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Arthur Gahan was born into a large farm family in Kansas on December 9, 1880. He attended Kansas State College, graduating in 1903. Then in 1904 he became assistant in the Department of Entomology of Maryland Agricultural College, and received an M.S. from that institution in 1906. He remained there as Assistant Entomologist, becoming interested in “parasitic” Hymenoptera in general and braconid parasitoids of aphids in particular. In 1913 he accepted a position with the U.S. Department of Agriculture, to work as a taxonomist at the U.S. National Museum. There, he worked on various groups of “parasitic” Hymenoptera, but ultimately concentrated on Chalcidoidea and became a leading authority of them and publishing copiously. He married in 1908, was active in civic affairs and the Entomological Society of Washington, becoming its president in 1922. He died on May 23, 1960, and was survived by his wife and two children.

Reference

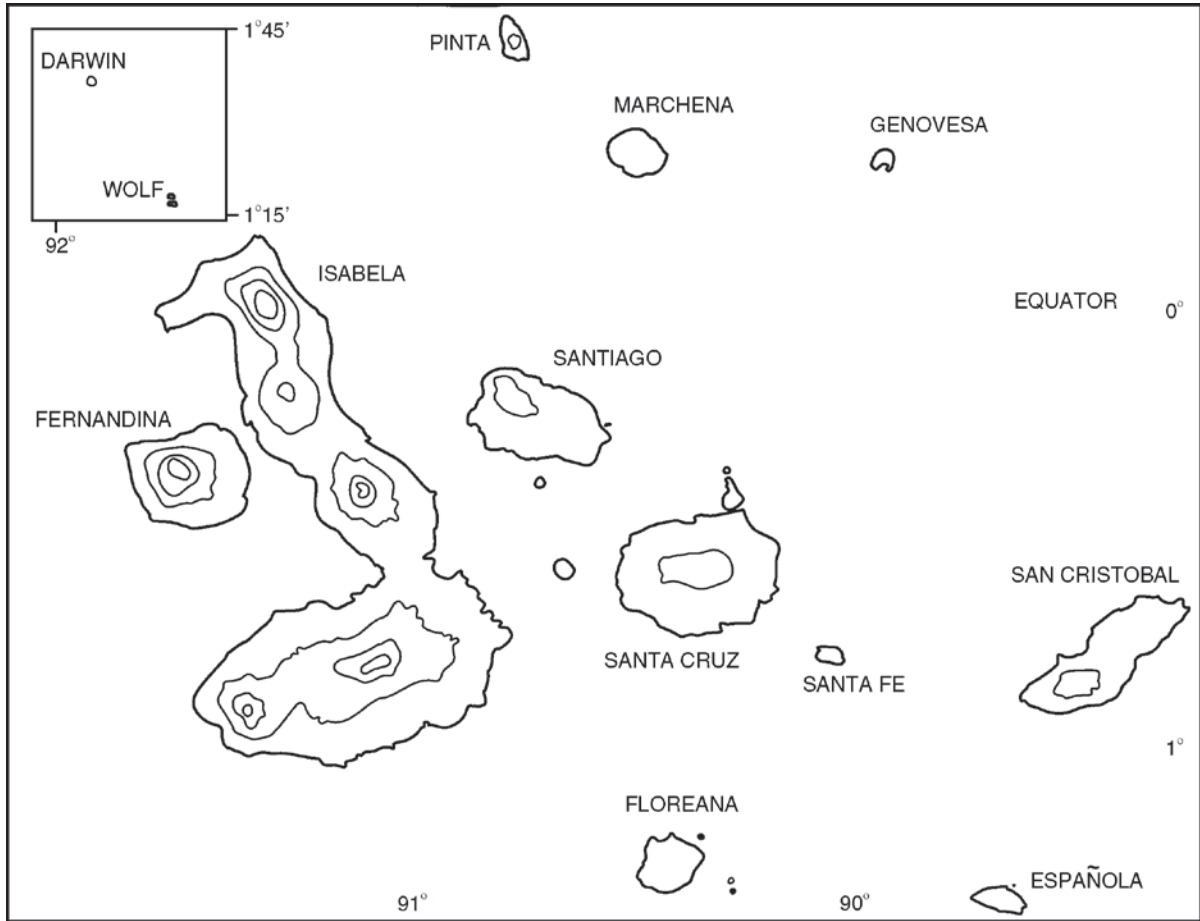
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Galápagos Islands Insects: Colonization, Structure, and Evolution

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The Galápagos archipelago of Ecuador has an interesting insect fauna that is now rather well known. The archipelago is composed of 19 islands larger than 1 km², with a total land area of 7,882 km². It is the world's only remaining tropical oceanic archipelago that is little altered by humans. The present islands, 800–1,000 km west of the Pacific coast of Ecuador, have been available for terrestrial colonization for 3–4 million years. The archipelago is a model system for assessing the dynamics of biotic dispersal to, and differentiation on, oceanic islands. They are a natural experiment which has been running in oceanic near-isolation for about 3 Ma. Each island (Fig. 1) is a replicate of an experiment in biotic dispersal, colonization, and differentiation. The present plants and animals can be seen to be a record of the successes in dispersal to the islands, and of the dynamics of their subsequent evolution in isolation. The story has been well (or even exhaustively) reported for many of the larger plants and vertebrates. This story, however, has not been well studied for the vast majority of insects and other terrestrial invertebrates.



Galápagos Islands Insects: Colonization, Structure, and Evolution, Figure 1 Map of Galápagos Archipelago.

The insect fauna (Tables 1 and 2) is now known to contain 23 of the world's 31 orders of insects, with at least 255 families, 1,057 genera, and 1,853 species, of which 736+ are endemic, 818+ are indigenous, and 295+ are introduced. Within the beetles (Coleoptera), the islands have 56 families, 297 genera, and 486 species (266 endemics, 110 indigenous, and 110 introduced species). The 376 native beetle species (indigenous and endemics combined) represent a rate of species accumulation of about one every 9,260 years (through successful colonization plus speciation through about 3.5 million years).

Charles Darwin is known to have been a keen collector of insects and especially beetles. However, as he wrote in his 1845 book "Voyage

of the Beagle," he was not impressed by the abundance or diversity of the insects of the Galápagos Archipelago. In fact, the entire biota of the Galápagos is generally not very impressive in appearance. But there are a few exceptions and these have received exceptional publicity. Most of the organisms are, however, small or drab when compared with those of the luxuriant tropical forests of mainland South America. This is partly a reflection of the isolation of the islands (800–1,000 km west of the coast of Ecuador), their youth (only 3–4 million years), the difficulty of dispersing to them, their seasonally harsh and semi-arid tropical climate, and the difficulty of establishment by colonizing species.

Galápagos Islands Insects: Colonization, Structure, and Evolution, Table 1 Numbers of native (endemics plus indigenous) genera, species, and single-island endemic beetle diversity, arranged by increasing island size. The larger islands have more genera, more species, more single-island endemics, and more species per genus. These generalizations also occur in the rest of the native insects fauna

Island	Area (km ²)	Total native Genera	Total native Species	Single-island species/ Endemics	Genus ratio
Caamaño	0.045	9	10	0	1.11
Beagle	0.08	1	1	0	1.0
Campeón	0.095	16	16	0	1.0
Plazas Sur	0.119	17	17	0	1.0
Eden	0.23	8	8	0	1.0
Daphne Major	0.330	3	4	0	1.33
Gardner at Floreana	0.812	7	7	0	1.0
Darwin	1.063	15	15	2	1.0
Bartolomé	1.24	16	17	0	1.06
Tortuga	1.298	3	3	0	1.0
Wolf	1.344	17	17	2	1.0
Seymour	1.838	31	33	0	1.06
Rábida	4.993	46	48	0	1.04
Genovesa	14.10	44	48	2	1.09
Pinzón	18.15	42	44	2	1.05
Santa Fé	24.13	40	48	2	1.20
Baltra	26.19	28	32	0	1.14
Pinta	59.40	76	87	0	1.15
Española	60.48	55	65	4	1.18
Marchena	129.96	56	63	2	1.13
Floreana	172.53	114	141	5	1.24
San Cristóbal	528.09	123	153	17	1.24
Santiago	584.65	119	148	14	1.24
Fernandina	642.48	72	80	1	1.11
Santa Cruz	985.55	186	258	27	1.39
Isabela	4,588.0	158	205	24	1.30

Colonization Processes

How do insects get to oceanic islands? The processes of colonization and any subsequent evolution on islands can seldom be directly observed. Usually, they are deduced from an analysis of the distributional and ecological patterns of the

organisms in conjunction with evolutionary and ecological theory.

There are two general groups of hypotheses about processes which place biotas on islands. One of these, the “Continental Drift” process of distribution of ancient biotas, is irrelevant for the Galapagos because of their geological youth and oceanic origin.

Galápagos Islands Insects: Colonization, Structure, and Evolution, Table 2 Summary of numbers of species and native genera of the insect orders of the Galápagos islands. Some orders have a disproportionate number of introduced species, especially on the islands with human settlement. A figure of 1.00 in the column of native species/native genus ratios shows that there has been no speciation in many insect orders after the natural colonization event of a single species in each genus, and comparatively little in the other orders

Order	Introduced	Native	Native	Species/Genus
	Species	species	Genera	Ratio
Collembola	3	35	22	1.57
Diplura	1	2	2	1.00
Archeognatha	0	1	1	1.00
Thysanura	1	2	2	1.00
Odonata	0	8	7	1.14
Orthoptera	4	29	13	2.23
Mantodea	0	1	1	1.00
Blattodea	11	7	3	2.33
Isoptera	0	4	3	1.33
Dermoptera	4	3	2	1.50
Embioptera	1	1	1	1.00
Zoraptera	0	1	1	1.00
Psocoptera	14	26	22	1.18
Thysanoptera	8	42	42?	1.00?
Hemiptera	118	198	86	2.30
Phthiraptera	8	80?	40?	2.00?
Neuroptera	0	8	5	1.6
Strepsiptera	0	1	1	1.00
Siphonaptera	3	1	1	1.00
Coleoptera	111	378	226	1.67
Lepidoptera	64	±300?	160?	1.88?
Diptera	66	±200?	150?	1.33?
Hymenoptera	46	±250?	160?	1.56?

Thus, all terrestrial colonists have crossed the oceanic water gap by one of four general dispersal mechanisms. The method of dispersal is a property of all the ecological, behavioral, and physiological characteristics of the species and of its mode and frequency of transport opportunity. Colonization is a property of both the life history requirements of the species and the characteristics of the new environment.

Aerial Transport (Actively by Flight and/or Passively by Wind)

This probably accounts for about half of the insects of the Galápagos. The mean body size of Galápagos insects appears to be smaller than for a mainland Ecuadorian fauna (but measurements are available for neither). Darwin first noted the small size of the insect fauna. The smaller body size would support

the idea that the majority of the insect colonists were carried as flying individuals by winds. In contrast to its importance for insects, it may seem surprising that wind transport may account for only 9% of natural seed-plant colonizations of the Galápagos.

Marine Transport

A significant component of the total insect fauna probably arrived on the sea surface, either on rafts of vegetation and flotsam or by floating themselves (as pleuston). This may be the most important mode for most of the flightless terrestrial arthropods. For the insects themselves, it is estimated that marine transport may also account for about half of the original colonists. Flightless or poorly flying groups of large-bodied beetles such as weevils and darkling beetles probably used this mode, as did millipedes, centipedes, terrestrial isopods, oribatid mites and others. Bostrichids, cerambycids and various other wood-boring and wood-associated beetles probably arrived by rafting in wood as adults or immatures. Flightless *Gerstaeckeria* weevils may have arrived on rafting pieces of their *Opuntia* cactus host plants.

Several groups of large-bodied wingless beetles such as endemic *Galapaganus* weevils and the three genera of Darwin's darkling beetles (genera of Tenebrionidae containing nine species that were first collected by Darwin: *Stomion*, *Ammophorus*, and *Blapstinus*) are represented by species that occur on more than one island. Such cases are usually within the older eastern and central group of islands. It is logical that these species originated (speciated) on one island and that they have then moved from this to another island, probably after being washed to sea during heavy El Niño rainstorms and floods.

Transport on or in Other Animals

Insect ectoparasites, such as all of the 80 species of Phthiraptera (chewing bird-lice) and the 8 species

of Hippoboscidae (louse flies, Diptera), as well as bird ticks, reptile ticks and chigger mites, undoubtedly arrived on their vertebrate hosts. Bird transport has also been important for seed-plants, because it is estimated that 79% of the angiosperms arrived as propagules with birds, either on or in their feathers or in their digestive tracts. Rafting terrestrial mammals and reptiles seem to have carried a few arachnid and insect ectoparasites. And invertebrate colonists themselves have also carried some of their own arthropod parasites. Examples are one strepsipteran (in leafhoppers), several dryinid wasps and some pipunculid flies (in leafhoppers). Among the beetles, there are two examples: one meloid blister beetle (on *Xylocopa* carpenter bees), and two rhipiphorid beetles (in wood-boring beetle larvae) probably arrived as parasitic immatures on or in their host insects. The parasitized bee hosts themselves probably arrived by rafting on floating wood and the hosts of the rhipiphorids in lumber imported for construction of buildings.

Human Mediated Transport

Humans have intentionally introduced many domestic animals and agricultural or horticultural plants to the Galápagos. Some of these have escaped and become feral. But there is only one example of the intentional introduction of an arthropod: the vedalia beetle (Coccinellidae) for the bio-control of the cottony cushion scale (*Icerya purchasi*, Hemiptera), an introduced pest. By 1998 there were at least 292 recognized examples of unintentional introductions of insect species and the number in 2004 was at 450 species of introduced insects. Such species are here called introduced species, but the term "adventive" has also been used for these. The first such introduced insect may have arrived with the first European landings of Bishop Tomas de Berlanga and his party in 1535, as *Dermestes* (dermestid) and *Necrobia* (clerid) beetles and cockroaches. These were all commonly associated with

humans and stored products in their sailing ships. Pirates, who used the islands from shortly after the time of their discovery until the early 1700s, and whalers and sealers, from the mid 1700s to mid 1800s, may have brought an alleculid beetle (and other dry-wood insects such as bark-beetles) in logs or firewood from the mainland.

Ships transporting both supplies and tourists have taken insects attracted to ships' lights to and between the islands. The orders with the largest number of introduced species are Coleoptera, Hemiptera, Lepidoptera, and Diptera. Some 111 beetle species are among the more commonly encountered species of insects introduced to date. Not all of the introduced species seem to have become permanently established; some long-horned beetles have not been found since their original collection. The introduced species occur in greatest diversity on the four large islands with permanent human settlements. There is now a program of agricultural quarantine control and inspection of goods and materials coming into the Galápagos in an attempt to limit future introductions of alien arthropods.

Sources of the Colonists

There is limited detailed data on the mainland distributions of either indigenous Galápagos insects or mainland sister species of the endemic species. The data now available seem to indicate that only a few of the Galápagos colonist insects came from southern South America (arid coastal Peru or Chile). Most of the faunal relationships are with the lowland semi-arid and seasonal Neotropics, along the Pacific coast from Mexico to Ecuador. The best phylogenetic and biogeographic analyses show a general biogeographic pattern of a western Neotropical source area and that the Galápagos species are relatively recently derived species.

Stochastic (Random) Processes in Colonization and Distribution

Colonization is seldom strictly predictable or linear even if the islands themselves are relatively linear in age or geography. As an example, one would predict that insect colonization was first to San Cristóbal and Española, which are the oldest and most easterly islands, and that the other islands were colonized sequentially northwestward as stepping stones as they formed through time. Exceptions to these predicted patterns do exist. This shows the lack of absolute predictability in present distributions through the randomness of the processes of either past dispersal, or colonization success, or extinction. For instance, the carabid beetle genera *Platynus* and *Scarites* are on Isabela and San Cristóbal islands, and not on Santa Cruz, which lies between them. The indigenous carabid *Halocoryza acapuliana* Whitehead is known only from small and central Rabida Island.

Neighbor islands are more likely to share endemic species. This is clear in a number of shared beetle species limited to island pairs such as Darwin and Wolf (the tenebrionid *Stomion cribicollis* Van Dyke and the weevil *Galapaganus darwini* Lanteri), and Marchena and Pinta (the tenebrionid *Stomion rugosum* Van Dyke). The isolation of Genovesa is evident in its failure to be colonized by flightless *Ammophorus* beetles and other insect groups. Flightless *Galapaganus* weevils are seemingly absent from Pinta and Marchena. Pinzón is famous for not having the widespread palo santo tree (*Bursera graveolens*), but this island's insects are not well enough known to evaluate a pattern of absence of insect species there.

Randomness is evident in the fact that some colonizations have been across the archipelago (from one side of the archipelago to the other). Molecular data suggest that Pinta Island was colonized by tortoises by oceanic transport from Española, and cladistic analysis suggests the same pattern in flightless *Stomion* beetles.

Structure of the Insect Fauna

An Unbalanced Fauna

Insect representation at the family level in the Galápagos is vastly different from that in the Neotropical fauna. The cause is the inequality of families in their ability to successfully complete both the sequential processes of dispersal and then colonization. When compared to the fauna of the Neotropical continental source area, it is evident that the Galápagos fauna is unbalanced (or disharmonic) and impoverished. This means that the taxonomic composition of the archipelago is significantly different in its makeup and proportions from that of the mainland.

The probable reasons for the absence of many insect families, subfamilies, and tribes are diverse. Difficulties of long-distance over-water dispersal and colonization must lie at the core of the reasons. Long distance dispersal is unlikely for many taxa and the lack of diverse and suitable habitats in the Galápagos is of undoubted importance. The absence of suitable food plants or prey items is involved. The taxa which are present can be viewed as able dispersalists, rugged colonists, and adaptable in acceptance of available microhabitats and food materials.

Trophic Generalists

Colonization is probably easier for trophic generalists (scavengers and predators) than for herbivores which are more likely to be specialist feeders. Island insect faunas in general tend not to be as rich in herbivores as the faunas on continents. In Galápagos beetles there are more trophic generalists (scavengers and predators) than herbivores. However, in Heteropteran bugs, colonization of islands by herbivores seems to be more successful than by predators.

Trophic Specialists

There is little evidence that Galápagos insects have narrow or restricted feeding niches. The few

examples are *Gerstaeckeria* weevils which feed only on the tissues of *Opuntia* cactus, and some host specific seed feeding bruchids and scolytids. *Ataenius* scarabs, usually associated with herbivorous mammal dung, feed on the dung of the herbivorous giant tortoises and land iguanas. This may or may not represent a shift to a new food type. Tortoise and land iguana dung appears similar to that of ungulates because it is mostly composed of poorly digested plant materials.

Ecological Escape

Plant or animal colonists on islands may be ecologically “released” through escape from their continental herbivores, parasites, predators, and competitors. Many cases of escape from insect herbivores or predators must exist, but few are recognized. One example is the seed-producing legume plants which have escaped many (but not all) of their seed predator bruchid beetles. The bruchid *Megacerus leucospilus* (Sharp) feeds on the seeds of the widespread beach morning-glory *Ipomoea pes-caprae* in Central America, but the plant seems not to have this seed predator on the Galápagos.

Parthenogenesis

If females of a species can reproduce without the presence of individuals of the male sex, the species is more likely to establish itself as a colonist. Several of the Galápagos insects are known to be parthenogenetic. But there is no apparent evidence that this has been disproportionately important in the colonization of the Galápagos.

Vegetational Zonation and Diversity

Terrestrial communities in the Galápagos are usually characterized according to the elevation-related (precipitation and temperature controlled)

zonation of the flora. The archipelago may possess the strongest or most compressed floristic zonation to be found anywhere in the world, passing through its six major vegetation zones in an elevational rise of only about 700 m; the littoral, arid, transition, humid forest, evergreen shrub, and above-treeline fern-sedge (“pampa”) zones.

Insect diversity also seems to display some zonation, with fewer species being known from the higher elevations. The arid zone has the largest area in the islands and the most native insect species. The other zones, at higher altitudes, have progressively less area and proportionally fewer species, but sampling has not been equivalent. This probably indicates that the arid zone has been a bigger target for colonization for a longer period of time. The introduced species are more evenly distributed in all zones. This might be a reflection of the more eurytopic (adaptable) nature of the introduced species.

Plants also support diversity in that they provide various structural parts that may be fed upon by feeding specialists. Host-specific plant-feeding insects could be expected to exhibit the same zonation as their hosts, but almost all Galápagos phytophagous insects seem to feed on several species of host plant. Data for genus and family-level host-plant diversity are not available. Host specificity, to be expected in groups which elsewhere are usually monophagous or stenophagous plant-feeders, such as chrysomelids, is slight in Galápagos phytophagous beetles. There is no additional evidence for host specificity in indigenous phytophagous insects other than in *Gerstaeckeria* weevils on *Opuntia* cactus and some bruchids and scolytids. Thus, phytophagous species are in the minority, few are host specific, and none seem to have co-evolved with the endemic vegetation.

Seasonality

Environmental conditions regulate periods of insect activity. Most adult insect species are present or active during the rainy months of January to

June. With the arrival of the Galápagos rainy season, insect activity increases and there are large and noteworthy outbreaks of beetles and other insects, which seem to be short-lived. These include *Calosoma* ground beetles, *Camponotus* ants, *Disclisiprocta stellata* Guenée (a geometrid moth), various sphinx moths, and other insects. These mass emergences are best noticed at lights at night and are environmentally triggered, but they also occur annually in coastal mainland Ecuador and seasonal forests elsewhere in Central and South America, so they are not a unique island feature.

Evolutionary Dynamics

Genus Level Endemism

Endemics are taxa limited to the geographic area under discussion. Genera endemic to the Galápagos probably represent an earlier time of colonization and a more prolonged period of isolation. Galápagos endemic genera are proportionally more frequent in the vertebrates and less frequent in the insects. This could mean that vertebrates differentiate at a faster rate or under stronger selective pressures, but more probably is a reflection of the more finely divided subjective criteria for what defines a vertebrate genus. Some endemic insect genera do exist. Among these endemics are some which can be called phylogenetic relicts or paleo-endemics and which have no close relatives, such as the eyeless cave staphylinid *Pinostygus* of Isla Santa Cruz, and the *Neoryctes* dynastine scarabs which occur as four species on four islands. Some genera, once thought to be Galápagos endemics, have since been found in mainland Neotropical localities and others may yet be detected.

Species Level Endemism

Most insect colonization has not been followed by much species multiplication; the mean for the native beetle fauna is about 1.35 species per

colonizing ancestor. About half the naturally occurring species are endemic, depending on the insect order. These evolved to endemic status following the colonization event of the ancestral species. The factors suppressing speciation in general in the Galápagos (as compared with other archipelagos) seem to be, in probable order of importance: lack of great ecological diversity, closeness to mainland source areas, and geological youth of the islands.

Different groups of organisms need not present equivalent amounts of endemism. This is obviously a result of differences in their vagility and the amount of gene flow between continental and island populations. In beetles, the good dispersers have lower levels of endemism, while poorer dispersers have higher levels. Comparison of the Galápagos and Hawaiian archipelagos shows a much larger mean number of speciation events from a single colonist ancestor in Hawaii. This is probably the result of Hawaii's greater age, area, ecological diversity, and isolation (this is to say that colonist arrival is less frequent, and that genetic dilution of island populations by mainland genomes is also less frequent).

Speciation

Most insect genera in the Galápagos are represented by only a single species. This shows that most colonization of the islands has usually been by only one species in a genus. This pattern was first noted by Darwin. Only a minority of the native insect genera which are present contain more than one species, either through multiple colonization, or species multiplication on the islands. The process of forming several species by allopatric speciation on a single individual island has not been a dominant evolutionary process in Galápagos beetles, while it has been a spectacularly exuberant process in the Hawaiian Archipelago.

Nevertheless, there are several insect genera which have undergone appreciable subspeciation or speciation in the Galápagos but none of

these approach the dramatic swarms of species (descended from a single ancestor species) of insects, snails, or birds that have evolved in Hawaii. For instance, while hundreds of species of *Drosophila* occur in Hawaii, there are only 13 species (many cosmopolitan) of in these in Galápagos.

Winged Endemic Species

In the winged insects the most common pattern of distribution is for a species to occur on more than one island. This is easy to understand. It is most likely that these evolved on a single island and then dispersed to other islands, usually by flight.

Loss of Wings

Loss of flight ability is one of the more pronounced phenomena associated with island insects. This is seemingly not a property of island life itself, but of habitat stability and homogeneity. Flightlessness also frequently occurs in insects in desert and semi-arid habitats. This last is the best single characterization of Galápagos environments, and beetles are prime examples. Flightlessness in some South African desert dwelling scarab beetles is a morphological correlate with water conservation capabilities. This may also be true and part of the adaptive strategies of such flightless Galápagos beetles as tenebrionids, carabids, and weevils. Beetle examples of more speciation in less vagile groups are in flightless carabids, weevils, and Darwin's darkling beetles (*Stomion*, *Ammophorus*, and *Blapstinus*). Interestingly, even within flightless genera in the arid lowlands, many species do occur on more than one island, and these are probably evidence of inter-island oceanic transport following the origin of the species on one island.

The single island endemics are usually restricted to either the arid lowlands or the moist uplands (of high islands). Groups that are actively in the process of losing flight ability, such as *Ataenius* and *Neoryctes* scarabs, show discrete polymorphic stages in reduction of hind wings. So, loss of flight ability in Galápagos insects is a significant

evolutionary theme. This has not always sponsored a major burst of species multiplication, but it has happened more often in groups that lost their flight ability on the Galápagos as a convergence rather than in groups that arrived already in a flightless condition. There is a parallel in birds: rails have reached many oceanic islands and then convergently experienced a reduction in wings and loss of flight ability.

Speciation and Flightlessness

Flightless terrestrial arthropods would certainly appear to have less dispersal potential than winged ones, and most species proliferation has occurred in the Galápagos beetles that are secondarily wingless. Nine genera of beetles probably colonized in a flightless condition, but only four of these have undergone island multiplication to three or more species. These groups have produced an average of 3.0 species per colonization event. Another 14 genera appear to have become flightless after colonization and these show even more species proliferation, with a mean of 3.6 species per colonization event.

