orders Diptera and Hymenoptera.

Lacewings (Order Neuroptera, Families Chrysopidae, Hemerobiidae)

These are delicate "nerve-winged" insects with large transparent wings that are often colored light green or brown as is the body. Depending on the species, they feed both as larvae and adults, and are considered important predators of aphids (perhaps second only to coccinellids) and have therefore been used in biological control programs. The larvae have hook-like piercing jaws that are used to suck up the body contents. The aphid prey is held up in the air while it is being eaten. In some species, the adult lacewing lays eggs with each one attached to the end of a vertical stalk which is quite visible when many eggs are laid together on a leaf.

Hoverflies (Order Diptera, Family Syrphidae)

As the name indicates, the adult flies hover in the air over one spot, and then dart to another location. The adults can be seen visiting flowers where they feed on nectar and pollen, and so are also called flower flies. The abdomen is often brightly colored with bands of white or yellow contrasting with a black background, perhaps as mimicry of wasps. It is not the adults that eat aphids, but rather the female lays her eggs close to or within an aphid colony. From each egg hatches a dipteran larva or maggot that is blind and legless, dorso-ventrally flattened and tapered at the anterior end. Like lacewings, the syrphid larva feeds on the aphid by piercing and sucking out the body contents, while holding the prey aloft.

Cecid Flies (Order Diptera, Family Cecidomyiidae)

These tiny flies are often called gall midges although the species that attacks aphids do not form galls on plants. Hence, these cecid flies are also called aphid midges, but the adult does not feed on aphids. Each female can lay about 100 eggs on leaves and stems of plants infested with aphids. It is the maggot-like larva that feeds by piercing the aphid with its long serrated mandibles, sucking out the body contents.

Anthocorid Bugs (Order Hemiptera, Family Anthocoridae)

These are called minute pirate bugs or flower bugs because they are often found on flowers where they may feed on plant juices. Most species are general predators on thrips, mites, and other small arthropods besides aphids. However, the two genera *Anthocoris* and *Orius* are predominantly aphid predators. Being hemipterans, they have simple or incomplete metamorphosis, and the adults as well as the nymphs feed on aphids by sucking out the insides through their styliform mouthparts.

Parasitoids

Parasitoids are insects (orders Hymenoptera and Diptera) in which the adult female attacks what is called the host, but she only indirectly kills the host because the female merely lays her egg in, on or near it. It is the larval offspring from the egg that actually feeds on and kills the host. In older literature, these parasitoids were called parasites, but this terminology was misleading because a true parasite (flea on a dog) usually does not kill the host (dog).

Parasitoids of aphids are micro-wasps (4 to 5 mm in length or smaller) in the order Hymenoptera, and are usually classified both taxonomically and behaviorally in only two families, Aphelinidae (superfamily Chalcidoidea) and Aphidiidae (or Family Braconidae and Subfamily Aphidiinae) (superfamily Ichneumonoidea). These parasitoids are quite host specific in using only aphids as hosts (and no other group of insects). But, even among the thousands of aphid species as possible hosts, different parasitoid species display a feeding behavior that ranges from a continuum of polyphagy to a certain host specificity of oligophagy to monophagy, so that many species of parasitoids limit their attacks to only one or a few species of aphids.

Using as an example a typical species in the genus Aphidius in the family Aphidiidae, the female micro-wasp is quite host-specific, and is called endophagous because she lays an egg inside the live aphid. Her ovipositional behavior is to attack the aphid with a quick thrust of her ovipositor which is usually brought forward between her legs, and is positioned in front of and beneath her head. After the egg has been successfully deposited inside the live aphid, the female departs to attack another aphid, and her involvement with the first aphid is ended. Her offspring, however, is the parasitoid larva that hatches from the egg inside the live aphid that will ultimately kill the aphid. Oddly enough, the aphid host usually continues to feed on the host plant as if nothing had happened and without changing its normal behavior. Over a period of approximately 8–10 days that varies with the species of aphid and parasitoid, the larva molts several times while gradually devouring the aphid internally, finally killing it. Then the fourth and last larval instar spins a cocoon inside the dead aphid, whose exoskeleton becomes hard and changes from its original color to brown (which is now referred to as a "mummy"). The parasitoid larva may fasten the ventral side of the mummy to the leaf. It pupates inside the mummy, and approximately 4–5 days later (or about 12–15 days after the original oviposition) the new adult wasp parasitoid cuts a circular emergence or exit hole in the mummy (usually in the dorsum of the abdomen) and pulls itself out. The adult wasp will find a mate within a short time after emerging from the dead aphid mummy. When fertilized, this new generation of adult female will start the cycle again by attacking and depositing her egg inside another aphid. Note that it is the parasitoid larva that feeds on and kills the host aphid, not the adult female that only oviposits inside the aphid and then departs. Remember that during the moderate summer months, there are long periods in the life cycle of an aphid colony when it is sessile and does not move very far away as long as the host plant provides sufficient nourishment. Perhaps for this reason, micro-wasp parasitoids of aphids have been used quite successfully in biological control programs around the world.

Hyperparasitoids

The micro-wasp parasitoid described above is technically called a primary parasitoid, and it is considered beneficial because it kills the aphid which may be a pest insect. However, there are other species of micro-wasps also in the order Hymenoptera, but not in the same families as the primary parasitoids of aphids just discussed. These micro-wasps have evolved to a higher trophic level so that we have an example of multitrophic ecology and behavior. At the 1st trophic level is the host plant, then at the second trophic level is the herbivorous or phytophagous aphid, and at the third trophic level is the carnivorous or entomophagous primary parasitoid. Finally, at the fourth trophic level is a different species of micro-wasp called a secondary parasitoid or hyperparasitoid that attacks the primary parasitoid while it is still inside the aphid. This food web involving four trophic levels of plant, to aphid, to primary parasitoid, to hyperparasitoid has been used as a model system in community ecology.

Since many aphid species are such worldwide pests, hyperparasitoids of aphids have been especially well-studied, and can be categorized as follows depending on their adult ovipositional and larval feeding behaviors: (i) The female wasp of endophagous hyperparasitoid species deposits her egg inside the primary parasitoid larva while it is still developing inside the live aphid, before the aphid is mummified. But, the egg does not hatch until after the mummy is formed, and then the hyperparasitoid larva feeds internally on the primary larval host still inside the mummy. (ii) The female wasp of ectophagous hyperparasitoid species waits until the primary parasitoid larva has killed the aphid and formed the mummy. Then she drills a hole through the mummy, and deposits her egg externally on the surface of the primary parasitoid larva inside. After hatching, the hyperparasitoid larva feeds externally on the primary larval host while both are still inside the mummy. In both cases, the hyperparasitoid larva then pupates inside the mummy, and as with the primary parasitoid described above, the new adult wasp hyperparasitoid cuts an emergence or exit hole in the mummy (usually in the dorsum of the abdomen) and pulls itself out. The adult wasp hyperparasitoid will find a mate within a short time after emerging from the dead aphid mummy. When fertilized, this new generation of adult female hyperparasitoid will start the cycle again by attacking and depositing her egg in or on a primary parasitoid larva inside another aphid.

There is an economic interest in hyperparasitism because if primary parasitoids are considered beneficial insects (especially when used in biological control programs) then it would seem that hyperparasitoids that attack primary parasitoids might be detrimental. On the other hand, some ecologists suggest that perhaps hyperparasitoids play a positive role in the ecosystem by preventing an excessive increase in the numbers of the primary parasitoids that might so reduce the phytophagous host as to result in the local elimination not only of the insect pest, but also the beneficial primary species as well. If more phytophagous insects of the same species (such as aphids for example) were to move into this local area without sufficient primary parasitoids to attack them, then there might be a resurgence of the insect pest.

Aphid Defenses

As mentioned earlier in the section on polymorphism, there are aphid soldiers in a few species that perform an altruistic role. These are female nymphs that have morphological adaptations to defend a colony against predators. Even if they are not killed in this action, they do not reproduce. Usually, species that have soldiers tend to form closed galls on their primary hosts (see section on Galling). However, the majority of aphid species do not have soldiers, yet many species are still capable of defending themselves by various means such as the following: aggressive kicking, thick defensive cuticles and/or spines, waxing predators and parasitoids, using stylets to attack and kill eggs of predators and even other species of aphids, or suddenly falling off the leaf onto the substrate as a tactic that permits their escape from an impending attack by an aphidophagous natural enemy. Some aphids also emit chemical alarm pheromones that warn other aphids nearby of imminent danger. In this regard, it is interesting that some aphid alarm pheromones may also act as kairomones (communication chemicals between different species) so that predator coccinellid beetles are actually attracted to the aphids.

Control of Aphids

Prevention of damage to plants is especially important when a major agricultural crop could be destroyed by aphids at great financial loss to the farmer. Even forest and shade trees have economic as well as esthetic significance when they are used for logging or as parks. Control involves using methods to protect the crop from aphid attack by various means such as chemicals, natural enemies (biological control), host plant resistance (HPR), modifying aphid behavior, and finally integration of these methods (IPM).

Chemical Control and Resistance

Prior to World War II, chemical control of aphids was limited to nicotine and arsenical products. These aphicides were sprayed on the crop, and at the time seemed to have little negative residual or systemic effects. After the war, however, DDT and other chlorinated hydrocarbons were developed and widely used as broad-spectrum insecticides that were considered to be a panacea not only for control of aphids, but for many other insect pests as well. Although not systemic, they did have residual effects that in the beginning seemed to be a benefit because they were long-lasting. But eventually, evidence from field studies demonstrated that these residues persisted in the ecosystem, and accumulated in the food chain causing unexpected dangers to non-target organisms, especially to fish, birds, and even mammals. In addition, the unintended killing of beneficial insects that were the natural enemies of the insect pest resulted in pest resurgence, traded-pests, etc. The excessive use of these chemicals with these dangerous side-effects was eventually banned in many countries around the world.

New generations of chemical insecticides were developed such as the organophosphates, carbamates, and pyrethroids. To control aphids, special aphicidal properties were emphasized:

1. Selective toxicity: predators and parasitoids not killed, nor any other non-target organisms.
2. Systemic activity: chemical is applied not only to foliage and seeds, but especially to the soil where the roots take it up via the vascular system where aphids feed on the phloem sieve tubes.
3. Residues: Some residual activity may be needed to prevent aphids from reinfesting the crop. In the case of food and fodder crops, however, chemical persistence can be dangerous. Aphicides on such

plants should decompose into harmless compounds before harvest.
4. Rapid action: to prevent transmission of non-persistent viruses, quick mortality of aphids is necessary. Some synthetic pyrethroids show repellent action that deters aphids from settling.
5. Low phytotoxicity: the aphicide should not harm the crop itself because the purpose of the chemical is to protect the plant from aphids without having a toxic effect on the plant.

Application of Aphicides

No general rule can be given because so much depends on local conditions, type of chemical, length of growing season, aphid population size, time of day, weather, etc. Sometimes soil or seed application is sufficient instead of dusting or spraying, and of these two, if the crop is dense, then perhaps dusting is better than spraying. Farm advisors should be contacted because they know the local situation for making recommendations.

Resistance

It is well-documented that chemical insecticides are powerful agents of natural selection so that over time some mutated insects such as aphids develop resistance. This renders the chemical inefficient, resulting in attempts to restore success by repeating applications, then increasing the dosage, etc. In addition, as mentioned above, the beneficial natural enemies are also negatively affected. There are reports of 20 or more aphid species that have developed resistance to various chemical insecticides. The green peach aphid, *Myzus persicae* (Sulzer), is an excellent example. It is a notorious aphid pest that not only has secondary hosts in over 40 different plant families, but it is one of the most important vectors of over 100 plant viruses. Although *M. persicae* is probably of Asian origin, it is now found worldwide.

As a result of many years of subjection to chemical insecticides, natural selection has developed resistance in large populations of many aphid species not only in the field, but especially in greenhouses. The biochemical cause of resistance in aphids is still being studied, and there seems to be a positive correlation between resistance and the activity of enzymes (esterases). It has also been suggested that symbionts are involved in resistance. In any case, although some chemical aphicides may still need to be used, they should be applied judiciously to avoid the typical insecticide treadmill cycle of excessive dependence on chemicals with unintended results such as pest resurgence, traded-pests, etc.

Biological Control

Biological control is the intentional use by humans of an insect pest's natural enemies such as beneficial insect predators and parasitoids as well as pathogens (bacteria, viruses, protozoa, fungi, nematodes, etc.) in order to lower the population level of the insect pest below the economic threshold so that crop loss is reduced and the farmer can have a successful harvest. In the field, the aphids'sessile feeding behavior for long periods of the year makes them especially attractive to natural enemies. In addition, aphids are amenable to studies in the laboratory where many species can be rather easily reared along with their natural enemies for research and experimentation in insect cages, growth chambers, and environmentally controlled walk-in rooms. As a result, and because of their worldwide pest status (especially in the temperate zones), aphids have been the target of many successful biological control programs.

There is an aspect of this method called classical biological control wherein the natural enemy is introduced as an exotic parasitoid or predator from another country or even more frequently from another continent. Also, the insect pest is often an exotic invader into a new habitat or the insect pest could be indigenous. In either case, it seems that the indigenous natural enemies are incapable of keeping the new or old insect under control so that it has now reached pest status. To obtain the exotic natural enemy involves foreign exploration and importation, mass rearing, colonization, establishment, etc. Three examples of this type of classical biological control of aphid pests are given here because they are so well documented, and can be easily referenced in the entomological literature:

1. The first case of successful aphid biological control was against the wooly apple aphid, *Eriosoma lanigerum* (Hausmann), a serious pest of apple in North America and now worldwide in distribution. Beginning in 1920, an aphelinid wasp parasitoid, *Aphelinus mali*, was imported from the United States and became established in 42 countries with generally satisfactory results.
2. Another success was with the spotted alfalfa aphid, *Therioaphis trifolii* (=*maculata*) (Buckton), which invaded the southwestern United States in 1953. Two aphidiid wasp parasitoids, *Trioxys complanatus* and *Praon exsoletum*, as well as the aphelinid *Aphelinus exsoletum* were imported from the Middle East, and resulted in excellent control of this exotic aphid. This case was also important historically because the concept of integrated pest management (IPM) was pioneered during this period by entomologists at the University of California.
3. Finally, although the pea aphid, *Acyrthosiphon pisum* (Harris), was a Palearctic species, it had existed as an exotic invader in North America since the end of the 1800s where it was a pest on alfalfa and peas. Indigenous predators and parasitoids seemed ineffective, so in 1958 the specialized aphidiid parasitoid, *Aphidius smithi*, was imported from India into the western United States. Later in 1963, the polyphagous aphidiid parasitoid, *Aphidius ervi*, was introduced from Europe into the eastern U.S. Both parasitoids have been successfully established resulting in good control. Of ecological interest here is that over time, it seems that *A. smithi* is being replaced in the west by *A. ervi* that was first introduced in the east. However, good control of the pea aphid continues across the continent.

Unlike these three examples of classical biological control involving exotic aphids, it can happen that for various ecological and behavioral reasons the aphid pest is indigenous and the native natural enemies do not control it. In this case, at least the conservation of the existing, indigenous natural enemies is of primary importance. This can even be assisted by augmentation and inundative releases of these indigenous natural enemies from mass-rearing insectaries. Sometimes, exotic but taxonomically closely related species to the indigenous species of natural enemy might be imported from abroad and used to complement the native species, thus improving the possibility of controlling an indigenous pest.

In comparison with chemical control, biological control is non-polluting, non-toxic, and self-perpetuating, and makes no claim about completely eradicating the insect pest. Instead, the population level of the pest is lowered to an economic threshold acceptable to the farmer. Since this involves a living ecosystem, biological control tends to be permanent, and therefore less expensive. Needless to say, whether the pest is an aphid or some other insect, proper scientific procedures demand that extensive research be done on the biological aspects of both the insect pest as well as the natural enemies (indigenous and exotic) in relation to the ecosystem.

Finally, pathogens such as bacteria, viruses, protozoa, fungi, nematodes, etc., can be used as microbial insecticides against insect pests. Aphid diseases have been recognized for over 150 years, but only entomogenic fungi in the order Entomophthorales have been considered as the main pathogen against aphids. Usually warm and humid weather can spread the fungus very quickly into an epizootic, especially when the aphid colony is crowded. The infected aphid becomes brown and inflated with liquid when it dies of mycosis. This can happen in the tropics and greenhouse, but in field conditions in temperate regions humidity is not that predictable. Much can still be done to use the potential of fungi in biological control programs against aphids. The other pathogens such as bacteria and protozoa do not seem to have been demonstrated to cause infections in aphids. Although baculoviruses and picornaviruses can be transmitted transovarially and reduce the longevity of an aphid, no viral epizootics of aphids have been reported.

Host Plant Resistance (HPR)

Many plant species have defenses against herbivores including insects that is genetically heritable, and hence controlled by one or more genes. Resistance of plants to insect attack is related to the heritable qualities of the plant that may reduce the damage. The main task of agronomists is to increase the yield and quality of a crop by standard breeding methods. However, this can also include trying to breed genotypes into crops that make them resistant to insect attack by using one or more of the following mechanisms:

1. Antibiosis: physico-chemical characteristics of the plant that kill the insect;
2. Antixenosis: pest insect is repelled by the plant or at least has no preference for it;
3. Tolerance: the plant can recover even after some feeding damage by the insect.

Plant characteristics vary depending on the species, but host plant resistance can be morphological (leaf size, shape, color, pubescence, thickness, texture), biochemical (lack of nutrients, allomones [feeding repellents, ovipositional and feeding deterrents, toxins], kairomones [attractants for natural enemies]). Entomologists work closely with the agronomists to test or screen the supposedly resistant crops (but still as high-yielding as possible) to see if indeed these genotypes are also resistant to a particular insect pest that is being studied. To do this, hundreds of insect pests are constantly being mass-reared in the insectary. These are used not only for laboratory studies of insect-plant interactions, but especially for the purpose of bringing them into the field for artificial infestation. In the field, these insect pests are placed on the cultivar to be infested and eventually evaluated as to the amount of damage caused to the plant as it grows. It must be stated, however, that HPR to one insect pest does not mean that a cultivar is resistant to other taxa or even to related species. Furthermore, the genotype may not be resistant to other biotypes or races of the same insect pest species that initially showed host plant resistance.

Concerning HPR for aphids, the same general principles and procedures are used as just mentioned above. Hundreds of cultivars have been developed for resistance to aphids for more than fifty important crop plants in the families Leguminosae, Gramineae, Compositae, Cruciferae, Cucurbitaceae, Rosaceae, Solanaceae, etc. The problem of biotypes or races also occurs among aphids because of their parthenogenesis, telescoping of generations, host plant alternation, etc.

Modifying Aphid Behavior

Aphid behavior can be modified by both prevention of landing by aphids in flight, and by repelling aphids that have already landed.

Flying aphids are attracted or repelled from plants by light of a particular wavelength. When winged aphids first fly, they are attracted to the blue-ultraviolet light from the sky. However, after a period of flight this is reversed, and instead of flying upwards, the sky may repel them and they are attracted to the orange-yellow-green light reflected from the leaves below. This behavior might be exploited by using yellow traps to lure them away from crops in a field (though as yet this has not been demonstrated). The yellow trap can be filled with some liquid that kills the aphids that have landed in them. Yellow traps are used extensively to monitor flights of aphids.

Plant odors are volatile substances produced by plants that attract aphids in their host selection. Aphids on agricultural crops tend to be polyphagous, so perhaps specific volatile cues are not too important. However, aphids on perennial crops and wild plants are more oligophagous and even monophagous for which plant odors are needed. Hence, attractant baits have been tried as well as repellent chemicals that may also have a role in aphid control.

Alarm pheromones are released by some species of aphids when they are attacked by natural enemies. It would be advantageous for flying aphids to avoid landing on a plant where aphid colonies are being attacked and have released an alarm pheromone. Synthetic alarm pheromones have been used successfully, but because some are highly volatile, a formulation with a slow release would enhance this control method.

Synthetic chemical repellents would be a non-toxic alternative to insecticides, and are safer to the applicator and to the environment. However, there is a problem with aphids that are vectors of a non-persistently transmitted virus. It would have to have its repellent effect act very quickly before the aphid makes its first probe. Even chemical aphicides have this difficulty in not acting fast enough to prevent that first probe by which an uninfected aphid picks up the virus, or if already infected, then before the aphid probes into a healthy plant. There is a continuing need to study the chemoreception of aphids and their resulting behavioral responses.

Cultural Control

This method involves the use of normal agricultural practices to reduce pest damage not only by aphids but also by other insects. Such cultural techniques can include the following: timing of planting and/or harvesting to disrupt the normal cycle of aphid landing and feeding; crop rotation varies the crop during the season or annually with another plant that would be unattractive to the aphid and/ or less important to the farmer; intercropping uses the same principle but alternates field rows or sections of the crop with another plant; tillage (mechanical manipulation of soil to reduce weeds, improve drainage by plowing, hoeing, etc.); sanitation is the removal of weeds or crop residues that might provide the aphid an alternate host; water management depends on the needs of the host plant and the biology of the aphid species.

Integrated Pest Management (IPM)

In their evolution, aphids have taken advantage of favorable agricultural habitats especially through monoculture, thus making the agroecosystem an attractive food source. Although different species of aphids vary in their host range from polyphagy to monophagy, they are often able to survive on herbs in the vicinity of the crop or simply to fly to another area where a more suitable host plant is more available. Realistically therefore, eradication is all but impossible. Because of various side effects mentioned earlier, reliance only on chemical insecticides should not be the main option. Instead, it is sensible to integrate as many of these control methods just discussed. This concept of integrated pest management (IPM) was first developed at the University of California during the late 1950s. An acceptable definition of integrated pest management (IPM) should include the following entomological and ecological aspects: a pest management system that utilizes all suitable control methods to reduce and maintain the pest population level below that causing economic injury, with special concern for the environment including the insect's natural enemies. This sound ecological philosophy should be applied to aphids and to other insect pests whenever possible.

Important Aphid Species

Although there are over 4,000 aphid species, only a small percentage of these are pests. Nevertheless, it is not surprising that general interest and most of the funded research at universities and institutes should be concentrated on aphid species that indeed are pests of agricultural crops, forest and shade trees because of their commercial and economic importance. With this bias in mind, listed in alphabetical order (English names) is a sampling of some important aphid species: black bean aphid, *Aphis fabae* Scopoli; black citrus aphid, *Toxoptera aurantii* (Fonscolombe); blue alfalfa aphid, *Acyrthosiphon kondoi* Shinji; brown citrus aphid, *Toxoptera citricidus* (Kirkaldy); cabbage aphid, *Brevicoryne brassicae* (Linnaeus); corn leaf aphid, *Rhopalosiphum maidis* (Fitch); corn root aphid, *Aphis* (*Protaphis*) *maidiradicis* Forbes; cotton or melon aphid, *Aphis gossypii* Glover; cowpea or black legume aphid, *Aphis craccivora* Koch; grain aphid, *Sitobion avenae* (Fabricius); green apple aphid, *Aphis pomi* De Geer; green peach aphid, *Myzus persicae* (Sulzer); greenbug, *Schizaphis graminum* (Rondani); oleander or milkweed aphid, *Aphis nerii* Fonscolombe; poplar petiole gall aphid, *Pemphigus populitransversus* Riley; pea aphid, *Acyrthosiphon pisum* (Harris); potato aphid, *Macrosiphum euphorbiae* (Thomas); rose aphid, *Macrosiphum rosae* (Linnaeus); spotted alfalfa aphid, *Therioaphis trifolii* forma *maculata* (Buckton); tulip-tree aphid, *Illinoia liriodendri* (Monell); walnut aphid, *Chromaphis juglandicola* (Kaltenbach); woolly apple aphid, *Eriosoma lanigerum* (Hausmann).

Several of these important aphid species are worth special mention:

Green Peach Aphid

Myzus persicae (Sulzer) is probably the most polyphagous of all aphids. As a result, it is the most important insect vector of plant diseases including transmission of over 100 plant viruses such as curly top of sugar beets, peach yellows, cranberry false blossom, aster yellows, and various potato viruses, etc. It is pr obably of Asian origin on its principal primary host *Prunus persica* (peach), and then followed this host wherever it was planted which is now worldwide in distribution. Its secondary hosts are in over 40 different plant families, including many that are also economically important. In temperate regions it is usually heteroecious holocyclic, but can be anholocyclic where peach is absent and the climate permits winter survival. Because it is relatively easy to rear in laboratories and greenhouses, this aphid's biology, anatomy, physiology, etc., has been intensely researched. In addition, because of its economic importance, the ecology of *M. persicae* has been studied, especially for use with biological control.

Black Bean Aphid

Aphis fabae Scopoli is also heteroecious holocyclic, and in Europe it alternates between *Euronymus* (strawberry bush) and various secondary hosts where it feeds on many agricultural crops including *Vicia faba* (broad bean) and other legumes. Besides this polyphagous behavior, it is a vector of more than 30 plant viruses. It is widespread in temperate regions of the Northern Hemisphere, as well as South America and Africa, except for the hotter parts of the tropics and the Middle East. *A. fabae* may be a complex of species, and outside of Europe where it seems to have originated, its taxonomic status is unclear. However, because of its importance, it too has been intensely studied in both field and laboratory research projects.

Cotton or Melon Aphid

Aphis gossypii Glover is very polyphagous not just on cotton and cucurbits, but also on such diverse crops as citrus, eggplant, okra, peppers, coffee, potato, cocoa, and many ornamentals such as *Hibiscus*. In addition, it can transmit over 50 plant viruses to important crops such as beans, peas, soybeans, crucifers, celery, cowpea, sweet potato, tobacco, tulips, strawberry. Its distribution is now worldwide including the tropics and many Pacific islands. In the temperate latitudes with cold temperatures where crops are raised in greenhouses, *A. gossypii* is a major pest. Perhaps it is of palaearctic origin because it is anholocyclic in Europe. However, it seems to be holocyclic in North America, China, and Japan.

Oleander or Milkweed Aphid

Aphis nerii Fonscolombe is an especially interesting aphid because of its attractive bright yellow color contrasted with black cornicles and cauda, and dark antennae and legs. Such aposematic behavior advertises and warns potential predators that it is unpalatable and even harmful. This is because while feeding, it has sequestered poisonous chemicals (cardiac glycosides) from its host plants mainly in the families Apocynaceae and Asclepiadaceae such as oleander and milkweed. It has thus coevolved by transferring for its own protection the "poisonous" defense of these host plants. Instead of using cryptic or camouflage defense as many other insects do, *A. nerii* demonstrates behavioral convergent evolution with the similarly bright warning coloration (orange and black) of the monarch butterfly that also feeds on milkweed. *A. nerii* then reinforces this aposematic behavior by forming dense colonies that are frequently concentrated on young stems. Also unusual is its life cycle that seems to be only anholocyclic with no sexual morphs. It is widely distributed in the warmer regions of the Old and New World, plus the tropics and subtropics.

Pea Aphid

Acyrthosiphon pisum (Harris) is a large aphid with slender appendages and long cornicles. There are both green and red-pink morphs, similar to the potato aphid, *Macrosiphum euphorbiae* (Thomas), that also has green and red-pink morphs with both aphid species being in the same aphidine tribe Macrosiphini. The pea aphid seems to be a complex of races and subspecies on different host plants, but mostly important legumes such as alfalfa, clover, peas, broad beans, etc. *A. pisum* is a vector of more than 30 virus diseases, and although probably palaearctic in its origin, it is now worldwide in its distribution where it is holocyclic in the temperate regions, and perhaps anholocyclic in warmer climates. Because it can be reared easily in the laboratory with its micro-wasp parasitoids, as mentioned earlier, it was an example of a classical biological control program that was successful.

Summary

Aphids fascinate the non-entomologist as well as amateur and professional entomologists because of their sometimes unique and always unusual biologies. Although small in size, their external morphology and internal anatomy as well as their polymorphism and polyphenism make aphids interesting. One marvels at their reproductive behavior (parthenogenesis, telescoping of generations, sex determination), life cycles (host plant alternation), ant–aphid mutualism, etc. Finally, of course, aphids have had an enormous economic impact as pests on the world's agricultural crops, forest and shade trees, not only by their feeding, but as vectors of plant viruses. This is a great challenge to humankind to control them by using ecologically safe as well as effective methods. Hence, aphids are a rewarding subject for observation and research.

► Bugs
► Transmission of Plant Diseases by Insects
► Plant Viruses and Insects

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Aphid Flies

Members of the family Chamaemyiidae (order Diptera).

► Flies

Aphodius Grubs (Coleoptera: Scarabaeidae)

At least two species of *Aphodius* are important pests of turfgrass.

► Turfgrass Insects and their Management

Aphrophoridae

A family of bugs (order Hemiptera, suborder Cicadomorpha).

► Bugs

Aphylidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Apiary

A location where honey bees and bee hives are kept.

► Apiculture (Beekeeping)

Apical

A term pertaining to the apex (tip) or outer end.

Apiculture (Beekeeping)

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The science and art of managing honey bees called apiculture or beekeeping is a centuries-old tradition. The first beekeepers were hunters, seeking out wild nests of honey bees, which often were destroyed to obtain the sweet reward, called honey, for which these insects are named. As interest in honey bees grew, so too did the entomological and biological knowledge needed to better manage colonies of *Apis mellifera*. The innovations that allowed modern beekeeping to arise were primarily developed in the 19th century. The most important include the moveable-frame hive, smoker and centrifugal extractor. It is remarkable that these continue to be the hallmark of the beekeeper a century and a half later.

Honey bees are native to the Old World, but were quickly introduced into the Americas and Australia as part of European settlement. This social, perennial insect is now found on all continents and in most environments. Although honey continues to be an important product of honey bees, their most valuable service is pollination. A large commercial pollination effort exists in many countries to ensure maximum quality and quantity of crops pollinated by honey bees. The major crops involved are nuts, berries, fruits and vegetables.

Although the technology employed in beekeeping is traditional, the problems facing present day apiculture are modern and formidable. This is due primarily to worldwide distribution of exotic diseases and pests that have devastated beekeeping industries and honey bees alike. The major problems affecting U.S. beekeeping over the last thirty years come from introduction of the tracheal mite (*Acarapis woodi*), Varroa mite (*Varroa destructor*) and small hive beetle (*Aethina tumida*). These have produced a new kind of beekeeping that is much more aligned with production agriculture because it has become associated with and/or reliant on chemicals. It is an irony that honey bees, heretofore considered wild animals needing minimal human intervention, have become more domesticated, requiring human help to survive human-induced introduction of exotic species.

In spite of the increase in time and effort needed to keep bees in the modern setting, the fascination presented by the honey bee and its products continues. Thus, a small but enthusiastic cadre of novice beekeepers appears each season to take up the challenge of managing one of nature's most complex creatures. This infectious "joy of beekeeping" continues to proliferate across the generations, afflicting both beginners and commercial beekeepers generations removed from the first person in their family to be smitten by the beekeeping bug.

The purpose of this article is to describe aspects of beekeeping that will be important for a basic understanding of the craft by both novice beekeepers and the general public. It includes information on the honey bee colony and its management, as well as that with reference to nectar and floral resources and the use of these important insects in commercial pollination.

Products of the Hive

Many people keep bees because they are fascinated by these social insects. The vast majority, however, are also interested in collecting the useful products of the hive, which include:

Honey: Modified nectar collected by honey bees that is mostly carbohydrate.

Pollen: The male floral part collected by honey bees that is mostly protein.

Propolis: A mixture of resins and oils collected by bees from plants used to "glue" hive parts together and patch holes.

Beeswax: The material that makes up the bee nest.

Royal Jelly: A high-protein food that is used to feed developing queens.

Venom: A mixture of compounds injected by bees for defensive purposes.

The Honey Bee Colony

Honey bee biology is described elsewhere in this document. The colony of *Apis mellifera* is composed of one queen (fertilized female), up to several thousand males (drones) and tens of thousands of workers (unfertilized females). For the purposes of the beekeeper, worker bees are the most important; they are often divided into two classes, young nurse bees (feed the young) and older forager bees (collect pollen and nectar).

Major Developments in Beekeeping

Most new ideas in beekeeping are not novel. A scan of the literature usually will show that they have been developed, sometimes on several separate occasions, by enterprising apiculturists in the past. Three eras have been identified in the development of the craft.

Beekeeping prior to 1500 was primitive (rustic), and consisted of little more than honey hunting, robbing the sweet from established nests. A famous rock painting at Cueva de las Arañas, Spain, depicts this activity as early as 5000 B.C. The Philistines dabbled in beekeeping as did the ancient Egyptians, Greeks, Sumerians, and others. Even before the honey bee was introduced to the Americas, other kinds of bees were kept for honey and wax. The Inca and Maya of the New World cultured the stingless bees (meliponidae). There is a renaissance in this activity in the American tropics, but the term "beekeeping" has always been reserved for those managing the Old World western honey bee (*Apis mellifera*).

From 1500 to 1851 (pre-modern beekeeping), great strides occurred in knowledge about honey bees. The queen was discovered to be female in 1586. Drones were first identified to be males in

1609. Pollen was determined to be the male part of plants in 1750. Drones were shown to mate with the queen in 1792 and recognized as parthenogenic in 1845.

Concurrently with biological knowledge, management technique evolved. For example, the concept of supering (adding boxes on top of colonies for honey storage) was developed in 1665. A wide variety of so-called "patent" hives were marketed in the 1800s, an era known for huge controversy over size and style of box, none of which were really suitable to launch a new kind of beekeeping.

The modern beekeeping era began in 1851 when the Reverend L.L. Langstroth discovered the significance of the "bee space," which led to the invention of the movable-frame hive. Other advances followed: Johannes Mehring developed the first foundation in 1857. Major Hruschka produced an extractor in 1865. Moses Quinby invented the smoker in 1875 and published his first bee book in 1853. Comb honey production began with W.C. Harbison of California in 1857.

The years 1859 to 1890 encompassed the era of comb honey, known as the "golden age of beekeeping." Samuel Wagner published the first issue of *American Bee Journal* in 1861. *Gleanings in Bee Culture* was first published in 1873; it became simply *Bee Culture* in the 1990s. Migratory beekeeping up and down the Mississippi River began in 1878 (it occurred much earlier in ancient Egypt on the Nile). Package bees were first used in 1879. J. George Doolittle developed the concept of commercial queen rearing in 1888, using the grafting (larval transfer) technique.

Lloyd Watson first used instrumental insemination of the queen bee in 1926. This technology spawned studies in controlled genetics, which led to selection of commercial lines such as "Starline" and "Midnite" honey bees. This continues to be of importance and increasingly is responsible for advances in selecting for hygienic behavior (disease resistance) and tolerance to pests.

With recognition that apiculture was a legitimate vocation, the honey bee has been spread worldwide by beekeepers. This continues even today. The Irish and Norwegians may have brought honey bees to the Americas as early as 900 A.D. They came to the colony of Massachusetts in 1665, where the aborigines called them "white man's flies". These insects may have been introduced sooner into the New World by the Spanish conquistadors via Mexico, Florida, or Cuba.

Italian bees (*Apis mellifera ligustica*) were first introduced into the United States in the 1860s, and Frank Benton imported Cyprian and Tunisic stock in the 1870s. Many more introductions succeeded these first attempts. African honey bees (*Apis mellifera scutellata*) were brought to Brazil in 1957. Semen from these so-called "killer bees" was introduced into the United States in the 1960s, but natural migration through Latin America allowed a population to become established in the United States only when it crossed the Texas border in 1990. *Varroa jacobsoni* (now known as *Varroa destructor*) was introduced to *Apis mellifera* in the 1950s via its original Asiatic host *Apis cerana*. This parasitic mite had spread to all continents except Australia by the 1990s. New bee foods, including high fructose corn syrup and the Beltsville Bee Diet® were introduced in the 1970s. Honey became a world commodity in the 1980s. The small hive beetle (*Aethina tumida*) was introduced from South Africa into the United States in 1998.

Sources of Information

Beekeeping information can be found many places. Traditional print resources include:

Bee Culture, A.I. Root Co., P.O. Box 706, Medina, Ohio 44258, phone 1-800-289-7668 extension 3220, fax 330-725-5624

American Bee Journal, 51 South 2nd Street, Hamilton, Illinois 62341, phone 217-847-3324, fax 217-847-3660

The Speedy Bee, P.O. Box 998, Jesup, Georgia 31598-0998, phone 912-427-4018, fax 912-427-8447

The Internet is now a prime source on information. However, it is suggested beginners find the bee inspector and state university extension educator in their state and address questions directly to them. Each year, the magazine Bee Culture publishes a comprehensive list in the April edition.

Equipment

Of all things in beekeeping that are affected by the modern world, perhaps beekeeping equipment is the best candidate to look at within the context of newly evolving technology. Plans for standard, traditional wooden beehives can be found in many publications. Some parts of a beehive are easily made at home, especially brood chambers, supers, tops and bottoms. However, others may not be; frame construction, for example, is best left to commercial manufacturers.

A major equipment consideration is use of beeswax, recycled from the bees themselves. Traditionally bees have been guided to make their nest (comb) through use of embossed beeswax "foundation." This material not only guides the bees in making worker cells, but also saves much time and energy in the bargain. Plastic (wax-coated or not) is being increasingly used for foundation.

Beekeeping equipment is available from many places across the nation. Several concepts are important when considering equipment. These are: (i) standardization, usually based on conserving the bee space; (ii) changes in nominal lumber size, contributing to availability and wastage problems in cutting wooden ware; and (iii) constant development and evaluation of new materials. Although plastics come to mind, there have even been hives made from concrete to withstand tropical conditions. Nevertheless, wood continues to be the material of choice by most beekeepers.

Because individual suppliers or equipment and prices are constantly changing, only an overview of beekeeping implements and paraphernalia is possible here. For up-to-date prices, it's best to consult the bee journals, which actively cater to the trade and bee supply outlets.

Protective equipment for the beekeeper has also followed the same route. New materials such as plastic netting, Velcro® and others have meant that beekeepers can work with more peace of mind during manipulation of colonies.

As already noted, traditional beekeeping equipment is made from wood. However, plastic equipment also is in use for the traditional bee box. Plastic is also widely used as a wax foundation base and in single component plastic frames. Plastic frames resist damage, do not require painting, and do not require assembly. However, it often takes more resources by the bees to "draw out" plastic or beeswax-coated plastic foundation. Some disadvantages of plastic are its tendency to warp and become brittle when exposed to sunlight and difficulty in being sterilized by heat. Various companies use plastic to make containers for bee products. Such containers eliminate the extracting phase of beekeeping and provide a container for honey in its natural comb.

There are all manner of gadgets used in the art and business of keeping bees that do not generally get mentioned in standard references. The following are some of these gems:

1. The slatted (or slotted) rack was used initially to take up the space of a deep bottom board. It assists in ventilation and reduces brace and ladder comb. Some beekeepers swear by it, some at it.
2. A division board feeder is a hollow insert filled with syrup that takes the place of a frame in a super when a population is small. Easily homemade from a board and nails, they quickly feed a small colony.
3. A robber screen can be used to protect small colonies from being foraged by larger colonies, especially during nectar dearth.
4. Top feeders come in various styles. These avert the necessity to open the colony and/or to fill a frame-style division board feeder. Top feeders hold more and are more accessible.
5. A screened ventilated bottom board provides air circulation during both summer and winter. Newer information also suggests these are useful in controlling exotic mite populations.

6. Various painted patterns on the front of colonies can help bees identify their own home, thus reducing drifting (bees losing their way and entering foreign colonies).
7. Drip boards serve several purposes. They collect errant honey leaks from supers stored on them, provide air space between the floor and honey stored in frames, and a space for two-wheeled hand trucks to grip the stack.
8. A screened division board placed between two alien colonies enables them to access each other's odors, while keeping them physically separate. The end result is two queens working together to produce a large population. Eventually they can be joined after this close but separate association, however, one of the queens is eliminated in the bargain.

Building Equipment

Although it can rarely be built more cheaply than it can be purchased, only basic woodworking skills and tools are needed to build wooden beekeeping equipment. Box joints are currently the most common, and according to some, the strongest kind to use in beekeeping applications. Producing them requires a jig, usually home made, to neatly and precisely cut the slots to line up with the fingers. Butt joints are more forgiving; two boards are butted together and simply nailed. The TIM joint is fast but weak. If a colony is not going to be moved, it will probably work okay. The dado joint, used by some manufacturers, is becoming more popular, and is strong enough to withstand the rigors of moving and manipulation. When building equipment, in all instances, respect bee space requirements and be sure to build your equipment to fit standard measurements.

Protecting Wooden Equipment

Some wood may last longer while some may last much less time, depending on the climate, but hives are definitely helped by some type of protective coating. The average life of a bee box is about seven years. Scraped and routinely painted, equipment can go much longer. Since the inside surfaces of bee hives should not be painted, the paint film on the outer surface is often stressed by water migrating to the film from the inside of the hive rather than from the outside. Oil-based paints will readily peel within just a couple of years. Due to ease of application and lower cost, latex paints are better. The rubber-based latex paints will flex and resist chalking and peeling much more than oil paints, but they, too, will finally succumb to mildew and peeling.

Some commercial beekeepers and beekeepers in other countries routinely dip equipment in paraffin or beeswax. This is a good finish that protects the wood from all sides and ends, but requires working around hot, flammable paraffin. Once the equipment has begun to show signs of wear, simply dip it again in hot paraffin to recoat the finish and to remove wax and propolis residue. In recent years, polyurethane exterior stains have become popular and have been consistently improved. As with paraffin impregnation, many of these stains are water repellent, resist mildew and fading, and clean up with water and soap.

A final warning concerns pressure-treated wood. The materials used to preserve the wood are usually toxic to honey bees. Thus, treated wood is not recommended for bee colonies. Even the sawdust is considered a health hazard and dust masks are recommended when working so-called Wolmanized® treated wood.

Wearing Protective Equipment

The most important protective equipment is the veil, which protects the face, the most sought-after target for guard bees. Veils can be used without a helmet, or attached to a pith-type helmet, made of plastic or other material. Almost any hat that keeps the veil material off the face and neck will work. Veils usually have a mesh bottom that is snugged down over the collar onto the shoulders with a variety of ties and/or strings. Veils that attach to the bee suit with a zipper are popular, mostly because they are convenient, easily maintained, and virtually bee proof. They are also more expensive.

Bee suits usually are light in color, but many wear what's available, simply to keep their clothes clean. The white coverall suit is most popular, with a variety of pockets, cuffs and attachments. White is also the most difficult to keep clean. They are made from a variety of materials – cotton, cotton blends and synthetics – each with its own peculiar attributes. Suits should be "roomy," to allow bending and stretching and lifting room, and for other clothes underneath. This also keeps the suit from stretching tautly over the skin underneath, which bees can then easily sting through.

Seasoned beekeepers seldom wear gloves because they feel they lose that "delicate" touch when manipulating colonies. However, many beginners start with them. Most gloves have cloth gauntlets of some type to seal the sleeves of the bee suit. Glove materials range from full leather to plastic to split leather to rubber. Some are ventilated, while others have no fingers. Wearing gloves can help build confidence in manipulating bees. As one gains experience, the finger tips can be cut off, which still protects most of the hand, while ensuring a more sensitive manipulation.

Boots and pants-cuff clasps range from high top rubber boots to baling twine. The goal is to keep bees on the ground from crawling up pants legs – an unnerving experience. Comfort, durability, safety and cost are all important. All equipment should fit the job. A hobbyist with a few colonies will use, and need, different equipment than a commercial pollinator.

Management

The "meat and potatoes" of beekeeping is management. It is often the best manager who makes the most honey from his/her bee colonies. Experience is extremely important if one is to manage bees successfully. There is no better piece of advice for the novice beekeeper than to begin small and only expand as experience is gained. A vital ingredient of this experience is permanent, detailed record keeping and knowing intimately the characteristics of the honey bee ecotype one is working with. One must also master the basics of opening and inspecting a colony with the aid of smoke, yet not destroying its cohesiveness.

Beekeeping knowledge comes about slowly and being able to implement it effectively often takes far longer than expected. In order to appreciate the techniques of beekeeping, one must first gain an understanding of the dynamics of the colony during the year. A recommended exercise for the beginning beekeeper is to construct a beekeeping calendar. Regional characteristics of beekeeping are easily identified through the use of the calendar, which shows average dates of bloom, colony population characteristics and bee manipulations. Such a timetable also can be broken down into a number of beekeeping activities, each requiring certain decisions. These include inspecting a colony in spring, feeding pollen and sugar, monitoring population buildup, controlling swarming, supering, monitoring and removing the honey crop, requeening, preparing for winter and migrating in search of better nectar resources or to move bees into commercial plantings for pollination.

No year is ever the same, so the beekeeper must learn to "think like a bee colony," closely watching environmental changes and anticipating the potential effects on colonies. Major management problems in beekeeping are controlling swarming (the reproductive process of a colony), requeening and managing diseases and pests. Swarming has befuddled even experienced beekeepers. Requeening and queen introduction techniques have been written about for many years, but still confound beekeepers on occasion. Several options often need to be considered for successful introduction of new queens, the life blood of any beekeeping operation. Finally, the challenges of diseases (American and European foulbrood) and exotic pests (mites, beetles) are complex, requiring an understanding of many possible treatment regimes under the rubric of Integrated Pest Management (IPM).

Although controversial, most beginners are advised to begin by managing two colonies. The reasons for this are several. If a hive begins to fail, there are resources in the other the beekeeper can use to help the weaker one along. If one colony is lost entirely, the novice beekeeper may easily lose interest if another colony is not present to take its place.

A Model Bee Yard

Somewhere the perfect bee yard exists, but if so, it is not the general rule. Most are the result of a beekeeper's style that fits both location and management philosophy. Bee yards should be right-up-next-to-the-hives easy to get to all year long. Newly plowed fields, suddenly erected fences, rising creeks, muddy roads, locked gates and the like should be anticipated, and avoided.

The most accessible location is worthless without something for the bees to forage on. There should be enough blooms to produce surplus honey for every colony in the apiary. Field crops, hay crops, tree canopies, weed species, horticultural or oil crops all can work. But there needs to be large areas of blossoms blooming a relatively long time. Water is required all season long, too. A lake, stream or pond is best. Swimming pools, cattle troughs or leaky faucets cause potential neighbor problems and should be avoided as bee watering possibilities.

A wind break, especially during the colder months in temperate latitudes, is recommended. A tree line, fence or hill works best. Air drainage is important. Cold air drains downhill; colonies at the bottom of a hill get "dumped on" in cold weather. Hill tops, too, suffer winds and wind chill problems. Avoid both. Exposure seems important to some. Colonies receiving morning sun start to forage earlier than those in the shade (at least with some races of bees). Southeast is the most common, and probably works best.

Bee colonies must be protected from all manner of pests and predators, including humans. Bear (electric fencing), skunks and possum (fencing), cattle and horses (regular fences, though stout), and neighbor prying eyes (screening, hedges) must all be considered. For large bee yards, an out-building that works as a storage shed, work area, extracting room (sometimes) and lunch room is needed. Most of all, a bee yard should be a pleasant place to visit. Scenic, quiet, distant and, most importantly, not a challenge to use.

Inspecting Honey Bees

The productivity of honey bee colonies should be actively monitored by the beekeeper, whose job it is to recognize certain conditions and help a colony overcome those causing adversity. Generally, inspection will determine the state of the colony in terms of reproductive ability (queen condition; population of worker bees), nutritional resources (honey and pollen stored in the comb) and whether diseases or pests are present.

The latter is increasingly important as exotic organisms continue to proliferate around the globe. Of special significance at the present are two introduced mites, the internal *Acarapis woodi* and external *Varroa destructor*. These mites have caused beekeepers to take a closer look at and often use chemical controls inside the living beehive with the concomitant risks that these substances may harm the colony and/or contaminate its products. As a consequence, honey bees have become much more domesticated, as they are increasingly reliant on beekeepers in many areas of the world to help control exotic bee mites. Other diseases that affect colonies are caused by bacteria, fungi, viruses and protozoans. Of particular significance are two bacterial conditions, American foulbrood (*Paenibacillus larvae* subspecies *larvae*) and European foulbrood (*Melissococcus pluton*).

American foulbrood, in particular, is caused by a spore-forming organism that can resist harsh ecological conditions. Epidemics of this disease are the reason state bee inspection services exist, although many of these have been discontinued recently due to budgetary constraints and lack of support. Discovery of sulfa drugs and later antibiotics has caused a shift in beekeepers' perceptions concerning the disease, which they have actively kept at bay for decades. Unfortunately, the recent appearance of antibiotic-resistant strains of *Paenibacillus larvae* subspecies *larvae* is causing second thoughts by many beekeepers concerning official inspection backed up by apiary legislation.

An important adult disease is known as nosema and is caused by the protozoan *Nosem apis*. This is probably present in every colony of honey bees, but only becomes epidemic when bees are put under stress. It may be far more important in determining bee colony health than is generally given credit.