Adaptive Radiation

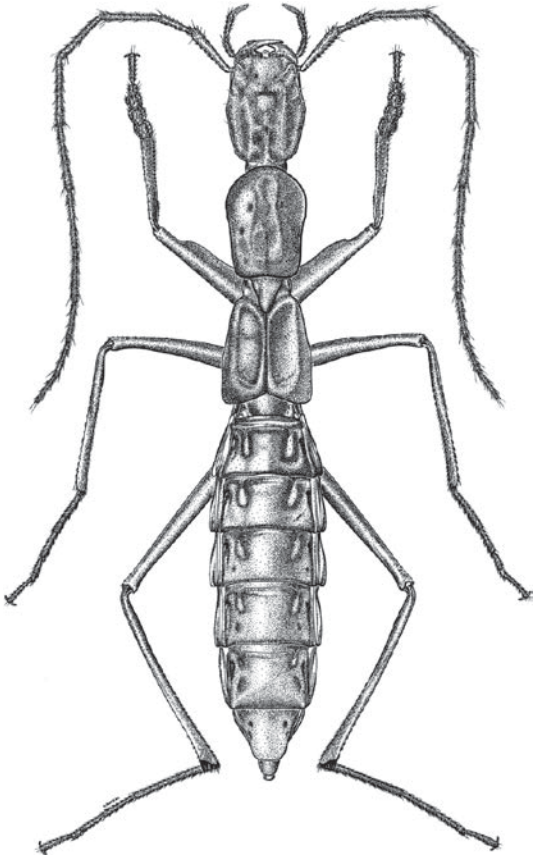
Adaptive radiation is a common phenomenon on islands. But it is important to note that adaptive radiation is much more than just the simple allopatric species multiplication that follows genetic isolation on separate islands. It is here defined as the set of evolutionary changes which occur in the diversification of a lineage that facilitate the exploitation of new resource types with different morphological or physiological traits. Thus, along with the morphological, physiological, and/or behavioral changes accompanying speciation must also come changes in either or both niche and habitat use. This is what has happened in the famous textbook example of Darwin's finches. Other examples can include the striking adaptive radiation in *Scalesia* trees and shrubs, and perhaps arguably in *Opuntia* cactus. In contrast, the famous giant

tortoises and less famous lava lizards have undergone much speciation or subspeciation, but there is little evidence for true adaptive radiation in these examples. Adaptive radiation is probably enhanced by competition for limited resources, as in the case of the finches, especially in times of drought. But, it is difficult to envision intense competition between generalist scavenger or generalist predator insects.

Are the few examples of adaptive radiation indicative of a generalization, or are they exceptions? How many of the monophyletic species swarms in the insects of the archipelago have undergone significant ecological, morphological, or behavioral differentiation that promotes life in a new niche or new habitat? In short, there seem to be very few examples within the insects in general. In the three genera of Darwin's darkling beetles (*Ammophorus*, *Stomion*, *Blapstinus*) there are some cases of congeneric species sympatry and there is some habitat separation between species based on preferences for different substrate types (sand versus volcanic ash), habitat distance from the sea-coast, and elevation. Most *Ammophorus* species inhabit the arid zone, but two are restricted to the moist highlands of San Cristóbal and Santa Cruz Islands. The same occurs in *Galapaganus* weevils. Thus, while the Galápagos are famous for having provided a classic example of the process and results of adaptive radiation in Darwin's finches, this is an exception. It is only a very infrequent or arguable result in Galápagos insects.

Subterranean Arthropods

A diverse assemblage of many eyeless arthropods occurs in the extensive systems of caves and rock crevices in the volcanic basalt bedrock of the Galápagos. Some ten species of arthropods such as geophilomorph centipedes, polydesmoid millipedes, soil dwelling earwigs, and darkling and carabid beetles are in eyeless (Fig. 2) genera which must have colonized the Archipelago in an already-eyeless condition. But at least another 23 species of



Galápagos Islands Insects: Colonization, Structure, and Evolution, Figure 2 The staphylinid beetle *Pinostygus galapagoensis* Campbell and Peck from a lava tube cave on Santa Cruz island. This eyeless and flightless subterranean endemic genus and species has probably changed more from its ancestral colonizing species than any other Galápagos animal. The beetle belongs to a group of visually hunting and flying arboreal predators which live in the canopy of tropical South American rainforests. No other members of its tribe occur in the Galápagos. The body length is about 2.5 cm, and this is the world's largest eyeless-wingless staphylinid beetle.

eyeless terrestrial arthropods, including seven beetle genera, are in normally eyed groups. These must have lost their eyes after colonizing the islands, and during the process of adapting to soil, litter or subterranean habitats.

Extinction

Extinction through time is a natural process and is to be expected. But extinction caused by human action is different and should be of great concern in the Galápagos. Insect species extinction through human causes is probable, but no documented individual examples are known. Some of the introduced insects, such as *Wasmannia* fire ants and *Polistes* wasps, are preying on or competing with indigenous and endemic insects.

Feral vertebrates have had a two-fold effect on beetles and other insects. (i) The vertebrates have caused the near or complete loss of insect host plants, such as *Opuntia* cactus on most of Floreana and San Cristóbal (eaten by feral goats and donkeys). This has led to the concomitant loss of host-specific insects such as *Gerstaeckaria* weevils. (ii) The vertebrates have also had an effect by being predators, such as mice or rats or pigs, feeding on *Neoryctes* scarab beetles or other large-bodied insects. Despite these examples, there is presently no strong or direct evidence of the actual archipelago-wide extinction of an insect species on the Galápagos through an action ultimately caused by human activity.

Human-caused habitat alteration has had a significant, but unmeasured effect on the native insect populations. The clearing of large areas of *Scalesia* forest for agriculture and pastures and the replacement of large areas of native vegetation by introduced crop plants, grasses and weeds on Floreana, Santa Cruz, San Cristóbal, and Isabela must have had some impact. The importance of all of these introductions and alterations has not been measured or even estimated for the beetles or other insects.

Future Research

Although much is now known about Galápagos insects, there is still much to learn, especially about the life histories and evolutionary relationships of the species and in comparing them with the continental South American insect fauna. The Galápagos National Park Service and Charles Darwin Research

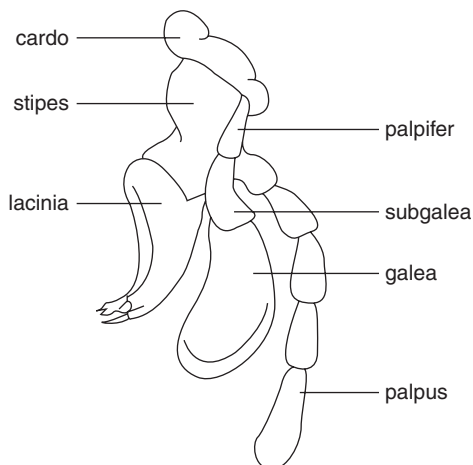
Station invite international research proposals and scientific collaboration with Ecuadorian personnel, students, and researchers. Information on past and present entomology research programs and details for scientific research permit applications can be found at <http://www.darwinfoundation.org/terrest/entomology.html> Research proposals of an applied and conservation orientation are especially welcome. General collecting without a research purpose is not permitted.

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Galea (pl. galeae)

The outer region of the maxilla, often a lobe (Fig. 3), and sometimes highly modified (Fig. 4) for feeding



Galea (pl. galeae), Figure 3 External lateral aspect of the left maxilla in an adult grasshopper, showing some major elements.

in Diptera, Lepidoptera and Hymenoptera. It forms the elongate, coiled proboscis in Lepidoptera.

► Mouthparts of Hexapods

Gall

An abnormal growth on a plant induced by insect or mite feeding, or a plant pathogen.

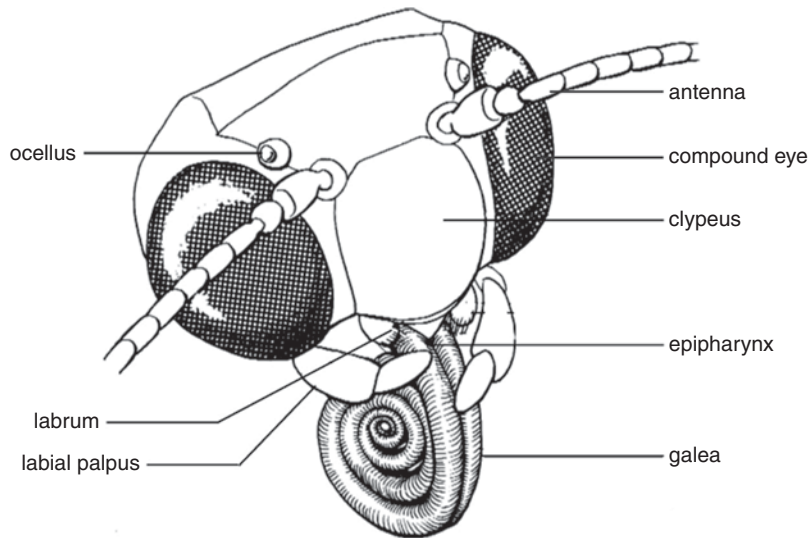
Gall Formation

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Galls are structures that form as a result of the abnormal growth activities of plants in response to gall-inducing organisms. Most galls are caused by nematodes, insects and mites, while a very small percentage are caused by bacteria, fungi and viruses. There are thousands of species of insects in the world that induce gall formation on the roots, stems, leaves, buds, flowers and fruits of plants in a wide variety of plant families. Insect galls range in complexity from simple outgrowths to more highly differentiated structures such as those typified by many of the cynipid wasp galls. Despite the large numbers and types of insect-induced galls, very little is known regarding the underlying mechanism or mechanisms of insect gall formation. In contrast, the mechanism of crown gall formation by the bacterium *Agrobacterium tumefaciens*, has been well characterized. An understanding of the mechanism of crown gall formation may provide some clues to the mechanism or mechanisms of insect gall formation.

Crown galls form as a result of wound inoculation on many species of plants by the soil dwelling bacterium *Agrobacterium tumefaciens*. Early studies showed that crown gall tissues exhibit autonomous growth and retain their tumorous



Galea (pl. galeae), Figure 4 The head of a moth (Lepidoptera) showing some components.

characteristics in the absence of the inducing bacterium. The ability of the bacterium to induce gall formation subsequently has been shown to be encoded by a tumor-inducing (Ti) plasmid that is transferred into the plant tissue. A small fragment (the T-DNA) of the Ti plasmid is integrated into the plant cell genome within the nucleus and is stably maintained and transcribed. It has been shown that the T-DNA contains genes that code for the production of plant hormones, the auxin indole-3-acetic acid (IAA) and for cytokinins. Cytokinins promote cell division in plant cells while auxins play a role in cell enlargement. Both of these hormones also affect tissue differentiation in plants as well as many other processes. Cytokinins have been shown to be produced by additional species of gall forming bacteria including *Erwinia herbicola* pv. *gysophila*, *Pseudomonas savastanoi* and *Rhodococcus fascians*. A linear plasmid with a cytokinin synthesis gene has been found in *R. fascians*, a bacterium that induces leafy galls.

While an understanding of the mechanism of crown gall formation may provide some clues to the mechanism of insect gall formation, it should be noted that insect galls have some important differences compared to crown galls. Unlike crown

galls, insect galls are organized structures, often with very complex morphologies. In addition, early studies have shown that unlike crown galls, insect-induced galls do not exhibit the autonomous growth that is characteristic of crown galls. Gall growth does not continue indefinitely once the gall-inducing insect is no longer present. The physical presence of the insect within the gall tissue is another unique factor that may play a role in the mechanism of insect gall formation, but the role of mechanical tissue disruption in the process of insect-induced gall formation has not been well studied. Instead, studies have focused on the role of chemicals in insect-induced gall formation.

Studies of Insect Extracts and Secretions

A number of studies have been undertaken to test insect extracts and secretions for gall inducing chemicals. Larvae of *Mikiola fagi*, a midge that forms leaf galls (Fig. 5) on the European beech (*Fagus sylvatica*), have been tested to determine if they secrete cecidogenetic (gall-forming) chemicals. When the larvae were placed on a lanolin



Gall Formation, Figure 5 Leaf gall caused by *Mikiola fagi* on the European beech (*Fagus sylvatica*).



Gall Formation, Figure 6 The eastern spruce gall caused by *Adelges abietes* on Norway spruce (*Picea excelsa*).

paste on leaves of beech and when a paste that larvae had previously been on, was repeatedly applied to leaves, changes involving cell division and cell elongation resulted, but galls did not form.

Studies of the eastern spruce gall on Norway spruce (*Picea excelsa*) have provided evidence for the presence of cecidogenetic activity associated with the salivary glands of the gall-forming adelgid *Adelges abietes*. The characteristic needle swelling associated with the early stages of gall formation (Fig. 6) has been mimicked by injecting spruce buds with a solution containing macerated adelgid salivary glands.

The willow leaf gall, caused by *Pontania pacifica*, is initiated by the accessory gland secretions of the ovipositing female sawfly while further development of the gall is dependent on the presence and activity of the larvae. When gland sacs were placed in developing galls from which larvae had been removed, galls continued to grow. If the glandular material was repeatedly injected over a period of several days, the galls continued to develop to normal size. Extracts of young *Pontania* larvae and extracts of female accessory glands were able to promote the continued growth of galls from which the larvae had been removed. Mixtures of chemicals were tested to see if they played a role in willow leaf gall formation. Rapid and sustained growth of galls was obtained with a periodic injection of a mixture containing a synthetic cytokinin kinetin, a naturally occurring auxin indole-3-acetic acid and adenine.

While the examples noted above provide evidence for gall-inducing factors associated with extracts and secretions, the specific cecidogenetic chemicals have not yet been identified. In addition, while there is evidence for cecidogenetic properties associated with glandular extracts and secretions, no one has been able to mimic the entire process of gall formation with an extract or secretion. This is not surprising given the difficulties associated with attempting to simulate the continual release of a gall-inducing stimulus from the precise location where the insect is normally active within the plant tissue.

Studies of Auxin and Cytokinin Involvement in Insect Gall Formation

Given the importance of plant hormones in plant development as well as in the mechanism of crown gall formation, a number of studies have focused on the roles of the plant hormones auxins and cytokinins in insect gall formation.

There were some early reports that applications of auxins to plant tissues resulted in structures similar to galls, while others reported failure in their attempts to induce galls with auxin. Applications of auxins to plant tissues have not resulted in the formation of structures that exhibited the complexity and the degree of hyperplasia of insect galls. Extracts

of the saliva of gall-inducing aphid species have provided evidence for the presence of the auxin indole-3-acetic acid (IAA) and some have concluded that IAA was the active cecidogenetic factor in the aphid species studied. However, it was not determined whether the aphids produced the auxin, or whether they accumulated it from the plant tissue.

IAA has been detected and analyzed in other galls and gall formers. Oak apple galls caused by *Cynips quercusfolii* on *Quercus robur* and *Quercus sessiliflora* were shown to contain twice as much auxin activity as normal leaf tissues, while *Pinus edulis* needles with galls induced by larvae of the midge *Janetiella* sp. near *J. coloradensis* were found to contain 3.7 times higher concentrations of auxin bioactivity compared to needles lacking galls on a fresh tissue weight basis, and 17 times more auxin activity per needle. IAA was detected in *Cynips quercusfolii*, but was not detected in the larvae of the midge *Janetiella* sp. near *J. coloradensis*. In a study of the goldenrod ball gall induced by larvae of the dipteran *Eurosta solidaginis*, the gall-forming larvae were shown to contain high levels of IAA with detection by gas chromatography-mass spectrometry (GCMS). Concentrations of IAA in the gall tissues were higher than in the stem tissues on a weight per stem length basis, but not on a weight per weight basis.

Some studies have shown high levels of cytokinins in gall tissues. Levels of four cytokinins were shown to be higher in developing galls induced by *Pontania proxima* compared to levels in leaf tissue. Levels of the cytokinin isopentenyladenosine were shown to be much higher in hackberry (*Celtis occidentalis*) gall tissues than in control leaf tissues. However, others have not found higher levels of cytokinins in gall tissues compared to normal tissues. Levels of cytokinin bioactivity found in galls formed by *Mikiola fagi* were not elevated when compared to healthy leaves, while cytokinin concentrations in gall tissues formed by a chalcid wasp on *Erythrina latissima* were lower than those in surrounding leaf tissues. Levels of four cytokinins were shown to be higher on a weight per stem length basis in goldenrod ball galls compared to normal stem tissues, but were not higher on a weight per weight basis.

Studies have also shown evidence for cytokinins associated with gall-inducing insects. Cytokinins have been detected in the oriental chestnut gall wasp (*Dryocosmus kuriphilus*) and in the larvae of a chalcid wasp that forms leaf galls on *E. latissima*. The high concentration of cytokinins in the larvae of the chalcid wasp could be responsible for nutrient mobilization by the larvae within the galls, and may also be responsible for the fact that galls containing larvae remain as green islands on senescing leaves, while those without larvae, senesce rapidly. Four different cytokinins have been detected by GCMS in the larvae of *Eurosta solidaginis*, the dipteran responsible for the formation of goldenrod ball galls (Fig. 7). The cytokinin isopentenyladenine was shown to be present at much higher concentrations in first instar larvae than in normal stem tissues. In contrast, in a study of willow galls induced by *Pontania pacifica*, growth promotion was found to be associated with two unidentified adenine derivatives in the female accessory glands of the sawfly, but no significant cytokinin bioactivity of gland extracts was detected.

In summary, studies have provided evidence for yet-to-be-identified gall-inducing factors associated with extracts and secretions of gall-inducing insects. In addition, there have been numerous reports of the presence of plant hormones in gall-inducing insects and gall tissues with detection not only by bioassay, but also by sophisticated state-of-the-art techniques. However, it remains to be seen whether gall-inducing insects have the ability to synthesize plant hormones such as auxins and/or



Gall Formation, Figure 7 The goldenrod ball gall caused by *Eurosta solidaginis* on *Solidago altissima*.

cytokinins, whether the gall-formers induce synthesis of the hormones in the surrounding plant tissue, or whether the hormones that have been detected in the gall-formers have just been accumulated from the plant tissue. The high levels that have been found in some species of gall-inducing insects are suggestive of synthetic capabilities. Despite the evidence for plant hormones in galls and gall-inducing insects, the specific role of plant hormones in the development of insect galls has not been determined. Given the important role that auxins and cytokinins play in normal developmental processes in plants as well as their well-characterized role in crown gall formation, it seems likely that they play an important role in insect gall development as well. As the evidence for the involvement of auxins and cytokinins in insect gall formation is more convincing for some of the gall systems that have been studied than for others, it is most probably the case that other yet-to-be-determined cecidogenetic agents will be identified as playing important roles in the mechanism of gall formation for certain types of insect galls.

- ▶ [Gall Midges \(Diptera: Cecidomyiidae\)](#)
- ▶ [Gall wasps \(Hymenoptera: Cynipidae\)](#)

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Gall Midges (Diptera: Cecidomyiidae)

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Cecidomyiidae are one of the largest families in the order Diptera, with more than 5,700 described species and many more undescribed and unknown species worldwide. The family belongs to the suborder Nematocera, and its closest relatives within it are the fungus-feeding gnats in the families Sciaridae and Mycetophilidae (in the broad sense). According to fossils from the Jurassic period, the family is at least 150 million years old, but has apparently experienced explosive speciation during the Cretaceous, with the appearance of flowering plants. Cecidomyiidae have a cosmopolitan distribution, although only the faunas of Europe and North America are fairly well known. This situation makes it impossible to estimate the actual number of species in the family. The common name “gall midges” refers to the gall-inducing habit of most species, which constitute the largest group of gall-inducing organisms. However, the family also contains many species that are fungus-feeders, predators, or feed on plants without inducing galls.

Classification

The Cecidomyiidae are divided into four subfamilies:

The Catotrichinae constitute the oldest subfamily and are considered ancestral to all other subfamilies. This group contains one genus (*Catotricha*) and seven species, which are known from the Holarctic region and from Australia.

The Lestremiinae are a diverse group of about 630 species that is ancestral to the remaining two subfamilies. Although many genera and species in this group are common and widespread, it is still largely unknown, and dozens of species belonging to it are yet to be described from the

Holarctic and the Australasian regions. Faunas of other parts of the world are poorly known. Lestremiinae are fungus or detritus feeders, and their larvae are found in decaying organic matter.

The Porricondylinae constitute a diverse, paraphyletic group of 635 species that are similar in habits to the Lestremiinae. A few species are consistently found in association with plants, such as in already infested fruit or in conifer cones, but are assumed to feed on decaying organic matter in these niches. Several species are known as fossils from the upper and lower Cretaceous. The subfamily is poorly known outside the Palearctic region, and relationships among its tribes are unclear.

The Cecidomyiinae are the youngest, largest, and most diverse subfamily of gall midges, with more than 4,400 described species worldwide. This is a monophyletic group that includes all the plant-feeding species in the family, as well as several unrelated groups of fungus feeders and predators. The Cecidomyiinae are divided into four supertribes: the species-poor Stomatosematidi and Brachineuridi, whose biology is largely unknown, and the very large and biologically diverse Cecidomyiidi and Lasiopteridi.

Morphology

Adult gall midges are tiny, fragile flies, usually 2–5 mm in length. Most species are inconspicuously colored, but some groups have color patterns, especially black and white, resulting from dense covering of scales and hairs. The head is made up largely of compound eyes that often touch at the vertex. The antennae usually number 12 flagellomeres, but their number vary among groups and sometimes also within the same species and even the same individual. Male flagellomeres are often composed of a large node and a long narrow neck, whereas female flagellomeres are mostly cylindrical with much shorter necks. Males of many species have two nodes on each flagellomere, each bearing sensory setae and circumfila – sensory hairs that girdle the flagellomere and sometimes

form very long loops. Male antennae of some groups in the family resemble those of the female. Mouthparts are usually greatly reduced and are only capable of liquid consumption; the adults of most plant-feeding species may not feed at all. The wing is usually transparent and has greatly reduced venation in most groups, with only 2–5 long veins, and long hairs along its margin. The legs are usually long and slender and comprise five tarsomeres. In the subfamilies Porricondylinae and Cecidomyiinae, the first tarsomere is considerably shorter than the second, and legs are easily broken beyond it. Tarsal claws are variably shaped, some with 1–2 additional teeth at their base. The ovipositor varies in length and is usually retracted inside the abdomen. Different groups have developed various modifications of the ovipositor, including conspicuous setation, or needle-like or sword-like parts to aid in oviposition. The male genitalia include gonopods that clasp the female during mating.

Larvae pass through three instars. They are legless and have a greatly reduced head capsule with no eyes, very short antennae, and mouthparts that are suited for piercing and sucking liquids. They are often bright yellow, orange, or red, but they may also be white, depending on the species. The third instar larva usually has a spatula, a dark, sclerotized structure on the ventral side of the prothorax, which is unique to the Cecidomyiidae. The spatula, which varies in shape and size among species, is used for digging in the soil or cutting through plant tissue, but many taxa have lost it altogether. Pupae may have diagnostic characters on their head and abdomen in the form of horns and spines that aid in cutting through plant material prior to adult emergence.

Biology

The gall-inducing guild within the Cecidomyiidae has received more attention than any other group in the family due to the large number of species and the remarkable diversity of host

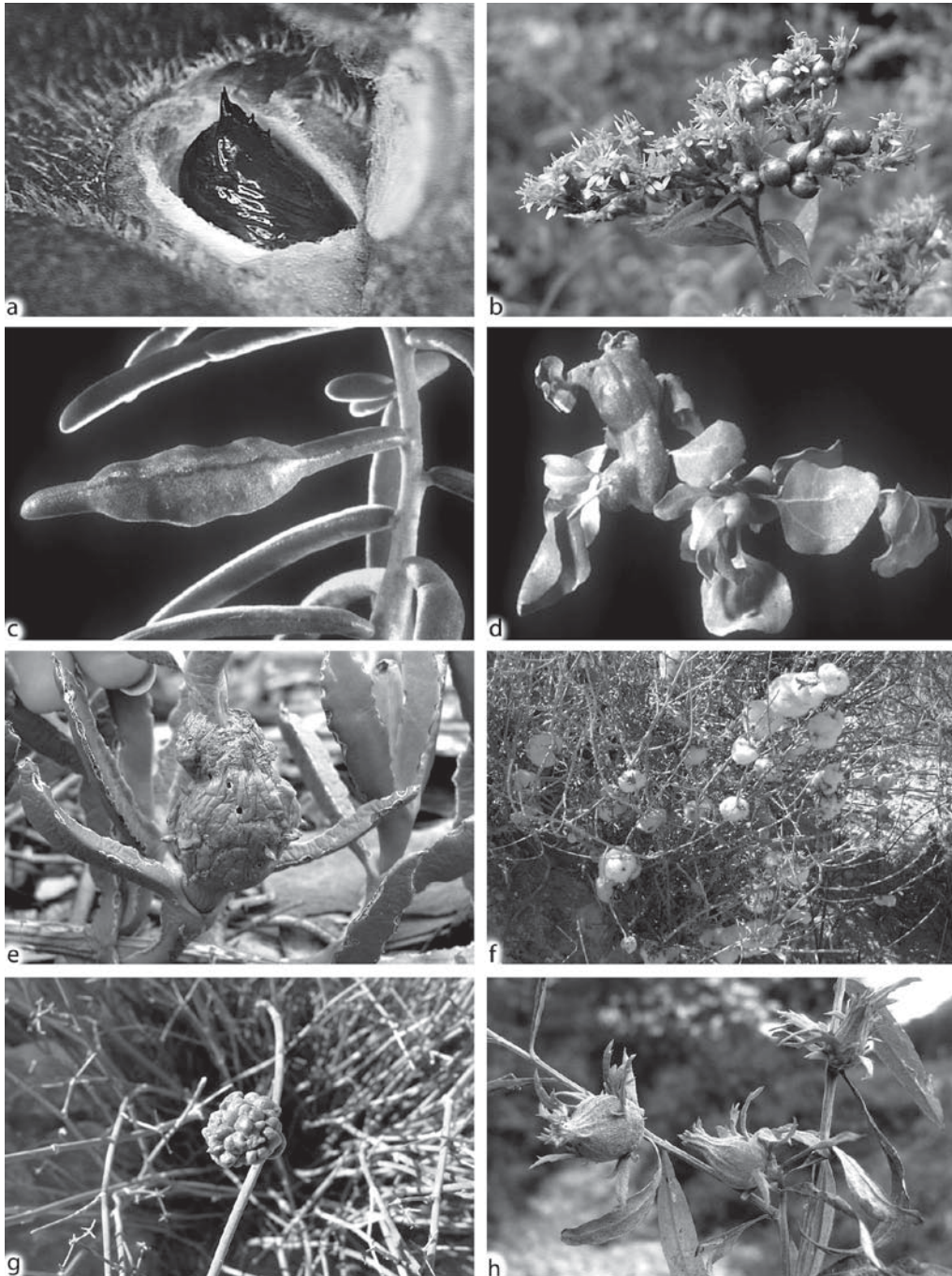
plants, gall structures, and life-history strategies exhibited by its members (Fig. 8). Roughly 70% of the known species in the family are gall inducers, most of which are monophagous (restricted to a single host), or oligophagous (feeding on a few related plant species). A few species are known to use a larger number of hosts that belong to several different families, either simultaneously or at different stages of their life cycle. Gall midges are found on hundreds of plant families all over the world, but certain families, such as the Asteraceae, Chenopodiaceae, Fabaceae, and Salicaceae, support especially high numbers of species. Galls range from simple leaf swellings, leaf curls, and unopened flowers to complex stem and bud galls that may comprise from one to many larval chambers and vary in the extent of tissue differentiation. Galls may be tiny or very conspicuous, green to bright red, hairy or smooth, and they may resemble the original structure of the affected plant organ or greatly deviate from it. The only other group of gall inducers exhibiting similar diversity in gall shapes and forms is the gall wasps (Cynipidae), but these are less species-rich and, as a group, are associated with much fewer plant taxa.

Although plant-feeding is by far the most common strategy in the family, feeding habits among cecidomyiid larvae are extremely diverse. Larvae of all Catotrichinae, Lestremiinae, and Porricondylinae, as well as some of the Cecidomyiinae, feed on fungi or decaying organic matter, while all plant feeders and predators belong to the Cecidomyiinae. Some species feed on or in plants without gall induction, or develop as inquilines, invading galls of other arthropods and feeding on gall tissues at the expense of the gall inducer. Inquilinism has evolved independently many times in the family, and while some genera are entirely or mostly composed of inquiline species, others include both gall-inducers and inquilines. Predatory larvae occur in many unrelated groups within the Cecidomyiinae and are either specialists or generalists that feed on various arthropods, particularly

Homoptera and mites. Certain groups within the subfamily are secondarily associated with symbiotic fungi that develop in their galls (e.g., many species in the tribes Asphondyliini and Lasiopterini), but larvae in these galls seem to feed on plant tissues rather than on the fungus, and the nature of this association is still unclear.

The life cycle of phytophagous gall midges is closely associated with that of their host plants. Species that are associated with trees are usually univoltine, whereas those that are associated with shrubs and herbaceous plants are often bivoltine or multivoltine, since these plants may continuously offer tissues that are suitable for galling. Females usually emerge from the pupae with their eggs fully mature and mate directly or after some courtship with males that wait for them on the host plant or on the ground. Sex ratios among emerging adults are often skewed towards females, and females of some species produce strictly unisexual (all male or all female) progeny throughout their lifetime, a phenomenon known as monogeny. While all Cecidomyiidae reproduce sexually, a few species in the Porricondylinae that feed on fungi may also reproduce by paedogenesis, a much shortened and simplified parthenogenetic life cycle during which larvae or pupae give rise to daughter larvae. This situation has evolved at least twice in the family and seems to be regulated by the availability of food; when food becomes scarce the population switches to normal, sexual reproduction through the development of adults.

Mated females cease to attract males and immediately engage in host seeking for oviposition. In most phytophagous species, the eggs are laid on the surface of plants or in between their scales or leaves. Some species in the tribe Asphondyliini have evolved a piercing ovipositor and insert the eggs directly into plant tissues. Whether eggs are laid individually or in batches is a species-specific trait, as is the morphogenesis of the resulting gall and its final shape and structure. Larval feeding cause modification of plant tissues around them to produce the gall, which often



Gall Midges (Diptera: Cecidomyiidae), Figure 8 Representative galls induced by gall midges (Diptera: Cecidomyiidae). *Top left*, leaf gall on *Solidago altissima* cut open to show a pupa of *Asphondylia solidaginis*; *top right*, flower galls on *Solidago rugosa* induced by *Schizomyia racemicola*; *second row left*, leaf gall on *Suaeda monoica* induced by *Stefaniola siliqua*; *second row right*; stem gall on *Atriplex halimus* induced by *Stefaniella atriplicis*; *third row left*, stem gall on *Carpobrotus acinaciformis* induced by *Asphondylia* sp.; *third row right*, bud galls on *Artemisia sieberi* induced by *Rhopalomyia navasi*; *bottom row left*, stem gall on *Deverra tortuosa* induced by *Paraschizomyia buboniae*; *bottom row right*, bud galls on *Artemisia princeps* induced by *Rhopalomyia longitubifex*.

reaches its final size when the larvae are still first instars. Both the physical and the chemical stimulation applied by the larvae are necessary for gall induction, and galls will cease to develop if the larvae are killed. Mature larvae either pupate in the gall or drop to the ground and pupate in the soil, depending on the species, and in some multivoltine species also on the time of year. Larvae of many species, especially in temperate areas, enter diapause in the soil or inside the plant for a certain part of the year until suitable plant tissues become available again. In multivoltine species, larvae of the last generation, and/or a certain proportion of the larvae in each generation, may enter diapause until the following year, and in some species dormancy may last several years.

Economic Importance

Many gall midges are pests of agricultural and food crops, ornamental plants, and forest trees. One of the most serious pests in the family is the Hessian fly, *Mayetiola destructor* (Say), whose larvae feed in the stems of wheat, and kill the plants or severely reduce their productivity. This species was introduced from Europe to North America during the Revolutionary War, presumably in Hessian soldiers' mattresses that contained infested wheat stems. Another serious European pest that was introduced into North America is the sorghum midge, *Contarinia sorghicola* (Coquillett), one of the most important pests of grains in the world, whose larvae feed in seeds and hinder their development. Gall midges from the genus *Orseolia* that develop in buds and stems of rice plants are serious pests of this crop in Asia and Africa. Control of pest species may be achieved by using natural enemies or chemicals, but control has been most efficient with the use of resistant plant strains and modifications of management practices.

Certain predatory gall midges are considered beneficial because they prey on agricultural pests. *Aphidoletes aphidimyza* (Rondani), for

example, is a biological control agent that is available commercially against numerous aphid pests. Adults of this species efficiently locate aphid infestations where females lay their eggs, and individual larvae may each consume dozens of aphids throughout their lifetime. Some phytophagous gall midges are successfully used as biological control agents of invasive weeds, although their impact is often too weak when not combined with other agents. Successful weed control projects involving cecidomyiid agents include the bud galler *Spurgia esulae* Gagné against leafy spurge in North America, and the flower-galling *Dasineura dielsi* Rübbsaamen against the Australian wattle *Acacia cyclops* in South Africa.

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Gall Moths (Lepidoptera: Cecidosidae)

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Gall moths, family Cecidosidae, total only seven species, with five species from southern South

America and two from South Africa. The family is in the superfamily Incurvarioidea, in the section Incurvariina, of division Monotrysia, infraorder Heteroneura. Adults small (7–26 mm wingspan), with rough head scaling; haustellum reduced, scaled; labial palpi short; maxillary palpi vestigial, 1-segmented. Maculation is somber, usually without spots but often with iridescence. Adults are probably diurnal. Larvae are gall makers on *Schinus* (Anacardiaceae) in Argentina.

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Gall Wasps (Hymenoptera: Cynipidae)

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The Cynipoidea [Hymenoptera: Apocrita (Parasitica)] superfamily contains plant-feeding (phytophagous) and parasitic wasp species, but is best known for the gall wasps (family Cynipidae). The superfamily includes about 3,000 described species. The number of families within the Cynipoidea is a matter of debate. Some researchers subdivide the group into six families: Cynipidae, Ibaliidae, Liopteridae, Figitidae, Charipidae, and Eucoilidae. Others use different classifications, including four families (Cynipidae, Ibaliidae, Figitidae, and Himalocynipidae), or five families (Austrocynipidae, Ibaliidae, Liopteridae, Cynipidae, and Figitidae).

Order: Hymenoptera

Suborder: Apocrita (Parasitica)

Superfamily: Cynipoidea

Family: Cynipidae

In general, cynipids are either gall-makers or inquilines in galls made by other species. About 1,360 species have been described, but it is estimated that 3,000–6,000 species actually exist. Gall-making cynipids (Cynipinae) are similar to true parasitoids in that they inject a kind of venom with their eggs into plant tissue. A gall forms because of the plant's response to the wasp's egg laying, presence of the egg, and/or feeding stimulation by the larva. Plant cells are usually modified and enlarged, the plant tissue surrounds the egg or larva, and the gall protects and provides nutritive cells for the gall-maker. Inquilines (e.g., Synerginae) cannot make their own galls on plants. Females lay eggs into other galls, and their larvae feed on gall tissue, sometimes changing the normal shape or size of the gall.

Gall Diversity

Cynipid galls come in a wide variety of forms, the shape and complexity being determined by the species of gall wasp that feeds within. Commonly attacked structures include catkins, seeds, flowers, petioles, branches, stems, and roots, but most galls occur on leaves and buds. The galls that cynipids make are generally described as blister, bud, bullet, oak apple, roly-poly, rosette, twig or stem galls. More than one gall species may also occupy a leaf or other structure. Some galls are single-chambered (monothalamous) and contain only one gall-maker, and others are multi-chambered (polythalamous) and contain many gall-makers. Those plants most often infested by cynipids are in the families Rosaceae, Asteraceae, Salicaceae, and Fagaceae. Oaks (Fagaceae: *Quercus* spp.), however, support the greatest diversity of gall-makers in North America, numbering at least 717 cynipid species.

Biology

Cynipid adults are small (1–6 mm), hard-bodied insects, with compressed abdomen, reduced wing venation, and simple, filiform antennae (Fig. 9). Most are drab-colored (e.g., black, brown, dark red, amber, or straw yellow), and may be either dull or shiny, but never metallic. Antennae of females are usually 13-segmented and males have 14 or 15 segments with the third often elongated and bent. The larvae are about 1–4 mm long, white, lack legs, and have distinct head and chewing mouthparts. Each larva develops within a discrete chamber of a gall, even when multiple gall-maker larvae develop in the same, polythalamous gall. Larvae apparently feed continuously, but do not produce fecal matter until pupation. Pupation always occurs in the gall, wherever the gall is located (e.g., on the plant or in the litter layer). Adults usually chew a circular hole upon exiting the gall.

The life cycle of many cynipids is complex, and involves heterogeny or alternation of generations. As such, a bisexual generation (both males and females) alternates with a unisexual generation (all



Gall Wasps (Hymenoptera: Cynipidae), Figure 9
Adult *Diplolepis rosae*, which develops in the mossy rose gall.

females). The female generation reproduces by parthenogenesis, and the unfertilized eggs develop into sexual offspring. Because of the haplo-diploid genetics of wasps, all males can develop from unfertilized eggs. However, females result from the replication of chromosomes inside an unfertilized egg's nucleus. The wasps of the two generations often look morphologically different and may attack the same or different plant structures and make very different galls. As a result, the insects of both generations have occasionally been falsely described as separate species.

Gall Inhabitants

Galls are good nutrient sources, and can be inhabited by other insects that feed on gall tissues or use the gall for shelter. Some of these insects can kill some or all of the gall-making larvae, either directly or indirectly by competition for resources. In addition to inquilines (e.g., *Synergus* spp. and *Ceroptres* spp. in oak galls), other insects feed opportunistically on gall tissue, including clearwing borers, longhorned beetles, metallic wood-boring beetles, weevils, gall midges, and others. Some of these opportunistic insects may have broad host ranges and also be pests on other plant species (e.g., dogwood borer). Some additional arthropods live externally on gall surfaces (e.g., mites, collembola), or in old, dry galls (e.g., ants). Natural enemies, especially parasitoid complexes, also inhabit galls and increase gall-maker mortality.

Abundance and Distribution

Populations of cynipids are sometimes greater on certain plants within a species than others, and several reasons why this occurs have been proposed. One possibility involves the adult female's choice of ovipositional sites and her ability to distinguish between host plants or structures that vary in size, nutritional quality, or defensive capability. Because her offspring are embedded in plant tissue, her

“choices” determine where eggs and subsequent offspring are dispersed. Especially important for those species that oviposit into buds before leaf flush is synchrony between insect hatch or emergence and plant budburst or leaf and shoot elongation. However, the plant’s genotype and ability to form a gall may still limit its use as a host for gall-makers. Thus, an egg may be laid into a bud, but the plant may not react to the stimulus to make a gall. In addition, because cynipids have limited sexual reproduction and dispersal ability, genetic variation within the population may be reduced, resulting in less adaptation to a variety of hosts and greater specialization on isolated host plants.

Economic Importance

Some galls and gall-makers are beneficial, and are used in biological control programs for weeds. And, historically, those galls containing tannic acid (e.g., oak galls) were used to make inks and dyes, and to tan leather.

Although galling insects are usually not considered pests, certain species can reach outbreak levels and cause either physical or aesthetic damage to high-value plants. Galling insects have been known to reduce photosynthesis and acorn production, discolor foliage, cause defoliation, branch dieback, and plant death. For example, the jumping oak gall wasp, *Neuroterus saltatorius* (Edwards) attacks Garry oak (*Q. garryana* Douglas) in the western United States and Canada, and causes severe and chronic mid-summer leaf scorching and partial defoliation. The rough oak bulletgall wasp, *Disholcaspis quercusmamma* (Walsh), forms galls on bur oak (*Q. macrocarpa* Michaux) and swamp white oak (*Q. bicolor* Willd) that disfigure trees and produce a sticky exudate, which attracts stinging insects. Other galls may hostinquilines that are pests of other plants. In addition, aesthetic disfigurement can be enough to prevent the sale of infested nursery stock. At present, little information exists on the effective management of galling insect

pests; pruning is labor-intensive and insecticide use may disrupt the natural enemy population, potentially leading to additional outbreaks.

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Gamagrass Leafhopper, *Dalbulus quinquenotatus* Delong & Nault (Hemiptera: Cicadellidae)

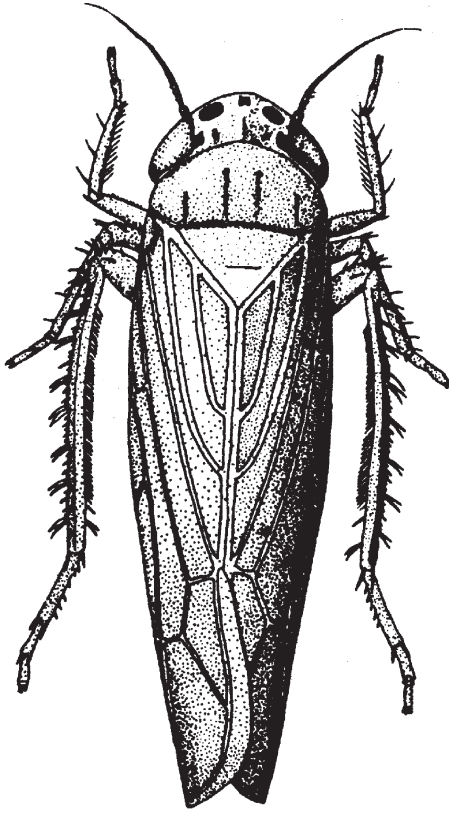
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The gamagrass leafhopper is a small (length 3.0–4.3 mm) deltocephaline, brownish orange in color, with five black spots on the head (Fig. 10). This species is found at low elevations (125–1,975 m) and occurs in central and southern Mexico and in Costa Rica.

Its developmental time from egg to adult eclosion is about 34 days at 24°C. Nymphs begin hatching on day 12 and peak nymphal abundance is reached on day 16. Generations develop continuously through the year on perennial gamagrasses (*Tripsacum* spp.).

This leafhopper has particular behavioral and ecological importance because it is among the few leafhopper species tended by ants. Unlike its non-tended congeners, *D. quinquenotatus* responds to

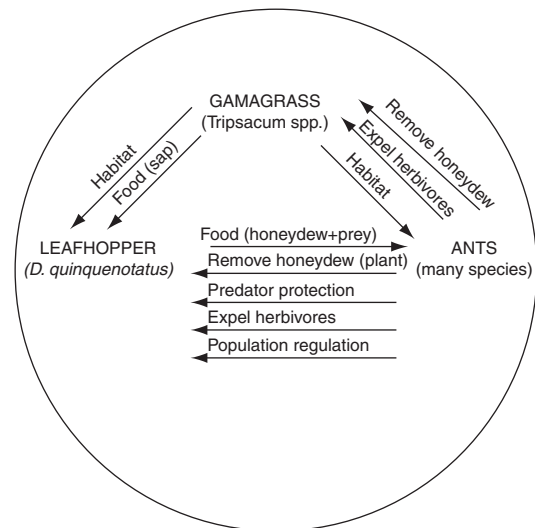


Gamagrass Leafhopper *Dalbulus quinquenotatus* Delong & Nault (Hemiptera: Cicadellidae), Figure 10 *Dalbulus quinquenotatus*.

stroking of the abdomen by ants' antennae by excreting and holding honeydew droplets until droplets are removed by ants. *Dalbulus quinquenotatus* excretes three to six times the volume of honeydew as do non-tended species. Moreover, droplets of *D. quinquenotatus* are about 23% larger in diameter and are excreted two to four times more frequently than its non-tended sister species. Nymphs and adults are sedentary and gregarious. They aggregate within leaves at the bases of *Tripsacum* spp. Sedentary and gregarious behaviors are typical in other hemipterans tended by ants such as aphids (Aphididae), treehoppers (Membracidae), and scales (Coccidae), but rare in leafhoppers. Because it has been broadly investigated, the gamagrass leafhopper can serve as model in the study of other hoppers tended by ants in the tropical and temperate regions.

The gamagrass leafhopper is tended by 18 ant species from four different subfamilies; however, the two most commonly associated ant species are *Brachymyrmex obscurior* Forel and *Solenopsis geminata* (F.). Other insects also inhabit the leaves at the bases of *Tripsacum* spp. where *D. quinquenotatus* is tended by ants. These include the decomposers *Coproporus* sp. (Staphylinidae), *Carpophilus* sp. (Nitidulidae), and *Haptoncus* sp. (Nitidulidae). These taxa occur during the wet season, and of these *Carpophilus* sp. is the most abundant. This species feeds mainly on the fermenting fluid of plants. The source of fermentation in this case is the carbohydrate contained in the honeydew excreted by *D. quinquenotatus*.

The mutualistic association (Fig. 11) between *D. quinquenotatus* and ants occurs because both receive benefits. The gamagrass offers habitat and food in the form of sap for the leafhopper most of the time, except at the end of the dry season, when gamagrass populations dry up. The sap is transformed by the leafhopper into honeydew and prey. The honeydew provides water, sugars, amino acids, lipids, and vitamins to ants. Moreover, ants consume some nymphs and adults thereby obtaining



Gamagrass Leafhopper *Dalbulus quinquenotatus* Delong & Nault (Hemiptera: Cicadellidae), Figure 11 Beneficial effects of the *D. quinquenotatus*- ants-gamagrass relationship.

protein and reducing the leafhopper population. Ants remove the honeydew produced by the gamagrass leafhopper. This leafhopper oviposits its eggs in clusters on the upper surface of midribs of basal leaves; therefore, removal of honeydew by ants reduces the death of leafhopper eggs by suffocation from accumulated honeydew and the formation of sooty mold on host leaves. Also, when the honeydew is removed the sooty mold is eliminated, facilitating plant photosynthesis. Ants protect *D. quinquenotatus* from arthropod predators such as spiders and nabids (Nabidae). Predators not only are expelled by ants when they try to approach *D. quinquenotatus*, but also are captured and transported to the ant nest and presumably used as food. Ants tending *D. quinquenotatus* also expel the related leafhoppers *D. gelbus* and *D. guzmani* that inhabit the canopy of *Tripsacum* spp. Adults of these two species respond readily to mechanical stimuli and avoid capture and predation by ants, especially on large gamagrasses.

The mutualistic association between *D. quinquenotatus* and ants on gamagrasses is affected by biotic and abiotic factors. Under greenhouse conditions, diet influences the response of ants to population of *D. quinquenotatus*. When ants are denied food, they prey upon and extinguish populations of *D. quinquenotatus*, but when supplied with prey (dead yellowjackets), large numbers of ants tend leafhopper populations that grow in size. Few ants tend leafhoppers when supplied with insect prey and honey. In natural conditions ants exploit other food resources to replace *D. quinquenotatus* honeydew during the driest months, when *D. quinquenotatus* populations are lower. That resource is nectar produced in extrafloral nectaries by the plants *Acacia pennatula*, *Leucaena esculenta*, *Lobelia laxiflora*, and *Lysilona* sp. that grow in the gamagrass community. In the wet season, when the host plants contain abundant green foliage, *D. quinquenotatus* and ants are most abundant on *Tripsacum* spp. The gamagrass populations, which grow in open areas in patches alongside herbaceous plants, shrubs,

and trees, tend to be maintained in an early state of succession because of frequently occurring fires during the dry winter months in Mexico. Burned gamagrass populations are colonized better than unburned gamagrasses by the gamagrass leafhopper and tending ants. Five months after fire, the mutualistic association is higher in burned than unburned gamagrass populations. Populations of leafhopper adults and ants are equal on gamagrass plants given extra doses of phosphorous, nitrogen, or potassium. This suggests that the mutualistic association between ants and gamagrass leafhoppers is not affected by plant nutrients.

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Gallinipper

This name is sometimes applied to any large mosquito, but it is more correctly applied to *Psorophora*

ciliata, a large and ferocious mosquito inhabiting most of the New World. Apparently it is America's largest mosquito. It is distinguished not only by its large size and painful bite, but by its hairy or shaggy legs. Interestingly, an American warship was named Gallinipper. It was part of a "mosquito fleet," a group of small boats, equipped with both sails and oars, which operated from Florida and patrolled the Caribbean in pursuit of pirates in the 1820s.

Gamete

A germ or reproductive cell, i.e., the sperm and ovum or egg.

Gamma Taxonomy

Study of the evolution and biology of taxa.

- ▶ Alpha Taxonomy
- ▶ Beta Taxonomy

Ganglbauer, Ludwig

Ludwig Ganglbauer was born in Vienna on October 1, 1856. By the age of six, he had become interested in plants and beetles. He was educated at the Schotengymnasium in Vienna, obtained a teaching diploma in zoology and botany from Universität Wien, and taught for a few years at a high school. He accepted a position at the Wiener Hofmuseum

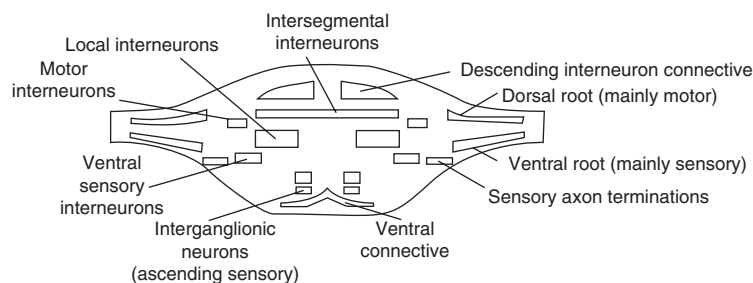
(which later was renamed Naturhistorisches Museum) and by 1881 had begun publishing on the taxonomy of Coleoptera. These early publications gained him acclaim, and in 1898 he was named Kustos in the zoology department, in 1904 head of the zoology department, and in 1906 director. In 1881 he became one of the founders of the journal *Wiener Entomologische Zeitung*, and served as one of the editors for three years. His major work, a four-volume book "Die Käfer von Mitteleuropa" (1892–1905), was unfinished because of his early death, in Vienna on June 5, 1912. The published volumes are still widely used.

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Ganglion (pl. ganglia)

A mass of nervous tissue, and the basic functional unit of the central nervous system. Many insects have three thoracic ganglia (the pro-, meso-, and metathoracic ganglia) in the thoracic region, though in others the meso- and metathoracic ganglia are fused. Each thoracic ganglion (Fig. 12) sends motor axons to the leg muscles of its respective segment, and receives input from sensor receptors in the legs. The meso- and metathoracic ganglia innervate the wing muscles. Ganglia also are found in the abdominal segments, though fusion of ganglia occurs here also. Nearly all ganglia support nerves carrying



Ganglion (pl. ganglia), Figure 12 Diagram showing the position of nervous tracts within a ventral ganglion.

both sensory and motor neurons laterally in the insect's body.

Garden Symphylan, *Scutigerella immaculata* (Newport) (Symphyla: Scutigerellidae)

- ▶ Potato Pests and their Management
- ▶ Symphylans

Gaster

The swollen, terminal abdominal segments of Hymenoptera; the region behind the constriction or pedicel.

- ▶ Abdomen of Hexapods

Gasteruptiidae

A family of wasps (order Hymenoptera).

- ▶ Wasps, Ants, Bees, and Sawflies

Gastric Caecum (pl. gastric caeca)

Bladder-like extensions of the midgut that function in food absorption.

- ▶ Alimentary Canal and Digestion

Gause's Principle

The principle that no two competing organisms can coexist in a stable environment without one species replacing the other. If seemingly equivalent species do co-exist, this implies that there are differences in their niches.

Gelastocoridae

A family of bugs (order Hemiptera). They sometimes are called toad bugs.

- ▶ Bugs

Gelechiidae

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

- ▶ Twirler Moths
- ▶ Butterflies and Moths

Gel Electrophoresis

The separation of molecules on the basis of size and electrical charge.

Gena

The side of the head (Fig. 13) beneath the compound eyes. The "cheek."