There continue to be numerous so-called "exotic" organisms that impact colonies of honey bees around the world. Ironically, two of these are ecotypes of honey bees themselves: the Africanized honey bee (*Apis mellifera scutellata*) and the thelytokus Cape of Good Hope bee (*Apis mellifera capensis*). In addition, various mites are found on Asian honey bees (*Apis cerana*, *Apis dorsata*, *Apis laboriosa*) that conceivably could transfer to *Apis mellifera* as *Varroa destructor* did previously. No better example of this constant threat is the surprise introduction of the South African small hive beetle (*Aethina tumida*) into the United States in the late 1990s.

Honey Bee Ecotypes

All honey bees are not the same. This statement, it seems, cannot be said too often around beekeepers and/or the general public. There are those who manage bees exactly the same whether or not their stocks have been selected for overwintering, swarming, rapid brood rearing, pollen collecting and/or stinging. The belief that all honey bees must behave or act similarly no matter the conditions is the root of many beekeeping controversies over the last two centuries, and the reason many lay persons fail to understand the complexities of these stinging insects. Usually, beekeeping "arguments" pertain to whether or not a certain management technique or a special kind of beekeeping apparatus is practical or efficient. The kind of bee a beekeeper has in his apiaries often will determine whether some concept or idea works or doesn't work. All too often, however, the bees' genetics are ignored when contemplating solutions to many of the mysteries of beekeeping.

Unfortunately, most beekeepers really do not know what kind of bee they are using. That's because present bee stock is literally a melting pot of honey bee genes. The predominant races (subspecies or ecotypes) of bees which make up the honey bee genetic mix found in the United States are: Italian (*Apis mellifera ligustica*), Caucasian (*Apis mellifera caucasica*), Carniolan (*Apis mellifera carnica*) and German (*Apis mellifera mellifera*), the dark bee. Each population evolved under certain ecological conditions and natural selection over a long period of time that have provided them with their own particular survival techniques. These ecotypes are thoroughly intermixed and are extremely difficult to separate in novel environments. In addition, other genes of other ecotypes also are present in small quantities.

Because there is such great variability, however, the possibility of quantum leaps in honey bee selection programs is possible. With the coming of the mite *Varroa destructor*, however, the honey bees' genetic base has narrowed in many parts of the world. But fortunately there remain pockets of bees that appear to be resistant (tolerant) and these may provide the foundation for rebuilding a honey bee stock devastated by this parasite.

Africanized Bees

One of the biggest biological stories of the Americas concerns honey bees. Introduction of the African honey bee ecotype (*Apis mellifera scutellata*) has been responsible for raising the public consciousness about these insects. This bee is nothing more than an ecotype adapted to tropical conditions, generally characterized by higher rates of defensive behavior and reproduction. Unfortunately, its fearsome reputation is an outgrowth of sensationalized press coverage of stinging incidents by these so-called "killer bees," which caused deaths of animals and people in Latin America. As a result many people now view honey bees as aggressive rather than defensive, and think them responsible for a good many human fatalities. The reality is that the number of verified deaths by honey bees is much smaller than reported (almost all stinging insects are routinely called bees). This over-sensationalized topic has affected beekeepers in several ways, most notably by loss of access to beekeeping locations. North America is the last frontier for the Africanized (or African) honey bee and its final distribution is still unknown. Nevertheless, the challenge for many beekeepers in the future will be to strike a balance in their communication with the public about the risks/benefits of their bees. Beekeepers also will have to adapt to this ecotype's different behavior, which often can be a radical departure from the European ecotypes previously present.

A special ecotype inhabits Africa known as *Apis mellifera capensis*. This bee is characterized by a high degree of thelytoky, which means workers can become laying queens, producing diploid females, in spite of laying unfertilized eggs. This ecotype has created a crisis of sorts in African beekeeping. It is hoped that this honey bee will not be moved out of its homeland by beekeepers and introduced to the rest of the world. The history of honey bee introductions around the world over the last two centuries, however, is not a good omen in this regard.

Smoking Bees

Within and outside the dark hive, bees communicate extensively by smell. Nectar, pollen, diseases, other insects, brood, the queen, drones – everything in the hive has an odor cue. As complicated as the bees' odor communication system appears to be, the manner that beekeepers have developed to overcome the bees' ability to perceive odors, both inside and outside the hive, is relatively simple, and that is to puff cool, white smoke in and around the hive. For reasons not clearly understood, smoke stimulates bees to move to honey stores and engorge, which reduces their propensity to sting.

Early smokers were little more than a smoldering fire beneath or near a hive. Later, tobacco pipes were modified to direct smoke into hives as were other devices. After evolving through many different designs and styles, beekeepers in North America have a small, but adequate range of smoker designs from which to choose.

Smoker fuels are as numerous as are the beekeepers who use them. Common types include grass clippings, pine straw, sumac pods, cloth rags, rotted wood, wood shavings, and burlap. Essentially, anything can be used that produces cool, white billowing smoke and has not been treated with pesticides, fire retardants or other noxious chemicals. Under normal conditions, smoke is effective for about 2 to 4 minutes before needing to be reapplied.

Moving Bees

Bees can be moved almost any way imaginable. Some, of course, are easier and safer than others. Commercial operations need the economy of size and efficiency. A large, flatbed truck serves that purpose. Some come with a flatbed trailer that attaches to the truck to increase efficiency. These trucks usually have customized tie-downs, tool boxes and equipment storage areas. Getting the bees on and off the truck can be done by hand (muscle) or machine.

Regular two-wheeled carts, sized to hold hives, often are used for moving. Motorized carts are common, as are booms and Tommy-lifts. Fastest are fork-lifts. There are several models available, from the standard, to large, specially designed models for specific bee pallets. Some have cabs, most have protective cages and large tires to navigate easily in muddy conditions. Some can swivel or pivot in the center.

Once loaded on the truck bed (many are built to hold an exact number of pallets), tie-downs can be regular rope, self-tightening straps, or wide canvas belts affixed to wooden frames that are used for extra security. A secure net is required at all times to avoid escaped bees on the road. Anytime bees are moved, the boxes should be fastened, entrances closed, the load netted and tied down to prevent shifting.

An important consideration in moving bees is temperature. Traditionally this has been managed by periodically spraying the load of bees with fresh water when signs of overheating are evident.

Package Bees

The most common way to start a colony, or start beekeeping, is to install a package of bees into an empty home-to-be by removing them from the shipping cage. Packages generally come in three- to five-pound sizes (3,500 bees equal a pound). And there are nearly as many ways to get bees from the shipping cage to the functioning unit as there are people doing the task. But basic biology dictates certain principles be obeyed. A starter box with some or all drawn comb is better than just frames with foundation, as it gives the bees some place to be, and store food immediately, and reduces the amount of gathered food required for wax production, freeing it for brood food.

Bees can be "moved in" by dumping them (they are often sprayed with water first to inhibit flying) inside the box (with three frames removed, then replaced, to accommodate the resultant mass); they also can be dumped directly in front, to march right in; or a combination of the above two techniques, where some are placed inside, the remainder outside. The empty package is removed in a day or so. Once installed, several precautions are recommended. The first rule is: feed, feed, feed. Then feed more, until they don't take any more. Feeding well into the summer may be required if adequate forage is not available.

Checking for queen acceptance, and then queen production is a must, but there is a fine line between too-often and too-seldom observations. It is safer to edge toward the too-often, but just barely. Once established, remove feeders, add supers and prepare for the honey flow and harvest.

Dividing Colonies

Splitting a colony is the easiest and least expensive way to increase the number of hives managed. But there are other reasons to split a colony, and there are nearly as many ways to split one as there are colonies to split.

The overall principle in making a split is to start with a large, healthy, populous colony (or colonies). The goal is to remove some uncapped brood, some honey and pollen resources to a new box, or two, to start a new colony. A new queen may, or may not be, added. Usually the parent colony should not be reduced to less than half its resources so it can continue to keep pace with the season. Bees, brood or food may be taken from more than one parent to successfully build a new split. Splits must have enough nurse bees to care for the brood, some foragers to gather resources, sealed brood for immediate colony expansion, younger brood for continued expansion and some resources for immediate consumption.

Splits are used to "make increase," or for other reasons. Popular swarm control/prevention measures include splitting a large colony to allow room for expansion, and to relieve brood-nest congestion. Often the "new" colony is rejoined to the parent when the swarming urge is over so the actual number of colonies does not increase. One technique used to reduce mite infestation is to divide a colony later in the season, eliminating the older, infested bees, and overwintering the younger, less infested bees.

Feeding Colonies

Providing food to colonies is one of the most time-consuming and tedious tasks facing any beekeeper. Two types of food are required: carbohydrate and protein. Generally, carbohydrates are provided by nectar in nature and the best analogy to this is sugar syrup, made up by dissolving cane sugar in water. This is then provided through various hive modifications or feeders, some of which are mentioned elsewhere in this article.

A relatively new bee food is high fructose corn syrup (HFCS) that is manufactured in huge amounts to service the soft drink and candy trade. Two types exist: 42 and 55. The 55 is generally considered more acceptable to bees because it has more sugar solids. Many beekeepers consider feeding both sugar syrup and HFCS, depending on hive condition. Sugar syrup high in sucrose is considered superior for colony population build up, while HFCS is used strictly to maintain populations.

Most suggested feeding regimens concentrate on providing carbohydrate. However, it must be complemented with protein for a balanced diet. This is provided by pollen to the honey bee in nature. The beekeeper, too, can trap and give back pollen or combine it with soy flour and/or yeast (supplement). Protein supplement often is sold ready-made in patties by beekeeping supply outlets.

Producing the Honey Crop

The beekeeper seeks to have as large a population of worker honey bees as possible coincidentally when the most nectar-producing flowers are blooming. This nectar is stored above a bee colony in the wild. Thus, beekeepers emulate this by adding extra boxes on top of hives (supers) into which bees place the nectar. Nectar is modified by the bees into honey. The insects add enzymes, changing the material chemically, and reducing the moisture content from 80% (nectar) to about 18.6% (honey). The bees determine when the moisture is correct and then cap over the honey with wax. When the supers are filled, they are removed and the honey is extracted from the comb using centrifugal force in special machinery (extractors). Sometimes honey is sold in the comb (known as section or comb and cut-comb).

Extracting the Honey Crop

A large honey crop is clearly a mixed blessing. The more supers that go on, the more honey to be processed. More honey means more work, but it also means more money. For years, clever people have tried to develop equipment to make the uncapping, extracting, pumping, filtering, and bottling procedure more convenient, even easy. Though "easy" extracting has not yet been achieved, the process has become much more streamlined. Old processing equipment was made from galvanized tin with lead solder joints. It was solid equipment that was built to stand years of heavy use. The clutch-drive mechanism was simple, heavy-duty, and a bit dangerous. Belts, drives, shafts, and pulleys were all exposed. In fact, a few early extractors were powered by low compression gasoline engines. Extracting was done outside on occasion, a practice that generally has been abandoned.

Stainless steel with welded joints is now used on extractors. Other metals may impart an objectionable odor. Smaller hobby-type extractors may use plastic barrels. In many instances, variable-speed direct-current (DC) drive motors are used that allow for the gentle extraction of full combs of honey. The equipment is mechanically simpler, but technologically more complicated. It's lighter and more maintenance free. Most commercial honey processing lines would be ordered as follows:

1. uncapper
2. extractor(s)
3. heated sump
4. honey pump
5. filter
6. settling tank
7. bottler

Other equipment in honey processing can include a barrel melter, a flash heater, wax spinner and other equipment-moving devices. A second line would drain honey from wax cappings to the sump. Dried cappings would be melted into beeswax, which could be returned to the bees as foundation.

Managing Swarming

Swarms can be both reproductive and migratory. Little can be done about swarming once the "impulse" is generated in a colony. The best ways to control swarming are providing room in the colony and/or regularly requeening with younger individuals. This is a "preventive" strategy that is much more effective. As stated earlier, once the impulse to swarm gets going, it is almost impossible to stop. Generally swarms are reproductive in nature, especially with European honey bees, and can be both a blessing and a curse. The blessing part is that one can be harvested and put to work in an apiary. A secondary blessing, obviously, is that a swarm happens. That means a colony is healthy enough to swarm, something all too rare in these days of increasing stress on managed honey bees.

The first thing to do with a swarm is collect it. At times this is easy, sometimes impossible. Swarms high in the air can be collected with vacuum devices, long ladders, or heroic gymnastics. Most can be collected into bags, boxes, supers or whatever and transported to permanent housing. The key is to provide ventilation; putting a strong swarm into an air-tight container is a recipe for disaster! Swarms are generally the gentlest of bees, but if left exposed for several days, they can become hungry and much more defensive. Always have a lighted smoker at the ready when working swarms.

The public relations aspect of swarm gathering should not be overlooked. But the macho image many beekeepers display while on the job communicate a mixed message. Once collected and transported, a beekeeper can do many things with this bunch of bees. The deciding factor is often the size of a swarm. Large swarms, about four or five pounds of bees (3,500 bees equal one pound), can easily survive by themselves. Smaller swarms of one to three pounds can be combined with other swarms to start a large colony; or added to another colony to boost its nectar- and pollen-gathering capability during a major flow.

To be safe, all swarms should be considered infested with mites and treated accordingly. As the queen heading the swarm is from essentially unknown heritage, replacing her with a young one of known parentage should be considered.

With the advent of the tropically adapted Africanized (*Apis mellifera scutellata*) honey bee, another kind of swarming is increasingly seen. This is the migratory swarm, thought to be brought on by stress such as lack of forage or water. This kind of swarm often behaves differently than the reproductive one and may be much more defensive, though not always so.

Managing and Rearing Queens

The queen is the key to managing the genetic component of a colony. She contributes one half of all the genes found in a colony, whereas a single drone provides for less than half (queens mate with 17 to 20 drones during a short period in their life just after emerging from the cell). The colony's characteristics, therefore, have a good chance of being perpetuated in the queen and research has shown that queen selection followed by open mating will ensure a good deal of progress in breeding bees with specific traits.

Queen rearing is one of the most demanding beekeeping activities, and more often than not is a true art form. Anybody can produce a queen, but rearing a quality queen with the correct genetic complement for a beekeeping operation is far more difficult. Queen rearing also is directly tied to a timetable, which must be rigidly followed. Often the question is raised whether or not one should produce queens him/herself, let the bees do it, or purchase a queen. There is no easy answer. The only reply may be to ask the question, "Whose quality control is the best under the circumstances, that of nature or of human beings?"

Again, the queen honey bee usually mates with many drones. This ensures large genetic variability, but also means a lack of controlled breeding. It is possible to instrumentally inseminate queen honey bees in an attempt to control genetics in a population. This is not easy, however, and can only be accomplished by trained workers. Most queen rearing facilities produce daughter queens from selected stock that are open mated (uncontrolled) in a natural setting.

Managing Wintering

The honey bee can live in almost any climatic environment, but is most stressed by winter in continental climates. Honey bees can produce a warm brood nest even in the coldest winters if supplied with the proper nutrition and number of workers. This leads to the adage that "honey bees never freeze to death, they starve to death." Beekeepers in cold climates, therefore, have a significant challenge to help their colonies overcome severe conditions of wind and cold. Many pack their hives wintered outdoors in various kinds of materials to conserve warmth. Others move their colonies indoors to protect them. The latter activity was employed by old timers who put their colonies into cellars. This was risky as too much warmth would stimulate a colony to begin to build population, a prescription for disaster. With development of refrigeration, however, it now is routine in some areas to bring smaller-than-normal hives (nuclei) into climate-controlled buildings and keep them in a kind of human-induced diapause, which reduces nutritional requirements to a minimum and conserves worker bee energy and vitality so they can begin to rear brood quickly and efficiently in spring.

An alternative to wintering is to simply collect all the stores and kill colonies off in winter, establishing new hives the following spring with package bees from more tropical areas. This was routinely practiced by Canadian beekeepers who simply purchased bees from the southern US until the border was closed in the early 1980s due to introduction of tracheal and then Varroa mites. To many beekeepers this was a repugnant practice and they were not sorry to see it abandoned. Effective wintering continues to be an important part of bee management as more colonies are lost during this trying time than other seasons of the year.

Nectar and Pollen Sources

Nectar and pollen are the only natural foods of honey bees, strictly vegetarian insects, and each geographic area has different sources of these important foods. Every good beekeeper, therefore, must be somewhat of a botanist in order to make sure the bees are located so they have an adequate food supply. Bee plants may also differ from each other in several ways, such as the kinds of nectaries (nectar glands) each supports and/or the time of day they may secrete nectar and/or produce pollen.

Nectar and pollen production by flowers is dependent on a great variety of environmental conditions such as soil moisture, pH, profile and fertility, as well as rainfall distribution, temperature and humidity. Over the last four decades, there has been an overall decrease in honey bee forage in the United States due to many factors, especially changing agricultural patterns and increasing urban development. Improving nectar production by genetically selecting for varieties of certain crops that produce large amounts of nectar, or purposely planting nectar-producing varieties in so-called "waste" land, along roadways or on lands reclaimed for mining, are some ways suggested to reverse this systematic reduction of bee forage.

Few plants produce the vast quantities of nectar the honey bee needs to make a large honey crop. In the state of Florida, for example, less than ten plants are responsible for sizeable honey crops on a consistent basis. Fortunately, in most areas a number of minor nectar crops usually are found which help support honey bees throughout the year, although they often contribute little to the beekeeper's honey crop. It is of more than passing interest to know that many introduced plants assist honey bees in a number of ways, and the insects may contribute to their proliferation.

Though not as readily available as honey, another type of sweet is collected and processed by honey bees. Aphids and other sucking insects often take more than they need from the plants. The excess is extruded and may be collected by ants or honey bees. The resultant product is honeydew. Some think this might have been the "manna" that descended from heaven as noted in the Bible (Exodus 16:1–36).

Commercial Pollination

Honey bees are cosmopolitan pollinators, transferring pollen both within and between flowers. Although important to many crops (fruits and vegetables), honey bees are not the most effective pollinators in many situations. This has led to some proclaiming that other bees should be used in preference, such as bumblebees (*Bombus* sp.) and/or blue orchard bees (*Osmia* sp.). However, honey bees have significant advantages including very large populations that are easily moved, and a well-known rearing technology.

There is no stable pollination service in the United States of the kind described by S.E. MacGregor in his classic volume on insect pollination. This means that pollination is carried out by a number of independent contractors. More recently, pollination brokers in the western United States have become more common. The vast majority of commercial pollination takes place in California on the almond crop. Literally hundreds of thousands of colonies are needed.

Commercial pollination is a service, a much different business than producing a product like honey or pollen. As such, it is not suited to all beekeepers and each should look carefully at the characteristics of this enterprise before dedicating many resources to it.

Recently, pollination has received more respect from the general public due to a scarcity of feral or wild honey bees caused by devastating effects of exotic bee mites. This represents a teachable moment for beekeepers, who can now describe with pride the value of their insect charges to the public at large.

Honey Contrasted to Pollination

Honey is a world commodity, and is labor intensive to produce. As such, the price of the product can always be expected to be influenced by societies with low labor costs. Indeed, beekeeping is being promoted aggressively as a development tool in many countries because it is relatively environmentally friendly and not capital intensive.

Although honey can be imported cheaply in many instances, a process exacerbated by globalization of world commerce, pollination services cannot. In addition, because no food product is involved, chemical treatment for exotic pests (mites) can be applied in a more forgiving way to colonies used strictly for pollination. This means that in the future there will always be a demand for pollination no matter the price of honey. Because commercial pollination seems more assured in the future, beekeepers should continually carefully consider this activity in their enterprise mix.

Conclusion

The future of beekeeping or apiculture continues to be mixed. On one hand, the honey bee will be more and more important as growers and the general public continue to realize how necessary this insect is for producing a quality food supply through pollination. Because honey is a world commodity, it also is continually under price pressures in developed countries, as it represents a good source of income for countries with a labor-intensive work force. Its reputation is also at risk, however, given the chemicals needed to keep (treated) bee colonies alive and the potential they have to damage the sweet's reputation through contamination. Whether or not honey and/or pollination are primary, there also are other reasons to keep bees, including using their products, both manufactured (royal jelly, honey, beeswax, venom) and collected (pollen, propolis), for the benefit of humanity, as well as for the general joy of communing with nature and one of its fascinating social organisms.

The history of beekeeping activities is long, and it takes time and experience to become a proficient manager of honey bee colonies. This article can provide only some of the basic information on the craft. The authors hope that it will serve as a catalyst for those thinking of taking up the activity, and also a source of basic information for anyone interested in one of humankind's most fascinating activities.

► Honey Bee
► Bees
► African Bee
► Cape Honey Bee
► Varroa Mite
► Small Hive Beetle
► Bee Louse
► Pollination by *Osmia* Bees
► Polination and FlowerVisitation

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Apidae

A family of bees (order Hymenoptera, superfamily Apoidae). They commonly are called bumble bees, honey bees, and orchid bees.

► Bees
► Honey Bee
► Wasps, Ants, Bees and Sawflies

Apioceridae

A family of flies (order Diptera). They commonly are known as flower-loving flies.

► Flies

Apivorous

Bee eating. Birds, and some predatory insects such as robber flies (Diptera: Asilidae) kill and consume honey bees or, in the case of blister beetles (Coleoptera: Meloidae), ground nesting bees.

Apneumone

A chemical released by a nonliving substance that is beneficial to the receiver. An apneumone is a type of semiochemical.

► Chemical Ecology
► Semiochemicals

Apodal

The condition of lacking "feet" (tarsi). Fly larvae and some beetle larvae, for example, have simple tubercles that aid in movement, but lack legs, including tarsi.

Apodeme

A thickened section of the exoskeleton that serves as a point for muscle attachment. On the external surface, it usually is marked as a suture or fold, but internally there may be a significant invagination.

Apodous Larva

A larval body form that is legless, robust, and C-shaped or spindle-shaped. The head may be well developed, or not. Apodous larval types include curculionoid, muscoid, and apoid.

Apoidae

A superfamily in the order Hymenoptera known as bees. It consists of several families.

► Bees
► Wasps, Ants, Bees and Sawflies

Apoid Larva

A larval body form that is robust, with a well-developed head, and cared for by nestmates or provisioned by the parent. It occurs in ants, bees, and wasps (Hymenoptera).

Apoid Wasps (Hymenoptera: Apoidea: Spheciformes)

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Apoid wasps are a morphologically, behaviorally, and ecologically diverse group of insects that are common in many habitats. Apoid wasps are most closely related to bees, and are placed with them in the superfamily Apoidea, one of three superfamilies of the so-called "stinging Hymenoptera" or Aculeata; the other two subfamilies are Chrysidoidea and Vespoidea (Table 7).

The subfamily Apoidea is subdivided into the series Apiformes and Spheciformes, the latter of which are the apoid wasps. Thus, the term "apoid wasps" refers to all members of the superfamily Apoidea that are not bees. Of the four families making up the Spheciformes (Heterogynaeidae, Ampulicidae, Sphecidae, Crabronidae), all but the Heterogynaeidae were formerly placed in the single family Sphecidae (*sensu lato*) in the superfamily Sphecoidea. But recent consensus splits the old Sphecidae into the Ampulicidae, Sphecidae (*sensu stricto*), and Crabronidae. The correspondence in taxonomic names between this recent family-level classification and what we might call the "classical" system represented in *Sphecid Wasps of the World* by Richard Bohart and Arnold Menke is given in the following table. The reason for the recent taxonomic reworking is sound. The "old" Sphecidae and Sphecoidea were artificial groupings evolutionarily, because the wasps in what we now call the Crabronidae are actually more closely related to bees than they are to the Ampulicidae or the "new" Sphecidae.

The Apoidea, as a whole, likely has its origins in the early Cretaceous, and it is the wasps that predate the bees. Species of over two dozen extinct apoid wasp genera, including members of the

Apoid Wasps (Hymenoptera: Apoidea: Spheciformes), Table 7 Superfamilies of aculeate wasps (classification of the Apoidea is after *The bees of the world* by Charles Michener)

Superfamily	Series	Families	Included groups
Chrysidoidea		multiple families	cuckoo wasps, bethylid wasps, and others
Vespoidea		multiple families	ants, social wasps, spider wasps, velvet ants, and others
Apoidea	Apiformes	seven families	bees
	Spheciformes	Heterogynaeidae	apoid wasps
		Ampulicidae	
		Sphecidae	
		Crabronidae	

Ampulicidae, Sphecidae, Crabronidae, and the extinct family Angarosphecidae, have been found in Cretaceous deposits. Over 9,500 described extant species of apoid wasps are unequally distributed among the four families and over 250 genera. Bees, in contrast, are divided among seven families, 425 genera, over 16,000 described species, and perhaps 30,000 species overall (Table 8).

As a group, apoid wasps share a number of traits that unite them with bees in a discrete evolutionary lineage: (i) a gap present between tegula (at the base of the wings) and the apex of the posterior edge of the pronotum; (ii) a broadly U-shaped pronotum when viewed dorsally; and (iii) the "propodeal triangle" on the dorsal posterior of the abdomen. A dozen or so shared traits link bees in a single clade within the Apoidea. For example, bees feed pollen and nectar to their young, and continue to eat both pollen and nectar as adults. In contrast, with perhaps one exception, all apoid wasps either feed their young arthropod prey or are brood parasites in the nests of other carnivorous wasps; the single exception is the genus *Krombeinictus* (Crabronidae) from India whose females provision with pollen and nectar. Adult wasps feed on nectar, sap, or honeydew, and some consume body fluids of prey. Another marked difference between apoid wasps and many bees is that body hairs are simple in the former, but often branched or even plumose in the latter, where they function to trap and carry pollen (though this may not have been their original function).

As a group, apoid wasps vary widely in habits and body size, form, and color. Most species are sexually dimorphic to a greater or lesser extent, females having almost universally larger body sizes and stouter mandibles. Also, only females have stings. Females of ground-nesting species also commonly bear two features not found in either males or in females of species that nest in other locations. The first feature is conspicuous rows of "rake spines" on their foretibia that aid in digging in soil. The second feature is flattened pygidial plates that aid in tamping soil in place during nest construction. Males of some species exhibit peculiar anatomical structures used in courtship and mate competition. Examples include the clypeal and abdominal hair brushes that male beewolves (*Philanthus*) use to disseminate sex pheromones, and the expanded translucent foretarsal plates of male *Crabro* that sport species-specific color patterns and which are apparently placed over female's eyes during courtship.

Heterogynaeidae

While the Heterogynaeidae are clearly apoid wasps, their exact relationship to the other three families is somewhat controversial. Heterogynaeids are small wasps, 1.5–5.0 mm in length, that are restricted in

Apoid Wasps (Hymenoptera: Apoidea: Spheciformes), Table 8 Correspondence of taxa names under the "classical" (Bohart and Menke 1976) and revised (Pulawski 2007) systems of classification of the apoid wasps. Note a few minor taxa have been left out of the table

"Classical" taxonomy	Revised taxonomy	Number of extant genera/species[a]	Some important genera (number of described species[a])	Nest type[b]	Host/prey orders[c]
not included	Heterogynaeidae	1/8	*Heterogyna* (8)	–	Unknown
Sphecidae: Ampulicinae	Ampulicidae	6/198	*Ampulex* (131)	C	Bla
			Dolichurus (48)	C	Bla
Sphecidae: Sphecinae	Sphecidae	19/731	*Ammophila* (201)	S	Lep
			Chalybion (45)	C	Ara
			Chlorion (20)	S, Pa	Ort
			Isodontia (61)	C	Ort
			Palmodes (20)	S	Ort
			Podalonia (66)	S	Lep
			Podium (23)	C	Blat
			Prionyx (59)	S	Ort
			Sceliphron (35)	M	Ara
			Sphex (118)	S	Ort
Sphecidae: Pemphredoninae	Crabronidae: Pemphredoninae	37/1021	*Arpactophilus* (43)	C	Hom
			Diodontus (73)	C	Hom
			Microstigmus (29)	Ps	Clm, Thy
			Mimesa (71)	S	Hom
			Passaloecus (35)	C, P	Hom
			Pemphredon (43)	C, P	Hom
			Pluto (58)	S	Hom
			Polemistus (36)	C	Hom
			Psen (92)	R	Hom
			Psenulus (159)	C	Hom
			Spilomena (86)	C, P, R	Hom, Thy
Sphecidae: Astatinae (part)	Crabronidae: Astatinae	4/151	*Astata* (80)	S	Hem
			Diplopectron (20)	S	Hem
			Dryudella (52)	S	Hem
Sphecidae: Astatinae (part)	Crabronidae: Dinetinae	1/12	*Dinetus* (12)	S	Hem
Sphecidae: Larrinae	Crabronidae: Larrinae	38/2686	*Gastrosericeus* (61)	S	Ort
			Larra (63)	Pa	Ort

Apoid Wasps (Hymenoptera: Apoidea: Spheciformes), Table 8 Correspondence of taxa names under the "classical" (Bohart and Menke 1976) and revised (Pulawski 2007) systems of classification of the apoid wasps. Note a few minor taxa have been left out of the table (Continued)

"Classical" taxonomy	Revised taxonomy	Number of extant genera/species[a]	Some important genera (number of described species[a])	Nest type[b]	Host/prey orders[c]
			Liris (350)	C, S	Ort
			Miscophus (183)	S	Ara
			Nitela (60)	C	Pso, Hom
			Palarus (34)	S	Hym
			Pison (196)	C, M	Ara
			Plenoculus (20)	S	Hem, Lep
			Sericophorus (69)	S	Dip
			Solierella (111)	C	Ort, Pso, Hem
			Tachysphex (391)	S	Ort
			Tachytes (294)	S	Ort, Lep
			Trypoxylon (629)	M	Ara
Sphecidae: Crabroninae	Crabronidae: Crabroninae	56/1886	*Belomicrus* (109)	S	Hem
			Crabro (88)	S	Dip
			Crossocerus (236)	C, P, S	Eph, Pso, Hom, Mec, Tri, Lep, Dip
			Ectemnius (184)	P, R, S	Dip
			Entomognathus (63)	S	Col
			Lindenius (60)	S	Dip
			Oxybelus (262)	S	Dip
			Podagritus (116)	S	Col
			Rhopalum (277)	P, S	Hom
Sphecidae: Nyssoninae	Crabronidae: Bembicinae[b]	84/1708	*Alysson* (42)	S	Hom
			Argogorytes (31)	S	Hom
			Bembecinus (187)	S	Hom
			Bembix (346)	S	Odo, Neu, Lep, Dip, Hym
			Bicyrtes (27)	S	Hem
			Clitemnestra (67)	S	Hom
			Gorytes (46)	S	Hom
			Harpactus (73)	S	Hom
			Hoplisoides (79)	S	Hom
			Microbembex (34)	S	Art[d]
			Nysson (102)	Bp	Apo[e]
			Stictia (28)	S	Dip
			Stizus (120)	S	Ort, Man
			Stizoides (29)	Bp	Apo[e]

Apoid Wasps (Hymenoptera: Apoidea: Spheciformes), Table 8 Correspondence of taxa names under the "classical" (Bohart and Menke 1976) and revised (Pulawski 2007) systems of classification of the apoid wasps. Note a few minor taxa have been left out of the table (Continued)

"Classical" taxonomy	Revised taxonomy	Number of extant genera/species[a]	Some important genera (number of described species[a])	Nest type[b]	Host/prey orders[c]
Sphecidae: Philanthinae	Crabronidae: Philanthinae	8/1141	*Aphilanthops* (4)	S	Hym
			Cerceris (868)	S	Col, Hym
			Clypeadon (9)	S	Hym
			Eucerceris (41)	S	Col
			Philanthus (137)	S	Hym
			Trachypus (31)	S	Hym

[a]number described species worldwide (see Pulawski 2007); genera included based on genus size and biological interest (but certain larger genera for which no biological data are available are left off the list).
[b]Bp = brood parasite in nests of other wasps; C = cavity nests; M = mud nests; P = nest excavated in plant stems; Ps = free-standing nest made of plant material bound with silk; R = nest excavated in rotten wood; S = nest excavated in soil.
[c]Apo = apoid wasps; Art = Arthropoda; Ara = Araneae; Bla = Blattodea; Col = Coleoptera; Clm = Collembola; Dip = Diptera; Eph = Ephemeroptera; Hem = Hemiptera; Hom = Homoptera; Hym = Hymenoptera; Lep = Lepidoptera; Man = Mantodea; Mec = Mecoptera; Neu = Neuroptera; Odo = Odonata; Ort = Orthoptera; Pso = Psocoptera; Thy = Thysanoptera; note that each species may prey upon a narrow range of families within each order.
[d]females are scavengers of dead arthropods.
[e]*Nysson* and *Stizoides* are brood parasites whose larvae feed on prey provisioned by other wasp species.

distribution to the eastern Mediterranean region, southern Africa, and Madagascar. Nothing is known about their biology, but there are hints that it may be unique among apoid wasps: females have such short wings as to make them flightless and they have been observed active at night; based on morphological evidence, it has been inferred that heterogynaeids are parasitoids, though they probably do not dig in soil.

Ampulicidae

The Ampulicidae have rather elongate bodies and legs that make them proficient runners; they range up to 3 cm or so in body size, and may be metallic blue or green in color. Though geographically widespread, ampulicids appear to be relatively consistent in their habits. Females of all species prey on cockroaches that are stung into temporary paralysis, placed singly in existing cavities, and quickly covered with debris after a single egg is laid on each prey. Venoms of certain species are known to have specific pharmacological effects on cockroaches, which are somewhat subdued following stinging, but remain active enough that the female wasp can lead them to the nest cavity, as if walking a tethered cow to pasture. Nests of ampulicids may have multiple cells separated by partitions made of plant debris, but are relatively simple compared to nests constructed by many Sphecidae and Crabronidae.

Sphecidae

The wasps in what is now called the Sphecidae are sometimes referred to as "thread-wasted wasps" in reference to their narrow cylindrical petioles. Sphecids often have quite striking body colors, including the metallic blue (*Chlorion aerarium*), black and yellow (*Sceliphron caementarium*), and black and orange with either silver (some *Ammophila*) or golden hairs (*Sphex ichneumoneus*). The family includes some of the largest apoid wasps, including members of the genera *Dynatus*, *Parasammophila*, and *Sphex* that can reach as long as 4–5 cm; sphecids are rarely less than 1 cm long, though this is the case for some *Ammophila* and *Prionyx*. Sphecids are more diverse in their nesting habits than are ampulicids. Some dig nest burrows in soil, others nest in existing cavities in wood or construct mud nests *de novo*. Certain species of *Chlorion*, on the other hand, are parasitoids that construct no nests at all, but simply sting their cricket prey and then place it back in its own burrow. Prey of sphecids include three orders of insects, along with spiders; some take prey that are large relative to their own body size. *Palmodes laeviventris* (which preys upon Mormon crickets, *Anabrus simplex*), *Sphex ichneumoneus* (which takes crickets and katydids), and certain *Ammophila* (that take large caterpillars) may provision with prey that approach or even exceed the adult female in body mass.

Crabronidae

The Crabronidae, the largest and most diverse of apoid wasp families, contains 90% of the apoid wasps. Crabronids range in size from 1.5 mm long *Spilomena* that prey on psyllids and thrips, to 35 mm long *Sphecius speciosus* that prey on cicadas, and 45 mm long *Editha magnifica* that take butterflies. Even individual genera can exhibit wide size variation; *Philanthus* in North America, for example, range from the 5 mm long *Philanthus parkeri*, predators of tiny andrenid bees, to 25 mm long *Philanthus bicinctus*, predators of worker bumble bees. As a group, crabronids prey on insects of at least 17 orders, along with spiders. The reproductive biology of the Ampulicidae, Sphecidae, and Crabronidae are covered in more detail below.

Reproductive Biology of Females

The reproductive strategies of female apoid wasps fall into three broad categories: parasitoidism, brood parasitism, and nest-provisioning. The nest provisioners include solitary, communal, and eusocial species, the latter two of which will be discussed in the following section. Unlike some apoid wasps, no vespid wasps or bees are parasitoids, and only the bees include brood parasites. However, apoid wasps have just barely crossed the threshold into eusociality, whereas bees and vespid wasps contain some of the most highly eusocial Hymenoptera.

Among apoid wasps, parasitoids lay their eggs singly on a host insect that has been stung by the adult female wasp; no nest is constructed by the female parasitoid, though she may return the host to its own burrow and cover it with debris. Parasitoids are found in the Ampulicidae, a few genera of Crabronidae (*Chlorion*, *Larra*), and perhaps the family Heterogynaeidae, though this has yet to be confirmed. Brood parasitic apoid wasps occur in the crabronid tribe Nyssonini (226 species) and genus *Stizoides* of the Gorytini (29 species). Brood parasites enter provisioned nest cells of other apoid wasps and deposit their own eggs (one per nest cell); the brood parasite larva then feeds on the host's stored prey, the host egg having been already killed either by the adult female parasite at the time of oviposition (*Stizoides*) or the parasite larva itself (Nyssonini).

The vast majority of female apoid wasps are solitary nest-provisioners that work without assistance from conspecifics to construct a nest and provision each of its brood cells with one or more paralyzed prey. The prey placed in a cell must provide all of the nourishment required by the maggot-like larva (one per nest cell in almost all species) that remains restricted to its own nest cell throughout development. Apoid wasp nest types can be grouped in five categories: cavity nests; nests excavated in plant material; nests excavated in soil; free-standing mud nests; and free-standing nests made of various materials bound with silk. In some genera, different species may construct nests in different categories.

Cavity nests, those built within existing cavities, are often constructed in old beetle tunnels in wood, but have also been found in such locations as empty snail shells, old plant galls, pitcher plants, rolled leaves, and gaps between stones or between boards on the siding of houses. Such nests usually contain multiple cells separated by a species-specific choice of materials; for example, *Chalybion* uses mud; *Isodontia*, chopped grass fragments and plant fibers; *Passaloecus*, conifer resins; *Nitela*, wood chips; and *Podium*, an eclectic mix of detritus, mud, and resin. Wasps that excavate their own nest tunnels in plant materials may tunnel through the pith of plant stems (e.g., in raspberry or sumac) or rotten wood in logs. Cells may be arranged in a linear sequence, and tunnels in the same nest may diverge into separate branches. Nests excavated in soil are, by far, the most common type of nest among apoid wasps. They may be simple, unbranched shallow tunnels terminating in the single brood cell, as is the case for some or all species of *Ammophila*, *Bembecinus*, *Bembix*, *Podalonia*, and *Prionyx*. Other species dig branched nests with side tunnels leading to as many as 1–2 two dozen brood cells provisioned in succession over a period of several weeks. Single and multi-celled nests can be found not only among different species of the same genus, but among different females in one species. Free-standing nests constructed *de novo* by females may be built of mud sculpted into species-specific shapes, as is the case for species of *Pison*, *Sceliphron*, and *Trypoxylon*. Mud nests may be attached to vines, trees, cliff faces, or nowadays, buildings; they may also have multiple cells.

In most cases, each nest cell is completely provisioned and closed off by the adult before the next cell is begun, but there is some variation in the duration and timing of provisioning relative to the developmental schedule of offspring. Most species are *mass provisioners* that completely provision cells with one or more prey before the egg hatches. More rarely, females are *progressive provisioners* that continue to bring in prey after the egg hatches, sometimes until the larva is ready, or nearly so, to spin its cocoon. Among solitary apoid wasps, only certain *Ammophila* provision two cells simultaneously. During provisioning, females of those species that hunt relatively small prey carry the prey in flight from hunting grounds to the nest. Prey are usually carried in the wasp's legs, sometimes with the aid of the mandibles, but some *Oxybelus* tote prey impaled on their stings, whereas *Clypeadon* females carry their ant prey grasped by the thorax using structures on the terminal abdominal segments aptly referred to as "ant clamps."

When they leave nests to forage, females of nest-provisioning apoid wasps face two problems in particular, other than the obvious need to find, sting, and transport their prey: the necessity to protect the unguarded nest from natural enemies and the need to find their way home again. Before departing to hunt, wasps often plug the entrance temporarily as a means of excluding intruders. And when a nest is completed, the female may construct an even more elaborate closure and take steps to conceal the entrance; in ground nesting species, this involves often elaborate and prolonged leveling of the mound of excavated soil adjacent to the nest entrance. Nevertheless, although these actions are likely successful in many cases, apoid wasp larvae are plagued by a variety of natural enemies that commence their attacks at varying times in the life cycle of the wasp. Brood parasites, which include not only other apoid wasps, but mites, flies (Phoridae, Sarcophagidae), and non-apoid wasps (Chrysididae) that feed on the wasps' own prey, may kill the wasps' young either directly or indirectly (through starvation). Parasitoids that feed directly on wasp larvae or pre-pupae include, among other insects, flies (Bombyliidae), beetles (Rhipiphoridae), and other aculeate wasps (Chrysididae and Mutillidae).

Several detailed studies attest to the fact that female wasps often have excellent homing abilities that lead them back to their nest, even when that nest is one of many hundreds or thousands densely packed into the apparently featureless soil surface of a nesting area. As far back as 1930, Niko Tinbergen's research showed that a *Philanthus triangulum* female can relocate her nest by learning the image of the landscape surrounding the nest and matching the memorized image to the configuration of local landmarks when she later returns with prey. The initial task of learning the image is apparently accomplished during an orientation flight, which in the case of *P. triangulum*, begins when the female circles the nest in flight, then gradually expands the diameter and height of her loops before departing for her hunting grounds. The form of the orientation flights varies among species, but females of all species share an uncanny ability to find their way home, even after being transported several hundred meters away by researchers.

When we examine the ovaries of female apoid wasps, we find several features that vary among species and correlate with overall reproductive strategies. First, although the paired ovaries of nest provisioning species each have three ovarioles (except for *Oxybelus* which have two), each ovary of brood parasitic species is comprised of four ovarioles (and sometimes five in *Stizoides renicinctus*). Second, although it is common for females of nest provisioners (especially progressive provisioners) to carry a maximum just one or two mature oocytes in their ovaries at a any time, brood parasites commonly carry 4–6 mature oocytes; and the parasitoid species *Larra amplipennis* can carry as many as 21. Third, the eggs produced by nest provisioners tend to be larger (relative to overall body size) than those of brood parasites or of *Larra*. All in all, this meshes with the fact that nest provisioning apoid wasps, because they invest so highly in individual offspring, have relatively low lifetime fecundities compared to parasitoids and brood parasites in their same families. Thus, it is likely common that even the most successful females of some nest provisioners can expect to have fewer than ten offspring during their lives. This contrasts markedly with the high potential fecundities of non-aculeate parasitoid Hymenoptera (e.g., Braconidae, Ichneumonidae).

Communal and Social Species

The vast majority of apoid wasps are solitary species, each of whose females occupies a nest alone and provisions it without assistance from conspecifics. Nests of both ground- and mud-nesters do sometimes occur in dense aggregations, but true communal and eusocial behavior is relatively rare among apoid wasps. Communal nests, in which small groups of females share a main nest burrow, but in which each provisions her own brood cells, have been reported in several genera (e.g., *Cerceris*, *Moniaecera*, *Spilomena*). In the Neotropics, *Microstigmus comes* is eusocial, inhabiting nests in which (i) two generations of adult females are present (likely a mother and her daughters), (ii) each nest cell is provisioned cooperatively, and (iii) one female is the primary egg layer. The nests, which are founded by one or more females, have as many as 18 brood cells and 10 adult females (as well as a smaller number of adult males). The nests of *Microstigmus* are unique among apoid wasps, that of *M. comes* consisting of a 1–3 cm deep bag of plant fibers embedded in a matrix of silk and suspended from the underside of a leaf by a short, coiled petiole. Other *Microstigmus* create similar nests, but embedding small pieces of bark, wood, leaf hairs, lichens, sand, or stone in the silk mesh. The use of silk produced by adults in nest construction is limited among apoid wasps to *Microstigmus* and other Pemphredoninae (e.g., *Arpactophilus*, *Psenulus*); however, larval apoid wasps commonly incorporate silk into their cocoons. Finally, whereas other social insects build nests gradually, expanding their size over time, *Microstigmus* construct their silken abodes all at once and so are limited to their confines until all cells in the nest are completed.

Mating Strategies

In 1960, a comprehensive review of the diversity of male apoid wasp behavior would have occupied a brief paragraph, but we now have a much better understanding of male behavior. Perhaps the best-known male behaviors are the so-called "sun dances" of sand wasps (Bembicinae) in which hundreds or thousands of males swarm over the surface of nesting areas seeking newly emerged virgin females (as in many species of *Bembix*). A variation on this theme sees males attempting to rendezvous with females at the point at which they emerge from the ground when they leave their natal nests (e.g., *Bembecinus quinquespinosus*, *Bembix rostrata*, and *Glenostictia satan*).

In other species, males defend discrete territories that are often plots of ground in emergence or nesting areas, as is the case for *Sphecius* (cicada-killers) and many *Philanthus* (beewolves). Or males may defend individual nests that are in the process of being provisioned by females (as in some *Trypoxylon* and *Oxybelus*, for example). Less commonly, males establish territories at hunting sites frequented by females (e.g., *Aphilanthops subfrigidus* which defend territories in mating swarms of prey, and *Mellinus rufinodus* which defend feces that attract flies hunted by females). In yet other species, territories are situated in locations that have no other apparent attractiveness to females other than the presence of the males themselves (e.g., *Eucerceris flavocincta*, *Philanthus basilaris*). While defending their territories, male wasps may engage in rowdy battles that involve, depending on the species, wrestling, biting, head butting, abdomen slapping, or mutual flights in which the contestants swirl about one another at dizzying speeds. One should not be left with the impression, however, that males of any given species have just one way to find a mate, as alternative mating tactics are common. Male *Stictia heros*, for example, may patrol the nesting area in the morning, but shift to defending territories later in the day. And some males of *Philanthus zebratus* patrol the air space above the nesting area, while others simultaneously defend scent-marked territories nearby.

Ultimately, it appears that in most cases it is the females that control which males are successful. Females, after all, are usually the larger sex, so are physically dominant to males (and in the case of *Philanthus basilaris*, may even prey upon them). So mating is sometimes, though not always, preceded by obvious courtship activities during which the male induces the female to copulate. This, however, is one of the least-studied aspects of apoid wasp reproductive biology.

Economic Significance of Apoid Wasps

A least one genus of apoid wasps, *Larra*, whose females prey on mole crickets, includes species that have found some success as biological control agents. Other genera contain species that may provide some natural control of pests such as aphids (*Passaloecus*), biting flies (*Bembix*, *Stictia*), cutworms (*Podalonia*), grasshoppers (*Prionyx*, *Tachysphex*), Mormon crickets (*Palmodes*), and leafhoppers (many genera). On the negative side of the ledger, apoid wasps can be a nuisance to those people that cannot abide the presence of a wasp, no matter what its activities. In North America, large territorial males of the cicada-killer wasp, *Sphecius speciosus*, sometimes bother homeowners and park visitors who mistake male investigatory flights for something more hostile. The large nest mounds of female cicada-killers that appear in otherwise immaculate lawns are considered unsightly by some. In Africa, *Palarus latifrons* and *Philanthus triangulum* can be outright pests when large numbers of females invade apiaries and decimate worker honey bee populations. And we know very little about the potential effect of apoid wasp predators on the biology of other beneficial insects such as native pollinators and biological control agents.

► Wasps, Ants, Bees and Sawflies
► Bees

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Apolysal Space

During molting, a very small space is created by the separation of the epidermis from the old cuticle. This space, called the apolysal space, contains molting fluid during the process of cuticle digestion.

Apolysis

Separation of the epidermal cells from the inner surface of the endocuticle. This is the first step in the process of molting.

Apomorphic

A character that is derived and not ancestral.

Apomorphy

When considering classification and phylogeny, a derived character state.

Apophysis

An internal or external elongate projection of the body wall.

Apoprogonidae

A family of moths (order Lepidoptera). They also are known as African skipper moths.

► African Skipper Moths
► Butterflies and Moths

Aposematism

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Aposematism is a strategy used by many organisms that increases their conspicuousness, and alerts or warns potential predators of their toxicity, their ability to inflict pain or, more simply, their unpredictability. Insects have evolved this strategy to a high degree, although it is found occasionally in other terrestrial organisms such as snakes, lizards, and frogs, and in aquatic organisms such as nudibranches. Aposematic signals usually are visual in nature and involve bright and contrasting coloration, usually black and red, yellow or orange or black and white. Visual signals may be enhanced by certain odors, sounds or behaviors, presenting a multimodal signal that predators may recognize and learn more easily.