- ▶ Head of Hexapods

Gene Amplification

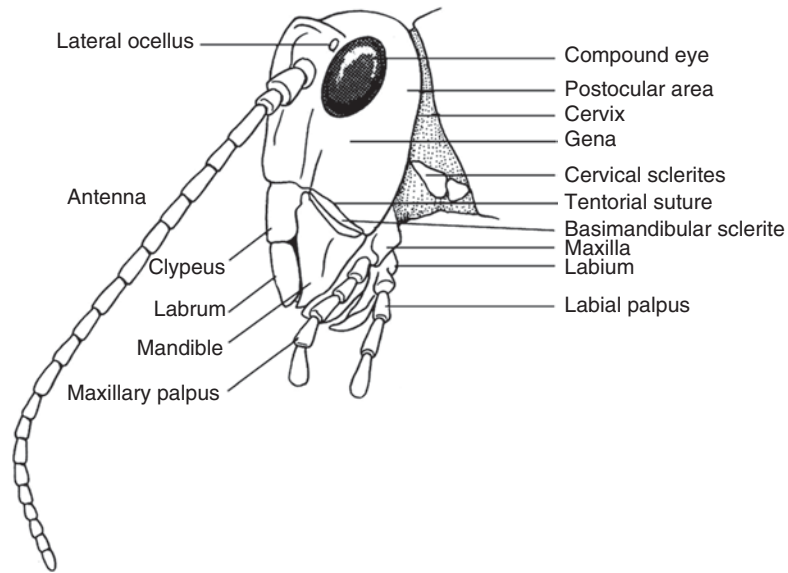
The production of multiple copies of genes in order to increase the rate of expression of a gene. Numerous genes are amplified in the developing oocyte of the mothers ovaries, providing for rapid translation of the genetic message into proteins for rapid embryonic development.

Gene Cloning

Insertion of a fragment of DNA containing a gene into a cloning vector and subsequent propagation of the recombinant DNA molecule in a host organism. Recently, cloning of a DNA fragment by the polymerase chain reaction has simplified the technology.

Gene Duplication

The duplication of a DNA segment coding for a gene; gene duplication produces two identical



Gena, Figure 13 Side view of the head of an adult grasshopper, showing some major elements.

copies which may retain their original function allowing the organism to produce larger amounts of a specific protein. Alternatively, one of the gene copies may be lost by mutation and become a pseudogene or a duplicated gene can evolve to perform a different task.

Gene Expression

The process by which the information carried by a gene is made available to the organism through transcription and translation.

Gene Flow

The movement of genes within and among populations as a result of cross fertilization.

Gene Gun

A method of propelling microscopic particles coated with DNA into cells, tissues, and organelles to produce transformation of the recipients.

Gene Library

A collection of recombinant clones derived from genomic DNA or from the cDNA transcript of an mRNA preparation. A complete genetic library is sufficiently large to have a high probability of containing every gene in the genome.

Gene Regulation

The mechanisms that determine the level and timing of gene expression.

General-Use Pesticide

This terminology was developed by the US Environmental Protection Agency to describe pesticides that are considered to be sufficiently safe that they can be used by the public without special training. Pesticides in this class can be purchased and used without license or permit. In contrast, more toxic or hazardous material are classified as “restricted-use pesticides” and can be purchased and used only by persons who are certified by the

appropriate regulatory agency in the state in which they work.

- ▶ Insecticides
- ▶ Regulations Affecting Use of Pesticides

Generalist

An insect that occupies a broad niche, or consumes a wide range of food.

Generation

The length of time from any given life stage to the same stage in its offspring, though it is usually considered to be egg to egg or adult to adult.

Genetic Modification of *Drosophila* by P Elements

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It became possible to genetically modify *Drosophila melanogaster* using recombinant DNA methods in 1982 when P elements (described below) were identified and genetically altered to serve as mechanisms (vectors) for inserting genes into the nuclear genome of *Drosophila*. The use of P-element vectors provides a powerful tool that has modernized *Drosophila* genetics and made it possible to study the role of many genes important in development and behavior. In addition, the P-element system has served as a model for scientists wanting to genetically modify other insects for use in pest management programs (Transgenic Insects).

P Elements are Disposable Elements

P elements are transposable (movable) elements that have been harnessed as a tool for genetically

modifying the fruitfly *Drosophila melanogaster* in a consistent manner. Transposable elements are independent genetic elements that can move within and between genomes; some call them selfish genetic elements. The development of P elements as tools (vectors) for inserting genes into *D. melanogaster* has revolutionized research on this important model insect, allowing fundamental studies of development and evolution.

Intact P elements are 2,907 bp long and encode a single polypeptide that has transposase (an enzyme that facilitates the movement of the element from one chromosome to another) activity. There are four exons (DNA sequences that are transcribed into protein, numbered from 0 to 3) flanked by inverted repeats 31 bp long. The presence of intact inverted repeats is required if the P element is to transpose (move).

Multiple copies of P elements (30–60) are dispersed throughout the genome of certain strains (called P) of *D. melanogaster*, but are not active because transposition is suppressed by factors in the P cytotype. Many P elements in *D. melanogaster*, and other *Drosophila* species, have some sequences deleted (are mutated), which also makes them incapable of transposing.

Movements of P elements cause mutations by inactivating genes, altering rates of transcription, or developmental- or tissue-specific gene expression. P-element movements can break chromosomes and cause chromosome rearrangements and germ cell (oocyte or sperm) death. Transposition of P elements in somatic cells reduces the life span of *D. melanogaster* males, as well as reducing fitness, mating activity and locomotion.

Hybrid Dysgenesis

P elements initiate a syndrome called hybrid dysgenesis in *D. melanogaster*. Hybrid dysgenesis occurs when males from a strain that contains P elements (P males) are mated with females lacking P (M females). Their progeny have high rates of mutation, chromosomal abnormalities and, sometimes, are

completely sterile. These abnormalities are caused by movement of *P* elements in the chromosomes of the ovaries or testes. The reciprocal cross does not generate hybrid dysgenesis because the *P* female's cytotype suppresses movement of the *P* elements.

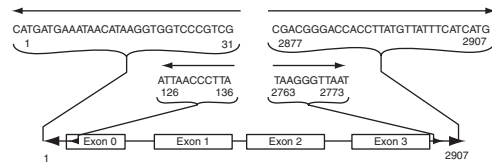
P Element Structure Varies

Many *P* elements in the *Drosophila* genome are defective. Some have internal deletions and are unable to produce their own transposase but, if they retain their 31 bp terminal repeats, they can move if supplied with transposase by intact *P* elements. *P* elements with defective 31 bp terminal repeats are unable to move because these repeats are the site of action of the transposase enzyme and important in movement and insertion of the elements into the chromosomes.

Transposition Method

P elements move from site to site in the genome (jump) by a "cut and paste" method. When a *P* jumps, it leaves behind a double-stranded gap in the DNA. The gap is repaired by using a matching sequence as a template. This matching sequence can occur on the sister chromatid or elsewhere in the genome. If the transposition occurs in an individual that is heterozygous for the *P* insertion, and the matching site on the homologous chromosome is used as the template for DNA replication and repair, there can be a precise loss of the *P* element sequence in the original site. There is no net loss in the genome because the *P* element has simply changed locations.

If a *P* jumps after the chromosomes have duplicated, but before the cell divides, one of the sister chromatids will still have a *P* in its original position. In this situation, the homologous *P* may serve as the template for filling in the (Fig. 14) hole left when the *P* moved to a new position elsewhere in the genome. Under these circumstances, the number of *P* elements in the genome is increased by one. The *P* element is replaced in its original site



Genetic Modification of *Drosophila* by P Elements, Figure 14 P-element vector diagram.

by gap repair and now is present in a new site in the genome, as well.

The cut and paste mechanism of transposition implies that *P* elements don't have to confer an advantage on the organism to invade and persist in the genome. In fact, a mathematical simulation model indicates that *P* elements can become fixed in populations even when fitness is reduced by 50% and many laboratory studies have shown that colonies can change from M to P strains relatively rapidly.

The location of the *P*-element in the chromosome is important in determining the frequency of transposition. Although transposition is more-or-less at random, *P*-element vectors containing specific gene sequences show some specificity by frequently inserting near the parent gene (which is called homing). *P* elements also tend to insert into upstream promoter regions of genes.

How Did P Elements Invade *D. melanogaster*?

P elements are relatively new to *D. melanogaster* populations. Surveys indicate laboratory strains of *D. melanogaster* collected before 1950 lack *P* elements, but most colonies collected from the wild within approximately the past 50 years have *P* elements. By contrast, *P* elements are relatively common in many other species of *Drosophila*. Surveys indicate that very closely-related, full sized and potentially active *P* elements are in *D. willistoni*, *D. guanche*, *D. bifasciata* and *Scaptomyza pallida*. *P* elements have been found in other dipteran families, including Opomizyidae and Trixoscelididae. Inactive *P* elements were found in the sheep blowfly *Lucilia cuprina* (Calliphoridae) and the

housefly *Musca domestica* (Muscidae). The presence of P elements in families other than Drosophilidae suggests that P elements may be more widely distributed than currently thought.

Phylogenetic analyses of DNA sequences from P elements in 17 *Drosophila* species in the *melanogaster* species group show that sequences from the P element family fall into distinct subfamilies or clades which are characteristic for particular species subgroups. These clades indicate that vertical transmission of P elements has occurred, but in some cases the P phylogeny is not congruent with the species phylogeny. More than one subfamily of P elements may exist within a group, with DNA sequences differing by as much as 36%, suggesting that horizontal transfer (movement between species) has occurred. In fact, horizontal transfer may be essential to the long-term survival of transposable elements.

P elements invaded *D. melanogaster* within the past 50 years. The donor species that provided a P element to *D. melanogaster* is thought to be in the *willistoni* group, which is not closely related to *D. melanogaster*. Because these species diverged from each other about 60 million years ago, there should have been sufficient time for considerable sequence divergence in the P elements if they had been present in both genomes prior to divergence (and transmitted vertically). However, DNA sequences of the P elements from *melanogaster* and *willistoni* are nearly identical, supporting the hypothesis of horizontal transfer. It is thought that the invasion of *D. melanogaster* by P occurred after *D. melanogaster* was introduced into the Americas.

Two mechanisms have been proposed to explain how the P element could have infected *D. melanogaster*. One involves horizontal transfer and the other involves interspecific crosses. Both *D. melanogaster* and *D. willistoni* now overlap in their geographical ranges in Florida and in Central and South America, but they apparently are unable to interbreed. Horizontal transfer could have been effected by a viral, bacterial, fungal, protozoan, spiroplasmal, mycoplasmal, or a small arthropod vector (perhaps a hymenopteran parasitoid or predatory mites). One candidate for

horizontal vector may be the mite *Proctolaelaps regalis*. *P. regalis* is associated with both *Drosophila* species; it has been found in laboratory colonies and in the field associated with fallen or rotting fruit, which is the natural habitat for *Drosophila*. Laboratory observations indicate that *P. regalis* feeds on fly eggs and can make rapid thrusts of its mouth parts into a series of adjacent eggs. This brief feeding on multiple hosts might allow it to pick up DNA from one egg and inject it into another. Mites from colonies of *Drosophila* with P elements in their genome were analyzed with several molecular methods that indicated the mites carried both P element and *Drosophila* ribosomal DNA sequences. Mites isolated from M colonies (which lack P elements) lacked P sequences.

For the mite *P. regalis* to have transferred P elements to *D. melanogaster* from *D. willistoni*, a number of events had to occur in the proper sequence. Females of *D. melanogaster* and *D. willistoni* had to deposit their eggs in close proximity and mites had to feed sequentially on one and then the other, in the correct order. The recipient egg had to be less than 3 h old, the germ line of the recipient embryo had to incorporate a complete copy of the P, the transformed individual had to survive to adulthood, and the adult had to reproduce.

Another potential mechanism for horizontal transfer of P involves interspecific crosses. Crosses between the sibling species *D. simulans* and *D. mauritiana* produce sterile males, but fertile females. When F₁ females are backcrossed to males of either species, a few fertile males are produced. Hybridization, although rare, occurs between some *Drosophila* species. Although *D. melanogaster* and *D. willistoni* are unable to cross, interspecific crosses may have allowed the transfer of other types of TEs between *Drosophila* species.

P Element Vectors and Genetic Modification of *D. melanogaster*

P-elements have been genetically engineered to serve as vectors to insert genes into the germ line

of *D. melanogaster*. A number of (Fig. 15) different vectors with different genetic characteristics have been produced subsequently.

Isolating pure *Drosophila* lines containing a single *P*-element insertion with a gene(s) of interest requires a sequence of steps over several generations. A *P*-element vector containing the gene(s) of interest inserted into it are microinjected into dechorionated eggs along with a helper plasmid that contains a complete DNA sequence coding for the transposase. The helper vector is unable to insert into *Drosophila* chromosomes by normal transposition methods because it lacks part of one inverted terminal repeat and lacks transposase (the gene of interest is typically inserted into the location of the transposase gene).

Embryos used for injection should be in the preblastoderm (an early embryonic stage prior to the development of the ectoderm, endoderm and mesoderm), when the embryo is still a syncytium

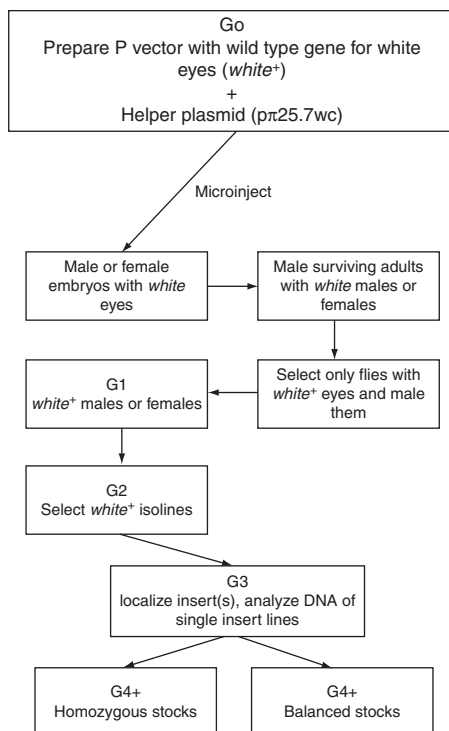
(the nuclei have divided rapidly but cell walls have not formed between them yet). Some of the injected eggs die, but those that survive to produce adults may contain some individuals that contain the introduced gene(s) of interest.

These adults (called G_0) are mated individually to uninjected males or females and their progeny are reared and evaluated to determine if they carry the injected gene, or any injected “marker” genes designed to allow discrimination between genetically modified and unmodified flies. The resulting G_1 progeny will be screened to determine if they carry the gene(s) of interest and the marker genes. Because insertion of the transgenes into the chromosome occurs nearly at random, multiple individual lines of transformed flies will need to be evaluated for fitness and level of expression of the inserted DNA as well as their stability.

Insertion of the genes into germ line chromosomes is enhanced if preblastoderm embryos are microinjected. At that stage, the cleavage nuclei are in asyncytium (lacking nuclear membranes) and exogenous DNA can more easily be inserted into the chromosomes. The preblastoderm embryos are in the process of forming the pole cells (cells that will give rise to the ovaries and testes). Insertion of exogenous DNA into the chromosomes of the germ line results in stable transformation, meaning that the transgenes are likely to be transmitted each generation. If only somatic cells contain the introduced genes, the flies cannot transmit the new trait to their progeny. Such adult flies may exhibit the trait, but are only transiently transformed.

Only a portion of the *P*-element vector inserts into the chromosome. The DNA inserted consists of the *P* sequences contained within the inverted terminal repeats. The plasmid DNA outside the inverted repeats should not insert and is lost during subsequent development.

Once transformed fly lines are obtained, the transgenic fly lines should be stable unless transposase is provided in some manner. Sometimes an experimenter wants to induce movements of the inserted DNA, and secondary transpositions can



Genetic Modification of *Drosophila* by *P* Elements, Figure 15 Steps in transformation of *D. melanogaster* with a *P*-element vector.

be induced if transposase is introduced by injecting helper elements containing the transposase gene into preblastoderm embryos.

Transformation success rates vary from experiment to experiment and experimenter to experimenter. Usually, it is important to obtain at least ten lines containing the gene(s) of interest. This may require microinjecting 600 or more embryos, because survival of embryos after microinjection averages 30–70% and, of these, only 50–60% survive to adulthood (G_0). Even after G_0 adults are obtained, damage caused by microinjection may result in early death or sterility in 30–50% of the adults.

Transformation may not take place in all germ line cells in an injected embryo. Usually only a small fraction of the germ line cells of a G_0 individual produces transformed G_1 progeny. Thus, it is important to maximize the recovery of G_1 progeny from each G_0 individual to increase the probability of detecting progeny in which integration of P elements occurred. The size of the introduced P element is another factor that may influence transformation success; the larger the construct, the less frequent the insertion.

Detailed information on the life history and culture of *Drosophila* are available in a variety of references, as are detailed protocols for transforming *Drosophila* with P-element vectors. The protocols provide complete information on the appropriate equipment for microinjection, how to prepare the embryos for injection, align them on slides, desiccate them, and inject them in the region that contains the pole cells. Directions are available for preparing the DNA for injection and for pulling the very fine glass needles required. P elements have been engineered to provide an array of vectors with different characteristics and functions.

Uses for P Element Vectors

When a P-element vector inserts into a nuclear gene, it has been tagged. This allows the researcher

to isolate and clone specific genes if the altered gene exhibits an altered phenotype in *D. melanogaster*. This process is called transposon tagging. Genetic engineering with P-element vectors in *D. melanogaster* also permit the expression of foreign genes from a variety of organisms.

P-element vectors also can be used to evaluate the effects of position on expression of a transgene by moving stably-inserted transgenes to other sites within the genome. The ability to replace or modify genes in their normal chromosomal locations in *D. melanogaster* is a very valuable genetic tool.

Transformation of Other Insects by P Elements

DNA from *D. melanogaster* has been introduced into other species of *Drosophila* with P-element vectors. Unfortunately, efforts to use P-element vectors to transform arthropod species outside the genus *Drosophila* have failed and research has shifted to the use of other types of transposable element vectors for this purpose. See the entry on Transgenic Arthropods for additional information on this topic.

Evolution of Resistance to P Elements

The spread of P elements throughout populations of *D. melanogaster* during the past 50 years has been remarkable, particularly since intact P elements can induce a variety of severe disadvantages in individuals in newly invaded populations. If P elements invade a small population, that population usually goes extinct. If evolution of repression systems (resistance to transposition) fail to occur quickly enough, larger populations also can go extinct.

In fact, several types of P repressor systems (resistance mechanisms) have been identified; they either are transmitted cytoplasmically (maternally

inherited) or through the nuclear genome, in which case the transmission is biparental. The repressor systems have been classified as P, M' or Q.

P fly strains have a strong maternally inherited system called P cytotype. P cytotype is mediated by a protein produced by differential splicing of the transcript of the complete element. When P females are crossed to a strong P line, less than 10% of the ovaries in their progeny become dysgenic, indicating that P strains strongly repress hybrid dysgenesis. By contrast, if P males are crossed to M females, more than 90% of the ovaries in their progeny are dysgenic. M' strains contain repressor elements of P, as well. Transposition repression in M' strains is due to the KP element. M' strains display intermediate levels of repression of dysgenesis when crossed to P males. Both males and females from M' strains are able to pass the repressing factor to their progeny. Q strains can strongly repress transposition and also display a low induction of transposition. Some Q strains show a maternal mode of inheritance of repression while others have biparental mode of inheritance. It thought that a repressor (SR) results from a deletion in the P element. The SR repressor cannot produce functional transposase but can produce the repressor protein and a novel protein, both of which may be involved in Q type repression.

Evolution of P, Q and M' repression systems was evaluated during two surveys of *D. melanogaster* populations conducted along a 2,900 km cline along the eastern coast of Australia. The first survey was conducted in 1983 and the second in 1993. In 1983, P populations were found in the north, Q populations at central locations, and M' populations in the south. After 10 years, Q and M' populations had increased their range at the expense of P lines. The surveyors speculated that the P and M' mechanisms of repression may be early, emergency responses to the harmful effects of transposition by P. The surviving *D. melanogaster* populations then may have the opportunity to evolve a superior mechanism to improve fitness by acquiring the biparentally transmitted Q repression system.

In many species of *Drosophila*, in which P elements have been present for a longer time than in *D. melanogaster*, no complete functional P elements have been found. Instead, many populations contain mutated elements which might encode repressor activity. These results reinforce the notion that active transposition of P is highly detrimental to species of *Drosophila* in the wild.

Using P Elements to Drive Genes into Populations

The interest in using transposable elements, such as P, as drivers for inserting engineered genes into natural populations for insect pest control has led to some computer simulation and empirical studies using *D. melanogaster* as a model system. Several different computer simulations suggest that transposable elements may be used successfully to drive specific genes into pest populations, including populations with different sizes, reproductive rates, density dependence and transposition frequency. Typically an equilibrium was reached quickly (usually within 50 generations), especially if 5 or 10% of the population carried the transposable element. However, if the "sweep" of elements does not occur rapidly, resistance mechanisms might develop that could reduce the effectiveness of the pest management program.

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Genetic Code

The rules that determine which triplet of nucleotides code for which amino acid during translation. There are more than 20 different amino acids and four bases (adenine, thymine, cytosine and guanine). There are 64 potential combinations of the four bases in triplets ($4 \times 4 \times 4$). A doublet code would only be able to code for 16 (4×4) amino acids. Since only 20 amino acids exist, there is redundancy in the system so that some amino acids are coded for by two or more different triplets (codons).

Genetic Control

A method of pest control that uses strains of insects with genetic mutations rendering them sterile or disadvantaged. When released into the natural populations of the target insect, the sterile insects mate with wild insects and produce sterile or disadvantaged offspring.

Genetic Distance

A measure of the evolutionary divergence of different populations of a species, as indicated by the number of allelic substitutions that have occurred per locus in the two populations. The most widely used measure of genetic distance is that of Nei (1972), $D = -\ln(I)$.

Genetic Engineering

The deliberate modification of genes by man. Also called gene splicing, gene manipulation, recombinant DNA technology.

Genetic Linkage

Genes are located together on the same chromosome.

Genetic Marker

An allele whose phenotype is recognized and which can be used to monitor the inheritance of its gene during genetic crosses between organisms with different alleles.

Genetic Sexing

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Genetic sexing refers to the methodologies enabling the separation of large numbers of insects according to sex (e.g., the separation or killing of females so that an all male population is produced). It is especially relevant for the Sterile Insect Technique (SIT) which is used to control or eradicate key insect pests by introducing genetic sterility into the target population. The primary active agent in the SIT is the sterile male, although in practice, both sexes have been released. A role for the sterile female in the SIT was sometimes debated, but direct evidence shows that females do not contribute significantly to the sterility induced in the wild population. In fact, releasing both sexes together at the high overflooding ratios required for the SIT to be effective leads to assortative mating among the released flies and, consequently, dilutes their effectiveness.

Genetic sexing can be achieved by utilizing natural differences between males and females (e.g., the time of emergence of tsetse flies, or the size of the pupae of certain Lepidoptera and mosquitoes). If such differences do not exist, then specific strains have to be developed using classical Mendelian genetic techniques. Two independent genetic modifications are required, the induction of a mutation that can be used as a selectable marker (e.g., affecting pupal color, or temperature dependent viability), and a chromosome re-arrangement (reciprocal Y-autosome translocation) that links the selectable marker to the male-determining Y chromosome. The most advanced and operational genetic sexing strains (GSS) are available for the Mediterranean fruit fly, *Ceratitidis capitata* (medfly). In this species, two mutations, white pupae (*wp*) and a temperature sensitive lethal (*tsl*), are used either to separate the sexes at the pupal stage using optical sorting machines, or to kill the females at the embryo stage by incubating the eggs at slightly elevated temperatures. Both mutations are found on chromosome 5. In the males of a GSS, the wild type alleles of these selectable markers, *wp*⁺ and *tsl*⁺, are linked to the Y chromosome.

Structure of GSS Based on the Selectable Markers *wp* and *tsl*

The structure of this Y-autosome translocation determines the stability of the GSS over time. Genetic recombination in the male between the selectable marker and the translocation breakpoint, leads to a reversal of the male and female phenotypes. Over several generations, such recombinants can accumulate and the GSS reverts to a standard bi-sexual strain. By choosing translocations where the selectable marker and the breakpoint are close together, and by incorporating recombination suppressors (inversions), GSS can be generated that are stable enough for large scale rearing as required for the SIT. The inclusion of a Filter Rearing System greatly increases

the useful life of a GSS in mass rearing factories. The structure of the translocation also determines the rearing efficiency. Ideally, the sterility linked to such chromosome re-arrangements occurs as early as possible with minimal affect on the rearing process/quality. The choice of the most appropriate selectable marker influences the cost effectiveness and the accuracy of the sexing procedure. The *tsl*-based strains currently in use in most medfly facilities allow females to be killed with an accuracy of 99.5% even at production levels of over 500 million males per week, and only inexpensive equipment (a water bath) is needed.

For the application of the SIT, the use of GSS offers the following advantages:

- Sterility is introduced more efficiently into the target population. Data show that 3 to 4 times more sterility can be induced if only sterile males are released.
- Production, handling and release costs are reduced. Only the active agents, the males, in the SIT have to be dealt with.
- Monitoring costs, in combination with female specific traps, are reduced, as only wild females are trapped and not sterile males.
- The males can be aged before release without mating, and as a consequence, they are released closer to sexual maturity.
- Sterile stings by females are eliminated, and SIT can be used for control as well as eradication.

GSS for the medfly are now used in most of the mass rearing facilities worldwide. In 2001, the overall production capacity was 1,400 million males per week. Research is ongoing to generate improved GSS (e.g., by introducing a marker for the discrimination of wild and released flies). In the future, it may be possible to use genetic transformation techniques to produce GSS for SIT programs. In addition, efforts have begun to construct GSS for other key pest species such as the screw-worm fly.

► [Sterile Insect Technique](#)

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Genetic Transformation

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Genetic transformation is a process that involves the introduction and expression of foreign genes in a host organism. This expression can result from the extrachromosomal, or episomal, presence of genes in nuclei that may persist if the introduced DNA has a mechanism for replication. Extrachromosomal expression, however, is most often transient as the DNA becomes diluted with cell division. Expression also can result from the integration of foreign DNA into somatic chromosomes that can persist through the lifetime of the organism, but not be inherited. Alternatively, foreign genes may

be stably inherited if incorporated into the genome of the germ-line, known as germ-line transformation. This is the most common type of genetic transformation in insects.

Transient or somatic transformation can be achieved in several ways, and most often is used for testing promoter regulatory sequences. Most simply, DNA, usually in the form of circular plasmid molecules, is introduced into tissue by microinjection, biolistic bombardment, or electroporation. The DNA within those plasmids that is taken up into nuclei usually are subject to transcription similar to chromosomal DNA. DNA also can be integrated into viral vectors that may persist extrachromosomally or integrate into somatic chromosomes, and this presents an effective means of transient gene expression. Viral vectors for this purpose include densovirus, subgenomic Sindbis virus, and pantropic Moloney murine leukemia virus (MoMLV). Transient expression in a foreign host also is possible by gene expression from bacterial symbionts in what is called “paratransgenesis.” This may be inheritable if the genes of interest are stably incorporated into the symbiont, and if the symbiont population is inherited. Examples of paratransgenesis include the expression of foreign genes in the bug, *Rhodnius prolixus*, via the bacterial symbiont *Rhodococcus rhodnii*, and the potential for foreign gene expression in *Wolbachia*.

Germ-line transformation that is stable and inheritable most commonly is achieved using transposable element, or transposon, based vector systems. This was first developed for *Drosophila melanogaster* using the *P* element transposon discovered in the same species. The *P* element belongs to a class of transposons that transpose in a precise or nearly precise fashion by using a DNA intermediate. These elements share general structural features including inverted terminal repeat sequences that surround a transcriptional unit that encodes a transposase enzyme. Transposases act at or near the terminal sequences to catalyze the transposition process that includes excision of the entire element from one chromosomal site and insertion

into another site. All of the transposons currently in use for germ-line transformation belong to this general class of elements, and are used in a binary vector-transposase helper system. In this system the transposon vector plasmid includes the inverted terminal repeat sequences and subterminal sequences required for mobility that surround a selectable marker gene and other sequences of interest. The transposase gene within the vector is either deleted or made defective, and vector transposition depends upon a separate helper plasmid that includes the complete transposase gene but not the terminal sequences necessary for integration. Thus, when transiently expressed in the germ cells, the helper transposase can catalyze chromosomal integration of the vector, but is lost in subsequent cell divisions allowing the vector integration to remain stable.

Currently, the two transposon systems developed for *Drosophila melanogaster* transformation, based on the *P* and *hobo* elements, do not function or are highly inefficient in other insect species. Four other transposon systems, discovered in other *Drosophila* species or other insects, function in a wide range of insects including *Drosophila*. These include the *Hermes* element from *Musca domestica*, the *mariner* Mos1 element from *Drosophila mauritiana*, *Minos* from *Drosophila hydei*, and *piggyBac* from *Trichoplusia ni*. Together, these systems currently have been used for germ-line transformation of more than 20 species within the Diptera, Lepidoptera, Coleoptera, and most recently, the Hymenoptera.

A critical component of transformation is the use of selectable marker systems used to identify transformed, or transgenic, individuals. Eye color markers are used routinely in *Drosophila*, and similar markers were used in the first transformation of tephritid fruit flies and mosquitoes. This was possible owing to the existence of mutant eye color strains and their wild type alleles cloned as recombinant DNA. Vectors carrying the wild type marker gene integrated into a mutant host strain allow transformed insects to be identified by visible detection of their wild type eye-color phenotype.

Later transformations in species not amenable to such “mutant rescue” selections relied on the use of dominant-acting visible marker genes. These include the green fluorescent protein (GFP) from the jellyfish, *Aequora victoria*, and variants of this gene that emit blue (BFP), yellow (YFP), and cyan (CYP) light under epifluorescence optics. The most recent fluorescent protein in use is the DsRed fluorescent protein from the coral *Discosoma striata*. Chemical and drug-resistance genes also have been used as dominant-acting selections, but these often have proven to be unreliable owing to natural resistance mechanisms resulting in the selection of non-transformed individuals.

In addition to the initial selection of transformant insects by marker detection or selection, transformation must be verified by molecular tests that include DNA Southern hybridization, DNA sequencing of the chromosomal integration site, and chromosomal in situ hybridization. These tests confirm chromosomal integration, determine the number of integrations, and assess whether integration has occurred by a transposon-mediated process. The latter confirmation is possible since most transposons duplicate their insertion site sequence, with some transposons integrating solely into a defined nucleotide sequence such as TA or TTAA. In some instances vectors integrate by a random or fortuitous recombination event resulting in integration of the entire vector plasmid, and often in a rearranged fashion. Such integrations can be useful, but may be problematic since rearrangements can disrupt genes within the vector, and in some cases the selection marker may remain intact while other genes of interest become nonfunctional. The potential for vector integration by recombination exists for all insect species, but thus far it is most prevalent in mosquitoes.

Transgenic insects have a wide potential of uses for basic biological analysis and practical application for pest and beneficial species. Transposon-mediated germ-line transformation is especially useful for insertional mutagenesis for functional genomics analysis. Transposon vectors are mutagenic since they can disrupt gene function

as a result of chromosomal insertion. Genes and regulatory sequences of interest that are interrupted in this way can be identified by a mutant phenotype or reporter gene expression, and isolated by probing for or amplifying the transposon vector sequences. Numerous genes and genetic pathways involved in development and behavior have been investigated in this way in *Drosophila*, and the availability of transformation vectors for nondrosophilid species now makes the use of these methods, and sophisticated genetic analysis, possible for a wide range of insects.

In addition to further investigating insect genetics and biology by functional genomics studies, strategies also are being modeled and tested in *Drosophila* for the use of transgenic insects for biological control. The first of these will improve existing programs such as the sterile insect technique (SIT) by creating strains that are genetically marked, and allow for genetic-sexing (due to female lethality) or male sterility. Sexing and male sterility should occur in response to a conditional or suppressible gene expression system so that the strain could breed normally under permissive conditions. Of considerable interest is the possibility for new strategies for biocontrol, also based on conditional systems integrated into transgenic strains, that result in the death of the released insects and their offspring in response to changes in diet or environmental conditions. The most common strategies at present include those utilizing a lethal gene expression system that is suppressed by the antibiotic tetracycline, or its analogs, which can be provided in diet but is not present in the field. Other strategies include use of temperature sensitive lethal genes that result in death of host insects at elevated field temperatures, but where strains can survive at lower laboratory rearing temperatures.

The greatest challenge for the effective use of transgenic insects in such highly promising strategies will be the comprehensive ecological risk assessment necessary for the field release of such strains. Transposons that are used as vectors are naturally mobile genetic elements, and many have

become distributed among insects and other species by horizontal transfer. Thus, a primary concern for their use in practical application will be the potential for vector movement into unintended host organisms. Vector mobilization or instability also will have serious consequences relating to the effectiveness of the transgenic strain, since the desired traits will be lost with the vector. These concerns for vector stability are diminished by use of vectors that are defective, so that they can be mobilized only by an exogenous source of transposase, or helper plasmid, such as that used for the transformation event. While the helper transposase should not persist in the host, the same or related transposon system may exist in the host or a symbiont or infectious organism resulting in mobilization, or instability, of the vector. Methods to more thoroughly evaluate vector stability, and the creation of new vectors that cannot be re-mobilized, will be our greatest challenge for the effective use of genetic transformation techniques to control pests and improve beneficial insect species.

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Gene Transfer

The movement of a gene or group of genes from a donor to a recipient.

Gengidae

A family of bugs (order Hemiptera, suborder Fulgoromorpha). All members of the suborder are referred to as planthoppers.

► Bugs

Geniculate

Elbowed or abruptly bent. When used with antennae it is equivalent to elbowed antennae.

Genitalia

The modified abdominal segments used in copulation and release of sperm or eggs.

Genome

The total complement of DNA in an organism. The total genetic composition of the chromosomes.

Genomes of Insects

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The total complement of DNA in an insect is the genome. Nuclear genomes in insects consist of the chromosomes, consisting of DNA and proteins. The nuclear genome is the largest contributor of genetic information within an insect. However, mitochondria, which are organelles in the cytoplasm, also are components of the genome. Mitochondria are derived from bacteria that became essential symbionts of eukaryotic organisms and contain a number of genes essential to the insect. Finally, in addition to the nucleus and mitochondria, many insects contain intracellular and extracellular microorganisms that provide essential services to the insect. Symbionts may be bacteria, viruses, fungi or spiroplasmas that live in or on

their insect hosts. Many insect symbionts are unable to survive outside their host and many insects cannot survive without the services of their symbionts. Thus, insects contain genetic information from several sources.

Nuclear Genome Size and Content

The nuclear genome is the most important and largest source of genetic information in the insect. However, the nuclear genome size in arthropods seems to bear little relationship to the complexity of arthropod morphology or to the number of genes encoded. Nuclear genome size varies widely among insects, with up to 250-fold differences in C values known. C stands for constant or characteristic and denotes the fact that the DNA content (size) of the haploid nuclear genome is fairly constant within a species.

C values vary widely among insect species. Size is usually measured in picograms (pg) of DNA or in kilobases (kb) of DNA sequence. For example, the locust *Schistocerca gregaria* has a C value of 9,300,000 kb, 52-fold more than that of the fruitfly *Drosophila melanogaster* yet it is unlikely that the locust is more complex genetically. Likewise, nuclear DNA content varies by five-fold among tenebrionid beetle species.

Genome size also can vary within insect species; diploid cells in the mosquito *Aedes albopictus* contain 0.18–6 pg of DNA and C values vary by three-fold (0.62–1.6 pg) among different populations. The amount of DNA in insect cells is difficult to measure because many tissues are polyploid (containing more than the normal two copies of each chromosome), with different tissues having different degrees of ploidy.

DNA consists of four types of nucleotides containing the bases guanine (G), cytosine (C), thymine (T) and adenine (A). The base ratios in insect DNA are lower than those found in vertebrates, with guanine + cytosine bases (G + C) comprising from 32 to 42% of the DNA bases, compared to 45% for vertebrates. If DNA base

composition were random, 50% of arthropod DNA would be G + C.

Sequencing Nuclear Genomes

The entire nuclear genomes of several model species, including humans, the mouse, the fruitfly *Drosophila melanogaster* and the nematode *Caenorhabditis elegans*, have been sequenced in an effort to understand the evolution of genes and genome function. To make the immense amounts of DNA sequence data available to scientists, databanks for depositing the sequences are expanding rapidly. There are three major database sites on the world wide web: the DNA Data Bank of Japan (DDBJ), the European Molecular Biology Laboratory Nucleotide Sequence Data Library (EMBL) and the GenBank Genetic Sequence Data Bank (GenBank). Subsets of the databases also have been organized. For example, there is a database of mitochondrial DNA sequences, a eukaryotic promoter database, a database of restriction enzymes, a database for intron sequences and a database for homeodomains.

The nuclear genome of only one insect, *Drosophila melanogaster*, had been sequenced completely by the date of this writing (2002). The genomes of other species may be sequenced in the future when costs for sequencing decline. The *D. melanogaster* genome contains approximately 180 megabases (Mb or million bases) of DNA located on four chromosomes. A third of the DNA is noncoding heterochromatin, meaning that it does not code for a protein. Heterochromatin typically is found in the centromeres, telomeres and other regions of the chromosomes that do not contain functional genes. Heterochromatin was named this because it stains differently than euchromatin, which is DNA that contains coding sequences. The 120 Mb of coding DNA is on the two large autosomes and the X chromosome; the fourth chromosome is mostly heterochromatin, with only about 1 Mb of coding DNA.

Prior to the start of the *Drosophila* Genome Project, approximately 3,800 different *D. melanogaster* genes had been mapped and many had been

associated cytogenetically with one of the 5,000 bands visible on stained polytene salivary gland chromosomes. Approximately 3,000 transcription units (DNA sequences that are transcribed into messenger RNA) had been placed on the cytogenetic map by localizing the DNA on specific polytene chromosomes by a molecular process called *in situ* hybridization. Nearly 10% of the total, 1,300 genes, already had been cloned and sequenced by individual laboratories.

The Genome Project initially was controversial because some feared that it would take funding away from individual research projects, would cost too much, and take too long. Despite this controversy, a *Drosophila* Genome Project was initiated as a collaborative effort among academic and government scientists with public funding. Later, a commercial company (Celera) initiated its own *Drosophila* Genome Project using a different approach.

The actual sequencing of the *Drosophila* genome by Celera began in May 1999. By late fall of 1999, sequencing was completed and multiple computers had assembled the DNA sequences in order! This amazingly rapid conclusion to the project was facilitated by the availability of the sequences produced by the public consortium. The genome sequences were published in the journal *Science* in March of 2000 and the project represents a major scientific milestone. The entire *Drosophila* sequence is available in GenBank and at FlyBase on the worldwide web. FlyBase is a database of genetic and molecular information and includes information on genes, alleles (variations of genes), phenotypes, transposons (movable genetic elements present in the genome), clones, stock lists, the locations of *Drosophila* workers, and bibliographic references (Table 3).

Several unexpected results were found in the *Drosophila* genome. Early analyses of the *Drosophila* genome suggest that there are only 13,600 genes, which is slightly fewer than the number found in the nematode *Caenorhabditis elegans*. This number (13,600) is far fewer than the 30,000 originally estimated for *D. melanogaster*. However, *Drosophila* has a relatively large number of

overlapping genes, so additions eventually may be made to the total.

Immediately after obtaining the *D. melanogaster*-genome sequences, a comparison was made to the genomes of *C. elegans* and the yeast *S. cerevisiae* in the context of cellular, developmental and evolutionary processes. These comparisons indicated there are many genes left to be studied in *Drosophila*.

Analysis of the *Drosophila* sequences also indicated this insect is surprisingly relevant to the study of genes and metabolic pathways involved in tumor formation and development in humans. Many of the well-studied signal pathways in tumor development in humans are conserved between flies and humans: at least 76 *Drosophila* genes are homologs to mammalian cancer genes and are under intensive study. Furthermore, 178 (62%) of the 287 known human disease genes can be found in *Drosophila*, including genes causing neurological problems (Alzheimer's disease, Huntington's disease, Duchenne muscular dystrophy, juvenile-onset Parkinson's disease). In addition, analysis of the *D. melanogaster* genome may prove useful in the study of renal, cardiovascular, metabolic and immune diseases, malformation syndromes, and cancer. The *D. melanogaster* genome represents a treasure trove of information that can be mined for years to come.

Chromosome Systems in Arthropods

Many insects are diploid (2n) in their somatic cells and haploid (n) in their gametes (eggs or sperm). Diploidy means that each chromosome type is represented twice. Diploid insects undergo meiosis prior to producing haploid eggs and sperm.

Some insect groups are parthenogenetic (females are able to reproduce without mating) and may be polyploid. Species in the Orthoptera (Blaberidae, Tettigoniidae), Hemiptera (Coccidae, Delphacidae), Embioptera (Oligotomidae), Lepidoptera (Psychidae), Diptera (Chamaemyiidae, Chironomidae,

Psychodidae, Simuliidae), Coleoptera (Ptinidae, Chrysomelidae, Curculionidae), and Hymenoptera (Diprionidae, Apidae) may be parthenogenetic. Polyploid insects usually are 3n or 4n, but exceptions include curculionid weevil species that are 5n and 6n. Parthenogenesis has not been found in the Diplura, Protura, Odonata, Plecoptera, Dermaptera, Grylloblattodea, Zoraptera, Megaloptera, Mecoptera and Siphonaptera, although it is not clear that species in these groups have been examined carefully for this attribute.

Parthenogenesis

Parthenogenesis is reproduction in which progeny are produced by unfertilized females. The mechanisms involved in parthenogenesis are diverse but can be divided into three major types: arrhenotoky, thelytoky, deuterotoky. Deuterotoky involves the development of unfertilized eggs into either males or females, and at least one insect, a mayfly, is reported to exhibit facultative deuterotoky. In the more common arrhenotoky, insects are haplo-diploid, with males developing from unfertilized eggs and females developing from fertilized eggs. The entire order Hymenoptera and many species in the Hemiptera, Thysanoptera, and Coleoptera are arrhenotokous. When the male of a species is haploid, its germ line nuclei contain half the number of chromosomes present in the corresponding diploid nuclei of the female and meiosis is modified so that the sperm remain haploid and do not undergo the typical reductional division.

Insects that exhibit thelytoky have females only. Thelytoky has arisen repeatedly in evolution and consists of several types. Thelytoky can be induced experimentally in a number of ways. In some cases of thelytoky, eggs only develop after penetration by a sperm (pseudogamy or gynogenesis), but the sperm nucleus degenerates without fusing with the egg nucleus so that the sperm makes no genetic contribution to the embryo. The sperm may be derived from the testis or ovotestis

of a hermaphrodite or from a male of a different, but closely related, species.

Thelytoky may be the sole mode of reproduction in a species or it may alternate with sexual reproduction in regular manner (cyclical thelytoky). Cyclical thelytoky is found in aphids, gall wasps and some cecidomyiids. In species that reproduce by cyclical thelytoky, genetic recombination is possible. In species with complete thelytoky, there is no way in which mutations that have occurred in two unrelated individuals can be combined in a third. Thelytokous reproduction can be induced in the eggs of many insect species by pricking the egg, or by exposing it to chemical agents or heat. In a number of normally bisexual insects, a few eggs deposited by virgin females can hatch spontaneously; the incidence of such egg hatch can be increased by artificial selection. The capacity for artificial parthenogenesis, induced thelytoky, or facultative thelytoky indicates that some capacity for parthenogenesis is probably present in all eggs. Thelytokous species or thelytokous populations of bisexual species have been found in the Diptera, Hymenoptera, Lepidoptera, Orthoptera and Coleoptera.

In the Hemiptera, both arrhenotoky and thelytoky occur, but even more complex genetic systems are found. For example, in mealybugs (Pseudococcidae), both males and females develop from fertilized eggs but, in the embryos that develop into males, the paternally derived chromosomes become heterochromatic (stain differently with a dye), are genetically inactive and not transmitted to male progeny. This genetic system has been called parahaploidy. Some method of chromosome imprinting is probably involved to ensure that the paternally derived chromosomes are eliminated in parahaploidy and not the maternally derived ones.

Endopolyploidy in Arthropods

Cells within insects may contain the typical diploid ($2n$) number of chromosomes or may contain

multiples of the haploid (n) number. The discussion of chromosome number (ploidy) is confusing because, in most insects, some of the somatic tissues exhibit high levels of endopolyploidy (multiple copies, greater than $2n$, of chromosomes may be present in some cells) while other cells may be diploid.

For example, haploid male honeybees (which have one copy of each chromosome in their testes cells) have about the same amount of DNA as diploid females (which are $2n$ in the ovaries) in some of their other tissues. This increase in chromosome number occurs because nuclei in some of the tissues of the male undergo repeated cell divisions so that equal amounts of DNA are present compared to the diploid ($2n$) females. In some cases, haploid insect males exhibit higher levels of endopolyploidy than the females of the same species.

Polyploidy of all cells in the body occurs when the chromosome number in an organism increases over the usual diploid ($2n$) amount, usually by duplicating the number of chromosomes to $3n$ or $4n$. Thus, polyploidy can occur in all cells of an insect or in just some tissues (endopolyploidy). A few insects are polyploid in all tissues, but many have polyploid tissues. For example, the diploid blood cells of the silkworm *Bombyx mori* contain 1 pg of DNA per blood cell, but a polyploid silk gland cell, which is metabolically much more active, in the same individual contains 170,000 pg of DNA. DNA content within cells also varies with developmental stage. At metamorphosis, the amount of DNA in *B. mori* declines by 81% after adults emerge from the pupal stage, which is probably due to histolysis of the polyploid larval silk glands and other polyploid cells that are not needed by the adult moth.

Noncoding DNA

DNA in the nuclear genome can be coding or noncoding. Coding DNA sequences code for enzymes (proteins that facilitate metabolic processes) and structural proteins. Coding DNA is transcribed

into messenger RNA and then translated into proteins. In addition, the coding DNA is transcribed and the resulting RNA is used directly (without translation into a protein) as transfer RNAs or ribosomal RNAs.

Noncoding DNA does not code for any known product, although it may have a function or functions. Noncoding DNA can constitute 30% to more than 90% of the insect nuclear genome. Noncoding DNA has been called junk or parasitic or selfish. There are several hypotheses to explain its persistence in nuclear genomes. One suggests that the noncoding DNA performs essential functions, such as regulating gene expression. A second hypothesis is that the noncoding DNA is maintained because it is linked physically to functional genes; the excess DNA is not eliminated because it does not affect fitness of the organism. A third hypothesis suggests that noncoding DNA is a functionless parasite that accumulates and is actively maintained by selection. A fourth hypothesis is that noncoding DNA has a structural function, perhaps for compartmentalizing genes within the nucleus, or for maintaining a structural organization (nucleoskeleton) within the nucleus. The lack of correlation between genome size, complexity and gene number remains a puzzle. Unless the noncoding DNA has a function, it should constitute a load upon the insect and be lost over evolutionary time.

Much of the noncoding heterochromatic DNA in insects is repetitive DNA, DNA sequences that are repeated several times to millions of times. Repetitive DNA is found in heterochromatin near centromeres (regions of the chromosomes to which spindle fibers attach so that chromosomes can be distributed to the daughter cells during mitosis or meiosis), telomeres (the ends of chromosomes) and other heterochromatic regions. Some repetitive DNA sequences are repeated 100 to 10,000 times and include genes that code for ribosomal RNA and transfer RNA.

Species vary in the amount of repetitive DNA in their genome. For example, *Drosophila melanogaster* has about 30% of its genome as heterochromatic DNA, but about 60% of the genome of

Drosophila nasutooides is repetitive DNA. Aphids have small amounts of repetitive DNA, and scientists have speculated that this reduced amount of repetitive DNA could be associated with a faster development time.

Satellite DNA is a type of highly repetitive DNA that differs sufficiently in its base composition from the majority of DNA in an insect that it separates out as one or more distinct bands when DNA is isolated by centrifugation with cesium chloride. Satellite DNA is rich in either A + T or in G + C sequences, and is found in long tandem arrays within the heterochromatic regions of chromosomes.

Even within an insect family, genome organization can vary. Total DNA in the genome of four mosquito species (*Anopheles quadrimaculatus*, *Culex pipiens*, *Aedes albopictus* and *A. triseriatus*) varies from 0.19 to 0.90 pg with the amount of repetitive elements varying from 0.01 to 0.15 pg. Generally, the amounts of repetitive DNA increase linearly with genome size in these mosquitoes. Intraspecific variation in the amount of highly repetitive DNA was found in *A. albopictus* colonies and may be due to differences in the number or type of transposable elements. Transposable elements are independent DNA or RNA elements that can move from one site to another in the genome and between genomes. The amounts of repetitive DNA in mosquitoes varies from 20% in *An. quadrimaculatus* to 84% in *A. triseriatus*. Because genome organization of relatively few insect species has been studied, it is difficult to determine the significance of these patterns.

Mitochondria

In addition to the nuclear genome, insects contain mitochondria in the cytoplasm. Mitochondrial chromosomes are circular, supercoiled, double-stranded DNA molecules. The mitochondrial chromosome of *Drosophila* contains approximately 18.5 kb of DNA and each mitochondrion contains several copies of the chromosome. Mitochondrial genes in insects lack introns (segments

of DNA in the middle of coding regions that are normally removed prior to translation into proteins) and intergenic regions (noncoding regions between coding regions) are small or absent. The ribosomes found in the mitochondria are smaller than the ribosomes in the cytoplasm. Mitochondria contain distinctive ribosomes, transfer RNAs, and aminoacyl-tRNA synthetases. Mitochondria have their own genetic code that differs slightly from the universal genetic code.

The complete sequences of a number of insect mitochondria are known, which allows comparisons of the organization and evolution of insect mitochondrial genomes. These complete mitochondrial genome sequences can be found in GenBank. One of the first mitochondria to be completely sequenced was that of *Drosophila yakuba* which was found to have 37 genes: 2 are ribosomal RNA genes, 22 are transfer RNA genes, and 13 are protein genes that code for subunits of enzymes functioning in electron transport or ATP synthesis. Partial DNA sequences of mitochondria have been obtained from many insects and also can be found in GenBank (Table 3).

Mitochondrial DNA is thought to be inherited only through the mother (in the oocyte) and males are not expected to transmit mitochondria to their progeny via the sperm. However, two studies have shown incomplete maternal inheritance of mitochondrial DNA occurs in *Drosophila simulans*. Most eggs and somatic cells contain hundreds or thousands of mitochondria, so a new mutation can result in a situation in which two or more mitochondrial genotypes coexist within an individual (heteroplasmy). Heteroplasmy, however, is

apparently a transitory state. Thus, the majority of individuals are effectively haploid with regard to the number of types of mitochondria transmitted to the next generation.

Mitochondrial DNA evolves faster than single copy nuclear DNA because mitochondria are relatively inefficient in repairing errors during DNA replication or after DNA damage. In Hawaiian *Drosophila*, mitochondrial DNA appears to evolve about three times faster than coding sequences in nuclear DNA. Because mitochondrial DNA does not code for proteins involved directly in its own replication, transcription or translation, it often contains a large number of mutations.

Mitochondrial DNA has been extensively used for systematics or population genetic studies. Genes can be amplified easily from mitochondria by the polymerase chain reaction (PCR) because there are multiple copies in each cell. Mitochondria are easier to purify than a specific segment of nuclear DNA.

Transposable Elements

Every genome probably contains several types of transposable elements. Transposable elements are genetic elements that can move from one site to another in the genome. Transposable elements have been divided into two classes, those that transpose with an RNA intermediate and those that transpose as DNA. Transposable elements have been found in the genomes of most organisms, including humans, bacteria, frogs, mice, maize, nematodes, protozoans and insects. An

Genomes of Insects, Table 3 Some relevant world wide web sites that provide information on insect genomes

The Interactive Fly is at: sdb.bio.purdue.edu/fly/aimain/1aahome.htm
FlyBase is at: flybase.bio.indiana.edu
<i>Drosophila</i> Virtual Library is at: ceolas.org/fly/
The SWISS-PROT protein sequence database is available at: http://www.expasy.ch/sprot / http://www.expasy.ch//sprot/ and http://www.ebi.ac.uk/swissprot/
The Protein Information Resource is available at: http://pir.georgetown.edu http://pir.georgetown.edu and http://www.mips.biochem.mpg.de

organism may contain multiple types of transposable elements. Most of them may be inactive because they have been mutated or suppressed by the host.

Highly mutated transposable elements probably are the source of much of the noncoding repetitive DNA. There are numerous types of transposable elements in insects. The ubiquity of transposable elements in the genomes of organisms has raised a number of unanswered questions about their evolutionary effects. Examples are still being discovered in which new transposable elements are in the process of invading and spreading within insect populations.

Symbionts of Arthropods

As noted above, mitochondria are derived from a microbial intracellular symbiont that became dependent upon its host cell early in the evolution of eukaryotes (organisms with a defined nucleus and cytoplasm). The relationship between mitochondria and the eukaryotic cell is now mutualistic and obligatory. Other organisms (viruses, bacteria, rickettsia, spirochaetes) also may have long evolutionary relationships with arthropods. Some are gut symbionts, while others are associated with the salivary glands and reproductive tracts. Some relationships are obligatory, others are not.