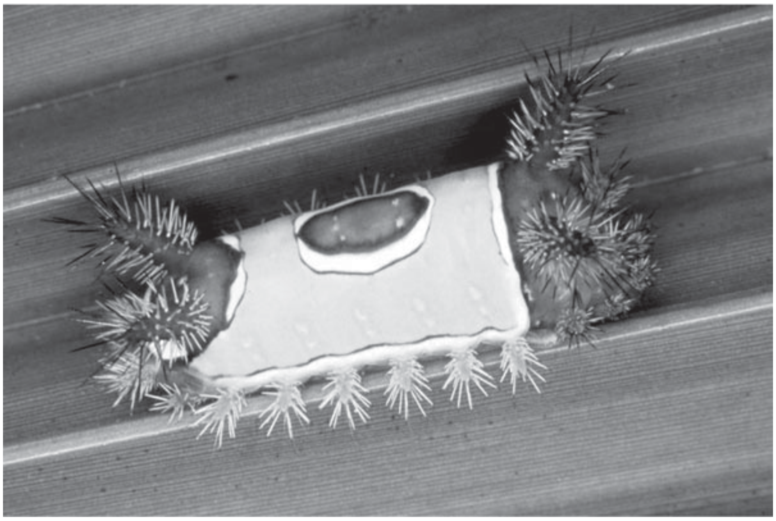
Visual aposematism as an antipredator strategy only works well against predators with color vision and good learning ability. Birds, and to a lesser extent lizards and amphibians, are the most common predators for which aposematic coloration (Figs. 66 and 67) is an effective deterrent. The naïve predator associates the particular color pattern of an aposematic organism with the unpleasant after effects of eating or attempting to eat it. Aposematic insects usually back up their warning signal with chemical defenses (unless they are harmless mimics of another toxic organism). These chemical defenses may be toxins that are stored inside the insect's body that could cause death if ingested and absorbed by the predator. However, the toxins themselves often are emetic (for example, cardiac glycosides in the Monarch butterfly, *Danaus plexippus*, and lucibufagins in *Photinus* fireflies), meaning that they cause the predator to regurgitate the prey item before a lethal dose of the toxin has been absorbed. The toxins also are often bitter so that the predator is less likely to pursue the attack once the bitter compounds have been contacted. In other insects, toxins are not stored within the body but are injected into predators through sharp urticating hairs or spines (for example, larvae of the saddleback moth, (Fig. 68) *Sibine stimulea*). In these insects, the predator is warned of the prey item's distastefulness without having to breach the cuticle of the aposematic organism.

The naïve predator may need only one trial to associate the color pattern of the aposematic insect with emesis or a bitter taste but more often, learning takes several trials. The speed of learning can be enhanced in several ways. If the predator encounters several toxic insects with the same aposematic pattern within a short period of time, it appears to learn the warning

Aposematism, Figure 66 **Aposematic insects are often aggregated, perhaps increasing the rate at which predators associate aposematic coloration with toxicity. The orange and black larvae of the oleander caterpillar, *Syntomeida epilais* (Ctenuchidae), aggregate in the early instars on oleander, *Nerium oleander*, a plant containing heart poisons (cardiac glycosides) (photo by James Castner).**

Aposematism, Figure 67 **The black and white larvae of the Giant African Skipper (Hesperiidae) also aggregate on their host plant (photo by Andrei Sourakov).**

coloration faster. This may explain why aposematic insects are often gregarious, living in small, usually related, groups. For example, oleander caterpillars, *Syntomeida epilais* and oleander aphids, *Aphis nerii* live gregariously on oleander which contains heart poisons. Other factors that can increase the rate of learning are the pairing of the visual pattern with acoustic signals or olfactory signals. Many aposematic insects hiss, stridulate or make some other noise when predators attack them. Arctiic moths and lubber grasshoppers, *Romalea guttata*, commonly do this. The association of sound with the color pattern and bitter chemical toxins in the aposematic



Aposematism, Figure 68 **Larvae of the saddleback moth, *Sibine stimulea* (Limacodidae), advertise their urticating hairs with a pronounced brown and white "saddle" on the lime-green bodies (photo by James Castner).**

insects help the predator better remember the color pattern. We are becoming increasingly aware that many insects release volatile pyrazine compounds when under attack. These nitrogen-containing compounds are extremely odorous at low concentrations and are thought to produce a universal warning odor in plants and animals.

Insects that are aposematic often exhibit what we might call bold behavior, at least for an insect. They are usually active during the day and are not cryptic, rather feeding in an exposed position. Aposematic adults may have an exaggerated slow flight, as do *Heliconius* butterflies and many arctiid moths. Larvae may wave tentacles and other long protuberances from their body to warn predators. Larvae of the Monarch butterfly (Fig. 69) integrate aposematic behaviors into their multimodal signal to warn of their toxicity. In addition to being conspicuously striped white, yellow and black, they release pyrazine from the head collar region when roughly handled and nod their heads up and down every 2 s while simultaneously twitching their anterior filiform tentacles.

► Allelochemicals
► Mimicry
► Chemical Ecology

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Aposymbiotic

Separated from its symbiotes, or symbiote-free; this usually refers to mutualistic symbiotes.

Aposematism, Figure 69 **Larvae of the Monarch butterfly, *Danaus plexippus* (Danaidae), use a multimodal signal to warn potential predators. Their aposematic coloration of black, white, and yellow stripes is enhanced with the release of pungent pyrazine and the behavioral display involving rhythmic nodding of the head and twitching of the filiform tentacles (photo by Lyle Buss).**

Apotome

A narrow anterior portion of each abdominal sternum, separated by a fold from the rest of the plate. They are present in Apterygota, but indistinct in Pterygota.

► Abdomen of Hexapods

Apparent Resources

Food resources (either insect or plant) that are "easy to locate" or apparent to potential predators or herbivores. Apparent resources often are protected against consumption by generalist and specialist predators, and generalist or specialist herbivores, by possessing broadly effective (though metabolically expensive) chemical defenses such as digestibility reducing substance (contrast with unapparent resources).

Appeasement Substance

A secretion presented by a social parasite that reduces aggression by the host insects, and aids parasites in being accepted as members of the colony.

Apple Maggot

► Apple Pests and their Management

Apple Pests and their Management

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Insects with chewing mouthparts inflict great damage on foliage, causing leaves to be skeletonized, riddled with holes, eaten around the edges, or entirely consumed (e.g., larvae of moths, sawflies, and beetles). Other insects suck sap from leaves, stems, or other plant parts, producing a characteristic spotting or browning, curling, or wilting. Feeding on stems or twigs results in dwarfing or wilting. Damage is caused both by removal of the sap and by injury to the plant tissue (e.g., scale insects, aphids, and true bugs). Also included in this category (Fig. 70) are mites, such as the European red mite and the two-spotted spider mite, which damage the leaves by piercing the cell walls with bristle-like mouthparts and ingesting their contents, including the chlorophyll. The injury results in off-color foliage that, in severe cases, becomes bronzed.

Scale insects are usually minute, but if they are abundant enough to encrust bark, twigs, or stems they can kill orchard and shade trees. Aphids produce a curling of the leaves and, when feeding on fruit, may cause it to be stunted or misshapen and may change the sugar content, greatly impairing the flavor.

Many insects feed as miners in leaves or as borers in stems, roots, or fruits. Feeding between the upper and lower surfaces of the leaf may cause as much defoliation as external feeding. There are about 500 leafmining species in the United States (e.g., spotted tentiform and apple blotch leafminers).

Tunneling causes serious damage. Insects that tunnel into fruit include codling moth, oriental fruit moth, apple maggot, and plum curculio. Damage with more serious consequences can be done by insects that tunnel into the tree trunk, bark, or foliar shoots, such as apple-boring beetles (roundheaded, flatheaded), dogwood borer, American plum borer, European corn borer, and oriental fruit moth.

Injection of a chemical into plant tissues while the insect feeds causes abnormal growth (e.g., rosy apple aphid) or produces a gall (woolly apple aphid). Each species of gall insect produces a characteristic gall on a certain part of a particular plant.

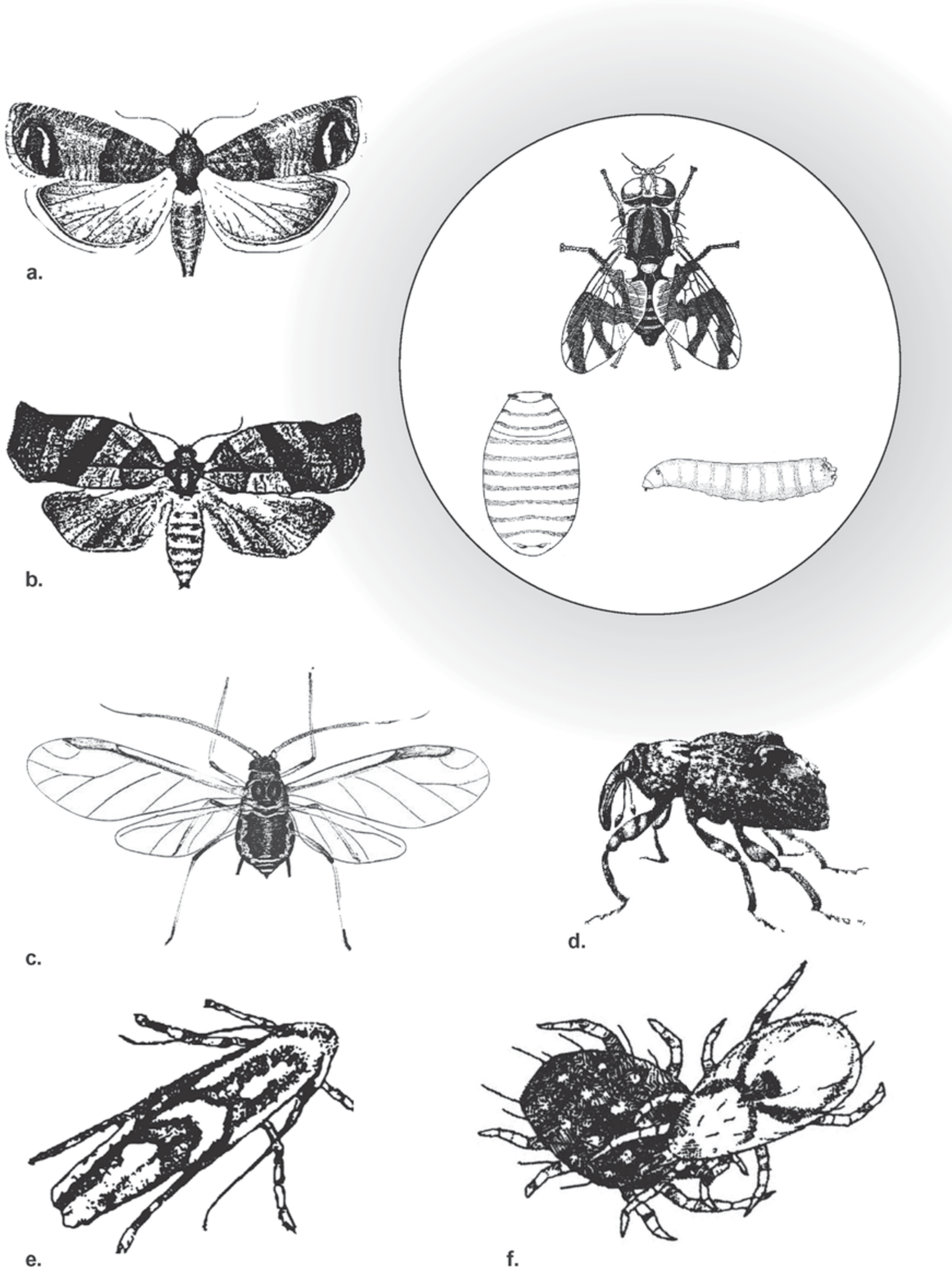
Insects at the larval and nymphal stages (e.g., woolly apple aphid) that live in the soil and attack the underground plant parts cause extensive damage.

Shelters in plants are built by leafrollers and leaf folders, which roll or fold the leaves and tie them with silk, feeding in the shelter so formed. Leaf tiers and webworms tie several leaves or even entire branches together, producing large silken webs or tents.

A few insects injure plants when they lay their eggs, particularly in stems or fruits (e.g., plum curculio, apple maggot, periodical cicadas, tree crickets, leafhoppers).

Major Economic Pests

Early researchers in New York estimated nearly 500 species of insects known to feed on apple. Fortunately, only a relatively small number of these ever reach economic pest status. A survey conducted in the northeastern U.S. identified a



Apple Pests and their Management, Figure 70 **Some North American apple pests: (a) codling moth; (b) obliquebanded leafroller; (c) rosy apple aphid; (d) plum curculio; (e) spotted tentiform leafminer; (f) European red mite attacked by predatory mite; within circle, apple maggot adult, larva and pupa.**

total of 191 phytophagous (plant-feeding) insect species in managed and abandoned apple orchards. Most numerous were species of Lepidoptera (mostly moths and their caterpillars, 43%) and Hemiptera (leafhoppers, plant bugs, aphids and scale insects, 32%). Current tabulations of actual economic pests list just over 60 species in New York, approximately half of which are considered important enough to warrant specific control recommendations. This compares with 17 pest species for pear, 12 for peach, and seven for tart cherry and plum. A similar accounting in other production regions reveals certain species with a worldwide distribution, and others, largely representing the above major orders, that are prevalent only in specific areas (Table 9). The following are some of the key pests in the northeastern U.S. growing regions.

Rosy Apple Aphid, *Dysaphis plantaginea* (Passerini)

Biology and Impact

The rosy apple aphid is the most damaging of the aphids that attack apple. Its saliva, injected while feeding, is translocated to nearby fruit, causing leaf curling and small, deformed apples. The rosy apple aphid can be distinguished from other aphids by its long cornicles and purple-rose color. It overwinters as an egg on twigs, in bud axils, and in bark crevices. The overwintering eggs of the rosy apple aphid are oblong and pale green at first, then turn shiny black. Rosy apple aphid nymphs are visible beginning around the tight cluster bud stage but are most easily observed at the pink bud stage. The first adults appear around bloom. Second-generation adults appear two to three weeks after petal fall. Some of these move to alternate hosts (such as narrowleaf plantain) and the rest remain in the orchard. The third generation develops by mid-July and moves to alternate hosts. In later summer, adult rosy apple aphids return to the trees to lay eggs.

Decision Making

Because rosy apple aphid populations are highly variable, it is important to assess their densities before making a treatment. Sampling can begin at the tight cluster bud stage but is better done at the pink stage when rosy apple aphid nymphs are more easily seen. Rosy apple aphid densities are estimated by sampling 10 fruit clusters from the interior canopy area of 10 trees. Treatment is generally recommended if one infested cluster is found, but for experienced samplers of rosy apple aphids, this is probably too conservative and a threshold of three to five infested clusters would be more appropriate.

Control

It is not known how important natural enemies (such as larvae of the fungus gnats, Cecidomyiidae) are in regulating rosy apple aphid populations. Several pesticides can effectively control this pest when applied at the pink bud stage. A material should be used that will conserve natural enemy populations, such as *Typhlodromus pyri*, an important mite predator.

Spotted Tentiform Leafminer, *Phyllonorycter blancardella* (Fabricius)

Biology and Impact

The spotted tentiform leafminer was introduced from Europe in the 1880s. Its host plants include apple, wild cherry, hawthorn, quince, plum, and crabapple. Spotted tentiform leafminer overwinters as a pupa in leaf litter on the ground. Adults emerge at the green tip apple bud stage and lay small, flattened eggs that are deposited singly on leaf undersides. Egg laying begins when leaves unfold after the half-inch green bud stage, and deposition is nearly complete by the end of the pink bud stage. Its five larval stages are divided

Apple Pests and their Management, Table 9 **Major insect and mite pests of apple**

Taxon scientific and common name	Geographical distribution	Plant parts affected
Acari: Eriophyidae		
Aculus schlechtendali (Nalepa), apple rust mite	North America, South America, Europe, Australia/New Zealand	Foliage
Eriophyes pyri (Pagenstecher), pearleaf blister mite	North America, South Africa	Foliage
Acari: Tetranychidae		
Bryobia praetiosa Koch, clover mite	North America	Foliage
Bryobia rubrioculus (Scheuten), brown mite	Worldwide	Foliage
Panonychus ulmi (Koch), European red mite	Worldwide	Foliage
Tetranychus canadensis (McGregor), fourspotted spider mite	North America	Foliage
Tetranychus kanzawai Kishida, kanzawa mite	Asia	Foliage
Tetranychus mcdanieli McGregor, McDaniel spider mite	North America	Foliage
Tetranychus urticae Koch, two spotted spider mite	Worldwide	Foliage
Tetranychus viennensis Zacher, hawthorn spider mite	Asia	Foliage
Coleoptera: Bostrichidae		
Amphicerus bicaudatus (Say), apple twig borer	North America	Twigs, Wood
Coleoptera: Buprestidae		
Chrysobothris femorata (Olivier), flatheaded appletree borer	North America	Cambium, Wood
Coleoptera: Cerambycidae		
Prionus imbricornis (Linnaeus), tilehorned prionus	North America	Cambium, Roots
Prionus laticollis (Drury), broad necked root borer	North America	Cambium, Roots
Saperda candida Fabricius, roundheaded appletree borer	North America	Cambium, Wood
Coleoptera: Chrysomelidae		
Nodonota puncticollis (Say), rose leaf beetle	North America	Fruit
Coleoptera: Curculionidae		
Anthonomus pomorum (Linnaeus), apple blossom weevil	Europe, Asia	Buds
Anthonomus quadrigibbus Say, apple curculio	North America	Foliage, Fruit
Conotrachelus nenuphar (Herbst), plum curculio	North America	Fruit

Apple Pests and their Management, Table 9 Major insect and mite pests of apple (Continued)

Taxon scientific and common name	Geographical distribution	Plant parts affected
Naupactus xanthographus (Germar), grape snout beetle	South America	Buds, Foliage
Phlyctinus callosus Boheman, banded fruit weevil	South Africa	Fruit
Scolytus rugulosus (Müller), shothole borer	North America	Cambium, Wood
Coleoptera: Scarabaeidae		
Macrodactylus subspinosus (Fabricius), rose chafer	North America	Foliage, Fruit
Popillia japonica Newman, Japanese beetle	North America	Foliage, Fruit
Dermaptera: Forficulidae		
Forficula auricularia Linnaeus, European earwig	Europe	Fruit
Diptera: Agromyzida		
Liriomyza brassicae (Riley), serpentine leafminer	North America	Foliage
Diptera: Cecidomyiidae		
Dasineura mali (Kieffer), apple leafcurling midge	North America, Europe, Australia/New Zealand	Foliage
Diptera: Tephritidae		
Anastrepha fraterculus (Weidemann), S. American fruit fly	South America	Fruit
Bactrocera tryoni (Froggatt), Queensland fruit fly	South America, Australia/New Zealand	Fruit
Ceratitis capitata (Wiedemann), Mediterranean fruit fly	South Africa	Fruit
Ceratitis rosa Karsch	South Africa	Fruit
Rhagoletis pomonella (Walsh), apple maggot	North America	Fruit
Hemiptera: Miridae		
Atractotomus mali (Meyer), apple brown bug	North America	Fruit
Campylomma liebknechti (Girault), apple dimpling bug	Australia/New Zealand	Fruit
Campylomma verbasci (Meyer), mullein plant bug	North America, Europe	Fruit
Lygidea mendax Reuter, apple red bug	North America	Foliage, Fruit
Lygocoris pabulinus (Linnaeus)	Europe	Fruit
Lygus lineolaris Palisot de Beauvois, tarnished plant bug	North America	Fruit
Plesiocoris rugicollis Fallén	Europe	Fruit
Hemiptera: Pentatomidae		

Apple Pests and their Management, Table 9 Major insect and mite pests of apple (Continued)

Taxon scientific and common name	Geographical distribution	Plant parts affected
Antestiopsis orbitalis Ghesquierei Car., antestia bug	South Africa	Fruit
Heteroptera: Tingidae		
Stephanitis pyri Fabricius	Europe	Foliage
Hemiptera: Aphididae		
Aphis pomi DeGeer, apple aphid	North America, South America, Europe	Foliage, Fruit
Aphis spiraecola Patch, spirea aphid	North America, South America, South Africa, Asia	Foliage
Dysaphis plantaginea (Passerini), rosy apple aphid	North America, Europe	Foliage, Fruit
Eriosoma lanigerum (Hausmann), woolly apple aphid	Worldwide	Roots, Twigs
Myzus malisuctus Matsumura, apple leafcurling aphid	Asia	Foliage
Rhopalosiphum fitchii (Sanderson), apple grain aphid	North America, South America	Buds, Foliage
Schizaphis piricola Matsumura	Asia	Foliage
Hemiptera: Cicadellidae		
Edwardsiana crataegi (Dg.), apple leafhopper	South America	Foliage
Edwardsiana frogatti Baker	Europe	Foliage
Edwardsiana rosae (Linnaeus), rose leafhopper	North America	Foliage
Empoasca fabae (Harris), potato leafhopper	North America	Foliage
Empoasca maligna (Walsh), apple leafhopper	North America	Foliage
Typhlocyba pomaria McAtee, white apple leafhopper	North America	Foliage, Fruit
Hemiptera: Cicadidae		
Magicicada septendecim (Linnaeus), periodical cicada	North America	Twigs, Wood
Hemiptera: Coccidae		
Parthenolecanium corni (Bouché), European fruit lecanium	North America	Wood, Fruit
Hemiptera: Diaspididae		
Aonidiella aurantii (Maskell), California red scale	North America, South Africa	Twigs, Wood
Chionaspis furfura (Fitch), scurfy scale	North America	Cambium, Fruit

Apple Pests and their Management, Table 9 **Major insect and mite pests of apple (Continued)**

Taxon scientific and common name	Geographical distribution	Plant parts affected
Epidiaspis leperii (Signoret), Italian pear scale	South America, Europe	Cambium
Hemiberlesia lataniae (Signoret), latania scale	South America	Cambium
Lepidosaphes ulmi (Linnaeus), oystershell scale	North America, South America, Europe	Cambium
Quadraspidiotus forbesi (Johnson), Forbes scale	North America	Cambium
Quadraspidiotus perniciosus (Comstock), San Jose scale	Worldwide	Cambium, Fruit
Hemiptera: Flatidae		
Metcalfa pruinosa (Say)	Europe	Fruit
Hemiptera: Margarodidae		
Icerya purchasi Maskell, cottony cushion scale	South Africa	Wood, Twigs, Fruit
Hemiptera: Membracidae		
Stictocephala bisonia Kopp & Yonke, buffalo treehopper	North America, Europe	Twigs, Wood
Hemiptera: Pseudococcidae		
Pseudococcus calceolariae (Maskell), citrophilus mealybug	Europe, Australia/New Zealand, South Africa	Fruit
Pseudococcus comstocki (Kuwana), Comstock mealybug	North America	Foliage, Fruit
Hemiptera: Psyllidae		
Cacopsylla mali (Schmidberger), apple sucker	North America, Europe	Foliage
Hymenoptera: Tenthredinidae		
Hoplocampa testudinea (Klug), European apple sawfly	North America, Europe	Fruit
Lepidoptera: Arctiidae		
Hyphantria cunea (Drury), fall webworm	North America, Europe, Asia	Foliage
Lophocampa caryae Harris, hickory tussock moth	North America	Foliage
Lepidoptera: Carposinidae		
Carposina niponensis Walshingham, peach fruit moth	Asia	Fruit
Carposina sasakii Matsumura, peach fruit moth	Asia	Fruit
Lepidoptera: Choreutidae		
Choreutis pariana (Clerck), apple-and-thorn skeletonizer	North America, Europe, Asia	Foliage

Apple Pests and their Management, Table 9 **Major insect and mite pests of apple (Continued)**

Taxon scientific and common name	Geographical distribution	Plant parts affected
Lepidoptera: Coleophoridae		
Coleophora multipulvella (Chambers), pistol casebearer	North America, Asia	Foliage, Fruit
Coleophora serratella (Linnaeus), cigar/birch casebearer	North America, Europe, Asia	Foliage
Lepidoptera: Cossidae		
Cossus cossus Linnaeus, European goat moth	North America, Europe, Asia	Cambium, Wood
Zeuzera pyrina Linnaeus, leopard moth	North America, Europe, Asia	Wood, Twigs
Lepidoptera: Geometridae		
Alsophila pometaria (Harris), fall cankerworm	North America	Foliage
Operophtera brumata Linnaeus, winter moth	North America, Europe, Asia	Buds, Foliage, Fruit
Paleacrita vernata (Peck), spring cankerworm	North America	Foliage
Lepidoptera: Gracillariidae		
Marmara elotella (Busck), apple barkminer	North America	Cambium
Marmara pomonella Busck, apple fruitminer	North America	Fruit
Phyllonorycter blancardella (Fabricius), spotted tentiform leafminer	North America, Europe, Asia	Foliage
Phyllonorycter crataegella (Clemens), apple blotch leafminer	North America	Foliage
Phyllonorycter elmaella Doganlar & Mutuura, western tentiform leafminer	North America	Foliage
Phyllonorycter ringoniella (Matsumura), apple leafminer	Asia	Foliage
Lepidoptera: Lasiocampidae		
Malacosoma americanum (Fabricius), eastern tent caterpillar	North America	Foliage
Lepidoptera: Lymantriidae		
Euproctis chrysorrhoea (Linnaeus), browntail moth	North America, Europe, Asia	Foliage
Lymantria dispar (Linnaeus), gypsy moth	North America, Europe, Asia	Foliage
Orgyia antiqua (Linnaeus), rusty tussock moth	North America, South America, Europe, Asia	Buds, Foliage
Orgyia leucostigma (J.E. Smith), whitemarked tussock moth	North America	Foliage, Fruit
Lepidoptera: Lyonetiidae		
Bucculatrix pomifoliella (Clemens), apple bucculatrix	North America	Foliage

Apple Pests and their Management, Table 9 **Major insect and mite pests of apple (Continued)**

Taxon scientific and common name	Geographical distribution	Plant parts affected
Leucoptera malifoliella (Costa), pearleaf blister moth	Europe, Asia	Foliage
Lyonetia prunifoliella (Hübner), apple lyonetid	North America, Europe, Asia	Foliage
Lyonetia speculella Clemens, apple leafminer	North America	Foliage
Lepidoptera: Noctuidae		
Amphipyra pyramidoides Guenée, humped green fruitworm	North America	Foliage, Fruit
Helicoverpa armigera (Hübner), cotton bollworm	Europe, Asia, South Africa	Fruit
Lacanobia subjuncta (Grote & Robinson), Lacanobia fruitworm	North America	Foliage, Fruit
Lithophane antennata (Walker), green fruitworm	North America	Fruit
Orthosia hibisci (Guenée), speckled green fruitworm	North America	Foliage, Fruit
Xestia c-nigrum (Linnaeus), spotted cutworm	North America, Europe, Asia	Foliage
Lepidoptera: Notodontidae		
Datana ministra (Drury), yellownecked caterpillar	North America	Foliage
Schizura concinna (J. E. Smith), redhumped caterpillar	North America	Foliage
Lepidoptera: Pyralidae		
Conogethes punctiferalis (Guenée), yellow peach moth	Asia, Australia/New Zealand	Fruit
Euzophera semifuneralis (Walker), American plum borer	North America	Cambium, Wood
Ostrinia nubilalis (Hübner), European corn borer	North America, South America, Europe, Asia	Foliage, Fruit
Lepidoptera: Sesiidae		
Podosesia syringae (Harris), lilac/ash borer	North America	Cambium, Wood
Synanthedon myopaeformis Borkhausen, apple clearwing moth	Europe, Asia	Cambium, Wood
Synanthedon pyri (Harris), apple bark borer	North America	Cambium, Wood
Synanthedon scitula (Harris), dogwood borer	North America	Cambium, Wood
Lepidoptera: Tisheriidae		
Tischeria malifoliella Clemens, apple trumpet leafminer	North America	Foliage
Lepidoptera: Tortricidae		

Apple Pests and their Management, Table 9 **Major insect and mite pests of apple (Continued)**

Taxon scientific and common name	Geographical distribution	Plant parts affected
Adoxophyes orana Fischer Von Röslerstamm, summer fruit tortrix	South America, Europe, Asia	Fruit
Archips argyrospila (Walker), fruittree leafroller	North America	Foliage, Fruit
Archips podana Scopoli, fruittree tortrix	North America, Europe, Asia	Foliage, Fruit
Archips rosana (Linnaeus), rose tortrix	North America, Europe, Asia	Fruit
Argyrotaenia citrana (Fernald), orange tortrix	North America	Fruit
Argyrotaenia pulchellana Haworth	Europe	Foliage, Fruit
Argyrotaenia velutinana (Walker), redbanded leafroller	North America	Foliage, Fruit
Choristoneura rosaceana (Harris), obliquebanded leafroller	North America, South America	Foliage, Fruit
Cydia lobarzewskii Nowicki	Europe	Fruit
Cydia pomonella (Linnaeus), codling moth	Worldwide	Fruit
Epiphyas postvittana (Walker), light brown apple moth	Europe, Australia/New Zealand	Foliage, Fruit
Grapholita molesta (Busck), oriental fruit moth	Worldwide	Fruit, Foliage, Twigs
Grapholita prunivora (Walsh), lesser appleworm	North America	Fruit
Hedya dimidioalba (Retzius), marbled orchard tortrix	North America, Europe, Asia	Buds, Foliage
Pandemis heparana Denis & Schiffermüller, fruittree tortrix	North America, Europe, Asia	Foliage, Fruit
Pandemis limitata (Robinson), threelined leafroller	North America	Foliage, Fruit
Platynota flavedana Clemens, variegated leafroller	North America	Foliage, Fruit
Platynota idaeusalis (Walker), tufted apple budmoth	North America	Foliage, Fruit
Proeulia auraria (Clarke), fruit leaf folder	South America	Foliage, Fruit
Pseudexentera mali Freeman, pale apple leafroller	North America	Foliage, Fruit
Sparganothis sulfureana Clemens, Sparganothis fruitworm	North America	Foliage, Fruit
Spilonota ocellana (Denis & Schiffermüller), eyespotted bud moth	North America, Europe, Asia	Foliage, Fruit
Tortrix capensana (Walker)	South Africa	Foliage, Fruit
Orthoptera: Gryllidae		

Apple Pests and their Management, Table 9 Major insect and mite pests of apple (Continued)

Taxon scientific and common name	Geographical distribution	Plant parts affected
Oecanthus fultoni Walker, snowy tree cricket	North America	Cambium, Wood, Twigs
Thysanoptera: Thripidae		
Frankliniella occidentalis (Pergande), western flower thrips	North America, Europe	Foliage, Fruit
Taeniothrips inconsequens (Uzel), pear thrips	North America, South America, Europe	Buds

into sap-feeders (instars 1–3) and tissue-feeders (instars 4–5). The second-generation adults begin emerging in early June in the northeastern states (average date is June 13 ± 8 days), and larvae are usually present in early July. Third-generation larvae are usually present in late August.

The spotted tentiform leafminer damages only foliage, which the larvae eat and mine. This causes reduced photosynthesis and possibly sequestered nutrients. Foliar damage can cause smaller fruit size, premature drop, and poor color. Damage caused by the second generation is usually of the greatest concern. Third-generation leafminers usually are not a problem if the second generation was controlled properly.

Decision Making

A sequential sampling plan can be used to classify spotted tentiform leafminer egg density at the pink stage or the density of sap-feeding mines immediately after petal fall. Treatment is recommended if eggs average 2 or more per leaf on leaves 2, 3, and 4 of a fruit cluster at the pink stage, or if sap-feeding mines average 1 or more per leaf on these leaves at petal fall. Sampling can be completed in approximately 10 min.

Proper timing is essential for both the assessment of second-generation leafminer densities and control, if required. If done too early, sampling will underestimate the population. If control is applied too late, it will not be effective. Sampling for "sap-feeding mines" should be done at approximately 690 degree-days (base 43°F) after the start of the flight of the second generation. On average, second-generation spotted tentiform leafminer moths begin flying in early to mid-June. A decision regarding the third generation is generally not required unless the density of the second brood exceeds two mines per leaf.

Control

Many parasitoids effectively limit spotted tentiform leafminer populations in some orchards. Most important are the wasps *Apanteles ornigis*, *Sympiesis marylandensis*, and *Pnigalio maculipes*. Insecticide sprays applied in July and August probably do the most harm to these natural enemies. Some leafminer pesticides are effective without being toxic to natural enemies such as mite predators. Depending on the product chosen, application can be made any time from initial egg deposition until the larvae enter the tissue-feeding stages.

Obliquebanded Leafroller, *Choristoneura Rosaceana* (Harris)

Biology and Impact

The oblique banded leafroller prefers plants in the Rosaceae family but will feed on many unrelated deciduous trees. This leafroller overwinters as a second-or third-instar larva on the tree within closely spun cocoons or hibernacula. Larvae become active in the spring when buds begin to open. As foliage pushes from the buds, larvae often tie leaves together and conceal themselves in the resulting chamber. Spring-generation moths emerge in early June in the northeast, with peak activity in mid-June. First-generation larvae complete their development in late July or early August. Summer-generation moths begin flying in early August. Second-generation larvae feed primarily on foliage, but may cause surface injury to fruit if they are very abundant. After feeding briefly, second-generation larvae enter their winter hibernacula.

Spring-generation larvae may eat away large portions of developing fruit. If the fruit survive, they are misshapen with large, deep cavities of healed-over injuries. Fruit damaged by first-brood larvae generally falls off the tree. If not controlled, this spring generation of obliquebanded leafroller may cause only small fruit losses (2–4%).

The principal impact of summer-generation obliquebanded leafroller is its feeding damage to the fruit. This generally occurs if a leaf is webbed to an apple or clustered apples touch each other. Feeding areas on the fruit are shallow, irregular, and may range from small punctures to large excavations. This injury is more serious than that caused by the overwintering generation because most injured fruits remain on the tree.

Decision Making

During bloom or immediately after petal fall, spring-generation larval densities can be classified as above or below a treatment threshold using a sequential sampling procedure. Treatment is recommended if more than 3% of fruit spurs contain live obliquebanded leafroller larvae. Sampling can usually be completed in approximately 10–15 min.

Sampling for the summer-generation larvae should take place approximately 600 DD (base 43°F) after the start of the first summer flight. On average, summer-generation obliquebanded leafroller moths start flying the first or second week of June. The value of knowing the precise date of this event on a local basis cannot be overemphasized. If information on adult moth flight is not available, July 5 to 10 is a rough approximation of the appropriate sampling period in the northeast. At 600 DD after the start of the adult flight, populations can be classified according to whether the average percentage of terminals infested with live larvae is greater than 3%.

Control

Several parasitoids attack the obliquebanded leafroller, but their effectiveness in regulating leafroller populations in commercial orchards is largely unknown. Most growers favor chemical sprays to reduce damage caused by this insect. A contact insecticide is sometimes applied at bloom to petal fall. Most orchards with a history of leafroller infestation require 1–2 pesticide applications against the second-generation larvae. Selective pesticides, including insect growth regulators and those that are based on the bacterium *Bacillus thuringiensis* are compatible with IPM because they are not toxic to natural enemies (especially mite predators).

European Red Mite, *Panonychus ulmi* (Koch)

Biology and Impact

The European red mite overwinters as an egg on the tree. Egg hatch is usually closely correlated with tree phenology, ordinarily beginning at the early pink bud stage and continuing into bloom. If egg hatch does not coincide with the pink stage, it is usually delayed and starts during early bloom. European red mite adults normally appear by petal fall, but few eggs are laid by the first generation of adults on leaves until the first week after petal fall. Early hatching European red mite nymphs feed on older fruit cluster leaves and may cause bronzing by petal fall if populations are high. Early season damage before petal fall is usually insignificant, but some studies have shown that heavy damage in early to mid-June can reduce yields during the next season.

In the summer months, the European red mite damages apple leaves by inserting its mouthparts to feed on plant juices. This injury reduces the capacity of the leaf to use sunlight as an energy source (photosynthesis), which may lead to reduced yield and fruit quality. Recent studies of European red mite impact have found that the only effect of moderate European red mite injury during the mid- to late season was a reduction in the color of some red varieties of apples. These results have identified the densities of mites that can be tolerated at various times of the growing season.

Decision Making

The natural mortality of overwintering eggs can be substantial but is highly variable (10–to 60%). Therefore, sampling or rating schemes are generally not used for predicting the potential early season severity of the European red mite in commercial orchards by assessing the density of overwintering eggs. During late bloom and petal fall, the European red mite is concentrated on older fruit cluster leaves, and therefore the overall density of the first generation will be overestimated by counting mites on the oldest leaves at that time.

Early control of the European red mite is essential to prevent early season damage during the postbloom period. One method used to quantify mite presence is the "mite-day" concept, which measures the number of mites and the period of time they are present on the leaves. One mite-day is equivalent to an average of one mite feeding on a leaf for one day. Thus 10 mite-days can be accrued by one mite feeding on a leaf for 10 days or 10 mites feeding for one day. The current economic threshold of approximately 550 total mite-days (for the growing season) assumes that no significant accumulations of mite-days occur before mid- to late June. Therefore, a protective prebloom oil treatment is currently recommended for control of early season European red mites.

During the summer, the need for a miticide to control the European red mite can be determined from a sample of the mite population in an orchard. A sampling procedure is available that determines mite presence based on examination of leaves of intermediate age. This procedure divides mite populations into three categories: greater than threshold, below threshold, and much below threshold. The last two categories provide an indication of when the population must be sampled again. If the density is much below threshold, the population should be sampled in 11–16 days. If it is minimally below threshold, it should be sampled again in 6–10 days. If mite predators are present, these intervals can be lengthened by approximately 50%.

Sampling involves recording on a chart the presence or absence of mites in distinct samples of leaves and continues until a decision on whether to treat them can be reached. From petal fall until June 30, a threshold of 2.5 mites per leaf is used. From July 1 to 31, the threshold is 5 mites per leaf. From August 1 to 15, a threshold of 7.5 mites per leaf is used. Treatment for mites is not currently recommended after mid-August. Adherence to these thresholds will prevent serious injury.

Control

The European red mite is an induced pest in commercial apple orchards. This means that pesticides used against other arthropods usually destroy naturally occurring mite predators, allowing European red mite numbers to increase to damaging levels. Several major predators of the

European red mite may be found in commercial orchards, depending on the part of the country where they are located:

Typhlodromus pyri (Scheuten)

Adults of *T. pyri*, a major predacious mite species, are present in the tree at about the time of the European red mite hatch. These predators control low to moderate densities of European red mites but do not regulate high populations. This mite predator is very effective against the European red mite and when present in substantial numbers it will eliminate the need for chemical mite control. *T. pyri* spends its entire life in the tree, overwinters as an adult female, and is active by bloom. It prefers to feed on the European red mite but will sustain itself on other food sources. Once established in an orchard, if it is not disrupted by pesticides, *T. pyri* will keep European red mite populations to densities of less than one mite per leaf year after year. It may take two to three years for *T. pyri* to become abundant in an orchard once a selective pesticide regimen is adopted.

Amblyseius fallacis (Garman)

A. fallacis is also an effective predator of the European red mite, but its continued presence in the tree from year to year is not reliable. It overwinters both in apple trees and in the ground cover beneath them. Ground cover, however, appears to have little influence on number and movement of *A. fallacis* in the tree. *A. fallacis* was previously believed to a poor biological control agent because it did not move into the trees until late in the growing season after the European red mite had reached problem levels. More likely, *A. fallacis* numbers often remain low until late in the season because pesticides toxic to them are used early in the season. If a site has a history of *A. fallacis*, pesticides should be managed to conserve it. Because *A. fallacis* remains in the tree year-round, even early season applications of pyrethroids are damaging to it.

Metaseiulus occidentalis (Nesbitt)

Predominantly found in drier climates such as the northwestern states, this predator can also provide biological control of the European red mite in commercial apple orchards. It has high reproductive and prey consumption rates, and disperses readily into orchards. However, it requires the presence of an alternative prey population in the orchard, such as apple rust mites, to preserve its population numbers when red mites are at low levels.

Zetzellia mali (Ewing)

This minute yellow mite is present in nearly all orchards, overwintering as a gravid female in concealed parts of the tree. Although it prefers older rust mites and the eggs and immature stages of European red mites and two spotted spider mites, it feeds on all stages of these species. It undoubtedly helps to control European red mites but is of little benefit if it is the sole predator species present.

Stethorus punctum (Leconte)

This small, black ladybird beetle feeds on several small arthropods, including European red mites. It is more common in orchards in the middle Atlantic states. Success in controlling European red mites depends on keeping a relatively high population of European red mites in the tree (3–5 mites per leaf).

For chemical control during the early season, petroleum oil is often recommended (a 2% solution at the half-inch green bud stage or 1% at the tight cluster stage) as an early season IPM program. Oil is relatively safe to predators, relatively economical, and European red mite populations have never shown resistance to it. Furthermore, a thorough application of oil applied before foliage is fully developed can kill nearly all the eggs present. Other early season treatment options include contact miticides or ovicides applied at the pink bud stage or at petal fall. Miticides will likely cover less of the foliage present by this time, and most are able to be overcome by the development of resistance in local mite populations, so this is a less desirable alternative.

Relatively few miticides can control European red mite during the summer. The available contact miticides must be chosen by their individual performance traits, including their activity against specific mite stages and beneficial arthropods, rate of action and length of residual effectiveness, optimal application conditions for each, and any possible resistance that may be exhibited by local mite populations. Because of the limitations of all contact miticides, good spray coverage is essential.

Some research has been done on the use of highly refined petroleum oils to control summer mite populations. Acceptable season-long control has been achieved by using a multiple-spray program starting at petal fall, followed by periodic monitoring throughout the summer. Potential difficulties with this approach include leaf damage and incompatibility with some of the fungicides used to control summer diseases.

Plum Curculio, *Conotrachelus nenuphar* (Herbst)

Biology and Impact

Plum curculio adults move into orchards from overwintering sites in hedgerows or the edges of woods and are present in the trees from the late pink stage to early bloom before the fruit is susceptible to damage. Adults are active in the spring when temperatures exceed 60°F. Adult females oviposit in fruit during both day and night but feed mostly at night. Depending on temperature, overwintering adults remain active for two to six weeks after petal fall.

Although adults may feed on blossoms, apples are not susceptible to damage until petal fall, at which time adults damage fruit by both feeding and ovipositing. Unlike fruit injured by other pests, many apples damaged by plum curculio will remain on the tree until harvest. Because adults are not highly mobile, orchards near overwintering sites, woodlands, and hedgerows are most susceptible to attack. Fruit damage is usually most common in border rows next to sites where adults overwinter.

Decision Making

Monitoring for the plum curculio is not often recommended because of the amount of time and labor involved and because it is generally assumed to be present in every orchard where populations are endemic. Nonetheless, various techniques have been used to monitor plum curculio damage and the presence of adults:

- Clubs or shakers can be used to jar adults from limbs into catching frames or cloths for counting.
- Polyethylene funnels hung under branches can be used to capture adult PC.
- Immature "scout apples" hung in trees near the edges of orchards serve to measure oviposition scars before petal fall so potential damage can be estimated before control sprays are applied.
- Oviposition scars on immature fruit can be counted in orchards starting at petal fall to estimate damage. Because substantial oviposition and damage can occur even after a single warm day and night, frequent scouting for damaged fruit is necessary after petal fall.

Control

Several species of wasps parasitize the eggs and larvae of the plum curculio. Ants, lacewings, and ground beetles prey on larvae in the soil, and some fungi kill larvae. These organisms are not usually sufficient to regulate populations of plum curculio in commercial orchards.

The plum curculio is difficult to control completely with insecticides. Relatively high rates and persistent applications are important because adults may be active for two to six weeks after petal fall depending on temperatures. Several commercial products are available to control this insect. In normal orchards that are not near woodlots or hedgerows and have not suffered previous damage, a single application at petal fall will provide seasonal control. In problem orchards, a petal fall application followed by a second spray 10–14 days later will provide adequate control. In orchards with chronic problems, or in seasons when adult activity is prolonged by unusually cool and wet weather, two cover sprays applied 10–14 days apart after petal fall may be necessary to prevent late damage. Research on heat unit accumulation and plum curculio oviposition has proposed that control sprays are no longer necessary whenever the last spray has been applied within 10–14 days after the accumulation of 340 DD (base 50°F) from petal fall.

Codling Moth, *Cydia pomonella* (Linnaeus)

Biology and Impact

The codling moth overwinters as a larva in a cocoon under loose bark on the tree trunk. Adults emerge during bloom, and the first flight continues until about 30 days past petal fall. Eggs, laid singly on the upper surface of leaves or fruit, start to hatch at petal fall and continue for two to three weeks. Larvae feed only on fruit. Surface bites, referred to as stings, cause blemishes, and deeper injuries are caused by feeding inside the fruit. Fruits injured by extensive internal feeding usually drop in the middle of June at which time early season damage becomes noticeable.

Adults from the second or summer generation of codling moth start to fly about mid-July, and the peak flight occurs around the first week in August. Larvae from this generation are active in fruit throughout August. Fruit damage by second generation larvae is generally more serious than that of the first.

Decision Making

Adult males can be captured in pheromone traps, but numbers of males captured in these traps cannot be related to potential fruit damage. Thus, pheromone traps are used only to monitor the seasonal activity patterns of adults within an area. It is not practical to monitor commercial apple orchards for CM eggs or larval fruit entries because of the theoretical zero tolerance for internal fruit damage. Developmental models, based on temperature accumulations after the first catch of males, can be used to predict the first egg hatch of codling moths. This approach is used to time initial control sprays for the codling moth at 250–360 DD (base 50°F) after first adult catch for the first generation, and 1260–1370 DD after this same biofix date for the second generation.

Control

The codling moth is attacked by both parasites and predators, but these natural enemies cannot effectively control this pest in commercial orchards. To kill the larvae before they enter the fruit, chemical sprays for the codling moth must be initiated before the eggs hatch. The codling moth is most effectively controlled by the same conventional insecticides used against the plum curculio, but it can also be controlled by more selective pesticides such as bacteria (*Bacillus thuringiensis*), insect growth regulators, viruses, and botanicals, although many of these products are less effective than standard insecticides.

Apple Maggot, *Rhagoletis pomonella* (Walsh)

Biology and Impact

The apple maggot overwinters as a pupa in the soil. Adults from the single annual generation of flies emerge in late June to early July. Females cannot lay eggs until they become reproductively mature, 7–10 days after emergence. Females lay eggs in fruit and the larvae develop there, emerging in the autumn after the fruit has fallen and entering the soil to pupate. Flies are active from July to mid-September, but commercial orchards require protection only from about mid-July through August. Flies do not reach orchards in large numbers until mid-July, and before this date, fruit remaining on the tree is unfavorable for larval development so early infestations do not cause sustainable populations in the orchard. In addition, for unknown reasons, fly activity between late August and mid-September generally does not result in serious damage in most commercial orchards.

Larval tunneling inside fruit causes it to become rotten and unmarketable. Early stings caused by punctures from female ovipositors may severely deform the fruit of some varieties, even though no larvae survive.

Decision Making

Monitoring to determine whether control sprays are necessary is recommended only in orchards that are not near large sources of outside infestation, such as abandoned orchards or those with no indigenous infestations of flies. In early to mid-July, red sphere traps baited with apple volatile lures are hung in trees along the edge of the block closest to an abandoned orchard or a stand of woods. These traps are checked one to two times per week. A spray of a suitable insecticide is applied if a cumulative average of 3–5 apple maggot flies per trap is captured. After spraying, trap catches are not checked again until after a 10 to 14-day period, during which spray residues would kill any immigrating flies.

Theoretically, there is absolutely no tolerance for apple maggot damage in fruit. In practice, apple maggot damage is not usually detected in normal fruit inspections unless there is approximately 3% fruit damage.

Control

Small wasps parasitize apple maggot larvae in fruit, and predators such as birds and crickets may eat larvae or pupae in or near the soil. In natural, unsprayed apple and hawthorn trees, apple maggot populations are not regulated by natural enemies. Parasites and predators are also ineffective at controlling apple maggot in commercial orchards.

Apple maggot flies have a limited migratory capability, so all apple and hawthorn trees within 1/4 to 1/2 mile of commercial orchards should be removed if possible. Dropped fruit should not be allowed to remain beneath the tree for more than one or two days. Eliminating fruit drops will break the life cycle of flies in an orchard by preventing larvae from exiting the fruit and entering the soil.

Apple maggot flies can be trapped in small, well-pruned trees that are not near large sources of outside infestations. A relatively high density of sticky red spheres (plain or volatile-baited) is required, approximately 1 trap per 100 apples. Mass trapping is usually less effective than chemical control, and apple maggot may still damage 1–5% of fruit from mass-trapped orchards.

Most commercial orchards have no indigenous populations of flies. Therefore, chemical control sprays are usually directed against flies immigrating into orchards from outside, unsprayed hosts, including both apples and hawthorns. Most broad-spectrum insecticides are remarkably effective in controlling adults. Insecticides must kill females before they oviposit in the fruit. Residual effectiveness of insecticides is particularly important in controlling apple maggot in commercial orchards when flies are continuously immigrating.