For additional details about the relationship between microbial genomes (contained within symbionts) and the insect genome.

► [Symbionts of Arthropods](#)

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Genomics

The study of genome data. The complete DNA sequences of organisms such as the human, mouse, rat, zebrafish, *D. melanogaster*, *C. elegans* and *Arabidopsis thaliana* can provide a plethora of information on entire families of genes and pathways of interacting proteins.

- [Proteomics](#)
- [Structural Genomics](#)
- [Functional Genomics](#)

Genotype

The genetic makeup of an individual (contrast with phenotype).

Genus (pl. genera)

The principal subdivision of a family. A group of species that are similar in appearance and appear to have a common ancestry.

Geographic Information System (GIS)

A management system for data associated with precise locations.

Geological Time

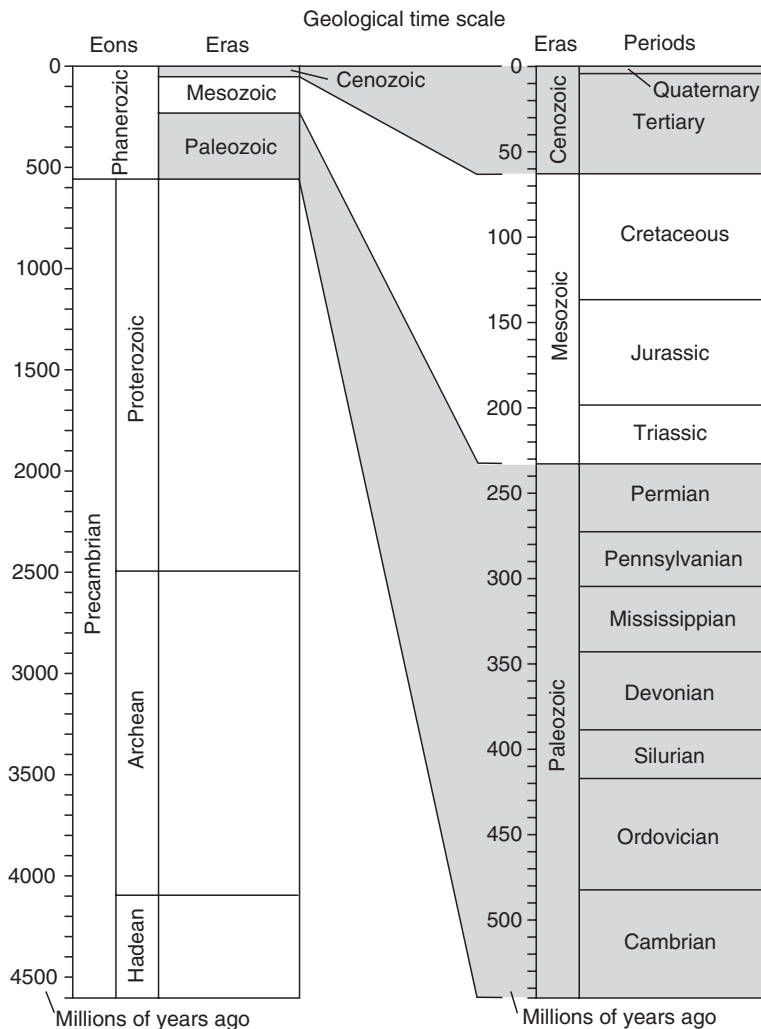
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The time line that describes the history of the earth has been divided into large blocks of time, but

each large block is normally subdivided, and subdivided again, for convenience (Fig. 16). The generally accepted divisions are eon, era, period, epoch, and age. The names given the block of time often have historical significance, and may be associated with occurrence of different fossils. For example, the Phanerozoic eon also consists of three major divisions: the Cenozoic, the Mesozoic, and the Paleozoic eras. The “zoic” part of the word comes from the root “zoo,” meaning animal. “Cen” means recent, “Meso” means middle, and “Paleo” means ancient. These divisions reflect major changes in the composition of ancient faunas, with

each era associated with domination by a particular group of animals. The Cenozoic has sometimes been called the “Age of Mammals,” the Mesozoic, the “Age of Dinosaurs,” and the Paleozoic the “Age of Fishes.” This is not entirely accurate, though there is some basis for these designations. Also, unlike most time lines, the time is expressed not only by date, but from the present. Thus, periods or events are commonly described in millions of years ago (mya). Different spans of time on the geological time scale are usually delimited by major geological or paleontological events, such as mass extinctions. For example, the end of the



Geological Time, Figure 16 A graphical depiction of the geological history of earth (adapted from the Geological Society of America).

Cretaceous period of the Mesozoic era is marked by the demise of the dinosaurs and of many marine species.

The oldest known meteorites and lunar rocks are about 4.5 billion years old, but the oldest portions of Earth currently known are 3.8 billion years old. Sometime during the first 800 million or so years of its history, the surface of the Earth changed from liquid to solid. Once solid rock formed on the Earth, its geological history began. This most likely happened to 3.8–4 billion years ago, but firm evidence is lacking. The oldest time period, the Hadean eon, is not a geological period *per se*. No rocks on the Earth are this old, except for meteorites. During the Hadean time, the Solar System was forming, probably within a large cloud of gas and dust around the sun. The Archean eon was marked by formation of land masses as the earth's crust cooled and plates began to form. The atmosphere was hostile to life as we know it today, consisting mostly of methane, ammonia, and other toxic gases. The only life known from this early period are bacteria and bacteria-like archaea, commencing about 3.5 billion years ago. Things got interesting only in the Proterozoic eon, when life became more plentiful and the first more advanced life (eukaryotic) forms began to appear and oxygen began to accumulate. Eukaryotic life forms, including some animals, began to appear perhaps as long ago as one billion years ago, but certainly by 500 mya.

The Paleozoic era was interesting because well-preserved fossils document this period. The seas were dominated by trilobites, brachiopods, corals, echinoderms, mollusks, and others, and toward the end of this period life appeared on land. On land, the cycads, primitive conifers, and ferns were abundant. The Mesozoic saw the radiation and disappearance of dinosaurs, mammals appeared, while more advanced land plants such as ginkgos, ferns, more modern conifers, and eventually the angiosperms began to appear.

The Cenozoic, the most recent era, is divided into two main sub-divisions: the quaternary and

the tertiary periods. Most of the Cenozoic is the Tertiary, from 65 million years ago to 1.8 million years ago. The Quaternary includes only the last 1.8 million years. The Cenozoic is particularly interesting to biologists because most of the life forms we see today developed in this period. It has been called the “age of insects” due to the development of great diversity, but could also be known as the age of flowering plants, birds, etc.; most of the flora and fauna we see today evolved during this period. The last 10,000 years (the Holocene) is sometimes known as the “age of man” and is also the time period since the last major ice age. The time period before the Holocene, the Pleistocene, is interesting because though much of the recent flora and fauna is the same as today, some interesting and now extinct megafauna were present, including mastodons, mammoths, saber-toothed cats, and giant ground sloths. The human species, *Homo sapiens*, also expanded during this time period, and as mentioned previously, there was a significant ice age period.

From an entomological perspective, the Phanerozoic eon (Table 4) was an exciting time. Arthropods ventured onto land during the Paleozoic, perhaps 400 mya, though the Silurian entomofauna consisted of primitive myriapods and arachnids. Fossil hexapods have been recovered from the Devonian, most notably springtails from chert. Insects proliferated rapidly during the remainder of the Paleozoic and thereafter. Interestingly, during the Mississippian (also called the Early Carboniferous) we have no fossil evidence of insects, whereas in the Pennsylvanian (also called late Carboniferous) we have numerous records of early (mostly now extinct) insect groups (e.g., protodonata and protorthopterans from deposits in France). At the close of the Paleozoic, the Permian period, the environment of earth was undergoing significant change, most notably a less tropical climate. Numerous insects from many deposits around the world document over a dozen orders of insects, including the occurrence of “giant” insects.

Geological Time, Table 4 Important time periods of the Phanerozoic eon (543 million years ago to present)

Cenozoic era (65 mya to today)	Quaternary period (1.8 mya to today)
	Holocene Epoch (10,000 years to today)
	Pleistocene Epoch (1.8 mya to 10,000 yrs)
	Tertiary Period (65 to 1.8 mya)
	Pliocene Epoch (5.3 to 1.8 mya)
	Miocene Epoch (23.8 to 5.3 mya)
	Oligocene Epoch (33.7 to 23.8 mya)
	Eocene Epoch (54.8 to 33.7 mya)
	Paleocene Epoch (65 to 54.8 mya)
Mesozoic Era (248 to 65 mya)	Cretaceous Period (144 to 65 mya)
	Jurassic Period (206 to 144 mya)
	Triassic Period (248 to 206 mya)
Paleozoic Era (543 to 248 mya)	Permian Period (290 to 248 mya)
	Carboniferous Period (354 to 290 mya)
	Pennsylvanian Epoch (323 to 290 mya)
	Mississippian Epoch (354 to 323 mya)
	Devonian Period (417 to 354 mya)
	Silurian Period (443 to 417 mya)
	Ordovician Period (490 to 443 mya)
	Cambrian Period (543 to 490 mya)
	Tommotian Epoch (530 to 527 mya)

The Triassic period of the Mesozoic era saw a warming of the earth, and fossil deposits document the occurrence of early insects such as Blattaria and some Orthoptera, Coleoptera, Odonata, Plecoptera, Neuroptera and Grylloblattodea. Transition into the Jurassic was not abrupt for insects, and the fossil record documents few marked changes, but increased radiation.

The Cretaceous period is notable for the radiation of angiosperms that took place. Because many insects are intimately associated with plants through phytophagy and pollination, they were profoundly affected by the availability of these new resources. Many of the modern taxa became established during this period, though more modern taxa such as some Diptera and Lepidoptera radiated later, in the Cenozoic. One very noteworthy feature of the Cretaceous is the great

availability of amber. The spread of resin-producing trees through this period and into the Tertiary provided an excellent preservation medium for insects. Thousands of species and perhaps 30 orders have been recovered from amber deposits around the world. As insects transitioned from the Cretaceous to the Cenozoic era, the earth witnessed the appearance of “modern” insect groups such as termites, scale insects, fleas, lice, batbugs, flies, bees, and ants.

► [Fossil Record of Insects](#)

► [Amber Insects: DNA Preserved?](#)

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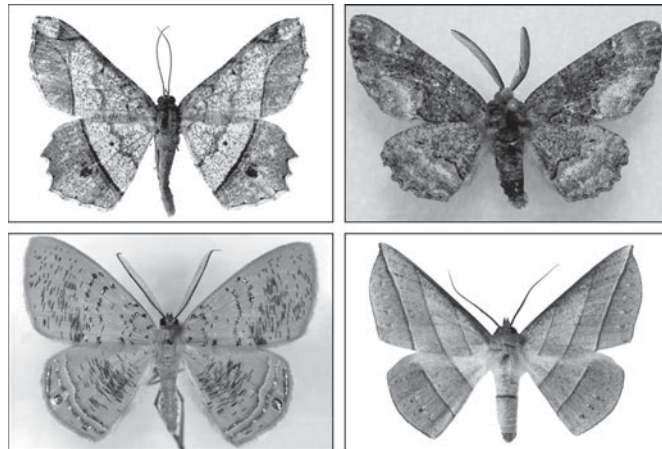
Geometer Moths (Lepidoptera: Geometridae)

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Geometer moths, family Geometridae, also called inch worms, are the second largest family of Lepidoptera, with about 21,150 described species from all faunal regions; the actual fauna probably exceeds 26,500 species. The major biodiversity is in the Neotropics, with over 6,500 species described, and the Indo-Australian region with about 6,670 species. The family is in the superfamily Geometroidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. The family is divided into eight subfamilies (recent past classifications mainly used only 6 subfamilies): Archiarinae, Oenochrominae, Orthostixiinae, Ennominae, Desmobaethrinae, Geometrinae, Sterrhinae, and Larentiinae. There are a very large number of tribal names used and much study and consolidation of overlapping groups is still needed in order to sort out all the valid tribes among the different faunal regions. Adults small to large

(8–120 mm) (most range 20–45 mm), with head scaling normal; haustellum naked; labial palpi upcurved; maxillary palpi small, 1 to 2-segmented; antennae various but mostly filiform (males usually with thicker antennae than females). Wings triangular, usually with somewhat pointed forewings (sometimes rounded), but sometimes emarginate or with falcate apex; hindwings more rounded in most species (rarely tailed); a number of genera have brachypterous or apterous females (Fig. 17). Body usually slender and delicate, but robust in some genera. Maculation extremely varied, but most species with somber hues of brown or gray; occasionally green (especially among Geometrinae) or very colorful among many tropical genera (especially in Ennominae). Adults mostly nocturnal, but also some crepuscular and diurnal groups. Larvae mostly leaf feeders, typically moving in looping fashion due to reductions in proleg numbers, and many remain motionless when disturbed and resemble small sticks or twigs. Some larvae deposit debris on their bodies to camouflage even further (Geometrinae); also known are attacking predaceous larvae (*Semiothisa* sp.) in Hawaii. Host plants include most all plant families. Some major defoliating pests are known in this family.



Geometer Moths (Lepidoptera: Geometridae), Figure 17 Examples of geometer moths (Geometridae): *top left*, (subfamily Ennominae), *Macaria monticolaria* (Leech) from Taiwan; *top right*, *Nacophora quernaria* (J. E. Smith) from Florida, USA; *bottom row left*, *Palyas auriferaria* (Hulst) from Florida, USA; *bottom row right* (subfamily Oenochrominae), *Sarcinodes aequilinearis* (Walker) from Taiwan.

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Geometridae

A family of moths (order Lepidoptera). They commonly are known as measuring worm moths or geometer moths.

- ▶ Geometer Moths
- ▶ Butterflies and Moths

Geophilous

This term, which literally means “ground-loving” is applied to organisms that live on the soil, or favor this habitat.

Georeference

Reference to the location on the earth’s surface based on latitude and longitude coordinates.

Geotaxis

Taxis response with respect to gravity.

Geotrupidae

A family of beetles (order Coleoptera). They commonly are known as earth-boring dung beetles.

- ▶ Beetles

Geridae

A family of bugs (order Hemiptera). They sometimes are called water striders.

- ▶ Bugs

German Cockroach, *Blattella germanica* (Linnaeus) (Blattodea: Blattellidae)

Blattella germanica is one of the most important nuisance species of cockroaches.

- ▶ Cockroaches
- ▶ Urban IPM
- ▶ School IPM

Germar, Ernst Friedrich

Ernst Germar was born in Germany on November 3, 1786. At 21 he moved to Leipzig and bought Hübner’s insect collection. In 1810 he obtained a doctorate in philosophy from Universität Halle. That was the year when the first part of his (1810–1812) work “Dissertatio sistens Bombycum species...” was published. In 1911, he traveled to Dalmatia, resulting in a (1817) book “Reise nach Dalmatien.” In 1813 he founded an entomological journal “Magazin der Entomologie” which ran for six years, was interrupted, and resumed publication in 1839–1845, at which time it was merged into “Linnaea Entomologica.” He married

Wilhelmine Keferstein in 1815. In 1817, he was appointed (at first without tenure) professor of mineralogy in Universität Halle. His other great entomological works were (1817–1847) “Fauna insectorum europae” and (1824) “Insectorum species novae...” He died in July 1853.

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Germarium

An area at the tip of the ovarioles (in females) or sperm follicles (in males) where egg or sperm formation is initiated.

Germ Band

During the blastoderm stage of embryogenesis a region of thickened cells called the germ band forms on the ventral side and elongates. Eventually it differentiates and invaginates.

► [Embryogenesis](#)

Ghilarov, Mercury Sergeevich

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M.S. Ghilarov was born on February 22, 1912, in Kiev (Russian Empire, now the capital of the Ukraine). He was educated at the State University of Kiev (1929–1933) where he specialized in entomology. After graduation from the University, he worked as an entomologist in the Ukrainian Station of Plant Protection. In 1936 he accepted the position of the senior scientific worker in the

State Research Institute of Rubber-bearing Plants in Moscow. He studied ecology of soil insects and influence of soil conditions on the fauna of pests in arable soils. In 1938 he obtained a Ph.D. degree. His further scientific interests turned into studies of general problems of insect adaptations to soil environment. In 1944 he moved to the Institute of Evolutionary Morphology, USSR Academy of Sciences (now the Institute of Ecology and Evolution, Russian Academy of Sciences) in Moscow where he remained until the end of his life. In the 1940s he developed the concept of the evolutionary role of soil as an intermediate environment in the course of transition of animals from the aquatic to terrestrial life. For this work he gained the degree of Doctor of Biological Sciences. His monograph “The specificity of soil as insect habitat and its role in insect evolution” (1949) served as the theoretical basis of soil zoology, the modern branch of soil natural history. In 1956 he founded the Laboratory of Soil Zoology in the Institute, and in the 1950–1960s he organized the broad comparative study of soil entomofauna in different regions of the Northern Palearctic. He found that the ranges of a number of soil-dwelling insects coincide with the particular types of the soil (“Zoological method of the soil diagnostics,” 1965). He headed the taxonomic study of soil insects and mites which were resulted in “Key of soil-dwelling insect larvae” (1964), and “Key of soil-dwelling mites” (Sarcoptiformes, 1975; Mesostigmata, 1977; Trombidiformes, 1978). He published more than 500 scientific papers devoted to various aspects of entomology. From 1973 he was the President of the USSR Entomological Society. In 1974 he was elected as a member of the USSR Academy of Sciences and in 1975 he was appointed the Academician-Secretary of the Division of General Biology of the Academy. Beginning in 1978 he also headed the Department of Invertebrate Zoology in the State University of Moscow. He was engaged in a broad range of international activities. He was a member (starting in 1956) and the Vice-president (1967) of the Permanent Committee of International Entomological Congresses, and

from 1976–1982 he was the vice-president of the International Union of Biological Sciences. His scientific awards include three USSR State Prizes (1951, 1967, 1980), the Philippo Sylvestry Golden Medal (1965), the Gustav Kraatz Medal of the German Agricultural Academy (1966), a medal of the International Committee on the entomofauna of Middle Europe (1975), a medal of the Zoological Society of France (1976), a medal of the German Academy “Leopoldina” (1977), the I. Mechnikov Golden Medal of the USSR Academy of Sciences (1978) and honorary memberships in entomological societies and academies of sciences of a number of countries. He passed away in Moscow, USSR, on March 6, 1985.

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Ghost Moths (Lepidoptera: Hepialidae)

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Ghost moths (sometimes also called swifts), family Hepialidae, comprise about 496 species and occur in all faunal regions, although most species are in the ancient refugia regions of Australia, South Africa and Chile. The family is the main component of the superfamily Hepialoidea, in the infraorder Exoporia. Adults small to very large (20–250 mm wingspan), with head roughened; haustellum absent or vestigial and no mandibles are evident; labial palpi small and 2- or 3-segmented; maxillary palpi are minute and 1 to 5-segmented; antennae are very short. Maculation is usually dull with light (Fig. 18) spotting, but can include some green or gold iridescent markings or other light spots or bands. The



Ghost Moths (Lepidoptera: Hepialidae),
Figure 18 Example of ghost moths (Hepialidae),
Zelotypia stacyi Scott from Australia.

hindwings tend to be large and overall the adults have large bodies. Adults are typically crepuscular or nocturnal, but a few are diurnally active. Larvae feed as borers on roots, trunks or under bark of trees, various bushes, or grasses, or even leaf litter. A few species are considered pests in Europe, Asia and Australia. This family has the record for egg deposition by a single female, of about 50,000 eggs, which are scattered over potential Host plants during flight. A few are economic. The largest species are the Australian *Zelotypia stacyi* Scott and the Amazonian *Trichophassus giganteus* (Herrich-Schäffer).

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Giant Axons

Very large neurons running through the abdominal ganglia of insects, and connecting by electrical rather than chemical synapses. Giant axons promote the rapid transmission of impulses.

Giant Coccids

Some members of the family Margarodidae, superfamily Coccoidea (order Hemiptera).

► Bugs

Giant Butterfly Moths (Lepidoptera: Castniidae)

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Giant butterfly moths, family Castniidae, total 170 known species, mostly Neotropical but with some species also in the Indo-Australian region; likely world total may exceed 180 species. Three subfamilies are known, with the more unusual groups being from Australia and Southeast Asia: Synemoninae, Neocastniinae, and Castniinae. The family is its own monobasic superfamily, Castnioidea, in the section Cossina, subsection Cossina, of the division Ditrysia. Adults medium to large size (24–190 mm wingspan), with head smooth scaled and eyes large; haustellum naked (rarely vestigial); labial palpi often with distal segment erect; maxillary palpi 2 to 4-segmented; antennae clubbed. Body robust. Wings quadratic and broad (Fig. 19); hindwings rounded. Maculation variable but often dark browns with lighter bands or other markings; often colorful with variously colored patches and markings, especially on the hindwings. Adults diurnal or crepuscular. Larvae are borers of monocot plants, including grasses (Gramineae), Cyperaceae, Bromeliaceae, Marantaceae, Musaceae, and Palmae, among others.



Giant Butterfly Moths (Lepidoptera: Castniidae), Figure 19 Example of giant butterfly moths (Castniidae), *Castnia licus* Fabricius from Peru.

A few are economic on banana plants, various palms, and sugarcane. One palm pest from Argentina has become established in southern Spain in recent years.

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Giant Hooktip Moths (Lepidoptera: Cyclidiidae)

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Giant hooktip moths, family Cyclidiidae, are a small family of 14 described species, all Oriental plus one species in the southern Palearctic. The family is in

the superfamily Drepanoidea, in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium to large size (56–85 mm wingspan), with head scaling normal; maxillary palpi small, 3-segmented; antennae serrate or filiform; body slender. Wings broad and triangular, with somewhat acute forewing apex; hindwings rounded (Fig. 20). Maculation mostly pale with gray striae or other markings; dark spot on hindwings in some species, otherwise similar to forewings. Adults are nocturnal. Larvae are leaf feeders. Host plants recorded so far only in Alangiaceae.

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Giant Lacewings

Members of the family Polystoechotidae (order Neuroptera).

► [Lacewings, Antlions, and Mantidflies](#)



Giant Hooktip Moths (Lepidoptera: Cyclidiidae), Figure 20 Example of giant hooktip moths (Cyclidiidae), *Cyclidia substigmata* (Hübner) from Taiwan.

Giant Lappet Moths (Lepidoptera: Eupterotidae)

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Giant lappet moths, family Eupterotidae, total 325 species worldwide (except the Nearctic), but most are Oriental (238 sp.); only four species are recorded in the Neotropics. Three subfamilies are recognized: Janinae (in Africa), Eupterotinae, and Panacelinae (in Australia). Some specialists now include Hibrildinae (plus Tissanginae) in Eupterotidae. The family is in the superfamily Bombycoidea (series Bombyciformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults small to large (23–140 mm wingspan), with head scaling roughened; haustellum (Fig. 21) absent (rarely vestigial); maxillary palpi absent; antennae bipectinate (sometimes tripectinate or serrate); body robust. Wings mostly broad and rounded. Maculation varies but mostly shades of brown or gray with few markings. Adults are nocturnal. Larvae are leaf feeders, usually with many secondary setae. Host plants among numerous different plants, including Acanthaceae, Boraginaceae, Gramineae, Leguminosae, Myrtaceae, Pinaceae, and Rubiaceae, among others. Few species are economic (e.g., rice or forest pests).



Giant Lappet Moths (Lepidoptera: Eupterotidae), Figure 21 Example of giant lappet moths (Eupterotidae), *Palirisa cervina* (Moore) from Taiwan.

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Giant Leaf Katyids

A subfamily of katyids (Phyllophorinae) in the order Orthoptera: Tettigoniidae.

- ▶ Grasshoppers, Katyids and Crickets
- ▶ Katyids

Giant Mealybugs

Members of the family Putoidae, superfamily Coccoidae (order Hemiptera).

- ▶ Bugs
- ▶ Scale Insects and Mealybugs

Giant Northern Australia Termite

A termite species, and family of termites called Mastotermitidae.

- ▶ Termites

Giant Silkworm Moths

Some members of the family Saturniidae (order Lepidoptera).

- ▶ Emperor Moths
- ▶ Butterflies and Moths

Giant Stoneflies

Members of the stonefly family Pteronarcidae (order Plecoptera).

- ▶ Stoneflies

Giant Water Bugs (Hemiptera: Prosorrhyncha Belostomatidae)

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These aquatic insects are also known as giant fish killers, electric light bugs, and toe biters. They are predators of insects and other small organisms up to the size of tadpoles, small water birds or even fish, and occasionally are known to inflict injury to humans. In humans, a belostomatid bite produces a painful burning sensation that lasts several hours.

Morphology

Belostomatidae are large-sized (up to about 110 mm), ovoid to elongate aquatic bugs. They are brownish, dorsoventrally flattened while ventrally convex. The head extends triangularly in front of the large eyes. They have a stout syringe-like rostrum or beak, which is the result of the pair of mandibles and the two pairs of maxillae evolved in long piercing stylets. The beak is three segmented. A pair of short, 4-segmented antennae are concealed in grooves beneath the head. Segments 2 and 3 have lateral projections. Belostomatidae possess a pair of large compound eyes, but lack ocelli. The head does not overlap the pronotum. The front wings are in the form of hemelytra, with a sclerotized basal region (corium) and a membranous apical region (membrane) with reticulate venation. The hind wings are completely membranous.

The front legs usually are raptorial. They are at least dexterous, as in the genus *Limnogeton*, but in most cases they act as a vice-like grip. Very dense short setae on the under surface of most front leg

segments help the insect grasp. Front femora are expanded to contain a powerful musculature that allows the tibia and tarsi to seize the prey. Except in the case of *Limnogeton*, the middle and hind legs are paddle-shaped, and well suited for swimming. They are flattened and broadened, and doubled-fringed with long, fine setae that increase the effective swimming surface. The tarsi may be 2-, 3- or more rarely 1-segmented. There may be a single claw, slightly or greatly reduced, or paired claws, like in the front legs of Horvathiniinae. A metathoracic scent gland system (MSGS) has been reported only in Lethocerinae. In nymphs, the dorsal abdominal scent glands are not functional.