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Apple Proliferation

This is an important insect-transmitted mollicute (bacterial) disease of apples in Europe.

► Transmission of Plant Diseases by Insects

Apple Rust Mite, *Aculus Schlechtendali* (Acarnia: Eriophyidae)

This is an important apple pest in some areas.

► Four-Legged Mites
► Mites
► Apple Pests and their Management

Apposition Eye

A type of compound eye found in diurnal insects in which the ommatidium is shielded by pigment. This type of eye is also called a phototopic eye.

Appressorium

The swollen tip of a fungal hypha that facilitates attachment to the host, and penetration by the fungus.

Apterae

Wingless forms, usually used in reference to wingless parthenogenetic female aphids.

► Aphids

Apteropanorpidae

A family of insects in the order Mecoptera.

► Scorpionflies

Apterous

A term used to denote that the insect is lacking wings.

Apterygote

Insect taxa that do not possess and never possessed (in evolutionary time) wings. A member of the class Insecta, subclass Apterygota.

Apystomyiidae

A family of flies (order Diptera).

► Flies

Aquatic Entomology and Flyfishing

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The use of aquatic insects as lures for fish dates back to the second century A.D. In the seventeen volume treatise, *De Animalum Natura*, the Roman Aelianus discussed his observations of fish consuming insects at the water surface and how Macedonian fishermen used dry flies or spinners to catch what were thought to be trout from the Astraeus River. Not until fifteen centuries later did Charles Cotton propose the utility of aquatic insects in fishing. In 1836, Alfred Ronald's *Fly Fisher's Entomology* was published. This publication elaborated on fly tying methods and fishing techniques from an entomological perspective. Most recently, fly anglers are attempting to increase their knowledge about insects, specifically aquatic insects, in terms of imitating fish food items or "matching the hatch." This quest for entomological knowledge by anglers, in addition to aquatic scientists and fish managers, has prompted the need for better taxonomic and ecological treatments friendly to both the scientist and the angler. In order to create a functional artificial imitation of an insect to improve one's chances of catching a trophy fish, the angler requires basic identification, ecological and behavioral information of both insects (prey) and fish (quarry).

Terminology: Entomology Versus Flyfishing

As with many fields of scientific study, understanding the complexities of both entomology and fly fishing requires an understanding of both languages. While the term "fly fishing" technically refers to only one insect order, Diptera, in reality it encompasses all insect and non-insect invertebrates used as food by fish. Representatives from several orders of terrestrial insects (e.g., Hymenoptera, Orthoptera, Diptera, and Lepidoptera) are common food items of fish and are mimicked with artificial flies. However, aquatic insects are the primary interest of anglers and are the majority of fly patterns mimicked. For example, there are thirteen orders of insects that are classified as aquatic. Only 3% of all insects have a life stage in an aqueous environment. Some of these orders are entirely aquatic whereas others have a few semi-aquatic representatives. Truly aquatic orders are those in which all of their members exhibit some portion of their life cycle in an aquatic habitat. The orders, Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies) are examples of truly aquatic orders. Semi-aquatic orders are largely terrestrial with a number of families exhibiting life stages in or near water. Coleoptera (beetles), Diptera (flies), and Lepidoptera (butterflies) represent semi-aquatic orders.

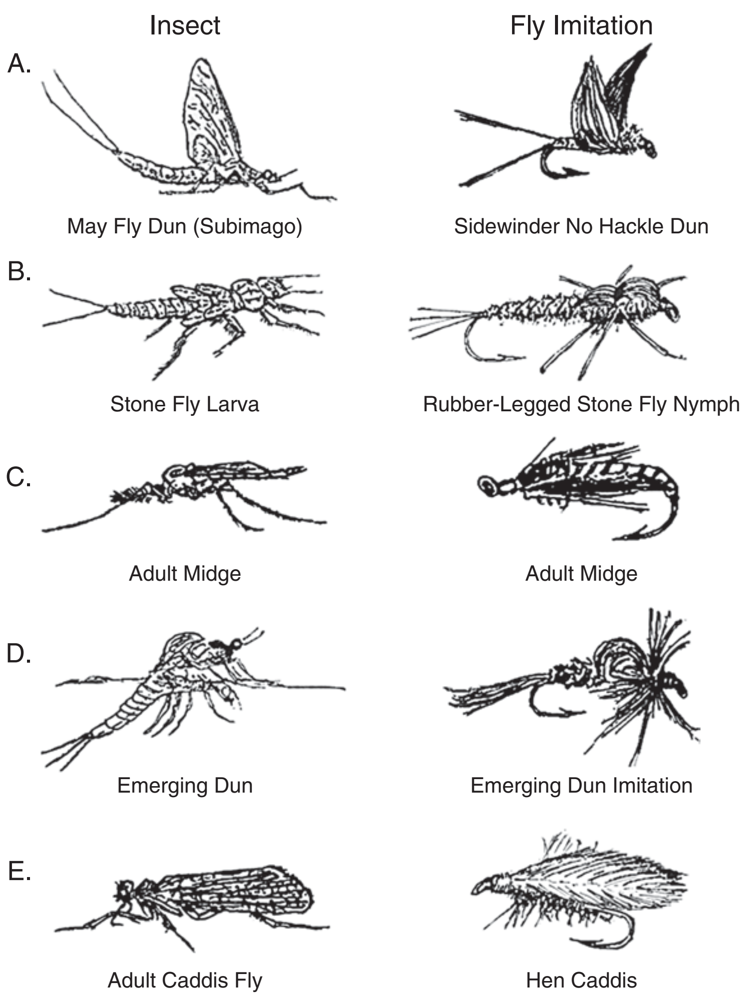
Typically, anglers refer to an emergence of insects (but more specifically to those with aquatic larval stages) as a "hatch." What the angler will call a nymph, the entomologist would refer to as the larval stage of an insect. Mayflies are the only group of insects that have a non-reproductive adult stage (the subimago); anglers refer to this stage as "duns." Post-ovipositing mayflies typically die with their wings spread on the water surface, and anglers term these "spinners," referring to the spinning action they exhibit while floating on the water surface. In addition, anglers refer to reproductively mature insects that end their life cycle on the water surface either by nature or that accidentally hop, fly or are blown onto the water surface as "dry flies." Fly patterns will mimic the larval and adult stages of both terrestrial and aquatic insects.

The sports angler often refers to insects by a number of colloquialisms. Educated fishermen often use the term caddis or caddisfly in reference to the order Trichoptera, fishflies for Megaloptera, and sandflies for some Diptera. Mayflies are known by a variety of names such as drakes or upwings.

Morphological Importance

Although the standard "mantra" of the dedicated fly angler is that the three most important aspects to catch fish are presentation, size and pattern, anglers must be familiar with many aspects of insect morphology. Most often, hand-tied flies incorporate the obvious features of the insect they are imitating. For many mayfly presentations, large characteristics such as wing size, caudal filaments, and body color are considered when tying flies. Small traits such as specific setation, paraglossae, and tarsal segments are often ignored largely due to their size relative to the insect and the investment of time that would be spent including these features in a fly. A fish will not recognize these small features because, at times, they may see the lure for only a few seconds.

Flies fit into two general classes based on their presentation. Dry flies are presented on the surface and signify the adult stage. Wet flies are fished below the surface and represent larvae. Success of the presentation is largely dependent on the time of the year. Presentation should mimic the natural life cycle of the native insects. A sample taken with a kick seine or observation of emergences will indicate what type of fly to use. An emergence of mayflies in the summer is the reason why an adult mayfly mimic presented on the surface may outfish a wetfly of a caddisfly. Several aquatic insect orders are often used as models for fly tying and as live bait. There are many fly imitations of caddisflies, mayflies and stonefly larvae (Fig. 71), as well as aquatic Diptera larvae and adults, due to their ecological importance of providing food for fish.



Aquatic Entomology and Flyfishing, Figure 71 A collection of common aquatic insects used as mimics for wet and dry artificial fly patterns. (A, C, D, and E = represent dry flies; B represents a wet fly or nymph). Illustrations by Mike Gouse (published in Swisher D, Richards C (1991) Emergers. Lyons & Burford Publishers, New York, NY).

Ecological and Behavioral Importance

Though fly fishing strategists argue over imitation vs. presentation, fly fishing tactics that employ ecological and behavioral aspects are as important as using a fly pattern based on the appearance of natural insects. Although insect abundance is important, fish will not eat the most abundant insect if it is not available to them. Three ecological aspects important in the availability of a particular insect include: stage of development, habitat use and activity (either associated with drift or foraging for food).

Although aquatic insect larvae are most abundant after hatching, they are not as available as fish food due to their small size and ability to avoid predators. In terms of energetics, a small insect is equivalent to small energetic payoffs. However, as aquatic insects grow and develop from one stage to the next they become more obvious to fish predators through their feeding activities. Thus, availability increases as insects grow and develop. Emergence for aquatic insects is a risky task. It is these emergers that are most available as they struggle to reach the water surface, plant stem or emergent rock from which they attempt to emerge as adults. Fish will concentrate feeding efforts on emerging insects if the adult stage escapes quickly. Those adult insects, both terrestrial and aquatic, that expire on the water surface are readily fed upon by fish.

Aquatic insects inhabit a wide variety of microhabitats within a given stream or pond, including rock or log surfaces, on plant stems or other submerged vegetation, as well as swimming openly in the water column. Habitat use by aquatic insects is relative to their needs. For example, foraging for food may put an insect in a different microhabitat other than used during non-feeding periods. Some mayflies may exhibit this behavior switch. Diel feeding activities among Phantom midges (Chaoboridae) also is an example of this type of behavior. Finally, phenological aspects of aquatic insect activity related to emergence, drift and oviposition increase insect availability. Some of these ecological/behavioral phenomena are tied to weather changes, lunar activity, water temperature and current regime.

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Aquifer

An underground formation of sand gravel or porous rock that contains water. Aquifers are an important source of water is some areas, and must be protected from pesticide contamination, affecting the type of pesticides and pesticide application technologies that are used.

Aradidae

A family of bugs (order Hemiptera). They sometimes are called flat bugs.

► Bugs

Arbovirus

Viruses transmitted by arthropods. This is an acronym for ARthropod-BOrne VIRUSes.

Archaic Bell Moths (Lepidoptera: Neopseustidae)

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Archaic bell moths, family Neopseustidae, include nine known species (six from Southeast Asia and three from Chile). The family forms a monobasic superfamily, Neopseustoidea, and the only member of the infraorder Neopseustina, of the suborder Glossata and subcohort Myoglossata. Adults small (14–27 mm wingspan), with head roughened; haustellum short, with vestigial mandibles; labial palpi 3-segmented and somewhat upcurved; maxillary palpi 5-segmented; antennae are mostly rather long and somewhat thickened. Maculation is pale, usually translucent with gray spots, and wing shapes rather broad and quadrate. When resting the wings are held in a rounded shape that resembles a bell. Adults are crepuscular or diurnal. Biologies and larvae remain unknown, but species in Chile are thought to possibly feed on native bamboos.

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Archaic Sun Moths (Lepidoptera: Acanthopteroctetidae)

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Archaic sun moths, family Acanthopteroctetidae, are very similar to Eriocraniidae, and include only four species, all North American except for one in the Palearctic (originally described in a separate family Catapterigidae). The family, plus the related Eriocraniiidae, are the only members of the superfamily Eriocranioidea, which form the infraorder Dacnonypha of the suborder Glossata. There are two subfamilies: Acanthopteroctetinae and Catapteriginae. Adults small (11–16 mm wingspan, with roughened head scaling and only short 2-segmented labial palpi; maxillary palpi are 5-segmented and folded; haustellum is reduced and vestigial mandibles are present. Maculation is more somber than in Eriocraniidae and adults are thought to all be diurnal. Larvae are blotch leafminers on *Ceanothus* (Rhamnaceae) in the single known biology.

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Archeognatha

An apterygote order of insects, also called Microcoryphia. They commonly are known as bristletails.

► Bristletails

Archipsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Arctics

Some members of the family Nymphalidae, subfamily Satyrinae (order Lepidoptera).

► Butterflies and Moths

Arctiidae

A family of moths (order Lepidoptera). They commonly are known as tiger moths, footman moths, or wasp moths.

► Tiger Moths
► Butterflies and Moths

Arculus

A small cross vein of the wing. The position of the cross vein (Fig. 72) varies among orders, but is associated with the cubitus vein.

► Wings of Insects

Area-Wide Insect Pest Management

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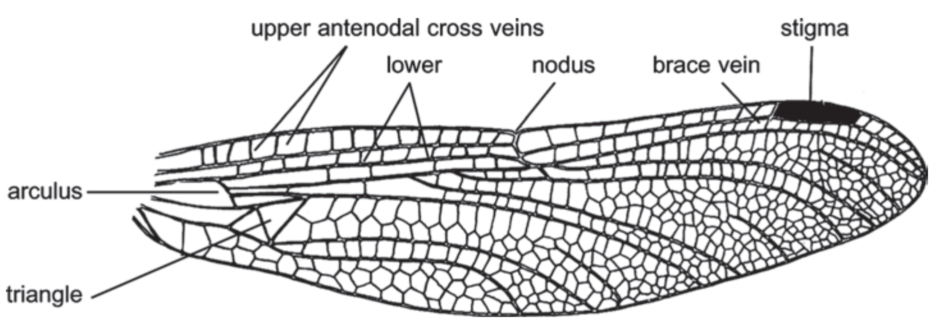
Area-wide pest management is one of several major plans or strategies for coping with pest problems. Management of localized populations is the conventional or most widely used strategy, wherein individual producers, other operators and households practice independent pest control. However, since individual producers or households are not capable of adequately meeting the challenge of certain very mobile and dangerous pests, the area-wide pest management strategy was developed.

The area-wide pest management strategy includes several substrategies including (i) management of the total pest population in all of an ecosystem, (ii) management of the total pest population in a significant part of an ecosystem, (iii) prevention, which includes containment of an invading population and quarantine, and (iv) eradication of an entire pest population from an area surrounded by naturally occurring or man-made barriers sufficiently effective to prevent reinvasion of the area except through the intervention of man.

Characteristics of Area-Wide Pest Management

Immigration of pests into a managed ecosystem prevents their eradication. However, it is easy to underestimate the tremendous impact of the immigration of pests from small untreated foci into a managed area. For example, very few codling moths, *Cydia pomonella* (L.) develop in the well managed commercial apple orchards, but researchers found that the number of codling moths that overwintered in the in Wenas Valley of Washington State dropped by 96% when a few abandoned orchards and neglected noncommercial apple trees were either removed or sprayed with insecticide. This study indicated that most of the codling moths in commercial orchards originated on untreated host trees that in aggregate were <5% of the host resources of the codling moth. Similarly, experience in coping with the pink bollworm, *Pectinophora gossypiella* Saunders,

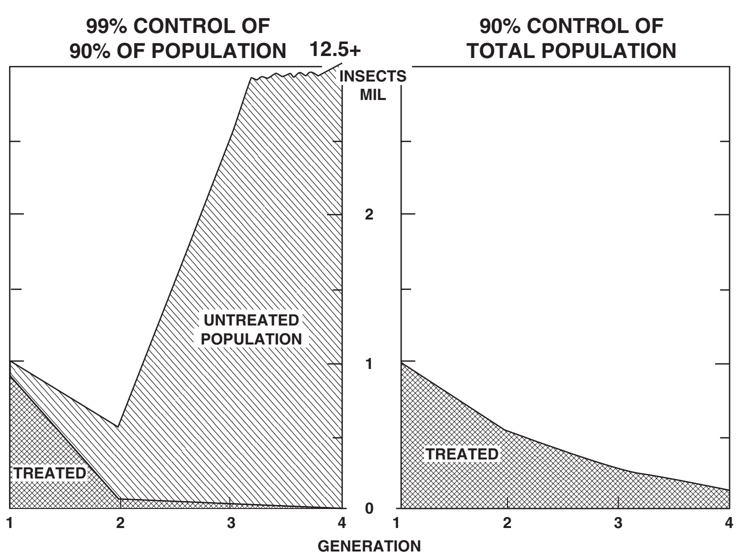


Arculus, Figure 72 **Front wing of a dragonfly (Odonata).**

and cotton boll weevil, *Anthonomus grandis* Boheman, have shown that a few growers who do not destroy crop residues immediately after harvest provide the food required by these pests to reproduce and to enter diapause. This lapse in field sanitation can directly cause the occurrence of devastating levels of these pests in the following season on neighboring farms.

The implications of allowing a small fraction of a population of a major pest species to reproduce without control can be seen graphically (Fig. 73). E. F. Knipling calculated that over a period of a few generations more pest individuals would be produced if 1% of the total population were allowed to reproduce without control, while 100% control was applied to 99% of the population, than if only 90% control was imposed uniformly on the total population. Thus, Knipling elaborated the basic principle of total population suppression: "Uniform suppressive pressure applied against the total population of the pest over a period of generations will achieve greater suppression than a higher level of control on most, but not all, of the population, each generation." Therefore, it is very important to eliminate any places of refuge or foci of infestation from which recruits could come to re-establish damaging densities of the pest population in areas of concern.

For the most part, the control of many highly mobile and very destructive pests is carried out by individual producers who rely heavily on the use of insecticides. Although other control technologies are often incorporated into the producer's integrated pest management (IPM) system, these technologies, too, are usually applied by producers independently of other producers. Such an uncoordinated farm-by-farm IPM strategy provides opportunities for the pest population to build up and to establish damaging infestations in well-managed fields. Consequently, on most farms insect pest populations increase to damaging levels each year, and the farmer is forced to apply



Area-Wide Insect Pest Management, Figure 73 **Results of a model that show that outcome of neglecting to suppress a small fraction of a pest population in an agroecosystem versus the effects of uniformly suppressing the entire pest population. On the left, 10% of the population is untreated and it produces a large number of individuals in four generations, while the 90% of the population that is treated declines. On the right, the entire pest population in the agroecosystem is suppressed uniformly and its numbers decline from generation to generation. (After Knipling, 1972. Reproduced with permission of the Australian Journal of Entomology.)**

broad-spectrum fast-acting insecticides as a rescue treatment (Table 10). This defeats the primary goal of the IPM system, which is to take maximum advantage of naturally occurring biological control agents.

Moreover, application of insecticides when an insect pest population reaches the economic threshold does not prevent the losses that occur before the threshold has been reached. For commodities that are planted on vast areas, such losses in aggregate are immense. For example, the world production of corn (maize) is roughly 600 million metric tons. Avoidance of a loss of 3% would make available 18 million metric tons, which could be a major factor in alleviating hunger. Some examples of crop losses caused by insects.

Area-wide pest management differs from the conventional pest management of local pest populations in several important ways. The area-wide strategy focuses on managing the insect populations in all of the niches in which they occur, while the conventional strategy focuses narrowly on protecting the crop, livestock, people, buildings, etc., from direct attack by pests. The area-wide strategy requires detailed multiyear planning and an organization dedicated exclusively to implementing the strategy. The conventional strategy involves less planning, tends to be reactive, and is implemented independently by individual operators or households. The area-wide strategy tends to utilize advanced technologies, whereas the conventional strategy tends to rely on traditional tactics and tools that can be reliably implemented by non-specialists.

The use of separate organizations to conduct area-wide programs provides opportunities to utilize sophisticated technologies and professional management. Computer-based models are utilized in planning and management. Satellite imagery is used in area-wide programs to identify localities of alternate hosts that can be treated to reduce pest populations that produce migrants that cause the damage in commercial production areas. Area-wide programs acquire or develop highly sensitive detection systems, and employ geographic information systems software to help manage data. They may implement approaches to prevent or retard the development of insecticide resistance or loss of host plant resistance. Computer programs and real-time environmental data to predict insect populations can be effectively used in an area-wide program but usually not on an individual farm basis. Thus, pest immigration patterns, analysis

Area-Wide Insect Pest Management, Table 10 Percent crop losses in the USA caused by various insect pests without and with control measures

		Percent loss	
Commodity	**Pest**	**Without control**	**With control**
Bean	*Helicoverpa zea*	37.0	6.0
Bean (snap)	*Epilachna varivestis*	20.0	9.9
Beet (sugar)	*Tetanops myopaeformis*	22.7	8.2
Corn (field)	*Diabrotica* spp.	15.7	5.0
Corn (field)	*Ostrinia nubilalis*	–	2.0
Corn (field)	*Helicoverpa zea*	–	2.5
Cotton	*Helicoverpa zea*	–	4.0
Cotton	*Pectinophora gossypiella*	35.5	10.0
Peanut	*Helicoverpa zea*	–	3.0
Soybean	*Pseudoplusia includens*	15.7	4.8
Sugar cane	*Diatraea saccharalis*	28.6	8.0

of weather to predict increase or decreases of populations, genetic analysis to determine resistance levels, etc., are utilized in area-wide programs.

Finally, area-wide programs are able to take advantage of the power and selectivity of specialized methods of insect control that for the most part are not effective when used on a farm-by-farm basis. These include the sterile insect technique (SIT), certain programs of inundative releases of parasites, semiochemicals, mating inhibitors, large scale trap cropping, treatment of hosts on public lands and in private gardens, etc.

Benefits of Area-Wide Pest Management

Experience has shown that pest suppression on an area-wide basis can be more effective than on a farm-by-farm basis for reducing losses caused by highly mobile pests and for capturing the benefits of highly mobile natural enemies. Area-wide programs enable many producers to pool resources in order to utilize technologies and expertise that are too expensive for individual producers. These may include mass rearing facilities, aircraft, information technologies and highly trained specialists. In addition, a coordinated area-wide program can achieve the avoidance or internalization of external costs. External costs (externalities) are the harmful effects arising from pest control operations that affect parties other than the pest control ker, but for which no compensation is paid to the persons harmed. For example, spray drift onto neighboring properties frequently provokes disputes. Also, pesticide use to protect agricultural crops has caused insecticide resistance to develop in insect vectors of disease.

Finally, economies of scale can be captured in area-wide programs, although complex trade-offs may be involved. The more mobile the pest and the more uniform the damage caused by the pest, the larger can be the area under coordinated management. The total costs of pest detection and monitoring and suppression per hectare of crop usually decline as the size of the managed area increases. However, the per hectare organizational costs usually increase as the project size increases because of the increased need for meetings and other communication costs. For these reasons, in very large programs such as the effort to eradicate the cotton boll weevil from the USA, the vast area was subdivided into a number of zones. Also, considerable organizational cost savings may be realized in instances where towns, municipalities or cooperatives already have structures in place for communication, decision-making, collection of fees, etc.

Contingencies Often Dictate Changes in Strategy

Contingencies often arise that require replacement of one strategy with another. For example, at various times during the 43-year campaign to remove the screwworm from the United States, Mexico and Central America, different pest management strategies had to be selected. This program began when an unusual series of frosts beginning early in December 1957 killed all screwworms in the southeastern USA north of a line in southern Florida from Tampa to Vero Beach. Sexually sterile flies from a culture in a research laboratory were released in a broad band north of this line to contain the pest population while a high capacity rearing facility was being readied. This containment strategy was replaced by the strategy of eradication in the summer of 1958 when the mass rearing facility was able to produce 50 million sterile flies per week, and eradication was accomplished in 1959.

A similar change of strategies was employed in eradicating the screwworm from west of the Mississippi River. Beginning in 1962, the parasite population was strongly suppressed north of the U.S. border with Mexico, and the influx of flies from Mexico was retarded by the release of sexually sterile flies in a 130 km-wide zone along the entire USA-Mexico border. (For political reasons in 1966, the U.S. Secretary of Agriculture declared the screwworm to be eradicated from the United States, even though it was obvious to entomologists that unless the parasite was removed from northern Mexico, it would continuously reinvade the United States.) However, the eradication strategy could be implemented soon after the governments of the USA and Mexico reached an agreement in 1972 to eradicate the parasite as far south as the Isthmus of Tehuantepec. Operations against the screwworm in Mexico began in 1974, and the last screwworm case occurred in the United States in 1982.

In the next phase, these containment and eradication strategies were employed to eradicate the parasite from all of Central America to Panama, where a sterile fly barrier was established in 2001.

Legal Authority for Area-Wide Pest Management

The legal authority needed for area-wide and other regulatory programs is still evolving. In about 1860, the grape phylloxera, *Phylloxera vitifoliae* (Fitch), was transported from the United States to France. Within 25 years of its arrival, this insect had destroyed 1 million hectares of vineyards or fully one-third of the capacity of France to produce grapes. In order to protect the German wine industry, the government of Germany in 1873 passed the first law that provided for quarantines and regulatory control of agricultural pests. Other governments quickly followed the example set by Germany. In 1881 representatives of many European countries met and developed a set of regulations governing the movement of grape propagating material.

In about 1880 the San Jose scale, *Aspidiotus perniciosus* Comstock, was established in California. Its rapid spread throughout the country on nursery stock, and the failure of a program to eradicate it, caused Canada, Germany and Austria-Hungary to prohibit the admission of American fruit and living plants beginning in 1898. This crisis led to the passage, by the U.S. Congress, of a series of eleven federal acts beginning in 1905 on quarantine and the regulation of interstate shipments in the USA. In 1999, most of these acts were consolidated into the Agriculture Risk Protection Act of 2000. Indeed, most countries adopted legislation on: (i) prevention of the introduction of new pests from foreign countries, (ii) prevention of spread of established pests within the country or state, (iii) enforcement of the application of control measures to prevent damage by exotic pests, to retard their spread or to eradicate them. In many countries, the law allows people who wish to organize a program against a pest to hold a referendum. If the referendum passes by a certain margin (usually 67%) then all parties at interest must cooperate in the venture.

Currently, in Florida, the program to eradicate citrus canker has been delayed for several years. This pathogen is carried considerable distances on driving rains, and to achieve eradication, the Division of Plant Industry has found it necessary to destroy all citrus trees within a radius of 578 m from an infected tree. Homeowners in urban areas, who do not understand the need for such drastic action, feel that workers who enter residential yards and destroy citrus trees as part of the eradication program violate their rights. Thus, the Broward County Circuit Court has ruled that program employees must have a separate court-issued warrant to enter each privately owned property. The need to apply for tens of thousands of warrants has prompted the Florida Department of Agriculture and Consumer Services to appeal this ruling. The outcomes of this and other judicial proceedings are likely to more clearly define procedures that must be followed in conducting eradication programs, and the levels of reimbursement owed to affected homeowners. Unfortunately, the tensions between urban and rural populations caused by the adversarial nature of this process are likely to persist for many years.

Apathy, Outrage and Area-Wide Pest Management

Some of the programs conducted on an area-wide basis, especially those aimed at eradication, have aroused opposition. The strategy of eradication emerged just over one century ago as the brainchild of Charles Henry Fernald of the University of Massachusetts. Under Fernald's leadership, Massachusetts attempted to eradicate an introduced pest, the gypsy moth, *Lymantria dispar* L., in an 11-year campaign from 1890 to 1901. Initially, the primary eradicant was Paris green spray. The use of Paris green, which suffered from modest efficacy and phytotoxicity, had to be abandoned because of adverse public reaction including threats of violence and mass protests.

Those stakeholders who are not primarily concerned with the economic dimension of the pest problem tend to be highly concerned with ecological, environmental, social and human health implications of area-wide programs. Therefore, leaders of area-wide pest management programs need to be highly sensitive to the perceptions and attitudes of the public toward certain program operations. Often, eradication efforts must be conducted by the ground rules of the urban rather than the rural setting. In programs to eradicate the Mediterranean fruit fly in California and Florida, members of the public strongly protested the aerial pesticide applications even if the same insecticide was used without dissent for mosquito abatement. On the other hand, the same public generally has applauded the release of Mediterranean fruit fly sterile males.

Normally the public is apathetic towards technological programs. However, certain factors inherent in programs and in the manner in which they are managed can precipitate an almost irreversible shift of the public's attitude from apathy to outrage. A sense of outrage can be evoked by involuntary exposure to pesticide residues, imposed levies or fees, quarantines, right of trespass, unfair and inequitable sharing of risks, costs and benefits, temporary loss of control of one's property or field operations, the perception that endangered species may be harmed, etc.

Acceptance of risk by the public is more dependent on the public's confidence in the risk manager than on the quantitative estimates of risk consequences, probabilities and magnitudes. The public' confidence in the managers of an area-wide program is of paramount importance.

In each area-wide program, a special effort must be made to anticipate and identify those factors that may be emotionally upsetting to various people and to take preemptive actions to avoid or mitigate adverse reactions. Public officials must be kept apprised, effective two way communication with the public must occur, surrogates of the public must be included in oversight and decision-making processes, and referenda may have to be conducted to secure support and funding for the program.

Invasive Pests, Global Trade and Area-Wide Pest Management

The rapid globalization of trade in agricultural products, and increasing tourism, have dramatically increased the spread of invasive harmful organisms. We have entered an era of an unprecedented level of travel by exotic invasive organisms. The greatest harm being done by non-indigenous invasive organisms is occurring on islands, and major pests are becoming established with increasing frequencies on all continents except, perhaps, Antarctica. For about one century many countries have relied on inspection of arriving cargo and passengers at the port of entry as a primary exclusionary strategy. However, volumes of arriving cargo are doubling every 5–6 years, and it is not possible to increase similarly the human and other resources devoted to inspection at ports of entry. Clearly exclusion at the port of entry is no longer sufficient to protect against exotic pests, even though a number of emerging technologies are likely to facilitate safeguarding activities. Thus, in order to stem the influx of exotic pests, it is important to shift primary reliance from exclusion at the port of entry to off-shore actions, namely on pest risk mitigation in the areas of production and elsewhere, certification at the point of origin, and preclearance at the port of export.

An important approach to offshore mitigation is the creation of pest-free areas. Indeed, countries that export raw agricultural commodities can effectively remove the threat of exotic pests to the importing country by creating and maintaining pest-free areas. A pest-free area is one that lacks a quarantine-significant pest species, and is separated from infested areas by natural or artificial barriers. There are two types of pest-free areas: (i) pest-free zones are large geographic areas, such as the entire country of Chile, that is certified free of tropical fruit flies of economic importance, and (ii) pest-free production fields, that require the demonstrated suppression of quarantine pests to non-detectable levels. Area-wide pest management is an important tool for promoting safe trade and contributing as much as possible to the complementary goals of food security and economic security for all countries.

Requirements to establish pest-free fields of crop production include a sensitive detection program, suppression of the quarantine-significant pest to non-detectable levels, strict control of the fields, and safeguards to prevent infestation during packing and transit to the port of export. For example, Florida is able to export grapefruit to Japan by creating pest-free grapefruit groves in about 22 counties. Regulatory experts from Japan inspect the entire process of production, packing and transit. Similarly fruit groves free of the South American cucurbit fruit fly, *Anastrepha grandis* (Macquart), have been created in Mossoro, Brazil and Guayaquil, Ecuador.

The concept of pest-free fields based on bait sprays and the sterile insect technique was pioneered during the early 1960s against the Mexican fruit fly along the Mexico-USA border Mexico. Also in the early 1960s, the Citrus Marketing Board in Israel developed a concerted area-wide program against the Mediterranean fruit fly that has been able to meet the certified quarantine security requirements of fruit importing countries. Chile used the sterile insect technique to rid the entire country of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). By 1980 the entire country of Chile had become a medfly-free zone, and since then Chilean fruits in huge volumes have entered the U.S. market without the need for any quarantine treatments. This has dramatically strengthened the economy of Chile. Now Argentina, Peru and other countries have sterile insect technique programs that they hope will enable them to become fly-free zones with free access to markets in southern Europe, Japan and the United States. Also Mexico has used the sterile insect technique to get rid of the Mediterranean fruit fly. Indeed Mexico is ridding large sections of its territory of all fruit fly species of economic importance. The Mexican states of Baja California, Chihuahua and Sonora have been freed of all economically important species of fruit flies, so that citrus, stone fruits, apples and vegetables are being exported from these states without any postharvest treatment.

A more recent, highly significant development has been the continuous area-wide release of sexually sterile male medflies over the Los Angeles Basin and around high-risk ports in southern Florida. This further reduces the risk of pest establishment in these port areas.

Selected Episodes in the History of Area-Wide Pest Management

Migratory Locusts

Migratory locusts probably were one of the plagues that caused prehistoric man to attempt forms of group or area-wide control. Because migratory locust swarms can be seen approaching from a distance and descending onto crops, it seems likely that people banded together and used whatever means at hand to stamp out as many as possible. No doubt invasions of armyworms, leafcutter ants and other insects caused people to cooperate in combating them. In China, since 707 B.C., more than 800 outbreaks of *Locusta migratoria manilensis* L. have been recorded along the floodplains of the Hwang, Huai and Chang Jiang rivers. In 1929, an outbreak devastated 4.5 million hectares of cropland. Consequently, about 120 million people were mobilized to modify the floodplains by damming, terracing and reforestation. Over almost 30 centuries, the Chinese slowly developed an area-wide pest management program that now folds together knowledge of biology, ecology, forecasting cultural practices, and water management.

During the late 1920s, catastrophic locust plagues were widespread in Africa and southwest Asia. Boris Uvarov and Zena Waloff of the British Ministry of Overseas Development responded by establishing the International Unit of Locust Research. This Unit became the Antilocust Research Centre and it provided the focal point for international cooperation in coping with plagues of the desert locust, the red locust and the African migratory locust. The Centre created databases and provided a sustained regular flow of information on the status of locust populations throughout their ranges. The Centre developed a system of monthly forecasting. Uvarov was able to interest the FAO in creating the International Desert Locust Information Service to coordinate forecasting and the planning of campaigns. Leadership in these vitally important functions has been assigned to the FAO's Locust Group.

In recent decades locust experts have attempted to shift the prevailing strategy from reactive to proactive, and eventually to outbreak prevention. The reactive strategy initiates interventions after plague status has been reached in order to contain the magnitude of the damage. The proactive strategy seeks to prevent the occurrence of plague status by intervening against localized outbreaks. Proaction requires early detection of bands and swarms, preferably still in breeding areas, and prepositioning of locust campaign supplies. The outbreak prevention strategy seeks to intervene before the phase shift from solitary to gregarious. Possibly the outbreak prevention strategy would rely substantially on inducing epizootics by inoculating breeding populations with selective pathogens. A difficulty in implementing the proactive strategy and moving toward the outbreak prevention strategy is that donor support tends to wane in the absence of full-blown plagues.

Insect Vectors of Human Diseases

Doubtless the scientific pioneers of area-wide approaches were influenced strongly by concepts from the field of public health and hygiene. About 2,500 years ago the Greek spirit and the Roman capacity for organization had produced a highly developed system of hygiene in what is now southern Europe. The Romans procured safe supplies of water by means of aqueducts, practiced daily bathing and removed garbage from cities. The rationale for these measures was explained by Varro (116–27 B.C.), who served Pompey and Julius Caesar. Varro asserted that minute living creatures cause malaria. He wrote: "In damp places there grow tiny creatures, too small for us to see, which make their way into our bodies…and give rise to grave illness." However, with the collapse of the Roman Empire and the storms of folk-migrations, classical hygiene eroded. Nevertheless, raging outbreaks of malaria, typhoid, typhus and bubonic plague during the latter Middle Ages reawakened concepts of hygiene and public health. Doctors and public authorities joined forces to erect walls against these plagues. Dr. Johann Peter Frank (1745–1821) had considerable success in persuading the rulers of Europe during the late 1700s and early 1800s to establish public hygiene policies and to enforce them vigorously. While only a 21-year old student at the University of Strasbourg, Frank called for "systematic action by the authorities" to intervene in the lives of all citizens in order to forestall or halt epidemics. The discoveries of Pasteur, Koch and others on the nature of diseases were foundation stones for rational policies of public health.

Mosquito-Borne Diseases

Through collective action within communities, even without an overall national plan and central coordination, malaria in southern Europe and North America largely disappeared in consequence of education, the universal adoption of window screens, destruction of habitats of *Anopheles* larvae and the treatment of all cases with quinine.

Investigations conducted in the late 1800s and in early years of the 1900s on the transmission by mosquitoes of deadly diseases led to widespread use of area-wide programs. Yellow fever, dengue, filariasis and malaria were shown to be transmitted by various species of mosquito. In 1892 Howard, and in 1900 Ross, began to recommend that the habitat of mosquito larvae over extensive areas be either treated with kerosene or drained. These practices were first implemented in west Africa to combat malaria, and soon adopted by communities in many countries. Mosquito abatement districts were pioneered by John B. Smith in New Jersey. The New Jersey Mosquito Extermination Association, founded in 1912, provided the model for the organization and operation of area-wide mosquito abatement districts of which there are about 260 in the United States and a thousand or more worldwide.

Yellow fever was wiped out in Havana, Cuba, under the leadership of Dr. W. C. Gorgas, who in 1898 implemented a strict sanitation program to prevent breeding of the disease vector, *Aedes aegypti* L. Subsequently, Gorgas implemented a program in the Panama Canal Zone against *Aedes aegypti* and *Anopheles* spp. vectors of yellow fever and malaria, respectively. This highly effective program was key to the successful construction of the Panama Canal.

Because the *Plasmodium* pathogen requires 12 days to develop in the mosquito vector before it can be transmitted to man, residual sprays can sufficiently reduce the proportion of mosquitoes that survive 12 days, and so interrupt malaria transmission. Therefore, in 1955 the World Health Assembly urged WHO to lead and organize worldwide eradication of malaria. By 1959, almost 65% of the people at risk were protected and this percentage rose to 74 by 1970. Malaria eradication was claimed in 37 countries, and the incidence of malaria had dropped dramatically in many countries. In Sri Lanka, the number of cases dropped from more than 2.8 million per year to just 17 in 1963, but then the effort floundered as WHO was unable to deal with the widespread hue and cry for local control. In 1969, the Global Program disintegrated. Soon DDT was banned in the United States and WHO's resources for malaria were reallocated. Malaria resurged to more than half a million cases per year in Sri Lanka and to more than 100 million cases worldwide.

In 1969 and 1970, the Indian Council for Medical Research and the WHO initiated several projects relevant to area-wide control. Unfortunately, in 1974 these projects became the target of a press campaign by writers who feared that these projects were actually a USA-funded effort to develop methods of biological warfare. Because the government of India was unable to restore confidence, the projects were terminated.

Many authorities maintain that the area-wide use of insecticide impregnated bednets is superior to house spraying for suppressing malaria, that a considerable pool of effective technology relevant to the application of the SIT against mosquito vectors was developed three decades ago, and that area-wide programs against malaria vectors can move ahead as soon as the international community develops the political will to do so.

Onchocerciasis Control Program in West Africa

River blindness is caused by the microflilariae of the *Nematode Onchocerca volvulus*, and is transmitted by the *Simulium damnosum* species complex of black flies. People and blackflies are alternate hosts of this parasite, and it has no other hosts. The female parasite lives in the human skin and gives birth to the microfilariae for most of her lifespan of 12 years. Microfilariae may invade the human eye, and blindness typically sets in between the ages of 30 and 39 years. A number of small-scale larviciding operations against the vectors were mounted beginning in 1950, and beginning in 1960 the European Development Fund financed a major campaign in a 60,000-km² zone at the intersection of Mali, Burkina Faso and Cote d'Ivoire (Fig. 74).

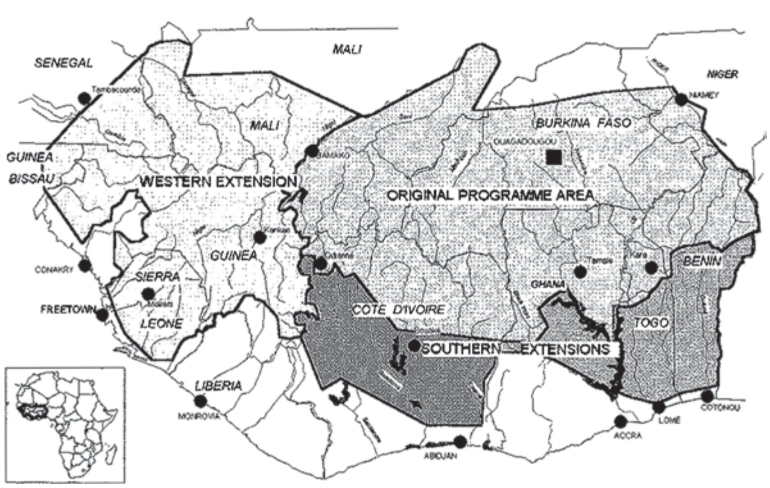
In 1974 the international community approved the Onchocerciasis Control Program and the World Health Organization was designated as Executing Agency. In order to manage the Program, National Onchocerciasis Committees were established in the seven participating countries (Benin, Burkina Faso, Cote d'Ivoire, Mali, Niger and Togo). A Joint Programme Committee has served as the supreme governing body and receives guidance from an Expert Advisory Committee. A Committee of Sponsoring Agencies coordinates the activities of the World Bank, FAO, WHO and UNDP. The Onchocerciasis Fund was created to accept donations, and the World Bank oversees it.

The Programme Director is assisted by seven units: Office of Director, Administrative Management, Epidemiological Evaluation, Vector Control, Applied Research, Biostatistics and Information Systems and Devolution. The latter conducts training and coordinates devolution activities with participating countries.

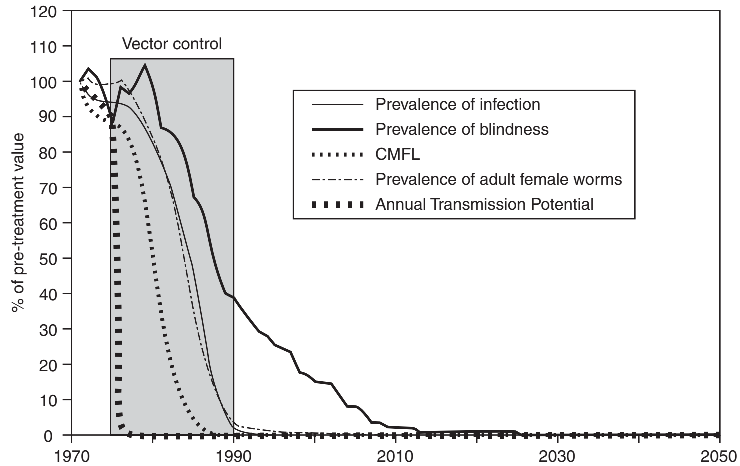
The limits of the program area were extended several times because of invasions of infective black flies over greater distances than initially foreseen. Thus the program area expanded from 654,000 km² in 1974 to 1,066,000 km² by 1990.

Two intervention tactics have been employed area-wide: larviciding largely by helicopter but also manually where streams are overgrown with vegetation, and treatment of humans with the microfilaricide, ivermectin. Because the period of development from egg to pupa rarely exceeds 1 week, larviciding must be carried out on a weekly basis. Seven insecticides are employed on a rotational basis to prevent the development of resistance. In order to achieve the proper concentration of insecticide in the flowing water, an automated hydrological surveillance network was created and real-time data are fed to an on-board computer to enable the pilot to properly manage spray operations.

The results of the program have been dramatic (Fig. 75). As a result of this program, 25 million hectares of land suitable for cultivation have become available, and rapid resettlement is underway. Because vector control operations were phased out in 2002, ivermectin remains as the only means of control.



Area-Wide Insect Pest Management, Figure 74 **The original area of the Onchocerciasis Programme established in 1974 and the subsequent western and southern extensions required to exclude migration of the black fly vectors. (After World Health Organization, 1994.)**



Area-Wide Insect Pest Management, Figure 75 Actual and projected impact of 15 years of suppressing black fly vectors of Onchocerciasis in the West Africa Programme. Reproduced from World Health Organization, 1994. CMFL is the community microfilarial load (geometric mean of microfilarial levels in all people in a given community).

Chagas Disease Vectors

Chagas disease, first recognized in 1909, has been ranked as the most important parasitic disease in the Americas. Although the infection is still largely incurable, transmission can be halted by (i) eliminating the domestic vectors, blood-sucking reduviids of the subfamily Triatominae, and (ii) screening blood donors to avoid risk of transmission through transfusions. Small-scale vector control programs began during the 1940s based on spraying the interior of homes with benzene hexachloride or dieldrin to control the primary vectors, *Triatoma infestans* (King) and *Rhodnius prolixus* (Stahl), as well as several other species of Triatoma. However, these programs suffered from under-funding and interruptions of funding, so that reinfestation occurred.

In 1983 a national program was launched in Brazil to eliminate the primary vector, *Triatoma infestans*, based initially on use of benzene hexachloride and later on pyrethroids. Although not without difficulties, this Brazilian program proved to be highly successful, and it inspired an area-wide program encompassing the Southern Cone countries (Argentina, Bolivia, Brazil, Chile, Paraguay, and Uruguay) plus Peru. This 10-year program was launched in 1991 under the leadership of the Pan American Health Organization with funding, in part, from the European Union. Total program costs were estimated at US $190 million to $350 million. The program's tremendous technical and economic success (internal rate of return of 30–60% largely based on savings in health costs) spurred a similar Central America Initiative (El Salvador, Guatemala, Honduras and Nicaragua) and an Andean Pact Initiative (Colombia and Venezuela).

Each program began with a centrally managed attack phase of about 3 years in which all homes are sprayed by trained professionals, followed by a more community-based phase, which relies substantially on the efforts of homeowners and local authorities. Adventitious transmission may be accomplished by sylvatic vector species, which can enter houses to form domestic colonies. In addition, migrant workers and other travelers can carry vectors. Currently, vector populations in Mexico and the Amazon Basin remain as major challenges. Elsewhere, the focus is shifting to epidemiological surveillance and care of people already infected.

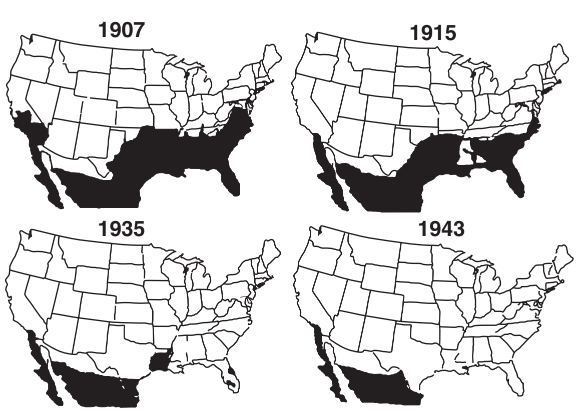
Cattle Ticks

The discovery in 1889 by Theobald Smith and colleagues that cattle fever is caused by a tick-transmitted parasite of red blood cells led to the initiation in 1906 of a county-by-county effort to eliminate the two *Boophilus* tick vectors (Fig. 76) from the United States. Many pastures were rendered tick-free by excluding all host animals until all ticks had starved to death. Livestock were dipped in an arsenical solution at 2-week intervals. Quarantines were used to prevent the movement of infested cattle into areas that had been cleared. By 1943, after 37 years of grueling effort, the ticks had been eliminated entirely from the United States for a total cost of about $40 million dollars, or the equivalent of the annual losses suffered before the program was initiated. Quarantines have been effective in preventing these ticks from becoming re-established from their populations in Mexico. A broadly shared vision sustained this program in spite of war and the great economic depression.

Contributions of Natural Enemies

Area-wide pest management began to be practiced widely during the nineteenth century using natural enemies. During the eighteenth and nineteenth centuries, people began to understand the roles of natural enemies in preventing insect outbreaks. Further, the powerful synthetic insecticides were not available to allow small holders independently to protect their crops and livestock. The beneficial work of coccinellids and other predators had been common knowledge for centuries, and they were collected and distributed for insect control. Insect parasitism was discovered only around 1700 by Leuwenhoeck in the Netherlands and in 1706 by Vallisnieri in Italy. Emperor Francis 1 of Austria ordered Vincent Kollar to publish his work on the role of natural enemies in suppressing pests. Kollar's great work appeared in 1837 and the English translation appeared in London's Gardner's Magazine in 1840.

E. F. Knipling has analyzed the potential contributions of parasitoids to area-wide pest suppression. Parasite augmentation could be an especially desirable preventive measure because the release of host specific parasites poses no danger to humans, beneficial organisms, or the environment. Highly misleading conclusions have been drawn from past augmentation experiments, because the experiments were done in small non-isolated areas. Most pest arthropods and parasites or predators are highly mobile. Therefore, meaningful results can be obtained only if augmentation experiments are conducted over large areas. Even though many species of natural enemies have developed efficient host finding by following odor plumes of



Area-Wide Insect Pest Management, Figure 76 **Progress in eradicating *Boophilus* ticks in the United States, 1906–1943.**

kairomones emanating from the host, under natural conditions the level of parasitization does not threaten the host with extinction. Augmentation utilizes the host resources in nature to produce large numbers of parasite progeny. If done properly, parasite augmentation for several generations can become a self-perpetuating suppression measure. Augmentation causes progressive increases in the rate of parasitism with each succeeding parasite generation, provided that the initial rate of parasitism is above 50%. In addition, a host-dependent species will tend to distribute itself proportionally to the distribution of its host. No other method of insect control has the characteristic of concentrating its suppressive action where it is most needed.

Lasting Suppression of Cottony Cushion Scale by Vedalia Beetle

That classical biological control can provide area-wide solutions was dramatically illustrated against an exotic pest in California in 1888 and 1889. At that time an introduced pest, the cottony cushion scale, *Icerya purchasi*, was killing hundreds of thousands of citrus trees. However Albert Koebele was able to introduce a scale predator, the vedalia beetle, *Rodolia cardinalis* (Mulsant), from Australia and New Zealand. Less than 11,000 vedalias were distributed, but they spread throughout the entire citrus growing area of southern California and saved the industry. The vedalia beetle continues to effectively protect citrus in California, and nothing needs to be done other than to avoid the use of certain insecticides, which would decimate this invaluable natural enemy.

Lasting Suppression of Cassava Mealybug by *Epidinocarsis lopezi*

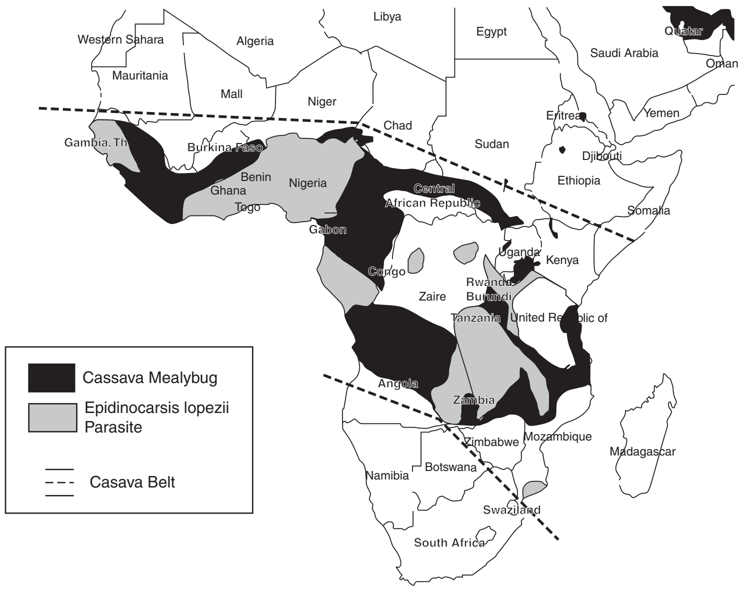
Almost exactly 100 years after the great vedalia success, a team led by Dr. Hans Herren of the International Institute for Tropical Agriculture (IITA) successfully implemented the largest classical biological control program in history. In 1973, cassava near Brazzaville and Kinshasa was found to be attacked by the cassava mealybug, *Phenacoccus manihoti* (Matile-Ferrero). In a few short years immature crawlers were dispersed by wind throughout sub-Saharan Africa.

The cassava mealybug created starvation and hardship for many of the 200 million people for whom cassava had become a staple crop. In 1981, an excellent parasitoid, *Epidinocarsis lopezi* (DeSantis), found in Paraguay by A.C. Bellotti, proved capable of bringing the cassava mealybug under control. The parasite was mass-reared and released by aircraft over 38 countries (Fig. 77) of sub-Saharan Africa (an area much larger than the combined area of the United States, Mexico and India) with excellent results. This singular accomplishment required strong and imaginative leadership and action by IITA, generous funding by donors, and brilliant scientific and technical work by Herren's team and their cooperators in Africa, Europe, and the Americas.

Area-Wide Conservation of Predators of the Brown Planthopper

In many cases, natural enemies are effective only if most smallholders in an area work to conserve them. Because both pests and natural enemies are mobile, their populations distribute themselves throughout the region in which their food sources are available. Even smallholders who do not participate in the conservation program receive some of its benefits. They get a free ride, and for them this is a positive externality of the program. On the other hand, the movement of natural enemies off the property of the participating farmer to that of the free rider is a negative externality.

The brown planthopper, *Nilaparvata lugens* (Stål), has been the scourge of rice production in southeast Asia for many years. However, during the 1980s, Indonesia (with technical assistance from FAO and Germany's GTZ) simultaneously



Area-Wide Insect Pest Management, Figure 77 **Biological control of the cassava mealybug in sub-Saharan Africa by mass rearing a parasite from Paraguay and distributing it by air over 38 countries.**

achieved substantial increases in rice production and major reductions in insecticide use. Generally, brown planthoppers are effectively controlled by indigenous spiders and other predators. Moreover, since insecticides have a greater impact on the predators than on the pest, the brown planthopper populations are able to resurge after being sprayed. In the past, farmers induced resurgence by beginning to spray at 40 days after transplanting the rice. However, cage studies showed that the smallholder who delays spraying until 65 days after transplanting saves two insecticide applications, and realizes a yield increase of about two tonnes, for a total benefit of US $588 per hectare.

It is possible to model what happens when some smallholders delay spraying to conserve natural enemies but others do not. If about 10% of smallholders conserve natural enemies, they gain only one-fifth of the potential benefit. If 30% of smallholders conserve natural enemies, they gain only one-quarter of the potential benefit, and the free riders gain about 7%. When 50% of small holders conserve natural enemies they gain one-third of the potential benefit, and the free riders gain about 18%.

When 70% of smallholders participate, they gain almost 60% and the free riders gain about 40%, and when 90% participate, they gain about 83% of the potential benefit, while the free riders gain 66%. Clearly, a conservation program is almost futile until about one-half of the smallholders participate, and the program becomes progressively more beneficial as the percent participation increases toward 100.

Bark Beetles

Dendroctonus pine bark beetles are dangerous pests in forestry because of their mass attacks on healthy trees. During the first decades in the twentieth century, foresters focused on destroying the developing broods of potentially destructive beetles before they could emerge and attack valuable trees. This was implemented by felling dead trees, peeling and burning the bark or by storing the infested logs in millponds until they could be sawed into lumber. The futility of such attempts by focusing directly on killing beetles became apparent when, in 1932, an extremely cold winter occurred and destroyed at least 80% of the beetles in western North America. The destruction of the beetle broods by frost was more complete, extensive and uniform than could be accomplished by forest managers. Yet, within 2 years the beetle populations had resurged and were again killing ponderosa pine on a vast scale.

However, forest entomologists recognized that the most vulnerable trees were those that lacked vigor or were in decline. Thus, in 1937 control of bark beetles based on susceptibility of trees to attack was pilot tested in California by a program called sanitation-salvage logging. In this approach, up to 20% of trees at highest risk of beetle attack were removed and sawed into lumber. During the first year following the removal of the most vulnerable trees, losses to bark beetles were reduced by 90%, and losses remained low for at least 10 years after the selective logging.

Boll Weevil Eradication in the USA

E. F. Knipling, with the support of the National Cotton Council, was determined to eradicate the boll weevil from the United States because the weevil necessitated the use on cotton of one-third of the insecticides used in U.S. agriculture. Also, highly insecticide-resistant boll weevil populations had emerged. Newsom and Brazzel, at Louisiana State University, had discovered that in the fall of the year the boll weevil enters a reproductive diapause and hibernates in trash along the edges of cotton fields. Brazzel showed that the number of weevils surviving the winter is reduced 90% if insecticides are applied just before diapausing weevils leave the fields. Moreover, Knipling's analysis showed that if insecticide sprays were targeted also to kill the generation producing individuals going into diapause, then the number overwintering would be reduced by more than 99%. Knipling's model was verified, and this ignited great interest in actually eradicating the boll weevil. An effective pheromone-baited trap was developed for detection. Weevils were sexually sterilized with the anti-leukemia drug, busulfan.

In 1971–1973, a large pilot field experiment to assess the feasibility of eradication was centered in southern Mississippi. The eradication zone was surrounded by three buffer zones. Very intensive suppression was implemented in the two inner zones, and farmers were expected to practice diligent control in the outer zones, although some grew cotton simply to qualify for government payments and with no intention to harvest a crop. Only one application of the suppressive system was made, because of a shortfall in appropriations. Nevertheless, the boll weevil was suppressed below detectable levels in 203 of 236 fields in the eradication zone. All of the 33 lightly infested fields were located in the northern one-third of the eradication zone and less than 40 km from substantial populations farther north. In the southern two-thirds of the eradication zone, no reproduction could be detected in any of the 170 fields. Knipling and some others concluded that the available technology was sufficiently effective to achieve eradication. Their experience with the screwworm indicated that eradication could be accomplished iteratively, following an application of the suppressive system that clears the pest from most of the target zone. Next, surviving populations are delimited and similar suppressive measures are applied to them. In this iterative fashion, the aggregate range occupied by the pest is progressively reduced toward zero. However, some felt that the technology was not adequate to mount an eradication campaign, unless a single application of the system of suppression eliminated all weevils in the target zone.

A Cotton Study Team appointed by the National Academy of Sciences drafted a very negative interpretation of the results. Because Knipling was a member of the Academy, he had access to this draft, and he wrote a strong rebuttal. Therefore, the Cotton Study Team wrote a "toned down statement" that continued to express strong reservations about the feasibility of eradicating the boll weevil, but concurred to conduct a new trial eradication program in North Carolina.

Grudgingly the Academy team legitimized the concept of continuing large-scale eradication experiments, but with the caveat that they would probably fail.

The new trial program, started in 1978 in Virginia and North Carolina, was highly successful. Subsequently, piece-meal programs, each run by a separate foundation, have removed the boll weevil from about 5 million acres in Virginia and the Carolinas, Georgia, Florida, south Alabama, California, and Arizona. These programs have caused significant reductions in pesticide usage, and the eradication efforts are continuing. Thus, the job is about half done. However, the corrosive effect of the Academy's report persists. The US Congress reduced the share of federal funds from the traditional 50 to <30% of the cost. However, such cost sharing is no longer guaranteed, and in 1997 the US Department of Agriculture initiated a program of making loans to officially recognized boll weevil eradication foundations. Moreover, the process of eradication is being conducted piece-meal with a minimum of technology. Pheromone traps are used to delimit infestations, and the attack begins with insecticides applied late in the growing season against weevil still reproducing and those entering diapause. As many as 15 insecticide applications per year are made against dense persistent populations. Planting by all growers is synchronized and delayed, short season varieties are grown, harvested as soon as possible, and stalks are destroyed immediately after harvest. Eradication is usually accomplished by the end of the third growing season.

Attempts to Sharply Define the Area-Wide Pest Management Strategy

A few scientists have attempted to sharply define the area-wide pest management strategy. Knipling stated: "Area-wide pest management is the systematic reduction of a target key pest(s) to predetermined population levels through the use of uniformly applied control measures over large geographical areas clearly defined by biologically based criteria." D. A. Lindquist wrote: "An area-wide insect control program is a long-term planned campaign against a pest insect population in a relatively large predefined area with the objective of reducing the insect population to a non-economic status".

Both of these definitions have considerable merit and they fit the majority of area-wide programs. However, slightly different definitions may be needed to describe programs on the conservation of natural enemies (which can tolerate some free-riders) and on classical biological control where the adaptation of the introduced biological agent to all new environments cannot be known in advance of making releases. Also, in programs to contain an invasive pest population, it may not be possible to clearly define the boundary of the pest population. In the similar vein, A. T. Showler stated: "Locust swarms can be highly variable, influenced by many factors, including geography, vegetative conditions, land-use patterns, environmental sensitivity, availability of resources and tactics, prevailing winds, insecure areas, and rainfall patterns. Reliance on a single control strategy is therefore unrealistic. A more appropriate approach would be to develop specific strategies that will fit with projected scenarios, mostly by harmonizing them with national contingency plans." The common thread that runs through all area-wide pest management programs is the strong emphasis on preventing the existence of any places of refuge or foci of infestation from which recruits can come to re-establish damaging densities of the pest population in areas of concern.

Benefit-Cost Assessment and Discounting Net Returns

Usually, investments in area-wide programs are made with the expectation that program benefits will accrue over a multi-year time horizon. Therefore, we must discount future benefits to balance them against present or near term expenditures. The stream of discounted annual benefits and costs for many years of an undertaking can be summed up and expressed as a single value, known as the present value net benefits (PVNB). The formula for calculating the PVNB for a 15-year project is as follows:

$$PNVB = NB_1 + w_2NB_2 + w_3NB_3 + w_4NB_4 + w_5NB_5 + w_6NB_6 + wtNB_t + w_{15}NB_{15}$$

where NB_t represents the net benefits in year t, and w_t represents the weighting factor for year t. The weighting factors are a function of a discount rate (r):

$$w_t = \frac{1}{(1+r)^t}$$

The discount rate is the opportunity cost of the money, or the interest value that money could earn if allocated to the best alternative use. This rate may be established by subtracting the national inflation rate from the bank interest rate for savings. In normal times, this procedure will generally produce a figure around 4 or 5% in developed countries. This represents the reasonable person's discount on the future, because people put their money in the bank to gain this premium, and otherwise they would spend it now. So, the benefit of eradication next year is worth 5% less if it is brought back to the present. Benefits in 20 years are only worth 37% of their face value when brought back to the present. In riskier economic environments, discount rates will be much greater, so the calculated net present value of future benefits may be insignificant. However, for programs involving vectors of human diseases, the futures of groups of people are at stake, and it does not seem appropriate to discount benefits in the manner appropriate for private investments. The health of the human population 30 years in the future seems just as important as the health of the population at present. Nevertheless, investments in vector control programs must be subjected to critical analysis in the interest of efficient and sound management. However, if high discount rates (e.g., 25%) are selected commensurate with economic risk in many developing countries, then it seem unlikely that vector control programs in these countries would ever be launched.

Knipling's Imperative

When the World Food prize was awarded to Knipling and Bushland, Knipling stated: "If major advances are to be made in coping with most of the major arthropod pest problems, then the tactics and strategies for managing such insects, ticks and mites must change. They must change from the current, limited scale, reactive, broad-spectrum measures to preventive measures that are target-pest specific and rigidly applied on an area-wide basis." Great and enduring strides can be made by adopting the strategy of area-wide pest management to help meet world food, health and environmental challenges.

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Argasid (Soft) Ticks (Acari: Ixodida: Argasidae)

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The family Argasidae is second to the family Ixodidae with regard to its medical and veterinary significance and the number of species. According to the novel classification based on a phylogenetic analysis of relationships at the generic to subgeneric level, the argasid ticks comprise four genera and about 185 species, among which three genera are represented by a large number of species: *Carios* (87 species), *Argas* (57 species) and *Ornithodoros* (36 species, one of which consists of three subspecies). The fourth genus (*Otobius*) is represented by three species. Not all researchers fully agree with the currently proposed systematic groupings of the family. This classification has its weaknesses but is considered superior to traditional classifications. In any case, further molecular taxonomic study is necessary.

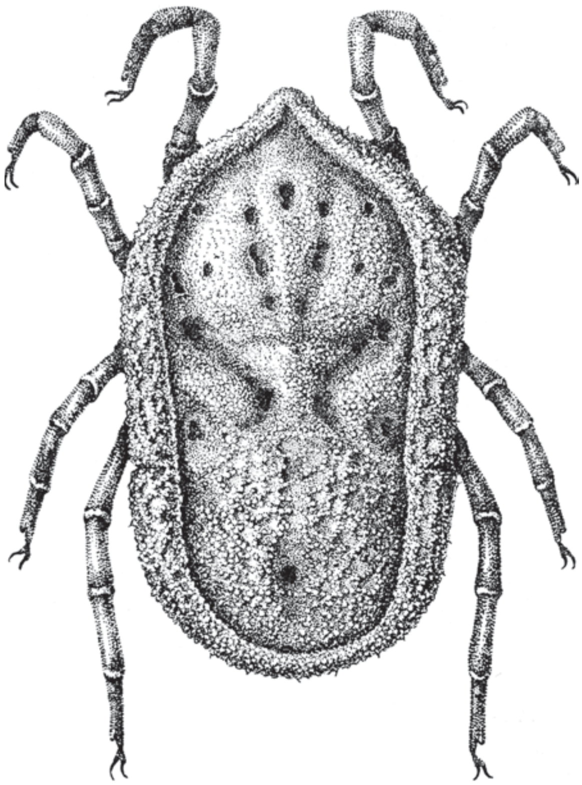
The main morphological difference between argasid and ixodid ticks is the lack of the scutum in argasids; thus, they are called "soft ticks." The lack of the scutum leads to the absence of such a clear sexual dimorphism in the adult stage of this family compared with ixodid ("hard") ticks. The integument of the Argasidae looks wrinkled and leathery. The mouthparts are located on the ventral side of the body, covered by the frontal margin of the body, and are invisible from above.

There are a number of significant biological differences between soft and hard ticks. Firstly, argasid ticks have several nymphal stages (instars), varying from 2 to 8, usually from 3 to 6. The number of instars is not constant, and is controlled by exogenous factors such as the size of the blood meal and the ambient temperature during development. Secondly, nymphs and adults of argasid ticks cannot engorge as much blood as ixodid ticks. The integument of adult argasids is strongly folded and capable of stretching during feeding, but does not grow at that time. Females of most argasid ticks increase their body mass after feeding by only 3–6-fold. The blood feeding time of argasid ticks is much shorter than that of ixodids, taking from several minutes to 1–2 h, and male gorging taking 1.5–2 times less than that of females. In contrast, nymphal argasids feed in much the same manner as ixodids; this is explained by their capacity to create new cuticle during feeding. Thirdly, adult ticks can gorge blood several times during their life, and can oviposit after each feeding. The maximal number of possible feedings is unclear, though as many as nine feedings have been documented.

Ecology

Argasid ticks are spread over all continents (with the exception of Antarctica) but have been studied very unevenly; in particular, there is insufficient information on this group in South America and Australia. Both in the Palaearctic and the Nearctic, soft ticks inhabit regions with a hot climate, mainly deserts, semi-deserts and southern savannas (steppes, veldts, prairies), but some species penetrate as far north as 50–55°N. The maximum number of species and their greatest abundance are known in foothill areas (300–900 m above sea level), but some ticks can be found at higher elevations (a maximum of 2,900 m above sea level for the cave tick *Ornithodoros tholozani* (Fig. 78) in the Pamirs).

Almost all species of argasid ticks are nidicolous, i.e., they live in or near shelters of various kinds. *Ornithodoros transversus* is an exceptional species that spends its entire life on the giant tortoises of the Galapagos Islands. Endophilous nidicoles inhabit bird and rodent nests, mammal burrows, and caves as well as stalls, poultry houses and farms. Harborage-infesting parasites live near nests or burrows, very often in rock or stone ledges as well as in human dwellings and temporary human-made cabins in places of resting, hunting or fishing. In such shelters, ticks inhabit all kinds of cover: cracks and crevices on walls, sandy or



Argasid (Soft) Ticks (Acari: Ixodida: Argasidae), Figure 78 **The cave tick, *Ornithodoros tholozani*.**

dusty soil surface of burrows and caves, spaces between nest fibers, etc. Ambient conditions, such as air temperature, relative humidity and light intensity, are more uniform and suitable for ticks in shelters than in the surroundings; this enables tick survival in extremely unfavorable areas. Being dependent on the hosts living in the shelters, the ticks have developed different patterns of adaptation, the main one being their unusual ability to persist without feeding. This is especially characteristic of nest and burrow inhabitants because death of the host or migration to another habitation are common phenomena, whereas active migration between shelters is not typical for most argasid ticks except in several species parasitizing ungulates and hares. Under laboratory conditions, unfed adult *O. tholozani* survived without feeding for more than 10 years and unfed adult *Argas lahorensis* for as long as 18 years.

As a rule, females of argasid ticks are characterized by gonotrophic harmony, though the number of eggs in each batch may fluctuate widely. After each complete blood feeding, they lay off-host from 50 to 200 eggs. If blood feeding is not complete, the number of eggs laid diminishes proportionally. During its entire life, a female can lay up to 1,200 eggs. Female oviposition depends on their insemination, which occurs off-host, and can take place either before or after feeding. Some cases of female insemination several months after feeding, followed by oviposition, have been described. One mating is sufficient for several ovipositions. Multiple gonotrophic cycles have been recorded among the Argasidae. There are some exceptions from gonotrophic harmony when a female lays eggs without feeding, using nutritional reserves remaining after nymphal feeding.

Feeding Behavior

Several feeding nymphal instars and repeated feedings in adult females allow us to describe the Argasidae (with a few exceptions) as multi-host ticks, though consecutive feedings may take place on the same host. Most argasid species feed on specific groups of hosts and, in a broad sense, can be considered specialists. Ticks of some subgenera of *Argas* parasitize birds available to them during nesting or resting. The genus *Carios* contains nearly all bat-associated argasids. When the ticks are offered unusual hosts, they either do not feed at all or have some abnormalities in their metamorphosis after such feeding. An extreme specialization was observed in Cuban *Carios natalinus* and *C. tadaridae*, which parasitize only bats of the genera *Natalus* and *Tadarida*, respectively. In contrast, such ticks as *Ornithodoros erraticus*, *O. tartakovskyi*, or *O. tholozani* must be considered generalists. They can feed on any mammals, birds and reptiles available to them. Among exceptions are the one-host *Ornithodoros transversus* and the two-host *Otobius megnini* and *A. lahorensis*. The latter species demonstrates some characteristics of exophilic ticks which are followed by adaptations to hot xeric environments. This tick has an extremely high critical temperature of the epicuticle (61°C in contrast to 42 to 54°C in other species studied) and minimal water loss under low RH. Among other adaptations are the development on the host from larval attachment until engorgement of nymphs of the last instar with a constant number of nymphal instars (3) and nymphal feeding at each instar for several days which increases the blood meal size and, hence, the number of eggs laid (300–500).

A capacity of unfed argasid ticks to parasitize and feed on engorged specimens of the same species presents an interesting phenomenon called homoparasitism (homovampirism, in Russian literature). Usually, unfed nymphs and males parasitize engorged nymphs of late instars and females. Unfed ticks prick the integument and gut walls of engorged specimens, and suck the gut contents. As a rule, such an operation is not followed by the death of the victim, so that this phenomenon cannot be called cannibalism. This phenomenon has been documented many times for a number of species of both *Argas* and *Ornithodoros* under laboratory conditions, but there are also a few observations from the field. Apart from this, feeding of unfed ticks on engorged specimens of other species has also been recorded.

Depending on the conditions of tick habitats, ticks have different forms of seasonal activity. The seasonality is absent or weakly pronounced in ticks inhabiting shelters with a relatively stable microclimate. In the tropical zone, ticks attack hosts, feed and oviposit all year round according to observations on the African tampan *Ornithodoros moubata*. A similar pattern of activity was recorded on *O. erraticus* inhabiting the Nile grass rat burrows in Egypt. In the subtropical and especially temperate zones, the seasonality in tick activity is much better defined. Ticks feed and oviposit during the summer and have one or two gonotrophic cycles during this period. In the winter months, a morphogenetic diapause in the form of ovipositional delay takes place in argasid species that parasitize migratory birds. Such diapause also occurs in ticks parasitizing bats, which hibernate in cool caves. Photoperiod seems to be the main but not the only factor regulating the induction and termination of diapause. A prolonged hunger is not considered diapause even when it continues for several years.

The abundance of argasid ticks in their shelters can be extremely high. A single cave inhabited by bats may contain hundreds of thousands of bat-parasitizing argasids. Cases have been documented when seabirds abandoned their nests in the middle of the breeding season because of enormous tick density. Especially high tick density has been noted in abandoned habitations of Central Asia. Such constructions are even more dangerous than dwellings; the longer ticks are without hosts and the hungrier they become, the more aggressively they attack occasional visitors. In past centuries special "bug traps" full of hungry argasids were used by Central Asian rulers for the torture of prisoners who died from exsanguination by thousands of ticks. The capability of argasid ticks to migrate varies depending on the habitation of a particular species. Endophilous nidicoles inhabiting nests, burrows and caves are usually considered non-migratory species because the distance to the host is very short. Harborage-infesting species can migrate over larger distances measured in many meters. As in the hard ticks, the migration toward a host is influenced by a spectrum of factors, such as CO_2, host body heat, various odors, etc. However, the effect of a single stimulus is weaker than for hard ticks, and the maximal effect has been observed when all stimuli worked together.

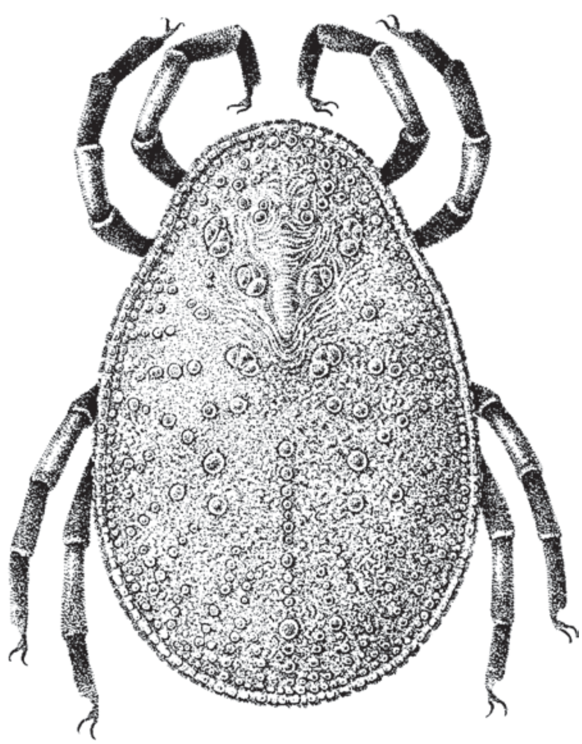
Evolutionarily, the Argasidae are more primitive than the Ixodidae. This primitivism is exemplified by a number of characteristics, such as rather narrow ecological patterns, low capacity for active migrations, existence of many nymphal instars, and slight morphological difference between the last nymphal instar and the adult stage. These characteristics are considered typical for more primitive forms among different groups of the Arachnida.

Medical Importance

The medical significance of argasid ticks is mainly determined by their participation in transmission of many species of *Borrelia* pathogenic to humans. These closely related bacteria are causative agents of tick-borne relapsing fevers. Each species of *Borrelia* is transmitted by its specific tick vector. *Borrelia duttoni* and its vector *Ornithodoros moubata* were the first combination of such kind recognized in Africa in the very beginning of the twentieth century. The disease occurs in the central, eastern and southern parts of the continent and humans are the primary reservoir host, which is unusual because in other combinations, mammals, especially rodents, are the main reservoir hosts. More than 15 combinations of *Borrelia* with particular species of argasid ticks are recently known worldwide. They occur in North, Central and South America, Africa, and the Mediterranean area, including some European countries, the Caucasus, Asia from the Near East to western China. In the western and southwestern United States the following combinations have been identified: *B. hermsi*-*Ornithodoros hermsi*, *B. parkeri* -*O. parkeri*, *B. turicatae*-*O. turicata*, *B. mazzottii*-*Carios talaje*. The ticks are capable of transovarial and transstadial passage of *Borrelia* for many generations, as well as of prolonged preservation of pathogens, even during prolonged hunger. The passage of pathogens from hungry to engorged specimens as a result of homoparasitism has been proved experimentally. Because tick vectors are nidicolous, the human infection depends on human closeness to tick habitation. Tick species inhabiting human dwellings, such as *Ornithodoros moubata* and *O. tholozani*, are especially dangerous vectors. In other cases the infection takes place only when humans intrude into tick shelters or settle themselves nearby.

Veterinary Importance

Some argasid ticks are also of veterinary importance. *Ornithodoros porcinus porcinus* and *O. erraticus* are the main vectors of the African swine fever virus, an acute contagious disease affecting domestic pigs and several wild representatives of the family Suidae. Epidemics of this disease have occurred in many African countries, as well as in some southern European-Mediterranean countries, but also in Brazil and Central America (Cuba, Dominican Republic, Haiti). *Ornithodoros coriaceus* transmits *Borrelia coriaceae*, the causative agent of epizootic bovine abortion in the western United States. Cattle, and especially sheep, densely parasitized by *Argas lahorensis*, may suffer from large losses of blood and often die. Some representatives of the genus *Argas* that are closely connected with poultry transmit destructive diseases of domestic birds. Fowl (or avian) spirochetosis caused by *Borrelia anserina* affects chickens, geese, ducks, turkeys, pheasants and some other fowl and decorative birds. The fowl tick, *A. persicus* (Fig. 79), the most important cosmopolitan poultry parasite, is the main vector of the pathogen. The pigeon tick *A. reflexus* (and,



Argasid (Soft) Ticks (Acari: Ixodida: Argasidae), Figure 79 **The fowl tick, *Argas persicus*.**

perhaps, other species from the *A. reflexus* group) also participates in transmission of the disease. The mode of transmission is unique for tick-borne borrelioses, by contamination from infectious tick feces. Transovarial passage of the pathogen has been proved. Fowl spirochetosis is spread worldwide: in North, Central and South America, Europe, Australia and many regions of Asia and Africa. *Argas persicus* is also responsible for transmission of a rickettsia, *Aegyptianella pullorum*, infecting some fowl. The disease is especially destructive for young chickens. *Argas walkerae*, whose adults transmit this disease in South Africa, also causes paralysis in chickens when its larvae feed on them.

A number of other human and animal pathogens have been isolated in nature from some species of argasid ticks, but there is not enough data to consider such ticks as competent vectors. On the other hand, some argasid ticks have been successfully infected by different pathogens in the laboratory, and maintained the pathogens for some time, but this also does not constitute proof of the tick importance in transmission of the disease. Nevertheless, the involvement of argasid ticks in the transmission of other diseases is very possible.

Human Response to Tick Feeding

Human skin reacts to argasid bites, sometimes rather severely. People are often insensitive at the time of the tick bite but later a strong itch appears followed by scratching and the appearance of ulcers. The strength of the human reaction depends on the tick species. Evidence of *Ornithodoros tholozani* bites may be in evidence for many months. *Argas* ticks living in towns and parasitizing pigeons often inhabit human dwellings, even some apartments in many-story buildings, and may cause allergic responses and toxicoses in humans. Many cases of anaphylactic reactions (sometimes even with fatal results) caused by bites of *A. reflexus* have been reported in European towns where pigeon populations increased dramatically during past decades. Such reactions are typical for other members of *Argas reflexus* group (e.g., for *A. latus* in Israel).

The most severe form of tick toxicosis is tick paralysis, which only occurs after prolonged feeding. In argasid ticks, the known cases of tick paralysis were described only for larvae characterized by prolonged feeding. Larvae of several *Argas* species cause paralysis of fowl with total recovery after all larvae drop off the host. Paralysis and death of sheep and cattle caused by *Argas lahorensis* has been reported from some European countries, Caucasus and Central Asia after attachment of 100–200 nymphal ticks of the slow-feeding third instar.

Management of Tick Populations

Personal prophylaxis is the basis of human protection from argasid ticks. It is necessary to avoid resting and overnighting in sites where tick attacks are possible. The most efficient method of tick eradication in human dwellings is the improvement of dwellings so that ticks are deprived of possible shelter. The maintenance of good sanitary conditions in poultry houses and farms with limited use of acaricides should maintain the abundance of fowl ticks at a low level. The acaricidal treatment of domestic animals infested by argasids is an effective mode of tick control. Some animal diseases, such as African swine fever, can be eradicated either by very severe quarantining of the infected herds or by destroying the infected herds together with the ticks infesting the animals. Only a small number of pathogens, parasites and predators of argasid ticks are known, thus it is impossible to estimate the prospects of their use for argasid tick control.

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Argentine Ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae: Dolichoderinae)

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Identification and Taxonomy

Argentine ants belong to the subfamily Dolichoderinae, or odorous ants, characterized in the worker caste by the presence of a single constricted petiolar segment, the lack of a sting, and a transverse slit-like anal orifice. Worker ants (Fig. 80) of the genus *Linepithema* can be further recognized by the combination of the anterior clypeal margin bearing a medial concavity and a distinct mandibular dentition bearing a series of larger teeth interspersed with two to three small denticles.

The Argentine ant is distinguished from all other *Linepithema* species in the worker caste by a lack of erect setae on the mesosomal dorsum, the presence of dense pubescence on the mesopleuron, large compound eyes comprised of 80–110 ommatidia, and the long antennal scapes that are as long or slightly longer than head length. Worker ants are uniformly reddish brown to dark brown and are between two and three millimeters in length. *Linepithema humile* males are unmistakable as they have an unusually robust mesosoma, longer than the gaster, that bears a distinctly concave posterior propodeal face.

Argentine Ant, *Linepithema humile* (Mayr), (Hymenoptera: Formicidae: Dolichoderinae), Figure 80 A foraging Argentine ant, *Linepithema humile.*

Much of the early literature about this species is found under the name *Iridomyrmex humilis*. The change to current nomenclature occurred when recent phylogenetic research revealed a number of new world dolichoderine species, including the Argentine ant, to be unrelated to true *Iridomyrmex*, a strictly Indo-Australian group.

Distribution

The natural distribution of *Linepithema humile* (Fig. 81) extends in the south from the Buenos Aires province across Paraguay to the Pantanal in the north, and is closely associated with major waterways in subtropical South America's Paraná River drainage. This species typically inhabits lowland forests and grasslands in the Paraná and Paraguay floodplains.

In the eighteenth century, *L. humile* began to appear elsewhere in the world, arriving on the Atlantic island of Madeira in the 1850s and in the southern United States and in Portugal in the 1890s. In spite of its humid subtropical provenance, this insect has been most successful invading Mediterranean climates. Thriving introduced populations are now found in California, Mexico, Hawaii,

Argentine Ant, *Linepithema humile* (Mayr), (Hymenoptera: Formicidae: Dolichoderinae), Figure 81 Current distribution of Argentine ant, *Linepithema humile*.

Ecuador, Colombia, Chile, Peru, South Africa, Japan, temperate Australia, New Zealand, numerous Pacific islands, and throughout the Mediterranean region. Occasional populations persist indoors in northern Europe and North America. Microsatellite evidence suggests that at least some of these introduced populations originated in Argentina near the port city of Rosario.

Biology

Like most ant species, Argentine ants are haplodiploid and eusocial. They live in colonies composed largely of sterile female workers and a smaller number of fertile queens and males. Unlike most ants, queens of *L. humile* do not fly, mating instead in the nest. Genetic evidence suggests that queens are singly mated. For reasons that remain obscure, up to 90% of queens in a colony are periodically executed by the workers. Males are present in early summer and disperse by wing at dusk. As for all Holometabola, metamorphosis is complete. Development time is dependent on temperature and has been estimated at 445 degree-days above a 16°C threshold for workers. Under field conditions, the process from egg to adult can take several weeks to several months.

Argentine ants possess a number of life history traits that facilitate colonization and possibly pre-adapt this species as a globally successful invader. First, Argentine ant colonies have a large number of fertile queens, in some colonies running into the thousands. This polygyny increases the chance that an isolated nest fragment will contain a queen and be able to grow into a successful colony. Second, colony reproduction occurs by budding. Argentine ants do not have to pass through the high mortality bottleneck at colony founding endured by haplometrotic species that found new colonies with single queens drawing on body reserves. Indeed, *L. humile* queens without workers are incapable of founding new colonies, but propagules as small as 10 workers with a queen or even female brood can mature into populous colonies. Finally, Argentine ants cope with frequent disturbance of nesting sites. Nests tend to be superficial and transitory, occupying the top level of soil or litter. The ants move among existing nests and establish new nests frequently in response to changes in moisture and temperature. In their native range colonies will climb trees to escape rising flood waters.

Argentine ant colonies can reach extraordinary sizes, inhabiting a diffuse system of interconnected nests spanning a few meters to several hundred kilometers or more. While colony networks in the native range are restricted to at most a few thousand square meters, introduced populations normally comprise unicolonial "supercolonies" on the scale of landscapes or even continents. Supercolonies are thought to arise following population bottlenecks at introduction that produce genetic homogeneity among descendents. Such colonies are normally diagnosed using aggression assays and have been documented to cover coastal Chile, California, most of Southern Europe, and parts of Australia.

Argentine ants, like all *Linepithema* species, are trophic generalists. They predate and scavenge a wide variety of protein sources, often arthropods, and display a high affinity for honeydew. Argentine ants recruit quickly to food sources using chemical communication and are often seen running in active foraging trails. The trail pheromone is (Z)-9-Hexadecenal, produced by the Pavan's gland at the tip of the abdomen.

Effects

Introduced populations of *L. humile* penetrate both human-disturbed and natural habitats. They disrupt ecosystem processes both through active predation and exploitative competition. Community diversity is often reduced following invasion, and Argentine ants have been documented displacing native arthropods in California, Hawaii, Japan, South Africa, and Spain. Long term effects of Argentine ant invasions have included changes in South African fynbos plant community structure via displacement of native seed-dispersing ants, and local extinction of *Phrynosoma* lizards in California following the decline of their native ant prey.

Damage to agriculture stems largely from the ants' association with honeydew-producing pests. The ants protect their insect symbionts from attack by predators and transport them to uninfested plants, leading to outbreaks in populations of aphids, scale insects and mealybugs. Argentine ants are especially problematic in orchards and greenhouses where they confound biological control efforts.

The extent of Argentine ant invasion is likely limited by a combination of abiotic conditions and interactions with other ant species. Invasions are facilitated in arid regions by development-related increases in moisture from irrigation and run-off. Highly competitive local ant communities may limit the spread of the Argentine ant. In the southeastern United States, for example, Argentine ant numbers declined following the introduction of the fire ant *Solenopsis invicta*.

Management

The diffuse network structure of Argentine ant colonies renders control more difficult than for many other ant pests, as extirpated nests are readily replenished from neighboring areas. Effective control is unlikely to be gained with any single strategy, and pest managers may have to experiment with different approaches to treat an infestation. Treatment of Argentine ants around homes should include cleaning indoor ant trails when they appear, removal of potential water and food sources, and sealing the ants' entry points into the house. Control using toxic baits is often effective, and boric acid-based liquid baits are generally more palatable to the ants than most commercially available ant baits. As a last resort, appropriate perimeter insecticides or repellents may be applied. For agricultural infestations, chemical or physical barriers applied to individual plants have reduced ant damage.

No specialized natural enemies are known for the Argentine ant, but this insect has received relatively little research in its native range and some may yet be discovered. Recent work suggests that native populations may be held in check by intraspecific competition among colonies and interspecific competition with species such as *Solenopsis invicta*, also native in the Paraná drainage. If this is the case, long-term strategies for limiting the effects of Argentine ants may include the maintenance of robust native ant communities.

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Argidae

A family of sawflies (order Hymenoptera, suborder Symphyta).

► Wasps, Ants, Bees and Sawflies

Argyresthiidae

A family of moths (order Lepidoptera). They commonly are known as shiny head-standing moths.

► Shiny Head-Standing Moths
► Butterflies and Moths

Arista

A large hair or bristle on the antennae of flies.

► Antennae of Hexapods

Armored Scales

Members of the family Diaspididae, superfamily Coccoidae (order Hemiptera).

► Bugs
► Scale Insects and Mealybugs

Army Ants

Ants that display group predatory and nomadic behaviors. The nest site is changed at regular intervals, and workers forage in groups.

► Ants

Army Cutworm, *Euxoa auxiliaris* (Grote) (Lepidoptera: Noctuidae)

This insect is found in the Great Plains and Rocky Mountain regions of the United States and Canada. It has been recorded from all states west of the Mississippi River, and as far east in Canada as Ontario, but attains high densities only in semiarid areas, especially along the western edge of the Great Plains.

Host Plants

Army cutworm has been reported to feed on a large number of plants. It is known principally as a pest of small grains, perhaps because these crops dominate the landscape where army cutworm occurs. It damages such field crops as alfalfa, barley, clover, flax, rye, sanfoin, sunflower, sweet clover, timothy, vetch, and wheat. Among vegetable crops, it has been reported to damage beet, cabbage, celery, corn, onion, pea, potato, radish, rhubarb, tomato, and turnip. Other crops injured include such fruit crops as apple, apricot, blackberry, cherry, currant, gooseberry, peach, plum, prune, raspberry, and strawberry. Army cutworm also feeds on noncultivated plants such as bluegrass, *Poa* spp.; bromegrass, *Bromus* spp.; buffalograss, *Buchloe dactyloides*; grama grasses, *Bouteloua* spp.; field pennycress, *Thlaspi arvense*; dandelion, *Taraxacum officinale*; lambsquarters, *Chenopodium album;* and lupine, *Lupinus* spp.

Natural Enemies

Many natural enemies have been found associated with army cutworm, and both hymenopterous parasitoids and disease have been documented to cause considerable mortality. In the central Great Plains, mortality studies over a 20-year period demonstrated parasitism levels of up to 33% and disease incidence of up to 57%. Not surprisingly, incidence of disease was greatest at high armyworm population densities. In a 3-year study in Oklahoma, researchers found that <12% of larvae were parasitized, with most parasitism due to two species, *Meteorus leviventris* (Wesmael) and *Apanteles griffini* Viereck (both Hymenoptera: Braconidae). A polyembryonic wasp, *Copidosoma bakeri* (Howard) (Hymenoptera: Encyrtidae), causes larvae to consume more food, to become larger, and live longer; this can result in the appearance of artificially high rates of parasitism, which sometimes exceeds 50%.

Among the other parasitoids known from army cutworm are such wasps as *Apanteles marginiventris* (Cresson), *A. militaris* Walsh, *Chelonus insularis* Cresson, *Macrocentrus incompletus* Muesebeck, *Microplitis feltiae* Muesebeck, *M. melianae* Viereck, *Rogas* sp., *Zele melea* (Cresson) (all Hymenoptera: Braconidae); *Campoletis flavicincta* (Ashmead), *C. sonorensis* (Cameron), *Diphyus nuncius* (Cresson), *Exetastes lasius* Cushman, and *Spilichneumon superbus* (Provancher) (all Hymenoptera: Ichneummonidae). Flies known to parasitize this species include *Bonnetia comta* (Fallen), *Euphorocera claripennis* (Macquart), *Mericia* spp., *Peleteria* sp., *Periscepsia cinerosa* (Coquillett), *P. helymus* (Walker), and *P. laevigata* (Wulp) (all Diptera: Tachinidae).

Several viruses are known to infect army cutworm, including entomopox, granulosis, and nonoccluded viruses. The relative importance of each is uncertain, but the granulosis virus is unusually pathogenic.

Life Cycle and Description

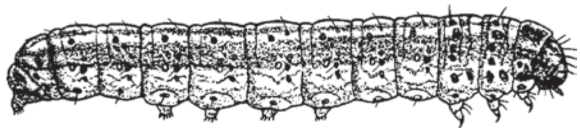
There is a single generation per year throughout the range of this insect. Eggs are deposited on soil in August-October. Eggs hatch in autumn or early winter, and larvae overwinter, feeding actively in the spring. Pupation occurs about a month before adults appear. Adults first become active in April-May in southern locations such as Kansas and Texas, whereas in more northern locations such as Alberta and Montana they may not appear until June-July. The moths migrate from the plains, where the larvae develop, to higher elevations in the Rocky Mountains, where the adults feed on nectar from flowers. The adults return to the plains in August-September.

Egg

Eggs are deposited singly or in small clusters just beneath the soil surface on a solid substrate. The eggs are a slightly flattened sphere, measuring about 0.6 mm in diameter and 0.5 mm in height. The egg is white to yellow initially, becoming gray to brown as the embryo matures. The egg is marked with about 18 very narrow ridges that radiate from the apex. Survival of eggs is reported to be affected by moisture, and above-average rainfall in late summer and autumn tends to assure good insect survival and damaging populations the subsequent year. Field-collected females were reported to produce 200–300 eggs, with the potential to produce about 500 eggs.

Larva

The eggs hatch in the autumn or early winter but the larvae are usually not noticed until spring when they increase in size and begin to consume considerable foliage. There are 6–7 instars, with head capsule widths of 0.26–0.30, 0.40–0.45, 0.65–0.72, 1.04–1.21, 1.70–2.10, and 2.90–3.40 mm, respectively, for instars 1–6 among larvae with only 6 instars. Additional instars apparently occur when larvae feed on less suitable host plants. The body color of the larvae is (Fig. 82) grayish brown, but bears numerous white and dark brown spots. There usually is evidence of 3 weak light-colored dorsal stripes. Laterally there tends to be a broad dark band, and the area beneath the spiracles is whitish. The head is light brown with



Army Cutworm, *Euxoa auxiliaris* (Grote) (Lepidoptera: Noctuidae), Figure 82 Larva of army cutworm *Euxoa auxiliaris*.

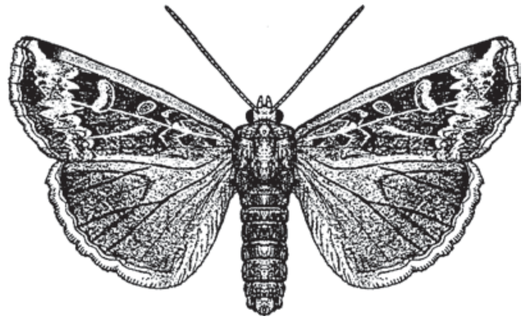
dark spots. Larvae attain a length of about 40 mm. They usually are found beneath the surface of the soil, emerging in late afternoon or early evening to feed. On cloudy days, however, they may be active during the daylight hours. Larvae will assume a migratory habit when faced with food shortage, and large numbers will proceed in the same direction, consuming virtually all vegetation in their path. It is this dispersive behavior that is the basis for their common name, and larvae have been observed to disperse over 4 km.

Pupa

Pupation occurs in the soil, in a cell prepared by the larva. The walls of the cell are formed with salivary secretion, which hardens and provide a degree of rigidity. The depth of pupation varies according to soil and moisture conditions, but may be any depth up to 7.5 cm. The larva spends about 10 days in the cell prior to pupation. Duration of pupation is 25–60 days. The pupa is dark brown in color, and measures about 17–22 mm in length and 6 mm in width.

Adult

The adults measure 35–50 mm in wingspan. They are quite variable in appearance, with five named subspecies, but moths generally assume two basic forms. One common form has the leading edge of the forewing marked with a broad (Fig. 83) yellowish stripe, and the remainder of the wing blackish but marked with white-rimmed bean-shaped and round spots, and a light transverse line. In another common color form the forewing is mottled brown,



Army Cutworm, *Euxoa auxiliaris* (Grote) (Lepidoptera: Noetuidae), Figure 83 Army cutworm adult, light form.

bearing bean-shaped and round spots but lacking bands and stripes. In all cases, the hind wings are brownish with dark veins, and darker distally. The brown body of the moth is quite hairy.

As previously noted, the adults are migratory, dispersing from the plains to the mountains annually. In transit and in the mountains they feed on nectar from flowering plants. They are nocturnal, and seek shelter during the daylight hours. They have the habit of aggregating in houses, automobiles, and other sheltered locations where they become a nuisance, soil walls, and induce allergic reactions among some individuals. They also may aggregate in natural shelters in mountainous regions, where they become prey for bears. In the Rocky Mountain region they are commonly called "miller moths".

Damage

These insects principally are pests of small grain crops grown in arid regions, although a number of irrigated crops also are at risk. Larvae readily climb plants to consume foliage, eating holes in vegetation initially, and eventually destroying the entire plant. Although they burrow into the soil during the daylight hours they do not normally feed below-ground. However, when succulent food is in short supply they will follow the plant stem down into the soil. When food supplies are exhausted large numbers of larvae may disperse in search of additional food.

Management

Adults can be captured in light traps and pheromone traps. However, males are attracted to the sex pheromone only during the autumn flight. Pheromone traps positioned at a height of 1 m or lower are more effective than those place higher. Larvae can be recovered from soil by raking through the top 5–7 cm.

Persistent insecticides can be applied to vegetation to kill army cutworm larvae when they emerge from the soil to feed; *Bacillus thuringiensis* is not effective. Larvae also will accept bran bait containing insecticide.

Cultural manipulations are not generally effective to prevent oviposition because moths will deposit eggs on barren soil. Delayed planting of crops can be effective, however, as larvae complete their development on weeds or starve before crops are planted. If larvae are dispersing, creation of deep ditches with steep sides, or filled with running irrigation water, may prevent invasion of fields.

To protect plants grown in the home garden, barriers are sometimes used to reduce access by cutworms to seedlings. Metal or waxed paper containers with both the top and bottom removed can be placed around the plant stem to deter consumption. Aluminum foil can be wrapped around the stem to achieve a similar effect. Because larvae will burrow and feed below the soil line, the barrier should be extended below the soil surface.

► Wheat Pests and their Management

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Armyworm, *Pseudaletia unipuncta* (Haworth) (Lepidoptera: Noctuidae)

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Armyworm also occurs in many areas of the world, including North, Central and South America, southern Europe, central Africa, and western Asia. It is known principally as a grain pest. It does not overwinter in northern latitudes, but disperses northward each spring, and then southward during the autumn. Because it is found widely, it has acquired several common names, including true armyworm, rice armyworm, and American armyworm.