In the apex of the abdomen (tergum 8), the Belostomatidae have a pair of retractable, strap-like appendages that allow snorkeling while the insect is under water. These special respiratory structures are the most distinctive feature of the group. Belostomatidae also are provided with static sense organs, associated with spiracles 2–7.

Taxonomy

Belostomatidae, as Belostomida, were recognized as a group by Leach in 1815. This family presently is arranged in three subfamilies: Lethocerinae, Horvathiniinae and Belostomatinae. Currently, 11 genera and approximately 150 species are recognized. The antennal and spiracular characteristics are most often used to identify subfamilies.

The Lethocerinae are 37–150 mm in length. Formerly it contained a single genus, *Lethocerus*, that was recently divided into three genera: *Benaucus*, with a single species *B. griseus*; *Kirkaldyia* also with a single species *K. deyrolli*; and *Lethocerus* with the remaining 22 species. *Lethocerus maximus* (Fig. 22) is the largest true bug and is among the largest insects. Males of Lethocerinae perform emergent-brooding, attending clutches glued to vegetation at the shore.

The Belostomatinae are between 9 and 70 mm in length. They are found worldwide, and contain most of the genera of Belostomatidae, and about a



Giant Water Bugs (Hemiptera: Prosorrhyncha Belostomatidae), Figure 22 Adult giant waterbug, *Lethocerus* sp. (photo courtesy of Dave Almquist, University of Florida).

hundred species. *Belostoma*, with approximately 60 species, is the most species-rich genus. Other quite species-rich genera are *Diplonychus* (approximately 6 species), *Abedus* (10 species) and *Apasus* (17 species), while *Sphaerodema*, *Hydrocyrius* and *Limnogeton*, among others, comprise very few species each. *Limnogeton*, with its unspecialized legs and its diet restricted to water-snails, is the most primitive genus. *Poissonia* and *Weberiella*, two monospecific genera, are poorly known. Belostomatinae males perform back-brooding.

Horvathiniinae, which measure 25–30 mm in length, are the least known belostomatid subfamily. In the unique genus *Horvathinia*, nine species were described, but recent revision (2005) left only two species: *H. pelocoroides* and *H. lenti*. Generally, only specimens attracted to light are known. However, recently two adults were collected for the first time in their natural habitat, but nymphs have never been observed. The real position of

Horvathiniinae is uncertain. Egg color is as in Lethocerinae, and the eggs are buried as in Nepidae (water scorpions), but those eggs lack the respiratory horn-like structures typically found in water scorpions.

Biology

Giant water bugs live in many freshwater environments. In Japan, rice fields have been reported to function as alternative wetlands for many aquatic insects, including belostomatids. Overwintering occurs in the mud at the bottom of the rice field. Giant water bugs in the subfamily Lethocerinae inhabit ponds, lakes and slow waters of streams and rivers. Belostomatinae prefer lentic waters, from small puddles to margins of large lakes. *Horvathinia pelocoroides* (Horvathiniinae) has been captured in the province of Corrientes, Argentina, in a permanent shallow pond of about 1 ha surface and 2.1 m depth; during the rainy season, the water level is high enough to drain into a stream. The pond was densely filled with floating hydrophytes dominated by water hyacinth, *Eichhornia crassipes*, and water lettuce, *Pistia stratiotes*. Other belostomatids shared the habitat with *H. pelocoroides*. Other fauna, including tadpoles and snails were reported to live in the area. Belostomatids are quite easily reared, so their biology has been extensively studied in laboratory trials.

Belostomatids are good flyers, and this ability is needed to escape (migrate) from drying ponds or streams, or due to shortage of prey. Migration may be related to the lunar cycle, as is the case in *Diplonychus rusticus* or *Lethocerus* sp. (in the latter case, during the full moon). Heavy rains also induce flight activity (called “rainfall response behavior”), primarily as an adaptation to migrate to breeding sites. However, the rainfall response behavior also ameliorates the risk of extinction due to flash floods. For *Abedus aberti*, there is a report that a torrential rainfall threshold of 8.0 min caused one-third of the adults to abandon a rapidly flowing stream; immatures respond more slowly to the flooding cue, usually requiring about

30 min of torrential rainfall. In this species, flash flood mortality normally causes less than 15% mortality because they can perceive danger through rainfall rate, while for most freshwater invertebrates exposed to such flooding the mortality may be more than 90%. Belostomatids are good swimmers, but in the case of *Limnogeton* and in Horvathiniinae, they are less efficient than the rest of the group. Positive phototropism (attraction to light, especially to mercury vapor lamps) of giant water bugs is the basis for their common name “electric light bugs.” Such lights interfere with their normal nighttime navigation as they normally navigate using star light.

Giant water bugs are carnivorous, and either ambush or actively pursue and capture the prey (foraging). They attack moving prey, but not still or immobile objects. Once grasped by the front legs with lightning speed, the prey is pierced with the robust rostrum. The bug then injects venomous saliva containing proteases, hyaluronidases, phospholipases, hemolytic enzymes and heart-stopping neurotoxins. This mixture, similar to that in snake venom, easily subdues (paralyzes and kills) the prey. As a result, the prey’s tissues are liquefied by external digestion, and the bug sucks out that liquid using a cibarial pump. Once grasped, the prey is never released, however it struggles to escape from the predator. The size of prey tends to match that of the predatory bug. The smallest belostomatids prey on water snails, which seems to be an ancient trait of the group. Increasing size allows them to prey on crustaceans, dragonfly nymphs, vertebrate larvae, small fish, and even frogs, salamanders, water-birds, larger fish, and snakes. Except for *Limnogeton*, a specialist in water-snails, the rest of the Belostomatidae have a diversified diet, always including vertebrates. It is hypothesized that the ancestral snail consumption, which requires quite precise movements and tight grasping, is a pre-adaptive trait (a trait evolved for one function but later co-opted for another) that allows the insect to handle more demanding prey such as vertebrates. Some species catch more prey than

they can eat, a hoarding behavior. Cannibalism is sometimes reported.

Although living in water, belostomatids need to breath air. Breathing is mediated by the special abdominal airstraps, which are protruded to the surface while lying motionless in the water. They transmit the air to the subhemelytral airstore by a channel, formed by the setae, which converge mesioventrally. Air finally passes to the tracheal system mainly through the dorsal first abdominal spiracle. In nymphs, respiration occurs from the airstore on the ventral surface of the abdomen, and cuticular breathing also plays a key role.

Defensive behavior is well developed in this group. The first reaction to a threat is the motion of the front legs as if to grasp the aggressor. Also, a foul-smelling liquid may be ejected from the anus for more than a meter. In Lethocerinae, the metathoracic scent gland does not play any defensive role, but seems to be essential in marking the trail to the clutch laid on the shore vegetation. The odor of the metathoracic gland does not prevent *Lethocerus* specimens from being eaten by humans in several parts of Asia.

Reproductive behavior of giant water bugs is unique among insects, as paternal care is the rule in most of them. Lethocerinae are emergent-brooders, while Belostomatinae are back-brooders. Only Horvathiniinae seem not to perform brood-caring, and eggs are half-buried in small groups in the wet sand of the shore. When paternal care occurs, a reversal of the typical sexual competition occurs, as the females fight for mates. Most probably, the big size of Belostomatidae, a primary trait, promoted ancillary selection of paternal care. Hatching occurs one or two weeks after egg laying, and nymphal development occurs in one or two months, requiring five molts.

Natural Enemies

Predation of eggs of *Belostoma* by water scorpions, *Notonecta*, has been reported. Also, young nymphs

of *Kirkaldyia* are preyed upon by the water scorpions *Laccotrephes*, *Notonecta*, and *Ranatra*, the giant water bug *Appasus*, and dragonflies of the family Aeschnidae.

Belostomatids such as *Belostoma* (Fig. 23) may serve as hosts of ectosymbiont platyhelminths such as *Temnocephala*. Also, *Bodo* kinetoplastid flagellates were isolated from the hindgut of *Lethocerus indicus*. Some belostomatid species have been reported as intermediate hosts for metacercariae of digenetic trematodes; this is the case for several *Belostoma* spp. that are parasitized by the trematode *Stomylotrema* in Brazil and Argentina. Trematode metacercariae lodge in the abdominal cavity of both male and female bugs.



Giant Water Bugs (Hemiptera: Prosorrhyncha Belostomatidae), Figure 23 Male giant waterbug, *Belostoma* sp., bearing eggs and young (photo courtesy of Doug Tallamy, University of Delaware).

Distribution

Although distributed worldwide, Belostomatidae are most diverse in the tropics. Lethocerinae have a pantropical distribution, with a few temperate representatives. *Benachus* lives in North America and the Caribbean regions, *Kirkaldyia* is distributed in East and Southeast Asia, and *Lethocerus* is a cosmopolitan genus. Belostomatinae genera differ in their distribution. For example, *Belostoma* is known from the Americas, while *Abedus* is restricted to the southwestern USA and to Central America. *Diplonychus* lives in Asia, India, China, and probably Malaysia. *Appasus* lives in Africa and Asia, *Hydrocyrius* is present in Saudi Arabia, Africa and Madagascar, and *Limnogeton* is found exclusively in Africa. Horvathiniinae have been recorded in Central and South America (northeastern Argentina, Uruguay, Paraguay, Bolivia and southeastern Brazil).

Ecological and Economic Significance

Belostomatids play a key role in freshwater ecosystems, where they perform as intermediate-stage predators in the food chain. Their control over invertebrate populations is greater in the absence of fish. *Belostoma* and *Lethocerus* species, among others, may be efficient controllers of freshwater snail populations. As a consequence, they may play a useful role in preventing human and veterinary schistosomiasis, as snails are an intermediate host. *Lethocerus* may be of concern in fisheries, as it may prey on specimens up to 20 cm long. Mosquito and/or chironomid larvae and/or pupae are actively preyed upon, and controlled to some extent, by *Belostoma*, *Diplonychus*, *Spherodema* and *Lethocerus* species. However, pesticide treatments targeted at mosquito larvae, or other biocide treatments for agricultural purposes, may poison water and prove harmful to giant water bugs. *Kirkaldyia deyrolli* is reported to be a threatened-vulnerable

species in the Read Data Book of Japan, most probably due to water pollution. Interestingly, *Bacillus* sp. spread to control larval mosquitoes may remain in belostomatid feces and dead bodies, acting as a mosquito-killing microbe repository.

Relative to humans, the main role of these insects is as a food source in several Asian countries where adults of *Lethocerus* are considered a delicacy, and are eaten both fresh and cooked. In Southeast Asia, some species are highly valued for extraction of a very expensive essence from the essence-producing glands. The “essence” is a sex-pheromone, and is produced by males to attract females. It is used by humans in cooking (dipping sauce).

Belostomatids may also be a nuisance because they are attracted to lights, especially when attracted to lighted pools where they might bite swimmers. The role of some giant water bugs as second intermediate hosts of digenetic trematodes may result in medical importance of giant water bugs in some regions. Thus, like many insects, belostomatids display several behaviors that could result in them being classified as either useful or harmful insects.

Evolution

In past times, giant water bugs likely took advantage of shallow waters teeming with small vertebrates or invertebrate larvae, an empty niche unavailable to large predatory fish, which need deeper water. The individuals best adapted to feed on larger prey succeeded over the predators taking smaller prey, in a feed-back cycle whose only limit was egg size and embryo nutrition. Thus, it appears that large body size, a primary trait under natural selection because it allows feeding on bigger prey, has shifted the evolution of Belostomatidae to their current large body size.

- ▶ Parental Care in Heteroptera
- ▶ Bugs (Hemiptera)

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Gill

A respiratory structure found in immature aquatic insects, through which they obtain dissolved oxygen. Gills take various forms, and are found at various locations.

Girault, Alexandre Arsène

Alexandre Girault was born in the state of Maryland, USA, on January 9, 1884. He earned a B.S. degree from Virginia Polytechnic Institute in 1903, and then in 1904 became employed by the U.S. Department of Agriculture. During that employment he worked as an applied entomologist on the plum curculio, Colorado potato beetle, and lesser peach

borer. In 1908 he moved to Illinois as assistant to the State entomologist and then as assistant in entomology at the University of Illinois. There he worked on insects of stored products, the Colorado potato beetle, and Cimex bed bugs. In 1911, he moved to Australia, as entomologist to the Bureau of Sugar Experiment Stations in Queensland. There, he worked on taxonomy of “parasitic” Hymenoptera. He also studied thrips. Three years later, he returned to the USA to work again for the U.S. Department of Agriculture, but this time in Washington, DC, on the classification of Chalcidoidea. He moved back to Australia in 1917, this time as assistant entomologist to the Queensland Department of Agriculture and Stock. His major work was a monograph (1912–1915) “Australian Hymenoptera Chalcidoidea” of over 900 pages. Many others of his over 300 papers were small notes, some of them badly printed on a small press of his own, and distributed to few institutions and hymenopterists, thus not readily available. He died in Brisbane, Australia, on May 2, 1941.

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Gizzard

This term is rarely used in entomology, but applies to a pouch-like structure at the juncture of the crop and stomach. This organ is used for filtering and grinding of food and usually is called the proventriculus.

► [Alimentary Canal and Digestion](#)

Glabrous

► [Smooth and without hairs](#)

Gladiators (Mantophasmatodea)

In 2002, German researchers announced the discovery of a new insect order, Mantophasmatodea. The order name is based on the names of their close relatives, the Mantodea (praying mantids) and the Phasmatodea (walking sticks). This was a significant find because a new order had not been discovered since 1915. Indeed, it remains to be seen whether the entomological community accepts the report that this is a new order. It has been a controversial topic since the initial discovery. Some have argued that Mantophasmatodea is a sister group of Grylloblattodea, and that they should be treated as suborders in the order Notoptera. Further, two of the three families were relegated to subfamily status in this system, and the insects were named “rock crawlers,” whereas the members of the sister taxon, were called “ice crawlers.”

Characteristics

Mantophasmatodea was first found in the Brandenberg Mountains of Namibia in southwestern Africa (since then they have been found widely in the western regions of South Africa, and in Tanzania). They were found at the base of grass clumps growing in rock crevices. In most respects these insects resemble stick insects (Phasmatodea), but have characteristics of praying mantids (Mantodea), and some unique attributes. Superficially, they resemble immature mantids, which are wingless like gladiators, but the gladiators lack the well-developed raptorial front legs of mantids. They differ from stick insects in that the head is hypognathous (pointing downward), the first thoracic segment is the largest, the first and second pairs of legs are raptorial, and the insects are carnivorous. Unlike mantids, the second pair of legs is used in feeding. The thorax appears to be armored, hence the name “gladiators.” They are also known as “heelwalkers” because they tend to elevate their tarsi when walking.

Gladiator insects are hemimetabolous, like other orthopteroids. The antennae are long and

filiform, the head hypognathous. The thoracic segments decrease in size from anterior to posterior. The femora of the first and second pairs of legs are broadened and armed with spines. The tarsi have five segments. There is slight sexual dimorphism. In males, the subgenital plate has a median projection. The cerci are one-segmented, prominent and clasping. In females, the ovipositor projects markedly beyond the short subgenital lobe. The female abdomen is widest in the middle, whereas in the male it is widest apically. Males are smaller than females. All insects are apterous. They generally are under one cm in length. They are brown or green, and may be uniform or mottled in color, often with a dorsal stripe or stripes. Polymorphism is common.

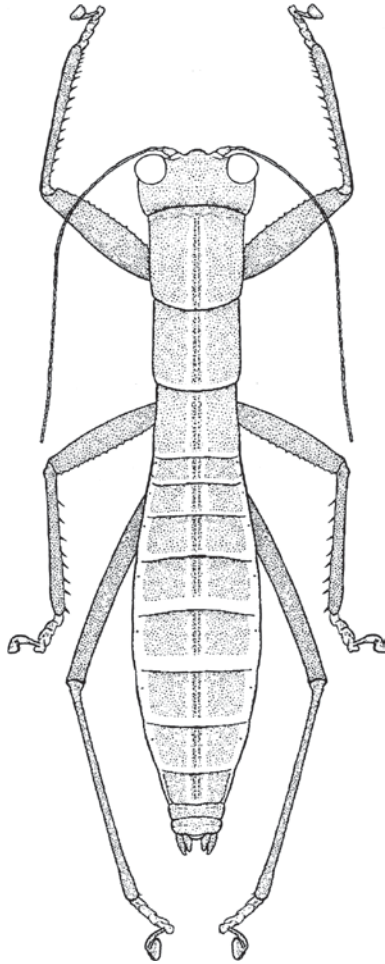
Biology

The eggs of gladiators hatch after the seasonal rains commence, with the nymphs developing during the wet months and the adults maturing at the end of the rainy season. The adults mate, lay eggs and die within two weeks. Mating can be protracted, lasting for 1–3 days. The eggs persist through the arid period in an egg pod in the soil. The pod is composed of sand granules glued together with an exudate. Each pod contains about 12 eggs, and females (Fig. 24) produce several pods.

Gladiators feed on small insects such as flies and bark lice. They may be nocturnal or diurnal. They frequent low vegetation such as tufts of grass. Apparently they communicate vibrationally, as they have been observed taping their abdomen on the substrate.

Taxonomy

The order presently consists of three or more families, several genera (some have yet to be placed in families) and perhaps 12 species. One genus, *Raptophasma*, is known from Baltic amber, dating back



Gladiators (Mantophasmatodea),
Figure 24 Female *Austrophasma* sp.
 (Mantophasmatodea: Austrophasmatidae)
 (adapted from Klass et al. 2003).

about 45 million years. These extinct insects differ from the modern forms in lacking the spines on the femora and tibiae of the first and second sets of legs.
 Order Mantophasmatodea

Family Tanzaniophasmatidae

Family Mantophasmatidae

Family Austrophasmatidae

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Glaphyridae

A family of beetles (order Coleoptera). They commonly are known as glaphyrid scarab beetles.

► Beetles

Glaresid Beetles

Members of the family Glaresidae (order Coleoptera).

► Beetles

Glaresidae

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

► Beetles

Glassy-Winged Sharpshooter, *Homalodisca vitripennis* (Hemiptera: Cicadellidae)

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The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) feeds on xylem fluid and is damaging to crops and ornamentals through the transmission of *Xylella fastidiosa*, a bacterium that causes phony peach disease, Pierce's disease in grapes, and leaf scorch in almond, plum, elm and oak. In Brazil, a strain of *X. fastidiosa* causes citrus variegated chlorosis, but the current geographic range of the strain does not overlap that of

H. vitripennis. *Homalodisca vitripennis* is native to the southeastern United States, and in the late 1980s or early 1990s spread from Texas to southern California, where Pierce's disease caused \$30 million in damage to California vineyards from 1994 to 2000. In California, *H. vitripennis* is a more important vector than the native species because it spreads the disease further into vineyards from surrounding vegetation. Furthermore, in the southeastern United States only muscadine grapes are grown successfully, because only the muscadine varieties are resistant to Pierce's disease. The range of *H. vitripennis* is restricted to areas with mild winters. However, *H. vitripennis* has been accidentally introduced to Hawaii, Tahiti, and Easter Island, Chile. Also, climatological models predict that *H. vitripennis* and *X. fastidiosa* could become established in Central and South America, southern Europe and Asia, Africa, Australia, and northern California.

The "sharpshooter" name refers to leafhoppers in the tribes Proconiini and Cicadellini (Hemiptera: Cicadellidae), and the name has two possible derivations. One reason for the name sharpshooter is the tiny "bullet holes" in branches and stems that are caused by the piercing-sucking behavior. In addition, adults and nymphs quickly move to the opposite side of a branch when startled, and this behavior is similar to the way a military sniper moves to the far side of a tree to avoid detection. The Proconiini tribe comprises 350 species in 56 genera, including *H. vitripennis*, and the

range of the tribe includes the Americas and Tahiti.

Homalodisca vitripennis adults (Fig. 25) are generally light brown with black and red wings, and are 11–13 mm in length. Adults usually align head to tail with their heads facing down when feeding, and feed on a wide range of host plants (>100 species), including hardwoods, softwoods, fruit trees, herbaceous crops, and grasses. Some preferred hosts include plum, holly, crape myrtle, citrus, grape and sunflower.

Feeding on xylem may limit the number of competitive interactions *H. vitripennis* encounters, as few insects feed on xylem fluid and there is little or no degradation of xylem quality with insect feeding. In addition, xylem fluid has little or no chemical defensive compounds, which may enable *H. vitripennis* to feed on such a broad host range. However, there are some disadvantages associated with xylem feeding, and *H. vitripennis* has developed some important adaptations to feeding on xylem fluid. To overcome the strong negative pressure associated with xylem tissue, *H. vitripennis* uses a large cibarial pump in the anterior portion of the head to extract the xylem fluid. Furthermore, xylem fluid is approximately 99% water, so a portion of the gut and the Malpighian tubules form a filter chamber that is designed to extract most of the water from the ingested xylem fluid. This process allows nutrients to be absorbed from a more concentrated solution. In addition, *H. vitripennis* feeds for long periods in order to



Glassy-Winged Sharpshooter, *Homalodisca vitripennis* (Hemiptera: Cicadellidae), Figure 25 Adult of glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar).

gain adequate nutrients. Hourly consumption of xylem is often 10–100 times greater than the dry body weight of the individual, so they must produce large amounts of waste. *Homalodisca vitripennis* has become a pest to the tourist industry in Tahiti due to the dense populations of adults and nymphs and the “rain” they excrete that falls on tourists. *Homalodisca vitripennis* excreta consist of a dilute mixture of water and ammonia, which is much less physiologically expensive than urea or uric acid. Most animals do not use ammonia as a waste product, due to the chemical’s toxic nature, but *H. vitripennis* waste products are too dilute to cause ammonia poisoning.

Glassy-winged sharpshooters have adapted high assimilation efficiency (about 99%) of amino acids, organic acids and sugars. This assimilation may be due in part to two species of endosymbiotic bacteria that live in the cytosol of *H. vitripennis* cells and aid in attaining the adequate nutritional requirements. Each species of bacteria complements the nutritional advantages of the other and is passed by females to offspring from generation to generation. One species, *Baumania cicadellinicola*, is related to endosymbionts of aphids, tsetse flies, and ants, but is a more primitive species and synthesizes most vitamins and cofactors. The other species, *Sulcia muelleri*, produces many of the essential amino acids that are not abundant in xylem fluid.

Adults often fly from plant to plant, sampling xylem fluid to find optimal hosts and adjust feeding rates to correlate with xylem nutrition. Flight behavior usually consists of short flights from plant to plant and *H. vitripennis* generally flies 2–3 m high, depending on the height of the surrounding vegetation. Dispersal rates vary with available host plants and seasonal conditions, but a single *H. vitripennis* can travel up to 100 m in a matter of minutes. Daily foraging usually occurs between 10 am and 2 pm, during peak xylem flow and this behavior allows adults to attain the best sample of a host in order to make a decision to stay and feed or move on. In addition, *H. vitripennis* may feed on different plants at different times

of the day to correlate feeding with maximum xylem flow in the plants. Foraging adults and nymphs are attracted to the color yellow, which may resemble new growth occurring in host plants. *Homalodisca vitripennis* also uses plant volatiles to locate host plants, but olfactory cues appear to be secondary to visual stimuli. Adults do not appear to use pheromones as aggregation cues or to locate mates.

When mating occurs, females line up head to tail on branches, while males fly from branch to branch looking for aggregations of females. Once the male selects a branch to land on, it walks down the branch in a spiral formation and looks for an accepting mate. If the female is not ready to mate, she will stick her legs and abdomen in the air and block off any potential suitors. Mating occurs in the morning or evening, and females deposit eggs at night. Eggs are inserted under the leaf epidermis on the underside of the leaf in groups of 3–28, although eggs are occasionally deposited in fruits or herbaceous stems. A single female can lay up to 1,000 eggs, and eggs hatch approximately 7 days after oviposition. Nymphs are gray and develop through five instars, usually lasting about two months.

Nymphs have different nutritional preferences than adults. Adults prefer to feed on xylem fluid that is high in amides (glutamine and asparagine), and nymphs prefer to feed on xylem fluid with a more balanced spectrum of amino acids. In addition, adults can feed on stems with thicker epidermis than nymphs, due to the adult’s thicker proboscis. Pubescent leaves and stems also deter nymphs from feeding, as first and second instars often feed on xylem in leaf veins, and have difficulty reaching the plant through the trichomes. Often eggs are laid on hosts that are acceptable to adults but do not support the development of nymphs, so the nymphs must disperse to find new hosts. However, nymphs have developed excellent dispersal abilities, and third and fifth instars can jump up to 68 and 79 cm, respectively. In addition, nymphs can traverse up to 10 m across a grassy field in three days, and neonates survive an average of 84 h without a host plant.

Nymphs and adults cover themselves in a light coating of lipid-protein molecules called brochosomes, which are produced by special cells in the Malpighian tubules. *Homalodisca vitripennis* secrete brochosomes from the hindgut after each molt and spread them over the integument with their hind legs. In addition, adult females often have conspicuous, white spots of brochosomes on their wings. Females cover their egg masses with these brochosomes by using their hind legs to brush the powdery substance from the forewing patch to the egg mass. All Cicadellidae species cover their integument with brochosomes, but only Proconiini species cover egg masses as well. The structure of brochosomes varies between species, and brochosomes that cover egg masses are structurally different than those that cover the integument. Brochosomes have repellent properties and probably aid adults, nymphs and eggs in the repellency of water and sticky substances, as well as protect against infections. In addition, brochosomes on egg masses may inhibit parasitism by egg parasitoids. Brochosomes may also protect against desiccation and UV light in some instances, as well as aid in thermoregulation.

In northern Florida and southern Georgia there are one or two generations per year. The first generation emerges from eggs laid by overwintered adults in forest edges, and migrates as adults to summer hosts and cropping systems in late May. The second generation migrates back to the forest in August and September, where they spend the winter in reproductive diapause and feed only during warm spells. There are two or three generations per year in California, with the highest oviposition periods in early spring and mid to late summer. During winter months in California adults actively feed on citrus, but do not reproduce. The close proximity of vineyards to these citrus orchards often increases the ease of movement between winter and spring hosts, and can increase the spread of *H. vitripennis* and Pierce's disease into vineyards.