Life History

Although not surviving year-round in cold winter areas, larvae apparently overwinter at intermediate levels, and in warm weather areas all stages may be found during the winter. The number of generations varies among locations, but in North America two generations occur annually in Ontario, Canada, whereas in the USA there are 2–3 generations in Minnesota and New York, 4–5 are reported in Tennessee, and 5–6 in southern states. A complete generation requires 30–50 days.

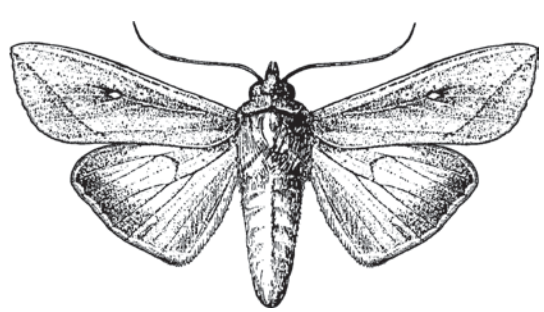
Females deposit eggs in clusters consisting of two to five rows, in sheltered places on foliage, often between the leaf sheath and blade, especially on dry grass. Often females seem to deposit large numbers in the same vicinity, resulting in very high densities of larvae in relatively small areas of a field. Nevertheless, the eggs are very difficult to locate in the field. The eggs are white or yellowish, but turn gray immediately before hatching. Eggs are spherical, and measure about 0.54 mm (range 0.4–0.7 mm) in diameter. The egg surface appears to be shiny and smooth, but under high magnification fine ridges can be observed. The egg clutches are covered with an adhesive secretion that is opaque when wet but transparent when dry. As the adhesive material dries it tends to draw together the foliage, almost completely hiding the eggs. Mean duration of the egg stage is about 3.5 days at 23°C, and 6.5 days at 18°C, but the range is 3–24 days over the course of a season. Hatching rates are affected by temperature, with cool weather more favorable for embryonic survival. In Tennessee, about 98% egg hatch occurs in early spring and autumn, with hatching rates dropping to less than 30% during the summer; this probably accounts for the evolution of the dispersal behavior in this species.

Larvae normally display 6 instars, though up to 9 instars have been observed. Mean head capsule widths (range) are 0.34 (0.30–0.37), 0.55 (0.49–0.63), 0.94 (0.83–1.12), 1.5 (1.29–1.70), 2.3 (2.08–2.56), and 3.3 (3.04–3.68) mm, respectively, for instars 1–6. Head capsule widths increase slightly with increased temperature up to about 30°C. Larvae attain a body length of 4, 6, 10, 15, 20, and 35 mm, respectively, during instars 1–6. Except for the first instar, which is pale with a dark head, the larvae of armyworm are marked with longitudinal stripes throughout their development. The head capsule is yellowish or yellow-brown with dark net-like markings. The body color is normally grayish green, but a broad dark stripe occurs dorsally and along each side (Fig. 85). A light subspiracular stripe often is found laterally beneath the dark stripe. Development time varies with temperature. During summer larvae complete their development in about 20 days, but this is extended to about 30 days during the spring and autumn, and greatly prolonged during winter. Instar-specific development times recorded during early summer in Tennessee are 2–3, 2–3, 2–4, 2–3, 4–5, and 7–10 days for instars 1–6, respectively. The larvae tend to disperse upward following hatching, where they feed on tender leaf tissue. If disturbed, they readily extrude silk and spin down to the soil. Larvae in instars 3–6 are active at night, seeking shelter during the day on the soil beneath debris or clods of soil.

Larvae pupate in the soil, often under debris, at depths of 2–5 cm. Pupation occurs in an oval cell that contains a thin silken case. The pupa is moderate in size and robust, measuring 13–17 mm long and 5–6 mm wide. The pupa is yellowish brown initially, but soon assumes a mahogany brown color. The tip of the abdomen bears a pair of hooks. Duration of the pupal stage is 7–14 days during summer but longer early and late in the season, sometimes lasting 40 days.

The adult is a light reddish brown moth with a wing span measuring about 4 cm. The forewing is fairly pointed (Fig. 84), appearing more so because a transverse line of small black spots terminates in a black line at the anterior wing tip. The forewing is also marked with a diffuse dark area centrally containing one or two small white spots. The hind wings are grayish, and lighter basally. Adults are nocturnal. Mating commences 1–3 days after moths emerge from the soil, and usually 4–7 h after sunset. Eggs are normally deposited within a 4–5 day period (range 1–10). Females produce an average of 4.9 egg masses (range 1–16). Reproductive capacity varies, with authors reporting mean egg production anywhere from 500 to 1500 per female. Feeding is necessary for normal oviposition. Mean longevity at warm temperatures is about 9 days in males and 10 days in females (range 3–25) whereas at cool temperatures mean longevity of males is 19 days and females 17 days.

Armyworm generally prefers to oviposit and feed upon plants in the family Gramineae, including weedy grasses. Thus, such grain and grass crops as barley, corn, millet, oats, rice, rye, sorghum, sugarcane, timothy, and wheat may be consumed, as well as wild or weed grasses. During periods of abundance larvae feed more generally, damaging such crops as alfalfa, artichoke, bean, cabbage, carrot, corn, celery, cucumber, lettuce, onion, parsley,



Armyworm, *Pseudaletia unipuncta* (Haworth) (Lepidoptera: Noctuidae) Figure 84 **Adult of armyworm, *Pseudaletia unipuncta* (Haworth).**

parsnip, pea, pepper, radish, sugarbeet, sweet potato, watermelon, and others. Adults feed on nectar of various flowers and sometimes feed on other sweet foods such as ripe and decaying fruit.

The importance of natural enemies, especially parasitoids, has been studied, though nearly all data are derived from periods of high armyworm density, which is not typical for this insect. Over 60 species of wasp and fly parasitoids are known, and vary considerably from time to time and place to place in importance.

Predators readily consume armyworm larvae. Ground beetles (Coleoptera: Carabidae) are especially effective because larvae spend a great deal of time in association with soil, but various predatory bugs (Hemiptera: various families), ants (Hymenoptera: Formicidae), and spiders (Araneae: Lycosidae and Phalangiidae) also feed on armyworm. Avian predators are often credited with destruction of armyworms. The bobolink, *Dolichonyx oryzivorus* (Linnaeus), prospers during outbreak years and has sometimes been called the "armyworm bird" in North America. Other birds of note include the crow, *Corvus brachyrhynchos* Brehm, and starling, *Sturnus vulgaris* Linnaeus.

Diseases commonly infect armyworms, especially during periods of high density. Bacteria and fungi, particularly the fungus *Metarhizium anisopliae*, are reported in the literature. Nematodes are sometimes considered to be important mortality factors. However, undoubtedly the most important diseases are viruses; several granulosis, cytoplasmic polyhedrosis, and nuclear polyhedrosis viruses often kill virtually all armyworms during periods of outbreak, especially when larvae are also stressed by lack of food or inclement weather.

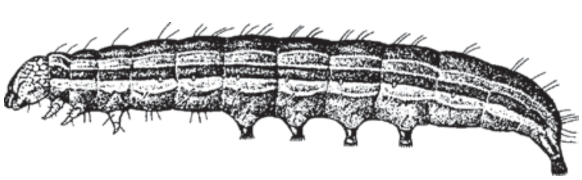
Armyworm attains high densities irregularly, often at 5–20 year intervals. The exact cause is unknown, but outbreaks often occur during unusually wet years and are preceded by unusually dry years. Armyworm is not well adapted for hot temperature; survival decreases markedly when temperatures exceed about 30°C. Consequently, at southern latitudes populations are higher early and late in the year, but at northern latitudes it is a mid season pest.

Damage

Larvae initially skeletonize foliage, but by the third instar they eat holes in leaves, and soon afterwards consume entire leaves. Larvae of armyworm (Fig. 85) are notorious for appearing out of nowhere to inflict a high level of defoliation. This occurs for several reasons: a highly clumped distribution of young larvae, with most of the crop uninfested until larvae are nearly mature and highly mobile; a tendency by larvae to feed on grass weeds preferentially, only moving to crops after the grass is exhausted; occurrence of a preponderance of feeding, about 80%, in the last instar; the nocturnal behavior of larvae, which makes them difficult to observe during the day; and the gregarious and mobile behavior of mature larvae, which form large aggregations or bands (hence the common name "army" worm). As previously noted, grasses and grains are preferred, but as these plants are consumed larvae disperse, often in large groups, to other plants. During outbreaks, few plants escape damage.

Management

Adults can be captured with blacklight traps, and a sex pheromone has been identified and can be used for population monitoring. It is advisable to examine crop fields for larvae, especially if moths have been captured in light or pheromone traps. Fields should be examined at dawn or dusk, because larvae are active at this time. If it is necessary to check fields during the day, it is important to sift through the upper surface of the soil and under debris for resting larvae.



Armyworm, *Pseudaletia unipuncta* (Haworth) (Lepidoptera: Noctuidae), Figure 85 Larva of armyworm, *Pseudaletia unipuncta* (Haworth).

Larvae will consume wheat bran or apple pomace baits treated with insecticide, but foliar and soil-applied insecticides are also effective, and used frequently.

Cultural practices have limited effect on armyworm abundance due to their highly dispersive behavior. However, grass weeds are a focal point of infestation, and should be eliminated, if possible. Not surprisingly, no-till and minimum tillage fields experience greater problems with armyworm, relative to conventional tillage fields. Proximity to small grain crops is considered to be a hazard due to the preference of moths for such crops, and the suitability of grains for larval development. In Virginia, destruction of winter cover crops by herbicide application is more favorable to armyworm survival than is mowing of cover crops, apparently because predators are more disrupted by herbicide treatment. Prior to the availability of effective insecticides, deep furrows with steep sides were sometimes plowed around fields to prevent invasion by dispersing armyworm larvae. Although this approach remains somewhat useful, it is rarely practiced.

► Turfgrass Insects and their Management
► Wheat Pests and their Management

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Arnett, Jr., Ross Harold

Ross Arnett was born on April 13, 1919, in the state of New York. He attended Cornell University and earned a B.S. degree in 1942. That same year, he married Mary Ennis, spent a short time working for the New York Conservation Department, then joined the U.S. army. His army duties had him controlling mosquitoes in Florida, and then teaching mosquito taxonomy in Panama. In October 1945, he was discharged by the army, and returned to Cornell University as a graduate student. He received his master's degree in 1946, having studied medical and aquatic entomology. For his doctoral research, he returned to his early interest in beetles, beginning a taxonomic revision of the North American Oedemeridae, and he received his Ph.D. in 1948. He was employed (1948–1954) by the U.S. Department of Agriculture as a taxonomist at the U.S. National Museum, 1954–1958 as professor of biology at Saint John Fisher College in New York state, 1958–1963 as professor of biology at the Catholic University of America (in Washington, DC), 1966–1973 at Purdue University (Indiana), and 1973–1979 at Siena College (New York state). Thereafter, he left academic life and derived his income from publishing. His research interests were in the family Oedemeridae. ("false blister beetles"), on which he published several scientific papers. However, it is as a teacher (he guided several graduate students in taxonomy of Coleoptera) and author of books and journals and publishing projects that entomologists knew him best. His "Beetles of the United States. A manual for identification" was the standard identification reference from its publication in 1962 until its replacement by the two-volume "American Beetles" (volume 1: 2000, volume 2: 2002) that he began. In 1947 he founded The Coleopterists' Bulletin and was for years its editor (it was later and ungrammatically renamed by others The Coleopterists Bulletin). In 1985 he founded the journal Insecta Mundi, which is now published by the Center for Systematic Entomology, of Gainesville, Florida, as a low-cost outlet for taxonomic publications on insects. He published a book on Coleoptera collections of North America, which later was greatly expanded to become "The insect and spider collections of the world" (1986) and still later (1993) was revised, and another (Entomological Information

Storage and Retrieval, 1970) on documentation, both of which were ahead of their time. He was author or coauthor of books on botany, on "How to know the beetles," of "Simon and Schuster's Guide to Insects," and of two volumes on "The Beetles of northeastern North America." His "American Insects" (1985) won the R.R. Hawkins award from the American Association of Publishers, but coleopterists would argue that his works on Coleoptera were far greater. He was the founder of a short-lived journal featuring colored photographs (hitherto rarely seen in entomology because of cost, yet common in everyday advertisements for commercial products) called Insect World Digest, and of two publishing companies (Flora and Fauna publications, and Sandhill Crane Press), which helped entomologists and other biologists to publish their works. He was the instigator in the 1970s of the "North American Beetle Fauna Project," whose ambition was to catalog and document all of the North American Coleoptera. He was the greatest proponent of North American coleopterology for over 50 years. He died on July 16, 1999, in Gainesville, Florida, survived by his devoted wife, Mary Ennis Arnett, who died on January 3, 2002, and eight children.

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Arolium

A pad or pads found between the tarsal claws or at the base of the tarsi.

► Legs of Hexapods

Arrestant

A factor that causes an insect to aggregate at the site of the factor, but not a factor facilitating long-distance orientation (i.e., not an attractant).

Arrhenogenic

A sex determining system, in which females produce male progeny only. Found in the blow fly *Chrysomya rufifacies* (Calliphoridae).

Arrhenophanidae

A family of moths (order Lepidoptera). They also are known as tropical lattice moths.

► Tropical Lattice Moths

► Butterflies and Moths

Arrhenotoky

A form of parthenogenesis in which an unfertilized egg develops into a male by parthenogenesis and a fertilized egg develops into the female. Arrhenotoky is found in many Hymenoptera.

Artematopididae

A family of beetles (order Coleoptera). They commonly are known as soft-bodied plant beetles.

► Beetles

Artheneidae

A family of bugs (order Hemiptera, suborder Pentamorpha).

► Bugs

Arthropleidae

A family of mayflies (order Ephemeroptera).

► Mayflies

Arthropod-Associated Plant Effectors (AAPEs): Elicitors and Suppressors of Crop Defense

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Interactions between plants and insects have played a significant role in the evolution of both groups of organisms. In response to herbivory, plants have evolved the ability to perceive and defensively respond to insect herbivores (or potential herbivores), either directly, by inducing biochemical changes that impede pest growth or indirectly, by promoting advantageous interactions with beneficial organisms, often through the release of volatile signals. These volatile signals indicate to parasitic and predaceous insects the location of potential prey. Insects may also partly inhibit these induced plant responses by limiting the accumulation of defense-related biochemicals at the feeding site. We collectively refer to substances that either negatively or positively alter plant responses to attack as arthropod-associated plant effectors (AAPEs). Those effectors that increase a plant's defense against an arthropod pest are termed elicitors while those that reduce a plant's defense are suppressors.

Research on arthropod-associated elicitors and suppressors of plant responses traces its roots to the 1972 discovery by Clarence Ryan and colleagues that feeding by Colorado potato beetle (*Leptinotarsa decemlineata*), as well as mechanical damage to tomato plants, rapidly increases the concentration of leaf protease inhibitors. This ultimately led to the discovery of systemin, an 18 amino acid peptide, and established the existence of peptide signals in plants. In 1988, Marcel Dicke and colleagues demonstrated that herbivory by spider mites (*Tetranychus urticae*) induced plant volatiles in lima bean (*Phaseolus lunatus*) leaves, which in turn served as attractants for predatory mites (*Phytoseiulus persimilis*). Shortly thereafter, Jim Tumlinson and colleagues demonstrated similar volatile-mediated tritrophic interactions among the beet armyworm (*Spodoptera exigua*) herbivore, corn (*Zea mays*), and host-seeking parasitic wasps (*Cotesia marginiventris*). In corn, this rapidly induced increase in volatile emission could not be stimulated by mechanical damage alone yet was readily mimicked by the application of beet armyworm oral secretions to wounded leaves. In 1997 the fatty acid-amino acid conjugate *N*-17-hydroxylinolenoyl-L-glutamine, termed volicitin, was discovered in the oral secretions of beet armyworm. This elicitor of corn leaf volatiles marked the first AAPE isolated and identified from insects.

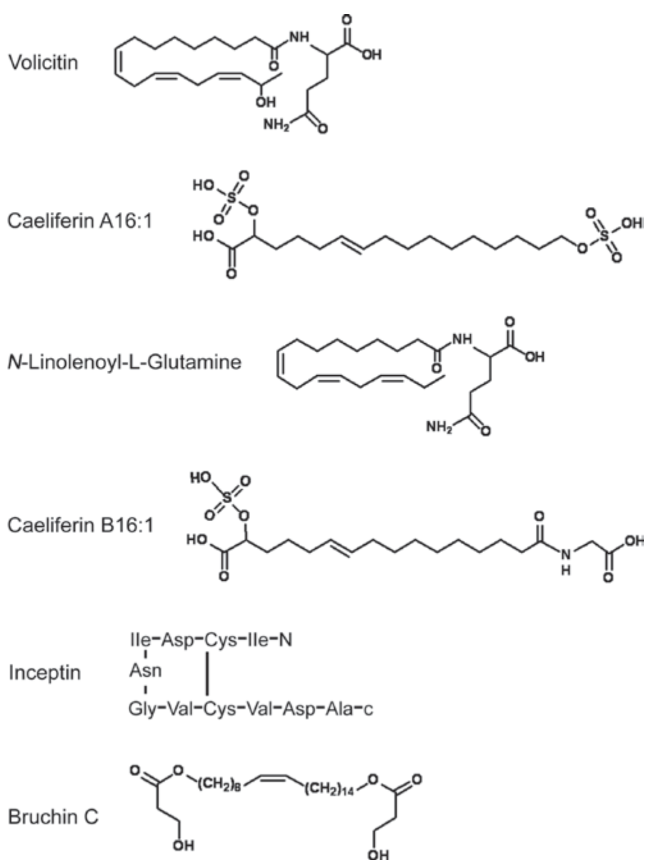
During arthropod feeding or oviposition, mechanical wound responses in the plant can be greatly amplified by the presence of elicitors. Elicitors are specific bioactive chemicals present at the plant wound-site that may be derived from the insect, the plant, or from the interactions between organisms. The mode of action of elicitors may vary, but increasingly some classes are predicted to act as ligands that bind plant receptors (likely membrane-bound extracellular leucine-rich repeat receptor kinases) initiating a complex cascade of signal transduction leading to induced plant responses. Typically, over the course of a few hours, elicitors will cause a rapid induction of defense-related phytohormones, including jasmonic acid, ethylene, and salicylic acid which serve as both markers and signals for subsequent plant defense responses. In contrast to elicitors, suppressors of plant defense may act through direct insect-derived protein/enzyme interactions within the plant. The majority of recently identified AAPEs described below act as elicitors of plant defense; however, glucose oxidase acts as a suppressor of plant defense.

Volicitin

In 1997, Hans Alborn and colleagues isolated and identified volicitin from the larval oral secretions of the beet armyworm (BAW), *Spodoptera* *exigua*. Subsequently, other analogous fatty acid amide elicitors have been identified in the oral secretions of several other species of Lepidoptera. This class of elicitors consists of plant fatty acids, typically linolenic, linoleic, and oleic acid, or their 17-hydroxy analogs, conjugated with glutamine or glutamic acid. They were initially thought to be specific for Lepidoptera but recently they have also been found in katydids, crickets and fruit flies. Thus far, three herbivore-produced fatty acid-amino acid elicitors, volicitin, *N*-linolenoyl-L-glutamine and *N*-linolenoyl-L-glutamate (Fig. 86), have been demonstrated to have significant activity in inducing plants to produce and release volatile organic compounds that are synthesized by several different biosynthetic pathways, including the lipoxygenase, shikimate and isoprenoid pathways. Fatty acid amides seem to have activity on a broad range of plants, although some clear exceptions exist (see inceptin below). A significant release of volatiles can typically be detected a few hours after an application of about 10 pmol volicitin/corn seedling.

Caeliferins

In the early 1990s, when working on the isolation of volicitin, the Tumlinson group observed that not only feeding by lepidopteran larvae but also feeding by the American grasshopper (*Schistocerca americana)* induced corn seedlings to release volatile organic compounds. This led to the recent discovery of a new type of elicitor named caeliferins. These



Arthropod-Associated Plant Effectors (AAPEs): Elicitors and Suppressors of Crop Defense, Figure 86 Structures of some elicitors.

compounds are comprised of saturated and monounsaturated, sulfated alpha-hydroxy fatty acids (with fatty acid chains of 15–20 carbons) in which the omega carbon is functionalized with either a sulfated hydroxyl or a carboxyl conjugated to glycine via an amide bond. In the oral secretions of the American grasshopper, the 16-carbon analogs are predominant and also most active in inducing release of volatile organic compounds when applied to damaged leaves of corn seedlings. It appears that caeliferins, which are the first non-lepidopteran elicitors of volatiles identified in insect herbivores, might be present in most, if not all, grasshoppers (members of the suborder Caelifera), but not in crickets or katydids (suborder Ensifera). Interestingly, oral secretions of at least some crickets and katydids contain some of the same glutamine and glutamic acid-based fatty acid amides that are found in Lepidoptera larvae. Preliminary results indicate that the activity of caeliferins might be restricted to monocotyledons where the response mimics that of volicitin. The typical lowest active dose is about 100 pmol/corn seedling.

Inceptin and Related Peptides

In cowpea (*Vigna unguiculata*) and beans (*Phaseolus vulgaris*), herbivory by fall armyworm (*Spodoptera frugiperda*) larvae and applications of oral secretions elicit phytohormone changes and induce volatile emission due to the presence of a disulfide-bridged peptide termed inceptin. Inceptin and related fragments are derived from the γ-subunit of chloroplastic ATP synthase (cATPC) present in leaf tissue. As a result of insect gut proteolysis, the oral secretion of larval fall armyworm contains a mixture of related peptides derived from cATPC, including additional amino acids at the N terminus and also C-terminal truncations. Inceptin is the one of the most potent AAPEs known to date, and has measurable elicitor activity starting at 1 fmol/leaf. Inceptin elicits a rapid and sequential induction of defense-related phytohormones, such as jasmonic acid, ethylene and salicylic acid, and also stimulates the emission of large amounts of volatile organic compounds. However, inceptin has additional roles in direct plant defense including upregulation of protease inhibitor transcripts and reduced growth of larvae on induced tissues. Similar to established peptide signals with known plant receptors, such as systemin and flg22 (derived from bacterial flagellin), inceptin is also believed to act as a ligand that specifically binds a plant receptor initiating these responses. In cowpea and beans, insect gut proteolysis following herbivory generates inappropriate fragments of an essential metabolic enzyme that enables plant non-self recognition.

Bruchins

The first beetle-derived elicitor of physical plant defense was described from the cowpea weevil (*Callosobruchus maculatus* F.). Oviposition of pea weevil (*Bruchus pisorum* L.) on pods of specific varieties of pea (*Pisum sativum* L.) promotes neoplastic cellular growths that impede entry of neonate weevil larvae into the pod and increase the probability of predation, parasitism and dehydration. This class of elicitors, collectively named bruchins, represents long-chain α,ϖ-diols, partly or entirely esterified with 3-hydroxypropanoic acid. Like the inceptin peptide, bruchins exhibit potent biological activity with as little as 1 fmol (0.5 pg) inducing neoplastic growth on pea pods. Supportive of a role for specific plant receptors, only pea plants harboring the yet uncloned Np allele exhibit these responses.

Glucose Oxidase

The first demonstration of a suppressive effect of AAPEs came from studies of the corn earworm (*Helicoverpa zea*) feeding on leaves of tobacco (*Nicotiana tabacum*). During herbivory larvae secrete the salivary enzyme glucose oxidase (GOX) from the spinneret which reacts with glucose to form hydrogen peroxide and gluconic acid. GOX levels in labial glands vary considerably dependent upon larval diet and host plants. Insect secretion of glucose oxidase limits the wound-induced accumulation of the toxic alkaloid nicotine following herbivory. As a product of GOX, hydrogen peroxide may either directly or indirectly inhibit wound-induced nicotine accumulation but this hypothesis awaits confirmation.

Other Systems for Consideration

Enzymatic activity consistent with β-glucosidase has been found in larvae of the cabbage white butterfly (*Pieris brassicae*). Applications of β-glucosidase preparations from almonds have been reported to promote volatile emission in excised leaves of Brussels sprouts (*Brassica oleracea* L. var *gemmifera*) that have been additionally wounded. Curiously, the role of β-glucosidase as an elicitor of plant volatile emission has not been followed up on in over a decade nor demonstrated outside of the aforementioned experimental system. Many lytic enzymes have the potential to influence plant physiological responses; however, clear and careful experimentation is required prior to demonstrating a substance to be a relevant effector.

Alkaline phosphatase activity has been demonstrated to exist in the salivary glands of adult whiteflies (*Bemisia tabaci* B biotype, syn. *B. argentifolii*) and is also secreted into artificial diets. This enzyme exists as a candidate AAPE but at this time no specific action on plant physiology has been shown. Alternatively, the pore-forming peptide alamethicin and larger polypeptides from preparations of cellulysin, originating from the fungus *Trichoderma viride*, are potent inducers of plant defense responses. These bioactive substances have been demonstrated to have activities similar to known AAPEs yet they are not known to exist in the secretions of arthropods at meaningful levels. Many additional plant-insect systems, such as the plant response to oviposition of insect eggs, have been clearly demonstrated to involve putative AAPEs, yet the majority of these await detailed characterization.

Significance of AAPEs

Many insect herbivores are vulnerable to predators and other natural enemies only during narrow developmental windows. For example, the parasitoid wasp *Cotesia marginiventris* must locate hosts before the end of the caterpillar's second instar. Long range attraction to the hosts is mediated by herbivore-induced plant volatiles, yet the amount of mechanical damage caused by first instar larvae is low. Elicitors, whether plant-or arthropod-produced, serve an important ecological function in amplifying plant signal transduction cascades such that a significant response (i.e., release of volatile organic compounds) is generated from a very modest initial injury.

Photosynthetic organisms have had to cope with biotic stress in the form of microbes long before the existence of insects. A significant component of plant pathology research focuses on the molecular aspects of how plants recognize pathogens and the mechanisms by which pathogens avoid recognition. Emphasis on this area of inquiry arose from necessity and the microscopic nature of the interactions. Entomologists have additional levels of complexity to confront including insect behavior, multiple instars of development and complex multitrophic interactions. Studies involving these visible markers have historically been more numerous than molecular level investigations. Plant breeders strive to maintain insect resistance in new crop cultivars, ideally one step ahead of emerging insect biotypes that overcome these defenses. Currently, numerous examples of genes responsible for plant resistance to insects are being identified as receptor kinases. These receptors are not directly toxic and by themselves do not result in plant resistance. Instead, ligand (i.e., elicitor) binding to receptors triggers induced plant responses that result in resistance. In plant pathology research, some virulent pathogens lack key biochemicals or possess slightly modified protein sequences enabling evasion of receptor-mediated plant recognition. We can fully expect the same interactions to be occurring in insect pests that are specialized on specific crops.

Once basic insect recognition systems are understood in plants at molecular and mechanistic level, strategies will be tractable to transgenically modify and promote a plant's ability to induce rapid defense responses. Some examples of future research on insect biotypes that overcome plant resistance will likely demonstrate mechanisms involving the alterations of receptor-ligand binding interactions. Currently not a single plant-insect interaction involving AAPEs is understood at this level. This research direction is essential for further progress. Understanding the chemistry of the AAPEs that mediate these interactions is more than just a research curiosity. AAPEs represent literal and figurative keys to induced plant defense and resistance to insect pests.

► Allelochemicals
► Tritrophic Interactions
► Plant Resistance to Insects

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Arthropods

Those members of the phylum Arthropoda. Animals with jointed legs. The principal arthropod taxa of interest to entomologists are:

Phylum Arthropoda
- Subphylum Trilobita – Trilobites (these are extinct)
- Subphylum Chelicerata
  - Class Merostomata – Horseshoe crabs
  - Class Arachnida – Arachnids (scorpions, spiders, ticks, mites, etc.)
  - Class Pycnogonida – Sea spiders
- Subphylum Crustacea – Crustaceans (amphipods, isopods, shrimp, etc.)
- Subphylum Atelocerata
  - Class Diplopoda – Millipedes
  - Class Chilopoda – Centipedes
  - Class Pauropoda – Pauropods
  - Class Symphyla – Symphylans
  - Class Entognatha – Collembolans, proturans, diplurans
  - Class Insecta – Insects

In addition, the Phylum Onychophora is sometimes considered to be arthropods, but it is best considered to be a separate phylum, evolutionarily intermediate between arthropods and annelids.

► Centipedes
► Diplurans
► Entognatha

- ► Millipedes
- ► Mites
- ► Pillbugs and Sowbugs
- ► Proturans
- ► Scorpions
- ► Spiders
- ► Springtails
- ► Ticks

Articulation

A connection or joint between two sections of the cuticle, or structures. Articulations take many forms, ranging from membranous or lightly sclerotized area between two plates, to a ball and socket joint.

Ascalaphidae

A family of insects in the order Neuroptera. They commonly are known as green owlflies.

► Lacewings, Antlions and Mantidflies

Ascosphaera apis

One of the best-known ascomycetous insect pathogens is *Ascosphaera* (Plectomycetes). *Ascosphaera apis* causes chalk-brood disease mainly in honey bees, a condition that may not necessarily be serious depending upon the hygienic behavior of the insects; colonies from which diseased brood is removed by worker bees appear to be resistant to the disease. The fungus is usually heterothallic, and during sexual reproduction the trichogyne (receptive female hypha) fuses with a nutriocyte, an inflated part of the ascogonium. The nutriocytes develop asci and ascospores that form into tightly packed spheres called spore balls. The chambers that encase the spore balls are termed the sporocysts, and these appear as dark specks on mummified larvae. Enzyme analysis has been used to identify strains of *Ascosphaera*, whereas certain morphological characteristics can facilitate separation of species. These characteristics include ascospore shape, size, color and arrangement, as well as the size, color, etc., of sporocysts. The location (i.e., subcuticular, external) of the cysts also can be relevant in identification, although it has been reported that cysts of *A. apis* can occur beneath the integument in carpenter bee larvae.

Ascosphaera spores can initiate infection in healthy bee larvae either by breaching the external cuticle or through the digestive tract. Chilling appears to facilitate the infection process, and the peripheral brood, where the temperature may be lower, is therefore more easily infected. Some species of the fungus can infect solitary insects; for example, *A. aggregata* commonly occurs in alfalfa leafcutting bees. The infection is initiated only by ingestion of the spores. The hyphae invade the midgut wall and hemocoel, and eventually replace most of the larval tissues. This species of Ascosphaera does not readily digest chitin, so that sporulation is subcuticular, in contrast to *A. apis* in which the mummified surfaces usually are covered with white mycelia and darkened cysts. When sexual reproduction in *A. aggregata* is complete, and the mature ascospores are formed, the fungal mat becomes dark brown and is hard and dry. This species requires a complex medium for *in vitro* growth and thus appears to be a true obligate parasite. Other species are considered to be opportunistic since they can grow saprophytically, or only infect stressed insects.

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Ascoviruses

The members within the proposed Ascoviridae family are characterized by the accumulation of virion-containing vesicles (asco = sac, or bladder) in the hemolymph of host noctuid larvae. The membrane-bound vesicles (1–10 μm) contain hundreds of enveloped allantoid shaped virus particles that are 300–400 nm in length and 130 nm in diameter. The outer surface of the bilayer viral envelope possesses a characteristic reticulate pattern. Purified ascoviruses contain a complex of 12 structural proteins ranging from 11 to 200 kDa. Ascoviruses encapsidate a circular dsDNA (140–180 kbp) having a G + C ratio of 60%. Comparative sequence analysis of the DNA polymerase genes suggests that ascoviruses and iridoviruses shared a common ancestor. Presently, ascoviruses have been detected in several noctuids including *Autographa californica*, *Trichoplusia ni* (TAV), *Spodoptera frugiperda* (SAV), *Heliothis virescens* (HAV), *Heliocoverpa zea* (HZV), and *Scotogramma trifolii* (STV). Southern blot hybridization studies have demonstrated that the SAV genome (140 kbp) differed from the closely related TAV and HAV genomes (180 kbp). Histological examinations revealed that TAV and HAV both replicated in the nuclei of epidermal and mesodermal insect tissues, whereas SAV replication was restricted to fat body tissue.

Ascovirus infections normally retard growth and development of diseased larvae. This virus, originally identified as a Rickettsial-like organism, is slow acting, causing larval death after a prolonged period (20–30 days) of arrested larval growth. These viruses infect a limited number of cells within a particular tissue. Examination of the milky infected hemolymph under light microscopy revealed the presence of numerous virion-containing vesicles. These vesicles are produced by infected cells that undergo an apoptotic-like cleavage. *In vivo*, infected larvae have been observed to discharge infectious virus from the eversible gland. The vesicles, when fed to neonate larvae, resulted in erratic infection patterns (2–85%). However, challenge with a minutin pin dipped in virus suspensions resulted in 100% infection rates. As few as ten vesicles are infectious when delivered into the insect hemocoel. Research has demonstrated that ascoviruses can be mechanically transmitted from infected larvae to healthy larvae during oviposition by parasitoids. The ascoviruses are able to outcompete the developing parasitoid and successfully infect host larvae. It has been suggested that the incidence of ascovirus in noctuid populations, ranging from 1 to 25%, may be associated with the presence of larval parasitoids.

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Asexual

Lacking separate sexes, and reproducing by parthenogenesis.

Ash-Gray Leaf Bugs

Members of the family Piesmatidae (order Hemiptera).

► Bugs

Ash Whitefly, *Siphoninus phillyreae* (Hemiptera: Aleyrodidae)

This species affects citrus and other shrubs and trees. See also, Citrus Pests and their Management, Hemiptera.

► Citrus Pests and their Management

Asian Citrus Psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae)

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The Asian citrus psyllid *Diaphorina citri*, is of Far Eastern origin and is also called the oriental citrus psyllid. Its known range of distribution covers tropical and subtropical Asia including India, Burma, Thailand, Nepal, Sikkim, Hong Kong, Ryukyn Islands, the Philippines, Malaysia, Indonesia, Ceylon, Pakistan, Afghanistan, Reunion, and Mauritius. It is also found in Saudi Arabia in the Near East, and Brazil in South America. This insect was first discovered in the United States in 1998, and is now widespread in southern Florida.

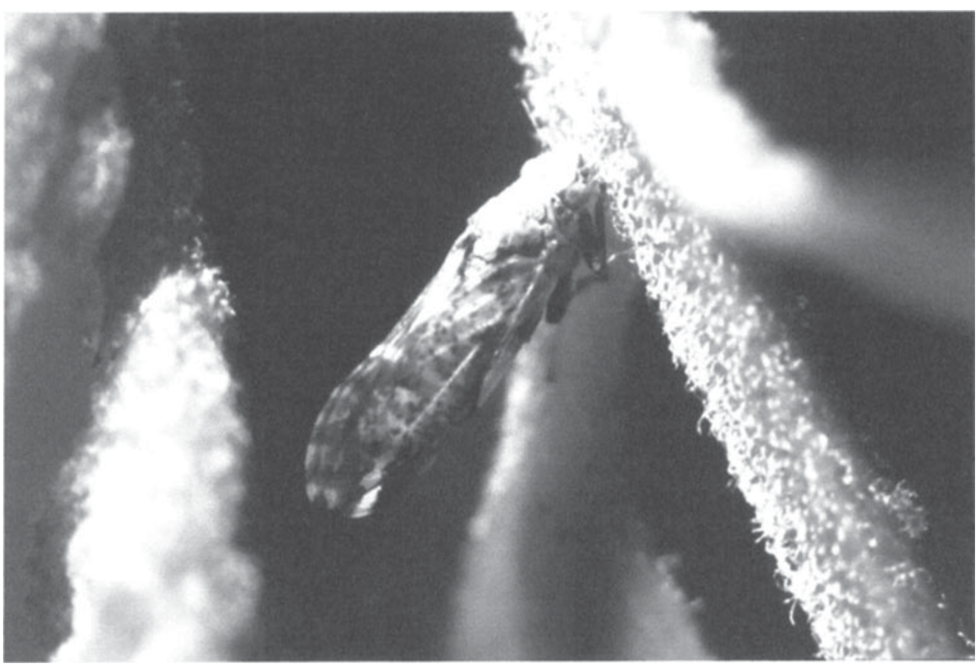
Diaphorina citri causes severe damage to citrus by: (i) withdrawal of a large quantity of sap from the foliage, affecting the overall growth of citrus, and promotion of sooty mold on honeydew secreted onto leaves, which results in reduction of photosynthesis; and (ii) efficient transmission of greening bacterium (*Liberobacter asiaticum*) by *D. citri*. The greening disease (Huanglungbin) is a limiting factor in citrus production in the Far East, though it does not occur in Florida. Citrus infected by the greening agent initially shows leaf mottling and chlorosis symptoms, followed by stunted growth, unseasonable bloom and leaf and fruit drops. Eventually, branch dieback and a general decline will result. Fruits from infected trees are small, uneven in size, off color, and having objectionable flavor. In Southeast Asia, mandarins and oranges are the main citrus trees planted in commercial groves, and they are the most susceptible cultivars. *Liberobactor asiaticum* is a phloem-limited, gram-negative bacterium which also can be readily transmitted by grafting and propagating with infected plant material. Both the nymph and adult can transmit the greening agent in 15 min acquisition feeding time. The incubation period in the vector is about 3 weeks. The infectious vector can retain the pathogen for life.

The length of the life cycle of Asian citrus psyllid varies from 27 to 117 days, depending on rearing temperature and host plants. The average developmental time for the immature stages is from 14 to 49 days within 15–28°C. *D. citri* nymphs undergo five instars. The adult longevity averages from 34 to 88 days within the temperature range of 15–30°C. The maximal longevity of individual females is 117 and 51 days at 15 and 30°C, respectively. The individual female may lay more than 748 eggs at 28°C. A total of 1,378 eggs have been reported to be deposited by a single female on grapefruit. Asian citrus psyllid can feed and breed on most citrus spp., two species of *Murraya* and three genera of Rutaceae. The developmental time of immature stages on various host plants varies significantly, ranging from 69 days on sour orange to 85 days on grapefruit. The average adult longevity on rough lemon is significantly longer than those on orange jassamine, grapefruit and sour orange. However, the females preferentially lay more eggs (averaging 858 eggs/female) on grapefruit than the other hosts mentioned above. The egg incubation period is about 4 days regardless of host plants. Eggs are deposited within 2 cm lengths of terminal tissue, including leaf folds, petioles, axillary buds, upper and lower surfaces of young leaves and tender stem. The egg is anchored on a slender stock-like process arising from the plant tissue. The egg is elongate, with a broad basal end and tapering towards its distal and curved end. The average size of egg measures 0.31 mm long and 0.14 mm wide. Freshly deposited eggs are light yellow, turning bright orange with 2 distinct red eye spots at maturity.

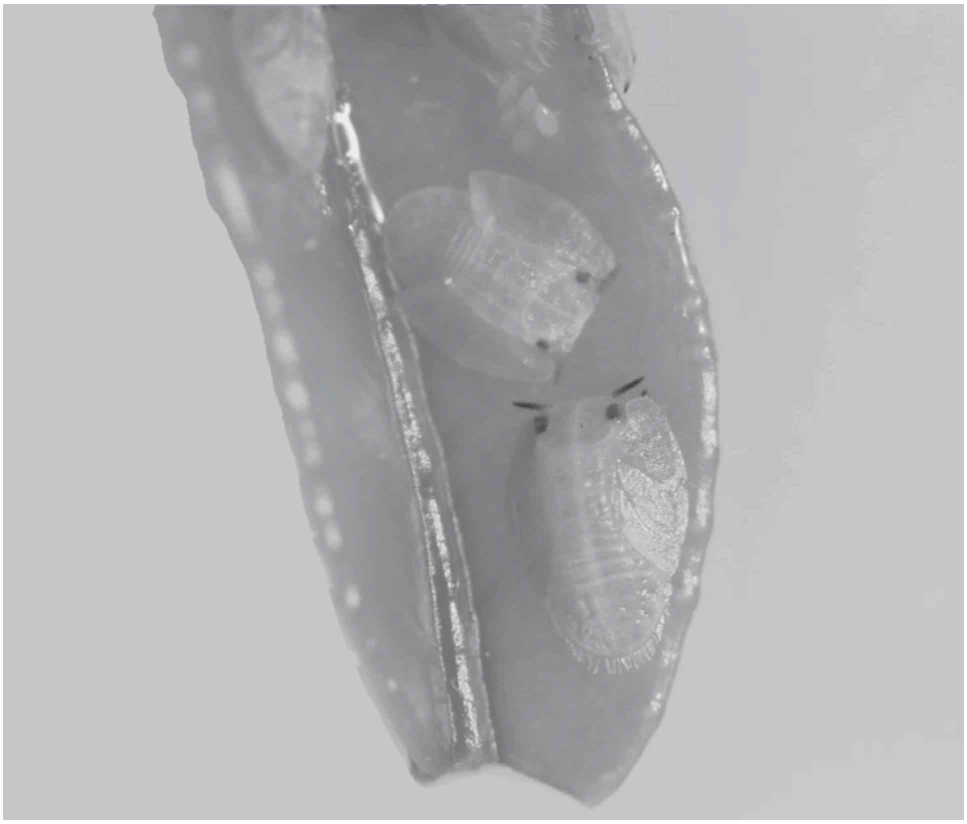
First and 2nd instar nymphs mostly aggregate and feed on the inside of folded leaves, the terminal stem and between the axillary bud and the stem of tender shoots. Young nymphs are quite docile and they only move when disturbed or overcrowded. The nymphs continuously secrete a copious amount of honeydew from the anus, and thread-like waxy substance from the circumanal glands, resulting in the growth of black sooty mold on the lower leaves. The average size of 1st instars measures 0.30 mm in length and 0.17 mm in width with light pink body and a pair of red compound eyes. The measurement of 2nd instars averages 0.45 mm long and 0.25 mm wide. The rudimentary wing pads are visible on thoracic dorsum. The average size of 3rd instars is 0.74 mm long and 0.43 mm wide. The wing pads are well developed and the segmentation of antenna is evident. The 4th instar averages 1.01 mm long and 0.70 mm wide. The wing pads are well developed; the mesothoracic wing pads extend towards 1/3 of compound eyes and the metathoracic wing pads extend to 3rd abdominal segment. The 5th instar averages 1.60 mm long and 1.02 mm wide. The mesothoracic wing pads extend towards the front of compound eyes; the metathoracic wing pads extend to 4th abdominal segment. In some mature nymphs, the abdominal color turned bluish green instead of pale orange.

Adults of *D. citri* (Fig. 87) are often found to rest on the terminal portion of plants, especially on the lower side of the leaves, with their heads pointing to the leaf surface at a 30° angle. When disturbed, they readily take flight to a short distance. The females only oviposit on the tender shoots. In the absence of suitable tissue, oviposition ceases temporarily. The average size of the adult female is 3.3 mm in length and 1.0 mm in width; the mean size of the adult male is 2.7 mm long and 0.8 mm wide.

Control of Asian citrus psyllid can be achieved by insecticide application. It is advisable to target the nymphs, (Fig. 88) as they are less mobile and concentrated on terminal tissue. However, other non-chemical control methods have been widely accepted; they include the use of such natural enemies as syrphids, chrysopids, coccinellids and parasitic wasps. The success in Reunion of using the eulophid (*Tamarixia radiata* Waterston) to control Asian citrus psyllid is a good example of biological



Asian Citrus Psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), Figure 87 Adult Asian citrus psyllid, *Diaphorina citri* (photo J. Tsai).



Asian Citrus Psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), Figure 88 **Nymphs of Asian citrus psyllid (photo Lucy Skelley, University of Florida).**

control. Other control measures, such as injecting infected trees with tetracyline antibiotics, establishing disease free nursery and monitoring and removing diseased trees from the grove are also known to be effective.

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Asiatic Garden Beetle, *Maladera castanea* (Coleoptera: Scarabeidae)

A native of Asia, this insect was accidentally introduced to northeastern North America where it became a turf pest. See also, Turfgrass Insects and their Management.

► Turfgrass Insects and their Management

Asilidae

A family of flies (order Diptera). They commonly are known as robber flies.

► Flies
► Robber Flies

Asiopsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Asiopsocidae

A family of psocids (order Psocoptera).

► Bark-Lice, Book-Lice or Psocids

Asparagus Aphid, *Brachycorynella asparagi* (Mordvilko) (Hemiptera: Aphididae)

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Asparagus aphid is found widely in eastern Europe and along the Mediterranean Sea. It invaded North America about 1969, where it was first detected in New York. It dispersed (or was dispersed) quickly, attaining North Carolina in 1973, British Columbia in 1975, Missouri and Washington in 1979, Alabama, Georgia, Oklahoma and Idaho in 1981, and California in 1984. Although it is abundant across the northern portions of North America, and very abundant along the west coast including southern California, it is uncommon in the humid southeastern states.

Life History

Oviparous aphids deposit overwintering eggs on asparagus ferns in September or later. Beginning in about March, eggs hatch into aphids that develop into stem mothers (fundatrices). Fundatrices move to asparagus spears and give birth to about 18 nymphs. Subsequent generations may be apterous (wingless) or alate (winged). Sexual forms are produced in the autumn, mate, and the females deposit eggs on the asparagus plant. Duration of a complete generation is about 15–19 days at 25°C.

The eggs initially are green in color, but turn shiny black within 1–2 days. Females produce, on average, 10.5 overwintering eggs during their life span. The elliptical eggs are deposited in the lower one-third of the asparagus canopy.

The grayish green nymphs exhibit four instars, the durations of which are about 2 days each, regardless of the morph or sex. Thus, nymphal development time averages about 8–9.5 days. Each female produces about 55 nymphs at 23°C, but only 27 and 9 at 14 and 32.5°C, respectively.

Both the alate and apterous adult viviparous aphids are present throughout the summer months, and reproduce parthenogenetically. The adults are relatively small, measuring 1.2–1.7 mm in length, and with short antennae. They are elongate oval in shape, and green or gray-green in color, often covered with a whitish waxy secretion. They blend in well with asparagus foliage, but impart a slightly bluish gray tint when the infestation is heavy. The most important character for distinguishing viviparous asparagus aphid from other asparagus-infesting species is the inconspicuous cornicles and long cauda of *B. asparagi*. Egg-producing females survive up to about 20 days.

This aphid feeds only on species of *Asparagus*. In addition to garden asparagus, *Asparagus officinalis*, it is known to feed on ornamental *Asparagus* spp.

A large number of native predators, parasitoids, and insect diseases affect asparagus aphid. Among the most important are ladybirds (Coleoptera: Coccinellidae), green lacewings (Neuroptera: Chrysopidae), and a parasitoid of many aphid species, *Diaeretiella rapae* (M'Intosh) (Hymenoptera: Braconidae). Other species of some importance are brown lacewings (Neuroptera: Hemerobiidae), the predatory midge *Aphidoletes aphidimyza* Rondani (Diptera:

Cecidomyiidae), flower flies (Diptera: Syrphidae), and other wasps (Hymenoptera: Braconidae and Aphelinidae). Natural enemies are reported to keep the population in check in eastern North America, but once attaining the arid western regions of North America asparagus aphid developed into a severe pest, and was seemingly little influenced by natural enemies. This suggests that climate plays a significant role, perhaps in conjunction with weather-sensitive natural enemies such as fungi.

Damage

Aphids feed on the new growth, causing shortening of the internodes, rosetting, dwarfing, and reduced root growth. Asparagus aphids deplete the sugars, particularly in the roots, and to a greater degree than some other aphids. Heavily infested plants have a bushy or bonsai-like appearance. Aphid infestation can kill seedlings or small plants in a relatively short time. Older, well established plantings may show damage and even death in the year following infestation by aphids, especially following a particularly cold winter. Freezing and aphid infestation are synergistic; together they reduce survival and vigor of dormant asparagus crowns greater than either aphid feeding or freezing alone. The threat of damage is much greater in western areas than in eastern North America, and it remains an infrequent pest in Europe.

Management

Egg hatch can be predicted from temperature models. Eggs can be separated from foliage by washing with petroleum cleaning solvent. Nymphs can be extracted from plants by heat or methyl isobutyl ketone. Aphid distribution tends to be clumped, with most aphids in basal regions of the plants. A sample of about 140 branches per field is optimal for making management decisions.

Foliar insecticides can suppress aphids, but multiple applications may be necessary, especially under high density conditions. Granular systemic insecticides may provide long term control. Some research has also been done to demonstrate the possibility of delivering insecticides to asparagus through the irrigation system.

Several cultural practices for suppression of asparagus aphid were investigated. Autumn and spring tillage reduce aphid overwintering but also reduce subsequent spear production. Mowing and herbiciding within asparagus fields can destroy early season aphids and delay the buildup of damaging populations. However, destruction of wild (volunteer) asparagus is the most important cultural practice available because it eliminates overwintering sites and limits invasion of aphids into commercial, aphid-free fields. Herbiciding, burning and removal of asparagus crowns by digging are all viable options to eliminate volunteer asparagus.

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Aspergillus spp. Fungi

Aspergillus spp. fungi cause a disease in honeybees called stonebrood. Several species may be involved, although *A. flavus* and *A. fumigatus* are most commonly implicated.

► Stonebrood

Aspirator

A device used to collect small terrestrial arthropods. Although there are many variations in design, the principle behind the designs is the same – air current causes the insect to be sucked (aspirated) into a tube or tubing that leads to a container/receptacle area. The key feature of the aspirator is that although the arthropod can be sucking into the container, it cannot be sucked further (inhaled in the case of mouth aspiration) because a fine screen blocks its egress, so it is retained/captured. The principal variables associated with aspirators are the form of suction (mouth or mechanical), length and shape of the tube/intake, and the size of the container/receptacle. This apparatus works well for small and/or weakly flying insects.

Assassin Bugs, Kissing Bugs and Others (Hemiptera: Reduviidae)

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The Reduviidae are a large, cosmopolitan, and morphologically diverse family of predatory true bugs. They include assassin bugs (genera include *Melanolestes*, *Psellipus*, *Rasahus*, *Reduvius*, *Rhiginia*, *Sinea*, and *Zelus*), wheel bugs (*Arilus cristatus*), kissing bugs (species of *Triatoma*, *Rhodnius* and *Panstrongylus*), ambush bugs (genera *Apiomerus* and *Phymata*), and thread-legged bugs (the subfamily Emesinae, including the genus *Emesaya*).

Taxonomy

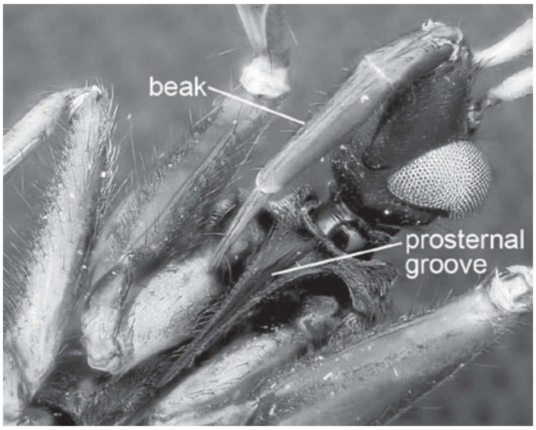
In 1843, Amyot and Serville recognized the reduvids as a discrete group. In its present systematic organization, the large family Reduviidae contains around 25 subfamilies, about 930 genera and 6800 species. Composition of subfamilies and relationships between them remain unsettled. Subfamilies Harpactocorinae (about 2,000 species), Reduviinae (about 1,000 species), Emesinae (about 900 species), Stenopodinae (more than 700 species) and Ectenodeminae (more than 600 species) together total more than 80% of known reduviid species. An additional five minor subfamilies contain only 3 or 4 species. Ten genera contain between a hundred and two hundred species each.

Morphology

Adult bugs vary greatly in body size, ranging from 3.5 mm in such reduviids as the genus *Empicoris* (Emesinae) to 40 mm in the genus *Arilus* (Harpactorinae). The body shape is also extremely variable. Reduviidae may be robust and oval, as occurs in the genus *Reduvius,* to elongate and thread-like, as in the genus *Empicoris*. Body coloration may be cryptic or aposematic. Most species are dark in color, with hues of brown, black, red, or orange. Others are masters of disguise and camouflage, colored to blend with their substrate or to resemble their prey. Many species are very hairy or spiny, with varied body expansions.

Reduviidae can be distinguished from other bug families by their elongated head, with a transverse groove behind the compound eyes, and the short, prominent, apparently three-segmented rostrum curved (Figs. 89 and 90) outwards from the head. A characteristic of the family is that the tip of the rostrum, in repose, fits into that groove.

The head has a pair of large compound eyes, usually two ocelli, and a pair of four-segmented antennae about the same length as the body. However, subdivision of antenna segments gives an appearance of antennae with a larger number of segments. The forewings (hemelytra) lack the costal feature, and the membrane usually has two elongated cells and a few veins emanating posteriorly. Legs are usually long, normally with 3-segmented tarsi, although the tarsal formula is variable.



Assassin Bugs, Kissing Bugs and Others (Hemiptera: Reduviidae), Figure 89 **A ventral view of the reduviid head, showing the curved rostrum and a groove located ventrally. A characteristic of the family is that the tip of the rostrum, in repose, fits into that groove.**

The male genitalia are usually symmetric and the ovipositor of females is usually plate-like. Eggs have three or more micropyles.

Biology

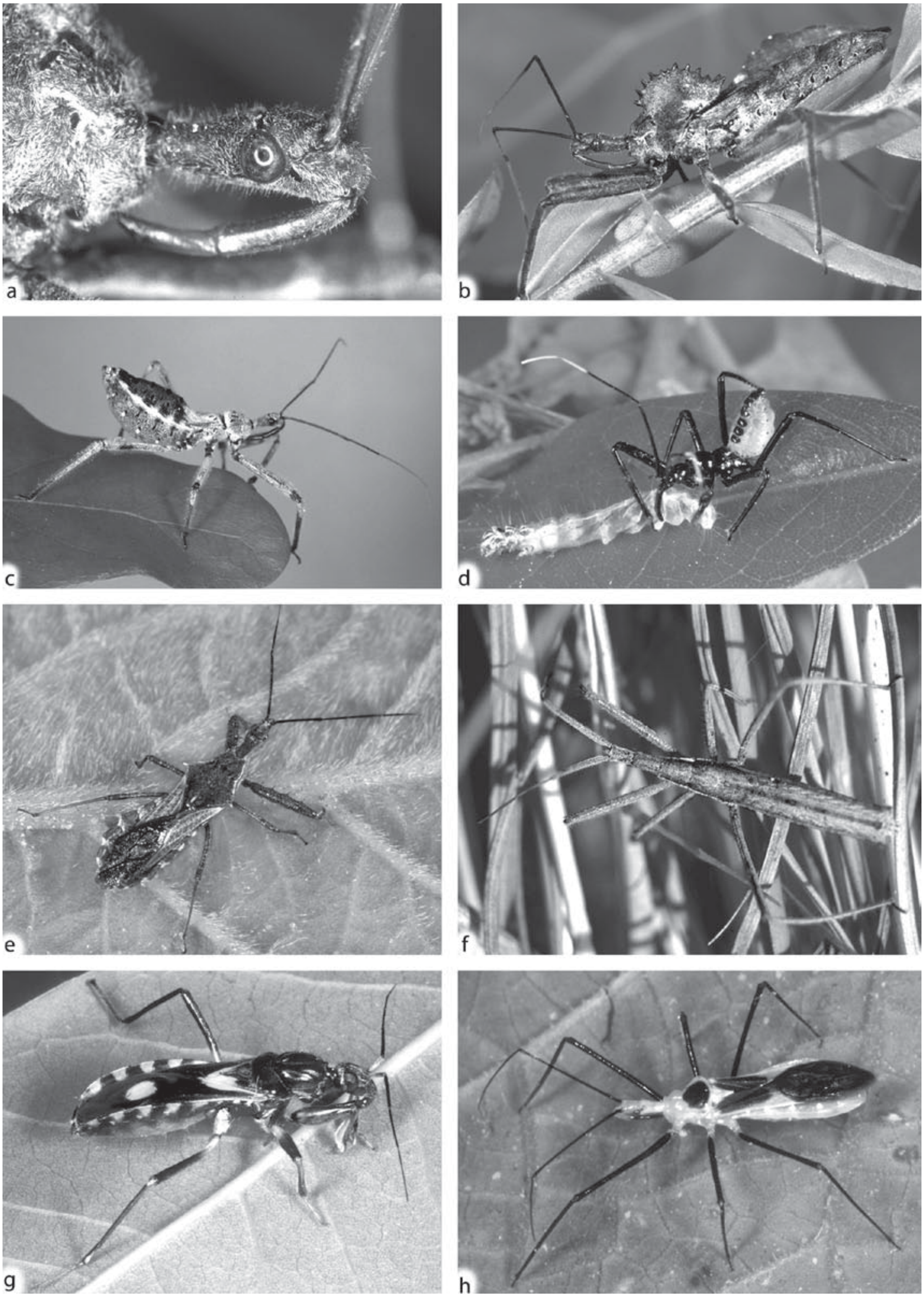
Despite their abundance and interest, reduviids have been largely ignored, and we do not know much on their biology. Triatominae are the exception, as their relationship with human diseases has stimulated their study under laboratory conditions.

Reduviidae may live in a variety of habitats in the wild, and tend to occupy warm environments. Sylvatic triatominae are found in burrows and nests of wild vertebrates, among rocks, fallen timber, hollow trees, roots, palms and bromeliads. In the subfamily Emesinae, some species are cavernicolous, but lack the characteristics common to many cave dwellers such as eyelessness or depigmentation. Among Emesinae and Triatominae, some species are domestic or peridomestic, which increase the medical importance of Triatominae as vectors of the protozoan *Trypanosoma cruzi*. The attraction of Triatominae to light also enhances the likelihood that they will enter inhabited structures and contact humans.

Reduviidae are well adapted for their physical environment. They may pass through inclement periods in the egg, nymphal or adult stage. Number of generations per year ranges from one to several, but in other cases the completion of life cycle may take more than 1 year. Longevity is also very variable among species. Some Salyavatinae live <2 weeks, whilst some Reduviinae live for about 7 months.

Except for Triatominae, which are hematophagous and feed on vertebrate blood, all reduviids prey on other insects. First step of attack is with the legs, whose length allow a longer attack distance. Also, the legs of some of these bugs are covered in tiny hairs that serve to make them sticky to grip prey while they feed in the manner of flypaper. Other assassin bugs (subfamily Apiomerinae) go one step further and collect certain plant resins which they spread over their front legs; these resins are very attractive to insects, and to bees in particular. Once the prey is grasped, the reduviid feeds by puncturing it with sharp stylets in their rostrum, injecting saliva which will paralyze the prey and liquify its tissues, to then finally sucking up the body fluids. The saliva is commonly effective at killing prey substantially larger than the predatory bug itself. In contrast, the genus of the small reduviid *Ptilocerus* uses chemical lures located in a special ventral abdominal gland to trap and prey on ants. The ants are very attracted by this secretion, which paralyses them. Also, reduviids that tackle large and dangerous prey like wasps or bees tend to make the first stab near the victim's head or neck, thus ensuring that their toxic saliva has maximum effect in the shortest possible time.

In Triatominae, ingestion of blood is possible thanks to different enzymes present in the bug saliva that counterbalances the hemostatic response on the part of the vertebrate host. Bug saliva is provided with anticoagulants (preventing the coagulation of host blood in the insect's suction apparatus), apyrases, platelet antiaggregation factors, antiserotonin, antihistamine, tryalisine (lytic protein which



Assassin Bugs, Kissing Bugs and Others (Hemiptera: Reduviidae), Figure 90 **Some reduviids: (a) Anterior view of a reduviid, showing their elongated head and the short, prominent, apparently 3-segmented rostrum curved outwards from the head; (b) adult wheel bug, *Arilus cristatus*. This is one**

permeabilizes mammalian cells), emollient factors, antithromboxane and a vasodilator. Blood is stored in the crop and stomach of triatomine. Several days later, erythrocytes are lysed, and the accessible hemoglobin is then digested. Blood ingestion is needed by nymphs to complete development, and by adults to perform reproduction, as cyclical egg laying is related to blood meals.

Reduviids are generally polyphagous, but there are also cases of prey specialization. For example, the subfamily Emesinae contains a number of genera (*Eugubinus*, *Ploiaria*, *Emesa*, *Stenolemus* and *Empicoris*) in which elongate, thread-legged member species feed on insects caught in spiders' webs, or on the spiders themselves. These slender, slow-moving bugs never get trapped in the spider silk, as they avoid the sticky spirals and walk very carefully so that they are not trapped in the spider silk. An extraordinary case of coprophagy is found in the Indian harpactorine *Lophocephala guerini*, which feeds on fermenting cow dung. Its microhabitat is underneath stones, in association with the formicine ant *Anoplolepis longipes,* and it is always attended and guided by these ants. However, the trophic habits of most reduviid species are still unknown.

Courtship behavior is much like in other insects, although it has some characteristic features. The sequential acts of mating behavior can be categorized into arousal, approach, riding over (precopulatory riding of Harpactorinae), nuptial clasp, extension of genitalia and connection, copulation, and postcopulatory acts. The fecundity varies between 50 eggs of the Stenopodainae to the 670 eggs of Harpactorinae. Eclosion and ecdysis occur usually in daytime.

Many species glue their eggs to the plants, often in a group, sometimes covering the eggs with a gelatinous material. Ground-dwelling species may bury their eggs in the soil, and some species of the subfamily Reduviinae have more well-developed ovipositors, suitable for the insertion of eggs into cracks.

A few species are known to guard their eggs, and in this case, the males perform the guarding. In the genus *Rhinocoris*, the female lays a batch of eggs on the plant leaf immediately after copulating. The male stands by and, when the female finishes laying, takes up his position aside the egg mass. Over the course of the next days the female lays additional egg batches. While the male is guarding he generally does not feed, unless an easily catchable prey comes his way. However, when the eggs have all hatched, he loses interest and moves away. Exceptionally, the guarding male may be relieved by a female that had copulated with him.

In the majority of nymphs and adults, the rostrum can be used to produce sounds (stridulation) by being scraped along a medially located, ridged groove on the underside of the thoracic segments. The aim of this acoustical communication may be mate attraction, courtship and copulation. In other cases, the aim is intimidation, and thus, some reduviids stridulate defensively. Non-receptive females may emit male-deterring vibrations.

Reduviids have an array of defensive and offensive behaviors, accompanied by morphological adaptations. These behaviors threaten other

of the largest and most easily recognized reduviids. It is found in North America and Central America, where it feeds on numerous insects, but also inflicts a nasty bite when handled by humans; (c) nymphal wheel bug, *Arilus cristatus*; (d) nymphal wheel bug, *Arilus cristatus*, feeding on a leaftier larva; (e) adult *Sinea diadema*. This species is found through most of North America including Mexico, where it inhabits meadows and crop fields. It often is reported to be an important predator of crop pests; (f) nymphal *Vibertiola cinerea*, an African savanna-inhabiting species that is now found in the Iberian Peninsula. Its host plant is the grass *Hyparrhenia hirta*, where it blends in well due to its elongated body; (g) *Rasahus* sp. bugs are found predominantly in the neotropics; (h) *Zelus longipes* is found throughout the western hemisphere where its often found feeding on caterpillars (photo credits: f, Eva Ribes, University of Barcelona; others Lyle Buss, University of Florida).

insects, aid escape from enemies and larger prey, and give protection from cannibalism. Some nymphs and adults of different subfamilies (Reduviinae, Cetherinae, Salyavatinae, Triatominae) will cover and camouflage themselves with debris, including soil particles or the remains of dead preyed insects, which are affixed by sticking objects to the viscid secretions of specialized setae located on the dorsum. The elongated slender bodies of *Rhaphiodosoma* and *Vibertiola* species (Harpactorinae) and stenopodaeines provide camouflage among the elongated grasses where they live, imparting protection from vertebrate predators. In other cases defense is active, as in harpactorine nymphs, which often fight to the death.

Some Aspects of Distribution

The distribution of Reduviidae is nearly cosmopolitan, though most taxa inhabit the tropical and subtropical regions, where they are particularly varied and abundant. Of the 6,800 species, 16% occur in Oceania, 37% in sub-Saharan Africa and 21% in the neotropics. Certain taxa with a wide distribution suggest transport by humans and their goods, or by migratory animals.

Ecological and Economic Significance

As predators, Reduviidae play a role in biological control. Their worldwide distribution, abundance, diversity, large pest prey record, amenability for mass culturing, ready synchronization and freedom from hyperparasites and predators are the merits of reduviids as potential biological control agents.

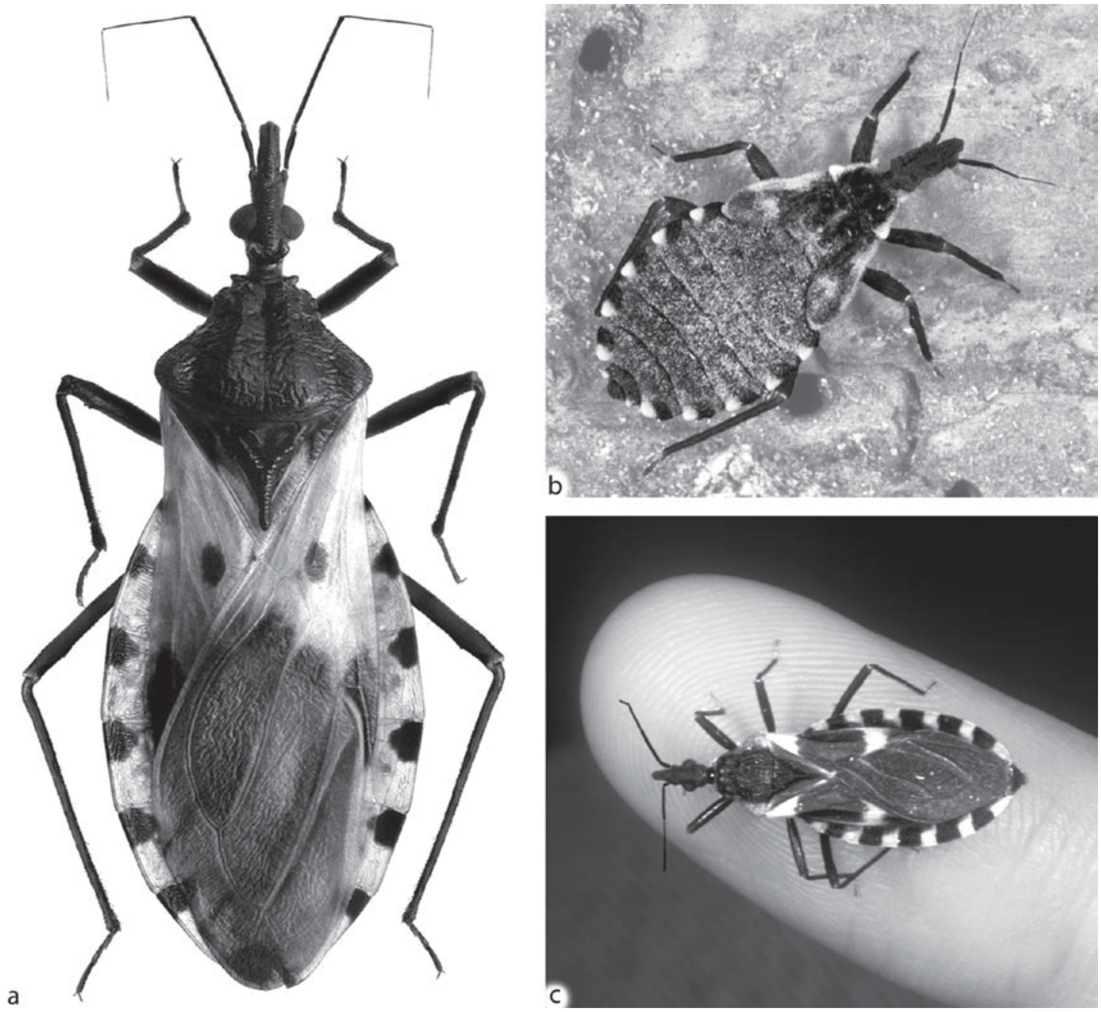
More than 150 reduviids predators belonging to 53 genera and seven subfamilies have been found preying upon a wide array of insect pests. Some species have been known to feed on cockroaches or bedbugs (in the case of the masked hunter *Reduvius personatus*) and are regarded in many locations as beneficial. They kill more prey than they need to satiate themselves. Reduviids exhibit a positive numerical response by killing more prey in terms of available prey population per predator at a given time, and by increasing their population through higher fecundity and survival.

In spite of their merits as beneficials, their potential as biocontrol agents of pests has been little studied. The better studied species in this area focus on *Rhinocoris fuscipes*, *R. kumarii*, *R. marginatus*, *Ectomocoris tibialis* and *Acanthapsis pedestris*. Other promising groups of predatory reduviids are species of *Sinea* and *Zelus*, which may help regulate insect pests on cotton. Recently, *Amphibolus venator* has been reported as a useful predator on last-instar larvae, pupae and adults of the stored-product insect pest *Trobolium confusum* (red flour beetle [Coleoptera: Tenebrionidae]). *Amphibolus venator* is commonly found in stored product facilities, shipments of groundnuts, warehouses or in rice milling facilities, and preys on other stored-product insect pests.

Because of their polyphagy, reduviids may not be useful as predators on specific pests, but they are a valuable help when a variety of insect pests occur. The counterpart of that polyphagy is that from time to time they may attack beneficial arthropods. A few of them appear to specialize on insects of some value; for example, several apiomerine reduviids feed on bees of the genus *Trigona*, that are useful pollinators.

Unfortunately, assassin bugs interact with human health negatively. They may become a nuisance, as many assassin bugs have been known to bite humans when not handled carefully. For some species the bite is known to be very painful, sometimes causing allergic reactions, and bites can become infected, as with any wound. Some of them are known to produce toxic saliva containing powerful enzymes similar to those in snake venom. As with any severe allergic reaction in humans, side effects of repeated bites may include shock and possible death. The fecal material of some reduviids can cause irritation of the eyes and nose and temporary blindness in humans.

Most important to human health are some blood-feeding triatominae species, also known as kissing bugs due to their habit of biting humans in their sleep on the soft tissue of the lips and eyes. A number of these hematophagous species are able to transmit a potentially fatal trypanosome disease known as human Chagas disease (HCD), also named American trypanosomiasis, caused by the protozoan *Trypanosoma cruzi*. These reduviids belong to genera *Triatoma*, *Rhodnius* and *Panstrongylus*, and the three most important species in this regard are *Triatoma infestans*, *T. dimidiata* and *Rhodnius prolixus* (Fig. 91). About 50 additional species belonging to the three genera mentioned above can also act as disease vectors, but they are more local in distribution so they are not as important, or as well known. Other genera involved locally in transmission of HCD are *Meccus* (Mexico), and *Microtiatomba* and *Parabelminus* (Brazil). Infestation rates of triatominae by *Trypanosoma cruzi* vary greatly from one area to another. As examples, in Brazil, 41% of 2412 triatominae bugs were infested whereas in Panama, 68.8% of 740 *Rhodnius pallescens* were infested, but only 17.7% of 94 *Triatoma dimidiata* were. In Yucatan (Mexico), infection rates of



Assassin Bugs, Kissing Bugs and Others (Hemiptera: Reduviidae), Figure 91 Kissing bugs or bloodsucking conenoses, *Triatoma* spp.: (a) adult *T. dimidiata*; (b) immature of *T. sanguisuga*; (c) adult of *T. sanguisuga* (photo credits: a, Ron Cave; others Lyle Buss, both University of Florida).

Triatoma dimidiata by *T. cruzi* ranged from 0% (in Tipoco) to 25% (in Tella). In Santander (Colombia), 48% of *T. dimidiata* contained the protozoan, while in Guayaquil (Ecuador), 50% were infested. Once infested, a bug may be infective for about 2 years. In contrast with other arthropod vectors (i.e., ticks), the protozoan cannot be transmitted to the offspring transovarially.

In 1909, the Brazilian doctor Carlos Chagas discovered the disease, and reported both the vector and the causative flagellate protozoan *Trypanosoma cruzi*. He recognized and described the disease in humans but also investigated the life cycle and other aspects of the protozoan and its insect vector. This disease is mostly found in rural areas, where the Triatominae can breed and feed on the natural reservoirs, such as opossums, raccoons, and armadillos. In fact, wild animals reported as infected with *T. cruzi* belong to the Orders Marsupialia (opposums), Edenteta (armadillos, etc.), Chiroptera (bats), Carnivora (cats, foxes, etc.), Lagomorpha (rabbits), Rodentia (mice and rats, squirrels) and Primates (monkeys). But, depending on the special local interactions of the vectors and their hosts, other infected humans and domestic animals may act as reservoirs too. Among domiciliary and peridomiciliary reservoirs are *Canis familiaris* (dog), *Capra hyrcus* (goat), *Cavia porcellus* (Guinea pig), *Felis domesticus* (cat), *Mus musculus* (mice), *Oryctolagus cuniculus* (rabbit), *Rattus novervegicus* and *Rattus rattus* (rats) and *Sus scrofa* (pig).

Trypanosoma cruzi may have both sylvatic and domestic cycles. The sylvatic cycle involves its circulation among wild small mammals and the Triatominae. The sylvatic cycle usually does not affect humans unless they enter in the wild and disturb the natural balance of wild fauna and flora. The domestic cycle, which has evolved more recently, involves humans, domestic mammals and a small number of Triatominae species that are able to live in domestic or peridomestic habitats. Although some reports on Chagas disease date back to precolumbian times, the real dispersion of the American trypanosomiases occured as a result of European conquest and the resulting disturbance of the natural balance and habitats of *T. cruzi*, its triatomine vectors, and its mammalian reservoirs.

Kissing bugs are strictly nocturnal, taking blood meal for 20–30 min and inflicting no pain to the host. When they feed, the bugs leave (infected) excrement behind on the skin. Transmission of the protozoan occurs when people scratch their bites and allow protozoa in bug defecations to infect their blood. Other forms of transmission are possible, though, such as ingestion of raw food contaminated with parasites, blood transfusion, organ transplantation and placental transmission (from infected mother to fetus).

The human disease occurs in three stages or phases: (i) the primary or acute phase, shortly after the infection, with an incubation of 15 (direct bite)-40 days (blood transfusion infection); symptoms are an inflammatory reaction, with necrosis around the bug bite site; meningoencephalitis and myocarditis are very severe consequences of this stage in children under 10 years old; (ii) indeterminate phase, 8–10 weeks after the acute stage and which may last for years without any symptom; the main danger is that the individual is unaware of being infested, acting as reservoir of *T. cruzi*; (iii) chronic stage that may develop up to 10 years after infection; the main signs are liver and heart dysfunctions, as well as, hypertrophy of the heart and certain parts of the digestive and/or excretory systems. The parasite circulates in the bloodstream, and infects, multiplies and ultimately destroys muscle and nerve cells all around the body, particularly in the heart and digestive system. The negative effects of the disease are reflected in a progressive deterioration of health, associated to increasing apathy, a decreasing capacity to perform work and a general reduction in the quality of life. If no action is taken, disease is lethal.

The disease is distributed in the Americas, ranging from the southern United States to southern Argentina, mostly in poor, rural areas of Central and South America. Domestic infestation in very poor rural zones may be of 1,000 insects per house. Human Chagas disease (HCD) has been spread into nonendemic urban areas by people migrating to cities from rural areas. In most countries where Chagas disease is endemic, testing of blood donors is already mandatory, since this can be an important route of transmission. Up to 18 million humans were affected by this disease in 1990, but recently data suggests nine million people affected, after coordinated initiatives throughout the endemic HCD area. Of some 100 million at risk of acquiring the disease in 1990, now about 60 million people are out of risk. About 200,000 new cases, and about 70,000 deaths are reported annually. Rates of human infection in endemic areas are very different, relating to different vector species or populations. In Zacapa (Guatemala), where *R. prolixus* is the principal vector, 38.8% of 373 people were infected. In contrast, in Santa Rosa (Guatemala), where *T. dimidiata* is the only vector found, only 8.9% of the 428 people studied had the protozoan. The same trends were reported in Honduras, in relationship to HCD vectors. Outside of the Americas, one genus and several bug species occur in India, where theoretically they may transmit Chagas disease.

Once infected, there are some pharmaceuticals useful to fight infections, but they are very toxic and have a lot of undesirable secondary effects. The best way to reduce HCD incidence is prevention, either by fighting the vector (*Triatoma*) or improving housing and sanitary conditions in the rural area. Vector insects may be eliminated by using sprays and paints containing insecticides (synthetic pyrethroids). Although resistance development is much lower than in mosquitos (due to long life-cycle and use of different insecticides), significant levels of resistance to deltamethrin and other pyrethroids have been reported in *Rhodnius proxilus* (Venezuela) and *Triatoma infestans* (Brazil and Argentina). Recently, oil-formulated *Beauveria bassiana* has been used against *T. sordida* and has proven to be useful in peridomestic areas of central Brazil. This could lead to implementation of integrated control by alternating application of fungi in the rainy season with synthetic insecticides in the dry season, or a combined application of fungi and insecticides in the rainy season. Those strategies could promote an efficient and permanent reduction of triatomine vectors in peridomestic areas. Also, several plant extracts showed insecticidal activity against triatomines. As examples, plants belonging to genera *Salvia*, *Annona*, *Neurolaena*, *Tagetes*, *Erythroxylon*, *Cassia*, *Senna* and *Cabralea* elicited an increase in the mortality rate (16–52%) of *Rhodnius neglectus*. Topical treatment of *T. infestans* with *Achryrocline* extracts resulted in a 45% mortality of triatomine bug. Five plant species (*Aspidosperma macrocarpon*, *Talauma ovata*, *Guarea guidonia*, *Guarea kunthiana* and *Simarouba versicolor*) from the Brazilian biome Cerrado, selected according to ethnobotanical information, have been tested in the form of 24 plant crude extracts on *Rhodnius milesi*. Most promising results were obtained from ethanolic extract of the root bark of *S. versicolor* (probably due to its antifeedant growth regulating activity) and the hexane extract of the root of *G. guidonia* (by a not yet clear activity). In addition to investigating new methods to kill triatomine bugs, considerable success has been made preventing bugs taking up residence in human domiciles.

However, the peridomicilium (considered to be the area within 100 m proximity of human dwellings) has been shown to be crucial in management of HCD. Henhouses, pigpens, corrals, perches, piles of tiles, bricks, wood and straw have to be taken into account. In research conducted in 121 peridomiciliary environments in rural areas of the state of Ceará (Brazil), triatominae (2670 specimens collected) were present in 30% of the environments, with 68.7% being shelters for domestic animals (mainly goat/sheep corrals, perches, henhouses and pigpens), and 32.3% were piles of bricks, roofing tiles or wood. Also, palm trees growing near human habitations are of great importance in HCD, as *Rhodnius* species breed in the crowns of many genera of palm trees. Specificity among insect and palm tree species may be very strict, as is the case of *R. brethesi* on *Leopoldinia piassaba*, or *R. colombiensis* on *Attalea butyracea*, but this is not always the case, as in *R. pallescens* or *R. pictipes*, which dwell in association with five host palm species each, or *R. prolixus*, with 13 host palm species. Peridomestic palm trees, especially in the presence of bird nests, may be regarded as high-risk habitats. In Ecuador, the palm seed endosperm (vegetable ivory or "tagua") and leaves of *Phytelephas aequatorialis* are used for handicraft manufacturing and roof thatching; as a result, those palms, which are the primary habitat of *Rhodnius ecuadoriensis* (a major vector of Chagas disease in Ecuador and Peru), are often found around dwellings.

For urban dwellers who spend vacations outdoors or camp in the wilderness, or who sleep at hostels or primitive houses in HCD-endemic areas, a mosquito net is recommended to reduce the risk of infection. If the traveler intends to travel to an area of HCD prevalence, he/she should get information on the incidence of Chagas disease from traveler advisories, such as the USA's Communicable Disease Center (CDC).

The Southern Cone Initiative against HCD was launched in 1991, following a resolution of the Ministers of Health of Argentina, Bolivia, Brazil, Chile, Paraguay and Uruguay. It focused on interruption of *T. cruzi* transmission by eliminating domestic vectors (particularly *T. infestans*), extending screening of blood donors, and promoting maternal screening and specific treatment of infected newborns. Similar initiatives were launched in 1997 for Central America and the Andean Pact countries. Those multinational initiatives, coordinated by the Pan American Health Organization (PAHO) allowed that on June 9, 2006, at the 15th annual meeting, the Intergovernment Commission of the Southern Cone Initiative against Chagas disease declared Brazil to be free of Chagas disease transmission due to *Triatoma infestans*. Also in Uruguay, Chile, most of Argentina, Bolivia, Paraguay and parts of Central America, transmission has been effectively eliminated. In 2004, a surveillance initiative was announced for the nine countries of the Amazon basin. To assure and increase the success obtained in this 15-year initiative, surveillance and control of the disease and its vector are currently on the agenda of all endemic countries. It is essential to keep in mind the perennial need of surveillance, data assimilation and selective interventions, as triatomines will always be present in the wild, as well as *T. cruzi* and its wild reservoirs. Schools and hospitals (obstetrics, blood donors, organ transplantation) are essential surveillance hot-spots where infestations may be detected and controlled.

► Bugs (Hemiptera)
► Trypanosomes
► Chagas Disease: Biochemistry of the Vector
► Area-Wide Pest Managment
► Chagas Disease or American Trypanosomiasis
► Parental care
► Acoustical Communication

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Assemblage

The species within a particular taxon at a location.

Associative Learning

The capacity to associate a stimulus, which itself has no positive or negative effects, with positive or negative effects. For example, bees can learn to associate color with food sources. Insects commonly display this ability.

► Learning in Insects
► Habituation
► Latent Learning
► Insight Learning

Assimilation Efficiency

The proportion of energy ingested by an animal that is absorbed into the body.

Astatidae

A family of wasps (order Hymenoptera).

► Wasps, Ants, Bees and Sawflies

Asteiid Flies

Members of the family Asteiidae (order Diptera).

► Flies

Asteiidae

A family of flies (order Diptera). They commonly are known as asteiid flies.

► Flies

Aster Leafhopper, *Macrosteles quadrilineatus* Forbes (Hemiptera: Cicadellidae)

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Aster leafhopper is native to North America, where it is nearly everywhere. It is most common, however, in the central region of the continent. Also, it overwinters poorly in cold areas. Most areas with aster leafhopper problems are invaded annually by leafhoppers originating in the southern Great Plains. In the mild-climate northwest, however, leafhoppers are able to overwinter successfully, and long-distance dispersal is not an important factor.

Life History

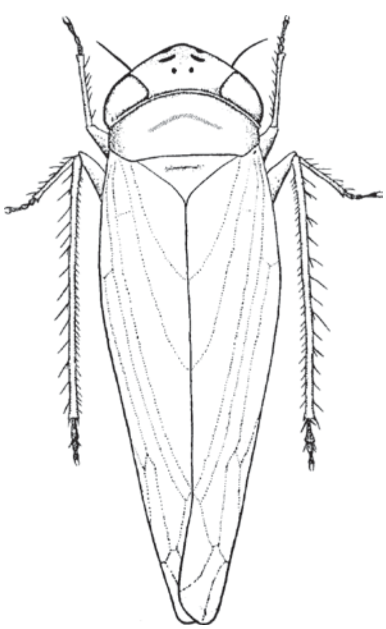
This insect overwinters in the egg stage in northern locations, and in the adult stage in warmer climates. In northern areas, there are three generations per year, whereas up to five generations may occur in more favorable midwestern locations. Because the generations overlap, and are initiated by both overwintering eggs and migrating leafhoppers, it is difficult to discern the generations. Total generation time requires about 27–34 days.

Eggs are deposited in leaf, petiole, or stem tissue, often near the juncture of the leaf blade and stem. They are deposited singly, but often in short rows of up to five eggs. They require a moist environment, and perish if the foliar tissue desiccates. The eggs are translucent when first produced, soon turning white. They average 0.80 mm in length (range 0.73–0.87 mm) and 0.23 mm in width. They are slightly curved, with one side concave and the opposite side convex, and taper to a blunt point at each end. The incubation period of the egg is about 7–8 days.

Newly hatched nymphs are nearly white, but soon become yellow and gain brownish markings, including dark markings on the head. There are five instars, the duration of which are about 3–4, 4–5, 3–4, 4–6, and 5–7 days, respectively, when reared at 21–25°C. The body length measures about 0.6–1.0, 1.2, 2.0, 2.5, and 3.0 mm in instars 1–5, respectively. As the nymphs mature, they gain spines on the hind tibiae, the number increasing from about 6–7 to 8–9. The tip of the abdomen also bears spines. The wing pads are indistinct through the third instar, but are apparent in the fourth instar, and overlap the abdominal segments in the fifth instar.

The adults (Fig. 92) are small, the males about 3.2–3.4 mm long, and the female 3.5–3.8 mm. These insects are light green in color, with the forewings tending toward grayish green and the abdomen yellowish green. There are six pairs of black spots, some of which are elongated almost into horizontal bands, starting at the top of the head and extending along the front of the head almost to the base of the mouthparts. The six pairs of spots are the basis for the other common name of this insect, "six-spotted leafhopper." Strong winds moving north in the spring transport adults into midwestern and northern crop production areas annually. Adults usually arrive in advance of egg hatch by overwintering populations, and populations of long-distance dispersants greatly exceed resident leafhoppers. Arrival time in the north varies, but May arrival dates are common.

When dispersal was studied in the western Great Plains of North America, the western edge of the principal migration path, overwintering of the adult leafhoppers was found only in Texas, USA, although north of Texas eggs may overwinter. By May, northward movement was evident, with adults present in Kansas, Nebraska, and South Dakota, where no nymphs had been found previously. By June the leafhoppers had progressed northward into Montana and North Dakota, and westward into Colorado and Wyoming. Thus, northward migration occurs rather rapidly, and the leafhoppers are present during most of the growing season in these areas.



Aster Leafhopper, *Macrosteles quadrilineatus* Forbes (Hemiptera: Cicadellidae),

Figure 92 **Adult of aster leafhopper, *Macrosteles quadrilineatus* Forbes.**

Aster leafhopper has a wide host range. It tends to overwinter on grains such as wheat and barley, and on grasses, clover, and weeds, then dispersing to other crops in the summer months. Several vegetable crops are damaged by aster leafhopper, including carrot, celeriac, celery, corn, lettuce, parsley, potato, and radish, but among vegetables only lettuce is consistently suitable for leafhopper reproduction. Other crops fed upon are barley, clover, dill, field corn, flax, oat, rice, rye, sugarbeet, and wheat.

In Washington, USA, studies indicated that the most important breeding areas were mixtures of clover and pasture grasses, followed by clover, sweet corn, oats, carrots, lawn grasses, rye, field corn, and various weeds. Among the weeds favored were fleabane, *Erigeron* spp.; ragweed, *Ambrosia* spp.; dandelion, *Taraxacum officinale*; wild lettuce, *Lactuca canadensis*; tumble mustard, *Sisymbrium altissimum*; and lambsquarters, *Chenopodium album*. Low, sparse, and young vegetation provided the best habitat. In Minnesota, large crabgrass, *Digitaria sanguinalis*; horseweed, *Conyza canadensis*; barnyardgrass, *Echinochloa crusgalli*; fowl-meadow grass, *Poa palustris*; and barley, wheat, and oats were especially suitable for reproduction. Carrot, dill, potato, and radish were important adult food plants, but not good breeding hosts.

Natural enemies are not well known, or very important in the population ecology of aster leafhopper. The most important enemies are the parasitoids *Pachygonatopus minimus* Fenton, *Neogonatopus ombrodes* Perkins, and *Epigonatopus plesius* Fenton (all Hymenoptera: Dryinidae). The best known among these is *P. minimus*, which has caused up to 37% parasitism.

Damage

Leafhoppers pierce leaf tissue of plants and remove the sap. The feeding punctures cause death and discoloration of individual plant cells, resulting in a yellow, speckled appearance in affected plants. This feeding damage, while unsightly, is minor in comparison to the damage caused to a great number of vegetable crops by transmission of aster yellows by leafhoppers.

Aster yellows is a plant disease caused by a mycoplasma-like organism (MLO), and is transmitted almost exclusively by aster leafhopper. Such crops as carrot, celery, cucumber, lettuce, potato, pumpkin, and squash are affected. Losses of 50–100% are reported due to this disease. MLO-infected plants are discolored, stunted, and deformed. On carrots, for example, the symptoms are red or yellow foliage and excessively hairy, bitter-tasting roots. On lettuce, symptoms are chlorosis, stunting, and lack of head formation.

Management

Leafhoppers are sampled with sweep nets, especially from grasses and grain fields. Yellow sticky traps are also useful and easy to use, and light traps equipped with fans for suction also have been used effectively to capture leafhoppers.

In addition to sampling for leafhopper abundance, it is also desirable to determine the proportion of leafhoppers that harbor the MLO. Formulas based on both insect number and disease incidence, called the "aster yellows index," have been developed to trigger control measures before the pathogen is widely transmitted to susceptible crops. Leafhoppers are collected before they enter an area, fed on aster plants, and the plants read for disease. This works effectively to alert large areas, such as entire states, but is not useful for local prediction.

Insecticides commonly are used to kill leafhoppers, and thereby minimize disease transmission. Because there are protracted acquisition and incubation times associated with this disease, chemical-based disease suppression is feasible. Insecticides are especially effective in the absence of long-distance dispersal by leafhoppers. Systemic insecticides are often favored due to their persistence, but contact insecticides can also be effective. Insecticides are often applied at 5–7 day intervals. Because it takes 10–15 days for infected plants to show signs of infection, it is not necessary to treat plants just prior to harvest.

Crop varieties differ in their susceptibility to infection with aster yellows; this is well studied both for carrots and lettuce, two of the more susceptible crops. Cultural manipulations can also enhance resistance. In studies conducted in Minnesota, very significant reductions in disease incidence were shown where aluminum foil mulch was used. Straw mulch was equally effective. Row covers, where economically feasible, should provide good protection against leafhoppers and disease transmission. Destruction of weed species known to harbor aster yellows is desirable.

Aster leafhopper acquires the MLO by feeding on infected perennial or biennial weeds or crop plants. Acquisition requires a prolonged period of feeding, usually at least 2 h, before the leafhopper is infected. Usually <2% of dispersant leafhoppers become infected. There is evidence that the MLO multiplies in the body of the leafhopper, and there is an incubation period of about 2 weeks in nymphs, and 6–10 days in adults, before the insects are capable of transmitting aster yellows. Leafhoppers remain infective for the duration of their life, but the MLO is not transmitted between generations through the egg stage. Thus, there is ample time for insecticides to interrupt disease transmission.

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Asterolecaniidae

A family of insects in the superfamily Coccoidae (order Hemiptera). They sometimes are called pit scales.

► Bugs

Aster Yellows

This is an important insect-vectored disease that affects many plants. See also, Transmission of Plant Disease by Insects.

► Transmission of Plant Diseases by Insects

Ateluridae

A family of silverfish (order Zygentoma).

► Silverfish

Athericid Flies

Members of the family Athericidae (order Diptera).

► Flies

Athericidae

A family of flies (order Diptera). They commonly are known as anthericid flies.

► Flies

Astrotaxis

Taxis response with respect to the sun, moon, stars or polarization of light.

Asymmetric Competition

Competition between two individuals or species in which one is more severely affected than the other.

Asymmetric PCR

Single-stranded DNA produced by providing an excess of primer for one of the two DNA strands. Asymmetric primer ratios are typically 50:1–100:1. Single-stranded DNA produced can be sequenced directly without cloning.

Asynchronous Muscle

Muscle in which the frequency of contraction is not controlled directly by nervous impulses, with the contraction frequency a property of the muscle. Asynchronous muscle produces several to many contractions in response to a single nervous stimulation. (contrast with synchronous muscle)

ATP

Adenosine triphosphate is the primary molecule for storing chemical energy in a cell.

Atrophy

Decrease in size of a tissue, organ, or part after full development has been obtained. In pathology, a condition in which the affected cells undergo degenerative and autolytic changes, become smaller, and have a lessened functional capacity.

Attelabidae

A family of beetles (order Coleoptera). They commonly are known as leaf-rolling weevils.

► Beetles

Attenuation

The process of decreasing the virulence of a microorganism.

Attractant

An odor, or the material producing an odor, that attracts insects.

Attraction of Insects to Organic Sulfur Compounds in Plants

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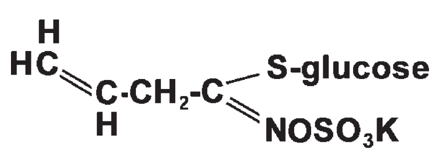
Among the secondary plant metabolites, two types of organic sulfur compounds are of considerable importance: glucosinolates and cystein derivative amino-acids, and their respective breakdown products. These compounds, in various ways, influence the diversity of organisms associated with plants bearing these compounds.

Glucosinolates

Glucosinolates (=mustard oil glycosides) occur predominantly throughout the order Capparales, consisting of Brassicaceae (=Cruciferae), Capparaceae, Moringaceae, Resedaceae, Tovariaceae, and sporadically in some other families (e.g., Caricaceae, Limnanthaceae, and Tropaeolaceae). About 50 different glucosinolates are found in Brassicaceae, and over 100 glucosinolates throughout the plant kingdom. Several to about twenty glucosinolates occur in each cruciferous species. For example, in leaves there are 14 glucosinolates in cabbage, 12 in cauliflower, 11 in Brussels sprouts, 7 in broccoli and Chinese cabbage. In roots, there are 18 glucosinolates in turnip and 8 in kohlrabi. In oilseeds, there are 9 glucosinolates in rapeseed and turnip rape, and 5 in mustard. Glucosinolates having a bitter taste are broken down to mustard oils (isothiocyanates) and other substances by enzymes which are known as myrosinases.

Isothiocynates, in general, have hot and pungent odors. However, those which have a bigger molecule lose pungent odor and have more sweet and mild odors. For example, 2-propenyl isothiocyanate (allyl isothiocyanate, C_3H_5NCS), which is (Fig. 93) split from sinigrin, has a very pungent odor; however, 2-phenylethyl isothiocynate ($C_6H_5CH_2CH_2NCS$), which is derived from gluconastrutiin, has a sweet odor.

E. Verschaffelt, a botanist from the Netherlands, first noticed the relationships between insects and glucosinolates early in the twentieth century. He found that the host plants of the large and small white butterfly larvae, *Pieris brassicae* and *P. rapae*, were limited to the plants containing glucosinolates. By smearing sinigrin on leaves which had been rejected before, the larvae came to readily attack and feed on some of these. Half a century later, this result was verified and developed by Thorsteinson and his group in Canada with the diamondback moth, *Plutella xylostella*, using artificial agar diet containing a known quantity of glucosinolate. Sinigrin, sinalbin, glucocheirolin, and progoitrin stimulated larval feeding in the presence of glucose. After these important works, the stimulation of feeding by glucosinolates, mainly sinigrin, was shown in a variety of specialist herbivores feeding on cruciferous plants: the cabbage aphid, *Brevicoryne brassicae*, the cabbage fly, *Delia brassicae*, the cabbage beetle, *Phaedon cochlearia*, and *P. brassicae*. The gravid female white butterflies tap the leaf surface with their forelegs (called "drumming") when they attempt to oviposit on leaves. They receive chemical



Attraction of Insects to Organic Sulfur Compounds in Plants, Figure 93 Chemical structure of sinigrin.

stimulation from glucosinolates in leaves via the sensilla on their tarsal undersurface. Glucobrassicin (3-indolylmethyl glucosinolate) is effective at 10^{-6} M, 1,000-fold more effective than sinigrin (2-propenyl glucosinolate), in initiating oviposition by *P. brassicae*. Each crucifer plant has a few or many glucosinolates so that they seem to work together.

In Japan during the 1950s, the olfactory stimulation of insect by isothiocynates was first proven by Sugiyama and Matsumoto with both of adults and larvae of the vegetable weevil, *Listroderes costirostris*. This species is a typical generalist, feeding on over 120 species in 28 plant families, in which Brassicaceae are among the important host plants. Each allyl-, 1-butyl-, 2-butyl-, phenyl-, benzyl-, 2-phenylethyl isothiocynate evoked every step of the chain reaction of host selection behavior in adults, consisting of the orientation (=attraction), antennae tapping and final continuous biting (=feeding) against the odor-material in the absence of any taste substances or nutrients. For newly hatched larvae, nine isothiocynates, methyl-, ethyl- to 2-phenylethyl, 1-naphtyl isothiocynates indicated a significant attractiveness, increasing with an increasing number of CH_2 groups. These results clearly show that not only the specialist herbivores, but also the generalist herbivores, use plant odors as the token stimuli for their host selection behavior. In Germany, the attraction of the flea beetles, *Phyllotreta crucifera* and *P. striolata*, by allyl isothiocynate was first shown in field trapping. Thereafter, allyl-isothiocynate was proven to be effective in attraction to the cabbage root fly, *Delia radicum*, the turnip root fly, *D. floralis*, *D. brassicae* adults, and also in stimulation of oviposition by *P. rapae* and *P. xylostella* females. The cabbage seed weevil, *Ceutorhynchus assimilis*, is attracted by isothiocynate mixtures similar to the composition of odor chemicals in oilseed rape plants. However, omission of two isothiocynate, 3-butenyl isothiocynate and 4-pentenyl isothiocynate from the mixture significantly reduces the attractiveness.

In general, favorable effects such as feeding and oviposition stimulation by glucosinolates and attraction by isothiocynates are observed in specialist herbivores on Brassicaceae. Contrarily, unfavorable effects such as feeding and oviposition inhibition and repulsion are observed in non-adapted herbivores, such as the bertha armyworm, *Mamestra configurata*, Colorado potato beetle, *Leptinotarsa decemlineata* and the desert locust, *Schistocerca gregaria*.

Plant breeding strategies have concentrated on reducing the glucosinolate content of rape seeds because of reducing the risk of causing goiter and organ abnormalities in livestock animals. However, the response of insects to the glucosinolate and/or isothiocynate content is not so simple. A worker reported that *Phyllotreta cruciferae* and *P. xylostella* larvae fed at equal rates on *Brassica juncea* and its low-glucosinolate lines, indicating that these species are insensitive to sinigrin. Another group of workers reported that the feeding activity, such as the proportion of time feeding and area damaged, by *P. xylostella* larvae is higher on the lines with low myrosinase activity than on the lines with high mirosinase activity. In contrast, the feeding activity of the southern armyworm, *Spodoptera eridania*, a generalist, is not related to myrosinase activity. Relative growth rates of both insect species are lower on cotyledons of lines with high glucosinolate content, but are not related to myrosinase activity in the lines. Thus, glucosinolate reduction is not always promising for protecting crops against the insects.

Organic Sulfur Compounds in *Allium* Plants

V. G. Dethier first proposed investigation of behavioral reactions of typical allium-feeders to organic sulfur compounds, which seemed to be characteristic of odor in allium plants. During the late 1950s to early 1960s, the fast progress of instrumental analysis brought forth the component data of onion volatiles. Allium plants produce very specific sulfur compounds. Cysteine derivative amino acids are converted by enzymatic splitting into sulfenic acids and thiosulfinates, which evolve into numerous substances. This results in production of odorous substances consisting mostly of mono-, di-, tri-sulfides, and n-dipropyldisulfide (n-DPDS, n-$C_3H_7SSC_3H_7$) and 1-propanethiol (1PTH, n-C_3H_7SH), which are reported to be the main components of onion odor. The attraction and oviposition stimulation of female onion fly, *Delia antiqua*, by these two compounds was first demonstrated by Matsumoto and Thorsteinson in laboratory experiments and field trapping in Manitoba, Canada in 1963–1964. However, no attraction nor oviposition stimulation was observed to di-methyldisulfide (DMDS). Newly hatched larvae also were shown to be attracted to over 20 compounds of various mono-, di-sulfides and alkyl-thiols, including DMDS. The larvae are likely to be less strict in the selection of odor chemicals.

Over 10 years later, the analysis of green onion-seedling odor was conducted in Canada and Japan independently, so that nine alkyl di- and trisulfides including n-DPDS and 1PTH were found. A propylthio (n-C_3H_7S) moiety was shown to be essential for a compound to induce attraction and oviposition stimulation activities. The compounds having butylthio (n-C_4H_9S) or amylthio (n-$C_5H_{11}S$) moiety also were reported to be attractive, although these compounds were not found in volatiles from onion. The green onion seedlings of susceptible cultivars give a larger quantity of propylthio compounds than those of resistant cultivars, because the allinase activity is higher than in the resistant cultivars.

Host finding by the leek moth, *Acrolepiopsis assectella*, an allium specialist, is also controlled by sulfur compounds, with propylpropanethiosulfinate (n-$C_3H_7SOSC_3H_7$) the most attractive. The adults of Diadromus pulchellus, an endoparasitoid of the young larvae of *A. assectella* and *P. xyllostera*, use the volatiles from the frass excreted by their hosts, and from the plant leaves fed by their hosts. In the volatiles from the frass of both moths, the same three disulfides (dimethyl, dipropyl, and methyl propyl) are the most abundant substances. Thus, volatile sulfur compounds in allium plants have been found to favor the host finding by an allium specialist, but to deter the approach and attack to the plant by generalists. This is similar as in glucosinolates.

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Audinet-Serville, Jean-Guillaume

Jean-Guillaume Audinet-Serville was born in Paris on November 11, 1775. The family wealth was lost during the French revolution, and Jean-Guillaume was sent to work in a coal store. The wife of the director of the store, Mme. de Tigny, author and correspondent of several notable entomologists, influenced him to collect and study insects. He married, and had three children before losing his wife. Latreille asked him to continue a work that Palisot de Beauvois had left incomplete due to the death of that entomologist. Thus, the 15th (last) part of “Insectes recueillis en Afrique et en Amérique…” was written by Audinet-Serville and published in 1819. Another famous work, Olivier’s “Encyclopédie méthodique,” was likewise incomplete, and here again Latreille persuaded Audinet-Serville, with help from Lepelletier de St. Fargeau and Latreille, to write volume 8, published in 1825. A third work, “Faune française” was also completed by Audinet-Serville in 1830, when he wrote the natural history of Coleoptera. Then, in 1831, he began publishing his own studies, first on the genus *Pirates*, and then “Revue méthodique de l’ ordre des orthoptères,” both in the pages of Annales des Sciences Naturelles. Other works followed, of which a notable one in 1839 was on “Orthoptères” and formed a supplement to Buffon’s series of volumes “Histoire naturelle….” He died on March 27, 1858. His collections were broken up and sold to various collectors.

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Audouin, Jean-Victor

Jean-Victor Audouin was born in Paris on April 2, 1797. He began to study law, but turned instead to medicine. His (1826) thesis was on the chemistry, pharmaceutical uses, and medical effects of “cantharides” (cantharidin), and on the beetles that produce it. He was made assistant to Latreille, and then succeeded Latreille as chairman of entomology at the Muséum National d’ Histoire Naturelle, and reorganized and enriched the collections. In 1829, he coauthored a book with Milne Edwards on natural history of Crustacea. His (1834) book “Histoire naturelle des insectes” was of several volumes. He contributed some of his work to Cuvier’s “Règne animal…” In 1838, he was elected a member of the Academie des Sciences. He did not build a personal collection of insects. He also published on applied entomology with a book (1842) “Insectes nuisibles à la vigne.” With Brongniart and Dumas he founded the journal Annales des Sciences Naturelles. He died in Paris on November 9, 1841.

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Augmentation

The practice of rearing and releasing biological control agents to effect pest suppression. This is also called augmentative biological control.

► Augmentative Biological Control

Augmentative Biological Control

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Augmentation involves efforts to increase populations or beneficial effects of natural enemies (parasitoids, predators, pathogens, entomopathogenic nematodes) of pest insects, mites and weeds. Various techniques can be employed in augmentation, but augmentation typically involves releases of natural enemies or environmental manipulation to enhance effectiveness of naturally occurring natural enemies. Environmental manipulation may involve providing alternative hosts or prey, food or nesting sites or modifying cropping practices to favor natural enemies.

Periodic releases may be labeled inundative or inoculative, depending upon the numbers of natural enemies released and the time interval during which they are expected to provide control. The distinction between inundative and inoculative augmentative releases may become blurred. Inundative releases involve releasing large numbers of natural enemies with the goal of achieving an immediate effect on pest populations. In essence, the natural enemies are "living pesticides." Pathogens and nematodes are commonly released inundatively. Parasitoids or predators are less often released in this manner because it is more difficult to mass produce high quality natural enemies inexpensively. For inoculative releases, relatively small numbers of natural enemies are released early in the cropping season and it is assumed that they will multiply and provide control of the target pest later in the season.

Examples of Augmentative Releases

Augmentation is an appropriate tactic to consider if indigenous natural enemies cannot suppress pest populations to an adequate level because the natural enemy population lags behind that of the pest, or if the natural enemies cannot persist over winter. Releasing natural enemies into crops that are sprayed with pesticides that are toxic to the natural enemies is unlikely to be effective unless the sprays are applied in a selective manner.

Examples of augmentative releases include releases of *Cryptolaemus montrouzieri*, a coccinellid predator of mealybugs into California citrus groves. This ladybird beetle has established permanently only in a narrow coastal area of California and does not overwinter elsewhere, so releases of 10–20 *Cryptolaemus* beetles per tree at the beginning of the summer can result in control of the mealybugs during the growing season. Periodic releases of the parasitoid *Aphytis melinus* are made to control California red scale on citrus grown in the coastal citrus region of California; approximately 200,000–400,000 wasps per acre are released. Several species of phytoseiid predatory mites have been released to control the two-spotted spider mite, *Tetranychus urticae*, in strawberries in California. Releases became essential and cost effective after this spider mite developed resistance to the pesticides used previously to control it. Releases of the parasitoid *Muscidifurax raptor* to control house flies, *Musca domestica*, on dairy farms can be effective if conducted as part of an integrated pest management program.

Augmentative releases are extensively employed in European glasshouses (or greenhouses). Releases of parasitoids or predators are made to control spider mites, whiteflies, leafminers, aphids and other pests on cucumbers, tomatoes and sweet peppers. For example, greenhouse whiteflies, *Trialeurodes vaporariorum*, are controlled by releases of a pathogenic fungus, *Aschersonia* sp. or a parasitoid wasp, *Encarsia formosa*. Several aphids can be controlled with releases of the cecidomyiid predator *Aphidoletes aphidimyza*, and the aphid *Myzus persicae* can be controlled by releases of the parasitoid *Diaeretiella rapae*. Leafminers, *Liromyza* sp., can be controlled by releases of several commercially available parasitoids. The two-spotted spider mite, *Tetranychus urticae*, a major pest of both ornamental and vegetable plants, is controlled by releases of the phytoseiid mite *Phytoseiulus persimilis*. Much of the information developed for releasing natural enemies in European glasshouses can be adapted to control glasshouse pests elsewhere because these pests are widely distributed.

Controversies about Augmentative Releases

Some augmentative release programs are controversial. For example, egg parasitoids of the genus *Trichogramma* attack eggs of many Lepidoptera. These tiny wasps have been mass reared and released against moth pests on millions of hectares of crops around the world. However, their efficacy rarely has been documented. It is suspected that efficacy may be less than expected because the wasps usually are reared, for economic reasons, on host eggs other than those of the target pest. Parasitoids produced on alternative host eggs may be of lower quality (small in size or with crumpled wings). Effective *Trichogramma* releases may require releasing as many as 150,000–500,000 wasps per hectare every 2 weeks during the growing season. Other elements of effective *Trichogramma* releases include collecting the species or biotype (specific strain) that attacks the target pest in the target crop for mass rearing. Reestablishing colonies on an annual basis using field-collected material has been recommended in order to maintain high quality.

Some augmentative releases of natural enemies have appeared to be effective because they induced the farmer to stop pesticide applications. However, the released natural enemy may not have provided control, which was actually provided by naturally occurring parasitoids, predators and pathogens. Knowingly using augmentative releases as a "placebo effect," in which the pest control is achieved by native natural enemies which are no longer disrupted by pesticide applications, is considered unethical because the consumer pays for unnecessary natural enemies.

Other releases of natural enemies may be of little direct benefit to the consumer purchasing them. For example, releases of some predators (such as some species of lady beetles or lacewing adults) may provide limited benefit at the release site because these predator species may be genetically programmed to fly long distances prior to settling down to feed and reproduce.

Another, more recent, issue that has been raised is whether some natural enemy species released in augmentative biological control programs could become permanently established in the environment. If the natural enemy is not native, some have questioned whether the natural enemies could have unintended effects on nontarget species in natural environments, perhaps reducing biodiversity. In the USA, importation of nonnative natural enemies, whether for classical biological control or for augmentative releases, must be approved by the U.S. Department of Agriculture after undergoing risk analysis.

When and Where are Releases Made?

Augmentative releases are most likely to offer practical alternatives to pesticides in situations where the crops are of high value, the natural enemies are reliably available at competitive prices, and guidelines on release methods, rates and timing are available. However, relatively few predators and parasitoids (probably <50) have been evaluated for efficacy, reliability and economic feasibility.

Augmentative releases can be hampered if high quality parasitoids and predators are not be available at the right time. Mass rearing of parasitoids and predators is restrained by high costs, lack of effective artificial diets, ineffective or limited quality controls and an inability to stockpile or store natural enemies during periods when they are not needed. Typically, parasitoids or predators are reared on insect hosts or prey, which are themselves reared on plants, making the rearing system complex and expensive. Maintaining pure and vigorous colonies of both hosts and natural enemies, as well as disease-free plants, requires skill and resources. If effective artificial diets could be developed for additional natural enemies, costs could decline and availability could increase. Although artificial diets for some arthropods are available, many diets are less effective than natural foods in producing high quality natural enemies. Concerns have been raised as to whether parasitoids or predators reared in insectaries are less fit than desired. For example, sex ratios in parasitoid populations reared in the laboratory often change due to inbreeding. Optimal methods for maintaining quality and genetic variability need to be developed to increase the effectiveness of natural enemies reared for augmentative releases in biological control programs.

Relatively few microbial products are available for pest management programs despite the fact that it may be easier and less expensive to produce viruses, bacteria or fungi than to rear parasitoids or predators. The commercial production of microbial pesticides involve a series of steps, including: isolating a suitable pathogen by screening a large number of isolates to identify those which show activity against the target pests; conducting laboratory and greenhouse tests to evaluate the efficacy of potential agents and to determine what environmental issues could affect their effectiveness;

producing commercial scale quantities of the product, which usually involves fermentation; developing the correct formulation of the microbe so the product can be stored, handled and applied effectively in the field; conducting efficacy trials of the agent under field conditions using commercial types of formulations. Microbial pest control products are expected to increase in popularity, but are not expected to replace synthetic organic pesticides. These microorganisms often are not pathogenic to predators and parasitoids, which can allow these agents to be compatible.

Several problems limit the use of microbial pesticides. Microbial products are not always reliable under field conditions due to limitations in both formulation and the microorganism itself. The activity of the microorganism may be too specific, which can be a disadvantage when there are multiple pests in the cropping system. Most microbial products have a short residual activity in the field (especially in comparison to synthetic organic pesticides), which makes it necessary to make multiple applications which increases labor and product costs. Microbial products may act slowly, making them appear ineffective or allowing excessive damage to occur in the crop.

Some Logistical and Ethical Issues

Augmentative biological control with releases of natural enemies requires that the user (grower, farmer, home owner) have considerable information. Consumers need to be informed before using augmentative biological control or consult with a knowledgeable pest control advisor. Some augmentative releases should be considered experiments because necessary information is lacking. It is possible that the release rates and timing may not have been evaluated under the specific climatic conditions and crop production conditions at the release site.

Detailed information about the pest species you wish to control is usually required for effective augmentative releases of natural enemies. Some natural enemies, such as some lady beetles, are generalists and will eat many species of aphids. However, even generalist lady beetles may not eat all species of aphids because the aphids are repellent or contain toxic chemicals. Many pests require specific natural enemies to achieve control. For example, a predatory mite that is known to feed on spider mites may not consume other plant-feeding mite species such as rust mites or tarsonemid mites. Many parasitoids have a very limited host range, sometimes limited to one or a few species. Thus, a taxonomic identification of the pest to species or strain may be required.

Next, the best natural enemy(ies) for that target pest need to be identified. Companies provide lists of pests against which their products may be applied, but these may be less than reliable. Consult your land grant university extension service, the U.S. Department of Agriculture or licensed pest control advisors for additional information as to which natural enemies are appropriate for your target pest.

One of the most difficult questions to answer is "how many do I have to purchase for release"? This question should be answered after careful consideration; if too few natural enemies are released, the releases will be ineffective and the funds used to purchase the natural enemies will be wasted. Furthermore, the additional damage to the crop caused by the pest could reduce yield or quality.

There are some common "rules of thumb" in release rates: for example, releasing 1 predatory mite for each 10 or 20 spider mites will provide relatively rapid pest population suppression. However, even this release rate is inadequate if the 10 or 20 spider mites have caused economic damage to the plant prior to the release; an average of ten mites per leaf results in different levels of damage than an average of ten mites per plant. Thus, information about the damage the plant can tolerate is needed. Different cultivars of a crop may vary in sensitivity to feeding by pests, so release rates and timing may have to be tailored to the specific crop cultivar.

To calculate the number of natural enemies required in an augmentative release program, the number of pests should be estimated by an effective sampling scheme. For example, it may be useful to estimate the mean number of spider mites per leaf, the mean number of leaves per plant and the mean number of plants per acre or hectare to calculate the total number of mites present and, thus, the number of predators to order. Do not forget to allow for a continued population increase between the time you calculate the pest population density and the time you receive the natural enemies (typically several days to a week later). The sooner the releases occur the less damage will accrue to the crop plant.

Once the natural enemies arrive, follow the directions on how to store them before releasing them, monitor the containers to be sure the natural enemies are healthy, and follow the directions on how to release them. Once the releases have occurred, know how to monitor the release site to be sure the natural enemies are performing as expected.

Time is of the Essence

Because natural enemies are relatively expensive, it is desirable to release them as early as possible in a pest population outbreak so that fewer natural enemies are required to perform the job. Waiting until the pest population is abundant increases costs and reduces the likelihood that the natural enemies will perform effectively.

Many natural enemies arrive from commercial producers as adults, and they may have been stressed during shipment. As a result, they may require a "lag time" before they feed or reproduce on the target pest. Furthermore, many natural enemies, such as predatory mites, typically live as adults less than a week; if we assume that the adults were collected immediately after emerging for shipping and the shipping process takes 1 day, such individuals will still have "lost" approximately 2 days in their potential effectiveness.

Ideally, augmentative releases will be planned prior to the start of the growing season and a monitoring program will be implemented so that releases can be scheduled as soon as the target pest population appears.

Costs of Releasing Natural Enemies

Costs of releasing natural enemies depend on the number that must be released. It is often the case that too few natural enemies are released and, as a result, in inadequate control occurs. In California strawberries, it was estimated to cost approximately US $600 per acre to release predatory mites to control two-spotted spider mites in strawberries. This cost was accepted because the spider mites were resistant to the currently registered pesticides and no other effective control method was available. Furthermore, the high value of strawberries (approximately $30,000 per acre) made this control cost feasible. In lower value crops, augmentative releases might not be economically justifiable.

- What is the specific pest you need to control?
- Which natural enemies are known to perform well on that specific pest species under similar climatic and geographic conditions?
- How many pests do you have? Per leaf? Per plant? How many plants per row or acre? How many acres?
- What is the effective release rate for that natural enemy? For example, should the natural enemy be released in a ratio of one natural enemy to each 10 pest individuals? If so, the earlier the releases can be conducted, the less expensive such releases will be. For example, If hundreds of spider mites are present on each plant, then it is expensive and difficult to release sufficient predators to suppress them; it would be better to make releases when less than one spider mite per leaf is present.
- Calculate the number of natural enemies needed based on release rate, area to be covered and abundance of the pest per plant, row, acre.

- Are multiple releases needed over days or weeks to achieve the necessary level of pest suppression?
- How should the natural enemies be stored and handled after your receive them from the commercial producer to reduce mortality and enhance effectiveness after release?
- When should releases be conducted (time of day, temperature conditions) and in what manner? For example, do natural enemies disperse readily or should they be released on each plant or each leaf.
- How can you monitor the results of the releases to know if the natural enemies are performing as expected?
- Does the commercial producer provide information on release rates, timing, methods, and guarantee quality of the natural enemies during shipping?

Key Research Needs

Additional resources committed to improving augmentative releases of natural enemies could increase the use of this pest management tactic. These include research to develop adequate quality control tests so that only high quality natural enemies are shipped from the commercial producers. Appropriate tests should be conducted to confirm that the correct natural enemy species is shipped, that it is disease free, vigorous and viable. Research should also be devoted to developing improved methods for producing natural enemies at peak demand times, or for storing natural enemies without a loss in quality, so that adequate numbers are available when needed. High quality, but inexpensive, artificial diets could reduce production costs. Shipping and storage methods could be improved; many natural enemies arrive stressed or, even, dead. Finally, accurate information on release rates and timing could be improved and developed for additional geographic regions and climates.

Because data are not available for all situations, many augmentative releases of natural enemies should be considered experiments and conducted on a relatively small scale initially until it is clear that the necessary information is available and appropriate for the new situation.

Future of Augmentation

Pests in greenhouses in Europe, in which eggplants, cucumbers and tomatoes are grown, are often under complete biological control due to augmentative releases of natural enemies. There are several moderately large companies that produce natural enemies for this market, provide information on release rates and timing, and provide other information. Control of pests of ornamental plants in Europe is less often achieved by augmentative biological control because damage to foliage or flowers reduces quality. Greenhouse-grown crops in other geographic areas may be limited due to difficulties in obtaining natural enemies in a timely fashion, differences in pest and disease complexes, and differences in climatic conditions.

Citrus growers in California have developed grower-owned cooperatives to produce natural enemies. This approach has proven successful for over 50 years, suggesting that grower-owned cooperatives might be a useful model for increasing the use of augmentative releases in other crops in other geographic areas.

Augmentative releases can be an effective pest management tool for many pests in a diverse array of crops. However, augmentative biological control requires that the pest manager have considerable information on pest and natural enemy biology, an understanding of pest-natural enemy dynamics, and the availability of adequate numbers of high quality natural enemies for release at the right time. Thus, it is an information-intensive and logistically critical management approach.

Augmentation has the potential to become a more dominant component of pest management programs if sufficient resources are devoted to

Some natural enemies considered suitable for augmentative biological control

Natural enemy	Pest
Predators	
Amblyseius barkeri	*Thrips tabaci, Frankliniella occidentalis*
Amblyseius cucumeris and A. degenerans	*Thrips tabaci, Frankliniella occidentalis*
Anthocorus nemorum	Thrips
Aphidoletes aphidimyza	Aphids
Cryptolaemus montrouzieri	Mealybugs and some scalaes
Chrysoperla carnea	Aphids
Hippodamia convergens	Aphids
Metaseiulus occidentalis	*Tetranychus urticae, T. pacificus*
Orius sp.	*Frankliniella occidentalis*
Phytoseiulus persimilis	*Tetranychus urticae*
Parasitoids	
Aphelinus abdominalis	*Macrosiphum euphorbiae*
Aphidius colemani	*Aphis gossypii*
Dacnusa sibirica	*Liriomyza bryoniae, L. trifolii, L. huidobrensis*
Diglyphus isaea	*L. bryoniae, L. trifolii, L. huidobrensis*
Encarsia formosa	*Trialeurodes vaporariorum, Bemisia tabaci*
Eretmocerus californicus	*Bemisia tabaci*
Leptomastix dactylopii	*Planococcus citri*
Metaphycus helvolus	Scales
Opius pallipes	*Liriomyza bryoniae*
Trichogramma spp.	Lepidopteran eggs
Pathogens	
Bacillus thuringiensis	Lepidopteran larvae
NPV-virus	*Spodoptera exigua*
Trichoderma harzianum	*Fusarium* spp.
Verticillium lecanii	Aphids
Entomopathogenic nematodes	
Heterorhabditis spp.	*Otiorrhynchus sulcatus*
Steinernema spp.	Sciaridae

obtaining the necessary information and improvements in rearing and deployment.

► Natural Enemies important in Biological Control
► Culture of Natural Enemies on Factitious Foods and Artificial Diets
► Rearing of Insects

An Important Website: http://www.cdpr.ca.gov/docs/ipminov/bensuppl.htm, which provides a list of commercial suppliers of natural enemies in North America. A variety of natural enemies are produced commerc ially for the control of greenhouse and other pests.

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Auricular Openings

Lateral, slit-like openings to the insect heart by which blood is admitted into the dorsal vessel. These are also known as ostia or incurrent ostia.

Australian Archaic Sun Moths (Lepidoptera: Lophocoronidae)

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Australian archaic sun moths, family Lophocoronidae, have six known species in Australia. The family comprises its own superfamily, Lophocoronoidea, and is the only member of the infraorder Lophocoronina, of the suborder Glossata. Adults small (10–15 mm wingspan), with head roughened; labial palpi 3-segmented; haustellum short and vestigial mandibles are present; maxillary palpi are long and 4-segmented. Maculation is pale monotone with some darker spotting. Biologies and larvae remain unknown, but adults are crepuscular in eucalyptus sclerophyll woodlands.

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Australian Lappet Moths (Lepidoptera: Anthelidae)

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Australian lappet moths, family Anthelidae, total 100 species, all from Australia. There are two subfamilies: Munychryiinae and Anthelinae. The family is in the superfamily Bombycoidea (series Bombyciformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size to very large (22–166 mm wingspan), with head vertex scaling (Fig. 94) rough; haustellum absent (sometimes short or more rarely long); labial short and mostly upcurved but some more porrect; maxillary palpi vestigial; antennae bipectinate (serrate to filiform in some females); body robust. Wings broadly triangular

Australian Lappet Moths (Lepidoptera: Anthelidae), Figure 94 **Example of Australian lappet moths (Anthelidae), *Munychryia senicula* Walker from Australia.**

and rounded (rarely somewhat acute or even falcate); hindwings rounded (rarely somewhat acute); rarely with micropterous females. Maculation mostly shades of brown with few markings, but some more marked or lighter. Adults nocturnal, but at least one species with diurnal males. Larvae are leaf feeders and generally colorful. Host plants recorded in several plant families, including Casuarinaceae, Gramineae, Leguminosae, and Myrtaceae, among others. Some species have urticating larval setae.

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Australian Primitive Ghost Moths (Lepidoptera: Anomosetidae)

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Australian primitive ghost moths, family Anomosetidae, comprise a single genus with 1 known species from Australia. The family is in the superfamily Hepialoidea, of the infraorder Exoporia. Adults small (18 mm wingspan), with head rough-scaled; haustellum short and vestigial mandibles present; labial palpi short, 3-segmented; maxillary palpi minute, 2-segmented; antennae short. Maculation is darkened with some darker forewing spots. Biologies and larvae remain unknown.

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Australian Realm

The zoogeographic region of Australia and nearby islands. It is characterized by a preponderance of marsupials, large flightless birds, and parrots, as well as an absence of mammals.

► Zoogeographic Realms

Australian Sheep Blowfly, *Lucilia cuprina* Wiedemann (Diptera: Calliphoridae)

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Sheep in many areas of the world are plagued by fly problems, but Australia, with 103,000,000 sheep, has the most severe fly problems. The problem starts when wool becomes excessively wet. Continually wet wool is irritating to the sheep's skin, and a condition called "fleece rot" develops. Fleece rot results in skin inflammation and the secretion of serum from the irritated skin. Such a site is soon teeming with bacteria. The wet, serum-containing wool is attractive to ovipositing flies, and soon the maggots hatching from those eggs feed not only on the fleece, serum, and bacteria, but the underlying skin. The problem is exacerbated by the presence of urine, feces, sweat or other animal secretions, all of which are attractive to flies. The attack of flies on sheep in this manner is called "flystrike," and this condition can result in the death of animals or the expense of treatments to prevent or cure this fly-based problem. The problem is greatest in environments where warmth and moisture occur frequently, and the cost for fly treatments and loss of sheep due to flies is estimated at $100–150 million annually in Australia. The principal problem fly is *Lucilia cuprina*, known in Australia as Australian sheep blowfly or primary green blowfly. It is responsible for over 90% of the flystrike in Australia, but other flies can be involved.

Beginning in about 1988, *L. cuprina* first appeared in New Zealand, greatly exacerbating the flystrike problem with sheep there, and extending flystrike attacks into a nearly season-long problem. In recent years, about half of the flystrike incidents in New Zealand were caused by *L. cuprina*, but the proportion attributable to this fly seems likely to grow as it continues to spread.

Sheep producers can take several actions to reduce or prevent flystrike. The mechanical removal of the wool around the tail, anus and vulva (in ewes) is called "crutching," and helps prevent flystrike because these sites are most likely to stay wet and soiled, and thus attractive to ovipositing females. However, the wool grows continuously, so repeated removal of wool is necessary for this process to be effective, and is not cost-effective for large producers of sheep. A more permanent treatment is the surgical removal of skin around the anus and vulva, resulting in wrinkle-free and wool-free tissue in these areas, which tend to remain clean and free of flies. This surgery is called "mulesing," and is normally conducted on lambs a few weeks after birth. It takes about 4 weeks for the wounds to heal, and should be conducted before flies are active, or they will be attracted to the wounds, making the problem worse. Mulesing is quite controversial because it is painful for the sheep, and is being phased out in Australia. The tails of lambs also can be docked to reduce the tendency of the anal region to remain soiled and wet, and this practice evokes less opposition. A common alternative to crutching and mulesing is chemical protection, though this also requires repeated treatment. Other alternatives include limiting sheep raising to regions that are too dry or cool for optimal fly population growth. Some breeds of sheep, such as Merino sheep, are particularly prone to problems because the are very wrinkled and have a very dense wool. Historically, Merino is the preferred sheep in Australia.

Over 90% of the flystrikes in Australia are initiated by *Lucilia cuprina*, an introduced species. As is generally the case with blowflies, the primary hosts are carrion, but when sheep are afflicted with fleece rot or have thick mats of wet wool, female flies will deposit eggs on live sheep. The presence of even a few flies (7–10 per hectare) is enough to cause severe problems if susceptible sheep are present. The adults are metallic blue or green in color, and about 9 mm long. Flies initiate oviposition only after completing a protein meal, which enables egg production, and then up to 250 eggs can be deposited in a single batch on soiled wool. Each female typically produces two to three egg clusters during her life span of 2–3 weeks. The eggs hatch within 8–24 h, and the maggots feed and grow to a length of 10–15 mm in about 3 days. They then drop to the soil, usually during the night or early morning, and pupate. About a week after pupation, the adults emerge and start the cycle again. Thus an entire life cycle is completed in about 2 weeks. They reproduce best under warm (at least 18°C), wet conditions, but cannot tolerate high (over 38°C) temperatures, so fly populations may decrease during the middle of the summer in hot areas. Thus, peak blowfly populations tend to occur in spring, and late summer or autumn, in Australia.

Sheep producers have several options when it comes to control of sheep blowfly. Producers can apply organophosphate insecticides for rapid fly control, but these products tend not to be very persistent (2–4 weeks), and resistance to some organophosphates is known. Insect growth regulators take longer to take effect, but persist longer (up to 14 weeks). Other products are available, of course, and confer different advantages. Resistance to pyrethroid insecticides is widespread in Australia. The insecticides are sometimes applied by hand, which is advantageous because they can be directed to the areas of the animal most susceptible to flystrike. To reduce labor costs, automated (walk-through) sprayers are sometimes used, but such applications are less directed and commonly less effective in their coverage of sheep. Applications are most common soon after shearing, and if applications are delayed, unacceptable insecticide residues on the sheep may result.

In addition to chemical treatment, growers have recently adopted the practice of trapping flies. Traps consist of buckets with special lids containing entrance cones that allow the blowfly to enter but not leave the trap. Each bucket contains a number of chemical lures that mimic the odors of fleece rot, urine, feces, and animal carcasses. Once trapped inside the bucket, the flies die from dehydration. Traps are distributed at a rate of one trap per 100 sheep, and they are recommended to be used early in the season when the fly population in naturally at its lowest. In addition to removing flies from the population, and thereby reducing the rate of flystrike, the traps are useful for monitoring population densities.

Optimal management of sheep blowfly is accomplished with implementation of an integrated or multi-faceted approach. This involves reducing the attractiveness of sheep to flies by docking lamb's tails, and by shearing, crutching or mulesing all sheep. Keeping the flocks separated helps reduce the movement of flies from flock to flock. Regular inspection of the flock is desirable, and catching and shearing of sheep, and spot treatment of sheep with fly infestations is desirable. Trapping and monitoring of adult fly populations with fly traps are helpful. Treatment of the entire flock may be necessary if the fly population becomes high, but timing needs to be optimized to avoid contamination with pesticide residues. Avoidance of pesticides with a history of fly resistance is important.

Some of the other calliphorid species associated with sheep in Australia, and their local common names, include:

- *Lucilia sericata* Meigen, the European green blowfly. This invader is the principal sheep blowfly in the United Kingdom, but only a minor pest in Australia. It is virtually identical to *Lucilia cuprina* in appearance.
- *Calliphora stygia* (Fabricius), the eastern goldenhaired blowfly. This fly is native to Australia. It is brown and about 13 mm long. It prefers cooler weather, disappearing in the summer months.
- *Calliphora augur* (Fabricius), the lesser brown or bluebodied blowfly. This native fly is a secondary species, not usually attacking sheep until other species have attacked. It is mostly brown, but has a metallic blue patch on its abdomen. It is about 11 mm long. It is found commonly in the summer. It differs from most other blowflies in depositing larvae rather than eggs.
- *Chrysomya rufifacies* (Macquart), the green hairy maggot blowfly. This is another native, secondary species. It is metallic green, and can be distinguished from *Lucilia* by the broad bands on its abdomen and its black forelegs. The adult is about 9 mm long. The larvae are distinctive, bearing sharp spines (the "hairs") over its dark body. It also is known to feed on other maggots.

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Australian Silkworm Moths (Lepidoptera: Carthaeidae)

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Australian silkworm moths, family Carthaeidae, are a monobasic relict family in Bombycoidea with a single species from western Australia. The family is in the superfamily Bombycoidea (series Bombyciformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults large (75–100 mm wingspan), with head scaling roughened; haustellum developed; maxillary palpi small, 3-segmented; antennae bipectinate, or apparently tripectinate (serrate in females); body robust. Wings broad and triangular but termen rounded; forewing with somewhat acute apex (Fig. 95). Maculation gray with large dark eyespot medially on all wings and band of gray-brown at base and along termen; hindwing reddish at apex with blue in eyespot. Adults are nocturnal (usually after midnight).

Australian Silkworm Moths (Lepidoptera: Carthaeidae), Figure 95 **Example of Australian silkworm moths (Carthaeidae), *Carthaea saturnioides* Walker from Australia.**

Larvae are leaf feeders, with numerous clubbed setae. Host plants are only in Proteaceae.

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Austrophasmatidae

A family of gladiators (order Mantophasmatodea)
► Gladiators (Mantophasmatodea)

Autecology

The ecology of individuals, or the effects of the physical and chemical environment on individual organisms (rather than on populations or communities).
► Synecology

Autocidal Control

The use of insects for self destruction, normally through release of sterile or genetically altered insects into a natural population.

Autoecious Life Cycle

A life cycle in which the insects (generally aphids) are host plant specific, living on a single host or some closely related hosts throughout the year. This is also called monoecious (contrast with heteroecious life cycle).
► Aphids

Attevidae

A family of moths (order Lepidoptera). They are commonly known as tropical ermine moths.
► Tropical Ermine Moths
► Butterflies and Moths

Aulacidae

A family of wasps (order Hymenoptera).
► Wasps, Ants, Bees and Sawflies

Aulacigastrid Flies

Members of the family Aulacigastridae (order Diptera).
► Flies

Aulacigastridae

A family of flies (order Diptera). They commonly are known as aulacigastrid flies.
► Flies

Australembiidae

A family of web-spinners (order Embiidina).
► Web-Spinners

Australian Parasite Moths (Lepidoptera: Cyclotornidae)

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Australian parasite moths, family Cyclotornidae, include only five known species from Australia. The family is in the superfamily Cossoidea (series Limacodiformes) in the section Cossina, subsection Cossina, of the division Ditrysia. Adults small (10–30 mm wingspan), with head scaling average; haustellum absent; labial palpi short; maxillary palpi absent; antennae filiform (thicker in males). Body robust. Wings elongated and rounded. Maculation somber hues of gray, with mainly a single forewing marking (one species is yellow and black). Adult activity uncertain but may be crepuscular. Larvae flattened, with lateral protrusions; highly evolved as parasites of leafhoppers, scale insects, or psyllids (Hemiptera) in early instars, and then as predators of ant larvae. The ants tolerate the predatory larvae, keep them in their nests and care for them, since they give the ants desirable exudates. Eggs are laid on plants frequented by likely hemipteran hosts and young larvae then search for a suitable host to parasitize upon hatching; eggs are tended by protective ants.

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Australimyzidae

A family of flies (order Diptera).
► Flies

Austremerellidae

A family of mayflies (order Ephemeroptera).
► Mayflies

Austroniidae

A family of wasps (order Hymenoptera).
► Wasps, Ants, Bees and Sawflies

Austroperlidae

A family of stoneflies (order Plecoptera).
► Stoneflies

Austropetaliidae

A family of dragonflies (order Odonata).
► Dragonflies and Damselflies

Autogenic Succession

A temporal succession of species that is driven by processes within the community (contrast with allogenic succession).

Autogenous

Among blood-feeding insects, the ability to produce eggs without a prior blood meal.

Autoradiography

A method for detecting radioactively labeled molecules through exposure of an x-ray sensitive photographic film.

Autoregulatory Control

Regulation of the synthesis of a gene product by the product itself. In some systems, excess gene product behaves as a repressor and binds to the operator of its own structural gene.

Autosomes

All chromosomes except the sex chromosomes. Each diploid cell has two copies of each autosome.

Autotomy

Self-amputation which functions as an escape mechanism. Under some circumstances, body parts are deliberately shed to avoid capture by predators. Arthropod legs are shed readily, and when this occurs early in life they can be regenerated, in whole or in part.

Autotroph

Organisms that obtain energy from the sun and other materials from inorganic sources (contrast with heterotroph).

Auxiliary Vein

A supplementary vein. The subcosta is often considered to be auxiliary.
► Wings of Insects

Auxiliae

Small plates beneath the base of the pretarsal claws, bearing the pulvilli (if present). These are sometimes known as auxilliary sclerites.
► Legs of Hexapods

Avermectins

Macrocyclic lactones derived from a soil-dwelling microbe, the actinomycete *Streptomyces avermitilis*. They are chloride channel agonists. These materials are considered to be broad spectrum, slow acting, natural pesticides, and display activity against helminths, insects, mites, and nematodes. They are used widely to treat animals for parasitic organisms, but also for insect and mite pests in agriculture. They degrade readily and lack persistence and mobility, so are valued in integrated pest management programs and even in some organic agriculture situations. Common commercial products include Abamectin, Agrimek, Avert, Avid, and Vertimec.

► Insecticides

Avian Malaria, Bird Malaria

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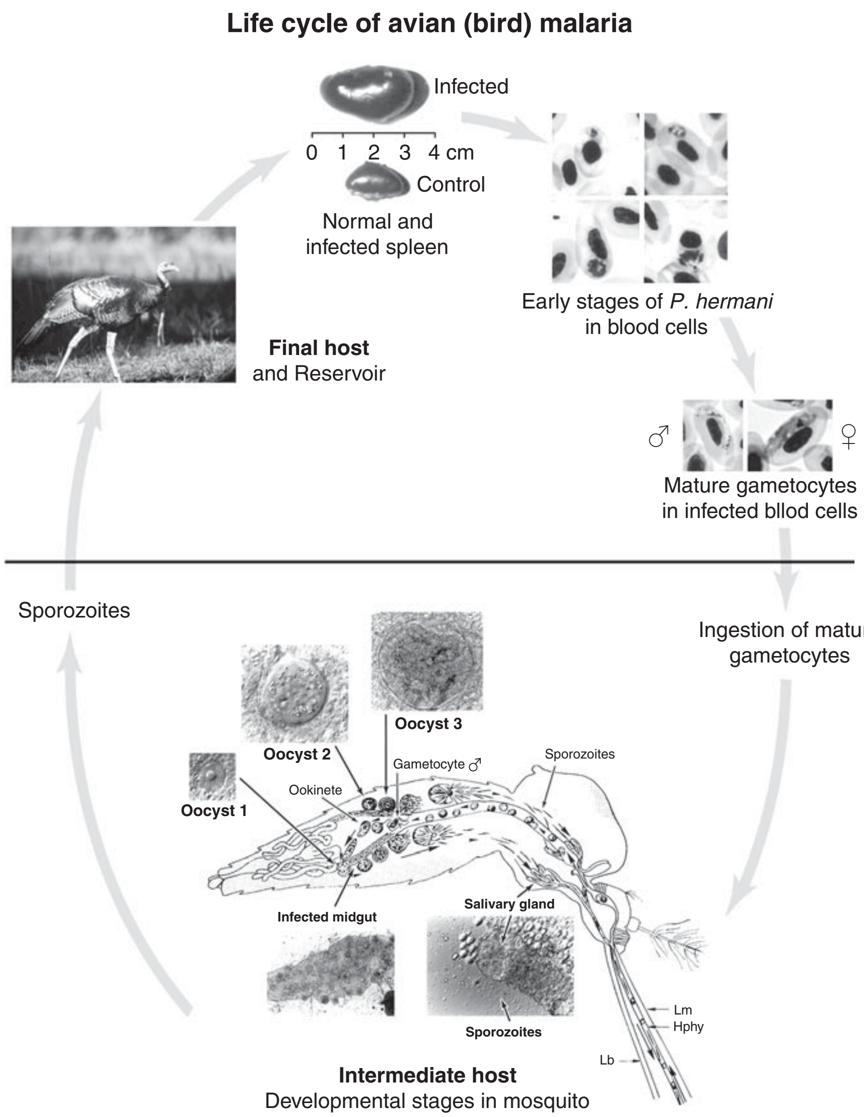
Avian malaria is an infectious disease and it is found all over the world, especially in tropical and temperate areas. It produces a wide range of effects in avian hosts, from no apparent clinical signs to severe anemia and death. It has served as an experimental model for human malaria during the early history of malaria research. Avian malaria is not one disease, but many and is caused by distinct species of a protozoan blood parasite, *Plasmodium*, that is transmitted by mosquitoes. It belongs to Class Sporozoa, Subclass Telosporidia, Order Coccidiomorphida and Suborder Haemosporidina, and Genus *Plasmodium*. There are about 30 species of *Plasmodium* parasites recognized that infect birds world-wide and they are grouped into four subgenera depending on the shape and size of the parasite in erythrocytes and presence or absence of schizogony: *Haemamoeba* species have round gametocytes; *Huffia* species have elongate gametocytes and schizogony in primitive red cells; *Giovannolaia* species have relatively large asexual stages and no schizogony; and *Novyella* species have small asexual stages and no schizogony.

Plasmodium parasites in birds are primarily blood parasites, but in the acute phase they do infect a variety of other tissues, the lungs, endothelial cells of capillaries in the brain, and the reticular cells of the splenic Malpighian body. The parasites multiply in all of these tissues. Later generations of the parasites are less selective in host cell preference and the parasites may be found in various other tissues. In the chronic phase the parasite causes little harm. Several species of mosquitoes belonging to genera *Anopheles*, *Culiseta*, *Mansonia*, *Aedes*, *Armigeres* and *Culex* are found to be experimentally susceptible to different *Plasmodium* species that infect birds, but the natural vectors are mostly *Culex* and rarely *Aedes* species.

The life cycle of *Plasmodium* (*Huffia*) *hermani*, a parasite of wild turkeys (*Meleagris gallopavo* L.) that was described (Fig. 96) from Florida in 1975, will serve as an example. This parasite was discovered after specialized subinoculation technique of blood (heparinized or citrated) from chronically infected wild older turkeys into young poults of broad-breasted-white domestic turkeys. In turkeys (both wild and domestic) the malaria parasite infection causes anemia, splenomegaly, and reduced weight gains in poults. Natural infection of the young turkey poults begins with the bite of an infected culicine mosquito. Sporozoites introduced with the salivary gland secretions are carried to the reticular cells of the splenic Malpighian body. After a minimum of three generations of exoerythrocytic development in these cells that takes about 10–14 days, the stage of parasite called merozoites may spill over in the blood circulation and invade basophilic cells of the erythrocyte series, or may continue asexual reproduction. These merozoites after invasion of basophilic cells of the erythrocyte series transform into trophozoites (uninucleated, either elongate or round), schizonts (rounded with 6–14 nuclei arranged peripherally as a rosette) and finally elongate slender gametocytes (male and female) with irregular margins in mature erythrocytes. Time required may vary from 2 to 4 days. In general erythrocytic avian merozoites appear to be able to choose among four possible fates. Most may continue schiozgony in erythrocytes, but some may become micro- and macro-gametocytes (male or female gametocytes, respectively) or they may re-initiate asexual reproduction in the tissues as phanerozoites. Northern bobwhites



Avian (Bird) Malaria, Figure 96 **Life cycle of *Plasmodium hermani*. Stages of avian malarial parasite in mosquitoes: oocyst 1 = young oocyst about 4 days old, oocyst 2 = about 7 days old, oocyst 3 = about 10 days old. Lm = labium, Lb = labrum, and Hphy = hypopharynx.**

(*Colinus virginianus*) in Florida is also a natural and experimental host of *P. hermani*.

Natural and experimental vector for *P. hermani* in wild turkeys and northern bobwhites in Florida is *Culex nigripalpus*, but experimental studies indicate that other culicines (*Cx. salinarius* and *Cx. restuans*) may be involved to a lesser degree. *Plasmodium hermani* is not transmitted by *Cx. quinquefasciatus* in Florida and it does not infect young chicks (*Gallus domesticus*). Three additional species of turkey malaria have been reported from other parts of the U.S.A. These are *P. hexamerium-like* from Texas, *P. lophurae* from Wisconsin, and *P. kempi* from Missouri, Wisconsin, Minnesota and North Dakota. Natural vectors of these species of avian malaria are presumably also culicines although they have not been determined. Experimental studies have shown that *Cx. tarsalis* and *Cx. pipiens pipiens* can be infected with *P. kempi*. Other species of *Aedes*, *Culiseta* and *Wyeomyia* can be experimentally infected with avian malarias, but their contribu tion in natural transmission of the parasite is unknown. In some of the experimental mosquitoes that are not natural vectors, a defense reaction occurs and development of oocysts in the mosquitoes is compromised by intracellular melanization of the developing oocysts.

The developmental cycle of the avian malarial parasite within the susceptible mosquito is similar in all vector species and begins with the ingestion of erythrocytes (blood cells) containing male and female gametocytes from the infected bird. As the blood meal passes into the gut, the change in the environmental factors induces gametocytes to emerge from the erythrocytes (within 4–6 h). The microgametes (male gametocytes) begin the prefertilization process by undergoing exflagellation. Soon thereafter individual microgametes are released, which swim actively to the macrogametes (female gametes) and penetrate them culminating in fertilization. This results in the formation of a zygote, which elongates and undergoes cytoplasmic changes and forms motile ookinetes (within 24 h). The mature ookinetes migrate intracellularly through the midgut cells and move into the outer wall of the midgut facing the hemocoel, where the ookinetes form a tumor like body, or oocyst. Within 8–12 days, the timing depending on temperature and species of the parasite, schizogony within the oocyst produces hundreds, or even thousands of sporozoites. Sporozites are spindle-shaped organisms measuring about 8–9 μm in length and about 1 μm wide. These are liberated into the body cavity by rupture of the oocyst wall, and some find their way into the salivary glands, where they mature in 1–2 days. A bite of an infected mosquito causes infection in young turkey poults and starts the life cycle all over again.

Recently, *Cx. nigripalpus*, *Cx. restuans* and *Cx. salinarius* were shown be experimental vectors of *P. elongatum* from 3 raptors species (red-tailed hawk, bald eagle and eastern screech owl) in Florida and *Cx. restuans* was shown to be the experimental vector of *P. forresteri* n. sp., from several species of raptors from Florida and Georgia.

Normally epizootics of avian malaria are rare. Several species of avian malaria, e.g., *P. gallinaceum*, *P. juxtanucleare* and *P. durae* are the most dangerous for poultry, producing up to 90% mortality. In addition, there are a few documented cases where avian malaria has been shown to either eliminate or reduce bird populations. Until 1826, birds were plentiful in Hawaii and mosquitoes were absent from the region. Introduction of *Culex pipiens* from ships traveling to Hawaiian Islands introduced a lethal form of avian malaria, which eliminated indigenous bird populations. In another case, it is suggested that an abnormally early rainy season over a 2-year period in southern Florida in the 1960s resulted in a widespread malaria epizootic in wild turkey populations, which caused a significant decline in the wild turkey population. In recent years, avian malaria has caused severe mortality in exotic bird populations, especially penguins, in zoos across the U.S.A.

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Axenic

Free from associated organisms. Including internal symbionts.

Axenic Culture

Culture of insects in the complete absence of other species (usually of microorganisms), including internal symbionts.

Axiidae

A family of moths (order Lepidoptera) also known as gold moths.

► Gold Moths
► Butterflies and Moths

Axillary

This refers to the point of origin of a structure, often a junction or angle. Thus, the axillary region of the wing is the wing base, and the axillary lobe in Diptera is the sclerite covering the base of the wing.

Axon

A portion of the nerve cell that transmits nerve impulses away from the cell body to a synapse. This also is called nerve fiber.

► Nervous System

Azadirachtin

This is a triterpenoid derived from the neem tree, *Azadirachta indica*. It is found in many parts of the tree, but is particularly concentrated in the seeds, from which it is extracted as used as an insecticide. It also has other properties, including medicinal. Although azadirachtin is a principal factor in insecticidal products, it is not the only active property, and is not especially useful as a feeding deterrent, though crude extractions of the tree contain feeding deterrents.

► Neem