Late in the summer in their native range most *H. vitripennis* eggs are parasitized by mymarid (Hymenoptera: Mymaridae) parasitoids. These

parasitoids include *Anagrus stethynioides* and several *Gonatocerus* species, most of which have been evaluated and/or used as biological control agents in California as part of a Pierce's disease management program. The most common parasitoids in the native range are *G. ashmeadi*, *G. triguttatus*, *G. morrilli*, and *G. fasciatus*. Eggs are susceptible to the different parasitoid species at different stages, but generally eggs older than 6 days are not susceptible. Once parasitized, eggs turn black as the parasitoid develops, and eventually the parasitoid chews a distinctive, circular exit hole and emerges. Parasitism often reaches close to 100% in the southeastern United States, but in California parasitism rates rarely exceed 19%. In addition to high mortality from parasitism, *H. vitripennis* populations suffer predation from several generalist predators, including spiders, anoles, dragonflies, and birds.

An entomopathogenic fungus, *Hirsutella homalodiscae*, often infects nymphs and adults, and is most common in mid to late summer. Infected *H. vitripennis* can be recognized by the fuzzy, white fungus growing on the exoskeleton. The generalist fungus *Beauveria bassiana* also infects *H. vitripennis*, but infection rates vary by strain and are generally low. Strains from natural populations in the southeastern United States and Texas are more efficient than commercially available strains. In addition, there are several chemical controls available that have strong effects on *H. vitripennis* nymphs and adults, but low effects on associated egg parasitoids.

The main focus in the control of *H. vitripennis* populations is on limiting the geographic spread of *H. vitripennis*. If *H. vitripennis* populations spread to the north from southern California, the damage to central California vineyards could be devastating. In addition, limiting the international spread is very important to the economic stability of vineyards in Europe and Australia and to the control of citrus variegated chlorosis in South America. The most important method to contain *H. vitripennis* is through the monitoring of horticultural shipments. This is a daunting task, due to the wide range of food and oviposition hosts used by

H. vitripennis. However, if this monitoring is not conducted there could be worldwide consequences.

- ▶ Bugs (Hemiptera)
- ▶ Leafhoppers (Hemiptera: Cicadellidae)
- ▶ Transmission of *Xylella fastidiosa* Bacteria by Xylem-Feeding Insects
- ▶ Management of Insect-Vectored Pathogens of Plants
- ▶ Transmission of Plant Diseases by Insects
- ▶ Citrus Pests and Their Management
- ▶ Small Fruit Pests and Their Management

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Glial Cell

A cell surrounding the axon, soma, and other portions of a neuron. Glial cells provide structural and nutritive support, and protect the nerve cell from outside chemical and ionic influences.

- ▶ Nervous System

Global Positioning System (GPS)

Georeferences based on transmission received from a network of satellites.

Globular Springtails

A family of springtails (Sminthuridae) in the order Collembola.

- ▶ Springtails

Glory Moths (Lepidoptera: Endromidae)

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Glory moths, family Endromidae, are a monobasic family of four species, with *Endromis* (one sp.) from Europe, *Dalailama* (one sp.) from Tibet, and *Mirina* (two sp.) from Central Asia. There are two subfamilies: Endrominae and Mirininae. The family is in the superfamily Bombycoidea (series Saturniiformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Adults medium size (29–74 mm wingspan), with head vertex rough-scaled; haustellum absent (or vestigial); labial palpi short, dropping (2 to 3-segmented); maxillary palpi vestigial; antennae bipectinate; body robust with very long hair-like setae. Wings broadly rounded with somewhat acute apex; hindwings rounded. Maculation dark orange brown, with various white spots and darker striae, or lighter and spotted (Fig. 26). Adult males are diurnal but females are nocturnal. Larvae are leaf feeders. Host plants recorded in Betulaceae, Caprifoliaceae, Salicaceae, Tiliaceae, and Ulmaceae.

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Glossa (pl. glossae)

The median lobes on the labium.

▶ Mouthparts of Hexapods

Glossinidae

A family of flies (order Diptera). They commonly are known as tsetse flies.

▶ Flies

Glossosomatidae

A family of caddisflies (order Trichoptera). They commonly are known as saddle-case makers.

▶ Caddisflies

Glossy

Said of a surface having the ability to reflect light. A measurable quality. The antonym is matte. Contrast with LUMINESCENT. Many authors fail to distinguish between these conditions, and erroneously write “shining” or “shiny.”



Glory Moths (Lepidoptera: Endromidae),
Figure 26 Example of glory moths (Endromidae),
Endromis versicolora (Linnaeus) from Germany.

Glover Scale, *Lepidosaphes gloveri* (Packard) (Hemiptera: Diaspididae)

Lepidosaphes gloveri is an important pest of trees and shrubs.

▶ Citrus Pests and their Management
 ▶ Scale Insects and Mealybugs

Glover, Townsend

Townend Glover was born in Rio de Janeiro on February 20, 1813. His parents were English, and it was in Leeds, England, that Townsend was sent on his mother’s death when he was only six weeks old. He became interested in natural history and enjoyed drawing. He was left an inheritance by his father, and this became available to him at the age of 21. He traveled to visit Munich, studied painting, and visited other European cities before returning to Leeds. His paintings, perhaps because he was shortsighted, were meticulous in detail. In 1836 he sailed for the USA to visit relatives, and traveled widely, especially in the South. In 1838 he moved to the state of New York, married in 1840, spent his time on natural history in the widest sense, and in 1846 bought his father-in-law’s country estate. In 1854 he joined the “Bureau of Agriculture” which had just been established in the U.S. Patent Office; his job was to collect information about insects. In 1856–1857 he was sent to British Guiana and Venezuela to collect new planting stock of sugarcane for Louisiana. Next, he worked on insect pests of citrus in Florida. He also studied plant diseases, soils, birds, mammals, reptiles, Indian mounds, and even human nature. In 1859 he resigned from the Patent Office and joined the faculty of the Maryland Agricultural College. In 1862 a new U.S. Department of Agriculture was established, independent of the Patent Office, and Glover was appointed United States Entomologist to it. He became a one-man Department of Agriculture, occupied with projects far



Glover, Townend, Figure 27 Townend Glover.

broader than entomology. He recommended fumigation of insect-infested shipments from abroad, a clairvoyant policy which has never been followed totally and adequately. He also was occupied with the biological collections of the (Fig. 27) Department of Agriculture. Ill and with failed vision, he resigned in 1878 and went to live in Baltimore with his adopted daughter. The copper plates that he assembled (273 of them) of his drawings of insects were never used to illustrate a major text on entomology but eventually, after his retirement, were bought by the U.S. Government Committee of Agriculture. He was succeeded as U.S. Entomologist by Charles Riley, another Englishman. He died in Baltimore on September 7, 1883, survived by his wife and adopted daughter.

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Glowworms

Although this term is sometimes applied to any insect that produces light, it is more correctly applied to *Arachnocampa* spp. (Diptera: Keroplatidae). These insects live in New Zealand and Australia, often in caves or other dark shelters. The best known are *A. luminosa* of New Zealand, and *A. richardsae*, *A. flava* and *A. tasmaniensis* of Australia. The larvae have organs that produce blue-green light. The light is used to attract prey, which are then ensnared in vertical silk threads coated with sticky mucous material that the larvae dangle from the ceiling of the cave or shelter. They are most frequent along streams, and suffer if exposed to low humidity.

Elsewhere, other light-producing flies include *Keroplates sesioides* in Sweden, *K. testaceus* in Germany, *K. nipponicus* in Japan, and *Orelia fultoni* in the Appalachian Mountains of the USA. Several relatives of these insects produce long sticky threads for prey capture but are not luminescent. Fireflies or lightningbugs (Coleoptera: Lampyridae) are sometimes called glowworms, but it is best not to apply this term to lampyrids.

Glowworms produce about 130 spherical eggs that measure about 0.75 mm in diameter. They hatch in 1–3 weeks depending on temperature. The larvae construct a hollow, tubular nest of silk and mucus, release sticky threads and begin light production. There are five instars, with the larva attaining a length of about 30–40 cm in about nine months. This is the only stage that feeds. The pupa is suspended by two silk strands, and in some species the pupal stage is luminescent. Pupation requires about two weeks. Upon emergence, the adults are quite different in appearance, the female being much larger and heavier. The adults live briefly, not more than one week, and the adult males are more active fliers. The adult females of some species luminescence intermittently. Mating occurs upon emergence and females mate only once. Females, being poor fliers, tend to lay their eggs near where they emerged.

Glowworms are not selective in their feeding behavior, taking anything that is captured on their sticky threads.

- ▶ [Butterflies](#)
- ▶ [Moths](#)

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Glycogen

A polysaccharide found in insects that is one of the two most common carbohydrate stored reserves (the other is trehalose) for insect flight. It occurs principally in the glycogen, fat body, and gut tissues. Glucose is released for metabolism from glycogen. Glucose usually is transported by the hemolymph as trehalose.

GLP

An acronym for “Good Laboratory Practice,” representing internationally recognized, sound standards of conduct and procedures. The objective of GLP is to ensure the generation of high quality and reliable test data. In entomology, GLP is usually reference to the context of pesticide assessment, but has broad application to laboratory-based science, and has a corresponding protocol for field research, “Good Field Practice” (GFP).

Glyphipterigidae

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

- ▶ [Sedge Moths](#)

Gmelin, Johann Friedrich

Johann Gmelin was born in Tübingen, Germany, in 1748, the son of a professor of medicine. In 1768, at the age of 20, he took a three-year journey through Holland, England, and Austria. In 1771, he became an untenured professor of medicine at Universität Tübingen, and three years later a tenured professor at Universität Göttingen. His (1787) treatise “Abhandlung über die Wurmtroknis,” which described effects of *Ips typographus*, was a major contribution for forest entomology. He contributed pages 1517–2224 to the 13th edition (1790) of Linné’s “Systema naturae...” He died in 1804 at the age of 56.

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Gnat Bugs

Members of the family Enicocephalidae (order Hemiptera).

- ▶ [Bugs](#)

Gnotobiotic Culture

Culture of insects when all the species (usually of microorganisms) are known.

Goat Moths

Some members of the family Cossidae (order Lepidoptera).

- ▶ [Carpenterworm Moths](#)
- ▶ [Butterflies and Moths](#)

Goblet Cells

Goblet-shaped cells found in the midgut of some insects. They house a proton ATPase pump that pumps hydrogen into the goblet cavity. Potassium is exchanged for hydrogen in the goblet cells, a process that creates transmembrane voltages, creates a high midgut pH, and aids in absorption of amino acids released in digestion.

Goblets

Small, round structures located on the spiracular plate of ticks.

Gobryidae

A family of flies (order Diptera).

► Flies

Goeldi, Emil (Emilio) August

Emil Goeldi was born in Ennetbühl im Obertoggenburg, Switzerland, on August 28, 1859. His schooling was in Switzerland until in 1882 he entered Universität Jena in Germany and studied zoology and anatomy. After he was awarded a doctoral degree, he was offered three job possibilities overseas, and of these he chose to become a professor in Rio de Janeiro. There, he worked in the Museu Nacional under the auspices of Brazil's emperor, Dom Pedro II. When a republic was proclaimed in 1889, he lost his job and went to live in the montane Colonia Alpina of Serra dos Órgãos. Later, the new Brazilian government offered him the job of founding a new museum at the mouth of the Amazon, so in 1894 he traveled to Belém, and in a few years had built a large institution, the Museu Paraense. He began two scientific journals, the Boletim and the Memórias of that museum which became known, even in his lifetime, as Museu Goeldi. His first name is usually written in Brazil as Emilio, in keeping with Portuguese

spelling. He collected extensively and published numerous papers on various animal groups. Some of those works were on insects, including Coleoptera and Diptera (a major work on the mosquitoes of the state of Pará). In 1907 he returned to Switzerland to teach at Universität Bern. He published (1913) a book on medical zoology, "Die sanitärisch-pathologische Bedeutung der Insekten und Verwandten Gliedertiere, namentlich als Krankheits-Erreger und Krankheits-Übertrager" drawing upon his experiences in Brazil. He died in Zurich on July 5, 1917.

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Gold Moths (Lepidoptera: Axiidae)

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Gold moths, family Axiidae, are a very small family of only six Palearctic species in the Mediterranean region, mostly in the genus *Axia*. The family is in the superfamily Drepanoidea, in the section Coscina, subsection Bombycina, of the division Ditrysia. Adults medium size (23–30 mm wingspan), with head scaling normal; labial palpi slightly porrect but very short; maxillary palpi vestigial; antennae bipectinate. Wings elongated and triangular, with relatively acute forewing apex; hindwings triangular and rounded (Fig. 28). Maculation mostly shades of brown to pink, but with at least one bright iridescent mark (often golden color); hindwings unicolorous. Adults nocturnal. Larvae are leaf feeders. Host plants all are in Euphorbiaceae.



Gold Moths (Lepidoptera: Axiidae), Figure 28
Example of gold moths (Axiidae), *Axia theresiae schelhornae* Amsel from Iran.

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Gomphidae

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

► [Dragonflies and Damselflies](#)

Gonad

The basic component of the reproductive system, possessed by both males (testes) and females (ovaries).

Gondwanaland Moths (Lepidoptera: Palaephatidae)

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Gondwanaland moths, family Palaephatidae, total only 31 known species, with 28 from Chile and Argentina and three from Australia. The family forms a monobasic superfamily, Palaephatoidea, in the section Nepticulina, of the division Monotrysia, infraorder Heteroneura. Adults small to medium (8–36 mm wingspan), with head roughened; haustellum is average length and naked (unscaled); labial palpi short and porrect, and 3-segmented; maxillary palpi 5-segmented (rarely 4-segmented and short), long and folded; antennae rather short. Wing venation is heteroneurous, with frenulate wing coupling, and usually with somewhat falcate forewing tips. Maculation is variable, usually with various spots; without large fringes (Fig. 29). Adults are thought to be diurnally active. Biologies are little known and the single known species has larvae that tie twigs together on its host plants (Verbenaceae and Proteaceae).



Gondwanaland Moths (Lepidoptera: Palaephatidae), Figure 29 Example of Gondwanaland moths (Palaephatidae), *Azaleodes micronipha* Turner from Australia.

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Gonopod

An appendage of the genital segment modified for copulation, insemination or oviposition.

Gonopore

The external opening of the ejaculatory duct (in males) or oviduct (in females).

Gorgas, William Crawford

William Gorgas was born on October 3, 1854, near Mobile, Alabama. The son of General Josiah Gorgas, William graduated from the University of the South in 1875. General Josiah Gorgas was an officer in the Confederacy during the American Civil War, so it is perhaps not surprising that William was denied entrance to the premier American military college, the United States Military Academy at West Point, New York. William was determined to have a military career, a prestigious career in earlier days, so he entered the military by way of a medical degree. In 1880 he entered the U.S. Army Medical Corps as an assistant surgeon.

William Gorgas' life was fairly average for about two decades after entering the military. However, he was stricken by yellow fever early in his career, and thereafter he was immune, so was

frequently drafted for service wherever yellow fever was a problem. Yellow fever was an enigma at that time, and its appearance, impact, and the inability to control the disease were quite puzzling. Gorgas was dispatched to Cuba during the Spanish-American War, in 1898, when yellow fever was seriously affecting American troops. The prevailing approach for the management of the disease at that time was fire, and the village and hospital to which Gorgas was assigned were torched in September of that year.

In 1898, Gorgas was made chief surgeon of Havana, Cuba, and he followed the generally accepted methods of yellow fever management, relying primarily on sanitation and isolation. However, it was not until the Cuban doctor Carlos Finlay, the English scientist Ronald Ross, and the U.S. Army doctor Major Walter Reed identified the *Aedes aegypti* mosquito as the vector of yellow fever that truly effective practices of management could be implemented. Prior to this time, yellow fever was thought to be transmitted from person to person via personal belongings or merchandise on which the organism was carried, and attempts to prove that mosquitoes could transmit the disease had been futile. Indeed, the earliest attempts to clean up Havana were unsuccessful because although the sanitation efforts cleaned up the water and debris, the relevant vector was favored by clean water and so prospered. However, once all mosquito breeding sites in the city of Havana were eliminated by either preventing mosquitoes from accessing water, or by oiling the surface of water where mosquitoes were likely to breed, yellow fever was effectively suppressed. Thus, Gorgas came to believe that environmental sanitation, and particularly mosquito management, could be used to reduce or eliminate yellow fever.

At the turn of the century, the development of the Panama Canal was in progress. The French were stymied in their efforts to complete the project due to yellow fever and malaria, losing 20,000 lives in an eight year effort to construct the canal. Ironically, the U.S. government seemed

similarly inclined to ignore taking adequate measures to prevent workers from contracting the disease. The Canal Commission considered health measures to be extravagant expenditures, but as disease extracted a lethal toll on workers, Gorgas' ideas on sanitation received a better reception. He promoted the draining of swamps in Panama, thereby mitigating malaria and yellow fever and greatly prolonging the life of workers involved in the construction project. Even after conditions improved, Gorgas' enemies were quite effective in discrediting him and his mosquito control policies, and it took the intervention of President Theodore Roosevelt to assure that his procedures would be implemented. Even then, the U.S. military attacked Gorgas' sanitary service. Gorgas prevailed, however, and made the Panamanian cities of Panama and Colon as safe as any city in the United States.

In 1914, based on his successes in Panama, Gorgas was appointed Surgeon General in the U.S. Army. He retired in 1918, but was commissioned to investigate the yellow fever situation in western Africa. Unfortunately, he experienced a stroke in 1920, and died a month later in London on July 4, 1920.

William Gorgas is remembered as the person whose sanitation skills allowed construction of the Panama Canal, a monumental achievement. His achievements at managing yellow fever in Havana are overshadowed by the Panamanian successes, but even the Cuban successes would accord him considerable recognition.

- ▶ [History and Insects](#)
- ▶ [Yellow Fever](#)
- ▶ [Malaria](#)
- ▶ [Reed, Walter](#)

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Gossamer-Winged Butterflies (Lepidoptera: Lycaenidae)

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Gossamer-winged butterflies, family Lycaenidae (including blues, coppers, elfins, hairstreaks, and harvesters), total about 5,955 species worldwide; the actual fauna probably exceeds 7,000 species. About 1,125 species are Neotropical. The family is in the superfamily Papilionoidea (series Papilioniformes), in the section Cossina, subsection Bombycina, of the division Ditrysia. Most of the relictual groups are Southeast Asian and African, such as the subfamilies Lipteninae, Poritiinae, Liphyrinae, Miletinae, and Curetinae. The family has eight subfamilies: those just noted, plus Lycaeninae, Theclinae, and Polyommattinae. North temperate species are only found in the latter three subfamilies. Some specialists include Riodinidae as another lycaenid subfamily, and also reduce the subfamily number to five (including the Riodininae), thus the classification is still in flux. Adults small to medium size (6 to 92 mm wingspan) (most average 20 to 39 mm), with body usually slender (rarely robust). Wings mostly rounded, but some with acute forewing apex; hindwings sometimes with tails (usually very narrow tails) (Fig. 30). Maculation varied but often with blues, greens or other bright colors, and with iridescence or lustrous shine, and often without many dorsal spots (more spotting usually on ventral sides of both wings); hindwings often with color spots near tails at the tornal corner of the wing margin (so-called “false heads”); and fringes short but often white or lustrous. Adults diurnal, but a few of the relict genera possibly crepuscular or only in dark forests. Larvae mostly somewhat slug-like, with tubercles and short setae; head usually retractable into thorax. Larvae feed as leaf feeders (some on other plant parts), but many are myrmecophilous and some even are carnivorous on ant larvae or hemipterans (especially Liphyrinae and Miletinae).



Gossamer-Winged Butterflies (Lepidoptera: Lycaenidae), Figure 30 Example of gossamer-winged butterflies (Lycaenidae), *Hypaurotis crysalus* (W. H. Edwards) from New Mexico, USA.

Some of the relict groups feed on lichens (Lipteni-nae). Host plants are in a wide variety of plant families, particularly Fabaceae and Leguminosae. A few economic species are known.

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Gracillariidae

A family of moths (order Lepidoptera). They commonly are known as leafminer moths or leaf blotch miners.

- ▶ Leafminer Moths
- ▶ Butterflies and Moths

Gradual Metamorphosis

This is a type of incomplete metamorphosis (hemimetabolous development) found in some aquatic insects (Odonata, Ephemeroptera, Plecoptera). Unlike insects displaying the typical form of incomplete metamorphosis, in which the immature and adult stages are substantially the same in body form (differing principally in the presence of fully formed wings among the adults), immature and adult stages of these aquatic insects differ slightly to significantly in appearance as compared to their adults. However, they lack a pupal stage, which is characteristic of insects with complete metamorphosis (holometabolous development). Because these insects depart from the typical pattern of hemimetabolous development, they sometimes are said to have gradual metamorphosis or paurometabolous development. Consistent with this differentiation, the immature are sometimes called naiads rather than nymphs (contrast with incomplete metamorphosis, complete metamorphosis).

- ▶ Metamorphosis

Graham, Marcus William Robert De Vere

Marcus Graham was born in the county of Durham, England, on March 25, 1915. As a boy, he became intrigued with natural history. At the start of World War II, he enlisted in the British army, and served in India from 1942 to the end of

1945. But he had begun to publish entomological papers in 1941. At the end of 1945, he entered Trinity College, Dublin, and graduated in 1950 with a B.A. degree and a B.Sc. degree. In Dublin, he studied the taxonomy of Braconidae, then turned to Chalcidoidea. He was soon appointed to the post of curator of the insect collections of the Hope Department of Entomology, Oxford University. He married in 1953. In 1955, he was awarded the degree of D.Phil. from Oxford University. He taught, took part in administration, and conducted taxonomic research on Hymenoptera until his retirement in 1981. His research was meticulous, he solved many puzzles resulting from inadequate descriptions by early taxonomists of Hymenoptera, and became the foremost authority on European Chalcidoidea. He produced major contributions on the European Pteromalidae, Tetrastichinae (Eulophidae), Encyrtidae, and Myrmaridae. He described 60 genera and 475 species of Hymenoptera. Apart from insect taxonomy and botany, he was interested in Romance languages and medieval literature, painting, and naval history. After retirement, he continued to work (his total production was some 200 papers) and was working on a revision of the genus *Torymus* (Torymidae) when he died, on March 27, 1995. He was survived by his wife, Nora, and son.

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Grain Beetles

Several beetles are important pests of stored grain.

► [Stored Grain and Flour Insects](#)

Grain Borers

Several beetles in the family Bostrichidae are important grain pests.

► [Stored Grain and Flour Insects](#)

Grain Weevils

Several weevils are serious pests of stored grain.

► [Stored Grain and Flour Insects](#)

Gramineous Lepidopteran Stem Borders in Africa

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Cereals, especially maize and sorghum, are the most important field crops grown in Africa by commercial and small-scale farmers. Sugar cane is also an important cash crop in many countries on the continent. Although maize and sorghum are grown primarily for human consumption, surpluses are used as fodder for livestock. Among the insect pests found attacking these crops in Africa, lepidopteran stem borers are by far the most injurious.

Given their great economic importance, an enormous amount of literature has accumulated during the past century. The aim of the following sections is to briefly summarize the current state of knowledge on these stem borer pests of cereals. Special attention is given to *Busseola fusca* and *Chilo partellus*, which are the principal borer pests of maize and grain sorghum in Africa, and to *Chilo sacchariphagus*, a serious pest of sugar cane on the Indian Ocean islands, which has recently invaded Mozambique.

Distribution of Major Stem Borers of Maize, Sorghum, Rice and Pearl Millet

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Lepidopteran cereal stem borers in Africa typically occur as complexes of species, with notable regional variation in their distributions. The noctuids *Busseola fusca* Fuller and *Sesamia calamistis* Hampson, and the pyralid *Eldana saccharina* (Walker), are present throughout most of sub-Saharan Africa, but there are important regional differences in the ecozones they inhabit, and their pest status. In eastern and southern Africa, *B. fusca* is a major pest of maize and sorghum at medium and high elevations (greater than 1,000 m), while in West Africa, it is considered to be important from sea level to 2,000 m. *Sesamia calamistis* generally is not a major pest in eastern and southern Africa, whereas in West Africa, this species is one of the most damaging to maize, sorghum and rice. *Eldana saccharina* is primarily a pest of sugar cane in South Africa, while in West Africa, *E. saccharina* is a major pest of maize, and attacks sugar cane to a lesser degree. In some areas of East Africa, *E. saccharina* attacks maize, but tends to arrive late in the season when the crop is less susceptible to yield loss.

Other important stem borers have more limited distributions. *Coniesta ignefusalis* (Hampson) (Crambidae) is the dominant stem borer of pearl millet in the Sahelian region of West Africa, but only a minor pest in other crops and other regions. It also has been recorded from Sudan, Ethiopia and Angola, and thus probably has a fairly wide distribution. *Chilo orichalcociliellus* (Strand) occurs in eastern Africa, mainly in lowland coastal zones, where it once was considered to be a major pest of maize and sorghum. However, recent studies suggest that densities of *C. orichalcociliellus* have decreased due to competition with *Chilo partellus*, an invasive Asian borer. *Chilo partellus* is thought to have arrived in eastern Africa in the early part of the twentieth

century, and has since spread to all countries in the eastern and southern parts of the continent. It seems likely that its distribution will continue to expand westward. *C. partellus* is generally the most damaging stem borer of maize and sorghum at elevations below about 1,000 m in eastern and southern Africa. *Sesamia cretica* Lederer, which occurs in Somalia, Sudan, Egypt, and Ethiopia, and *S. nonagrioides botanephaga* Lefebvre, which is found in both East and West Africa, are both important locally. *Chilo aleniellus* (Strand) has been reported as an important pest of maize in Ivory Coast. In addition to stem borers, there are several lepidopteran cob borers in Africa, one of which, *Mussidia nigrivenella* Ragonot (Pyralidae), is an important pest in West Africa. This species is discussed in a later section. The important stem borers of maize, sorghum and millet are listed below (Table 5), along with an approximation of their relative importance in different regions.

Information on rice stem borers is primarily from West Africa, and the Indian Ocean Islands, as these are the areas where rice is an important food crop. *Chilo zacconius* Bleszynski is considered to be the most important stem borer of rice throughout West Africa. *Maliarpha separatella* and *S. calamistis* also are of economic importance in the region. *M. separatella* is the only rice borer that has a widespread distribution in sub-Saharan Africa, and also occurs in the Comoro Islands and Madagascar. Other stem borers in rice in West Africa include *Scirpophaga* spp., *Chilo diffusilineus* (de Joannis), and *S. nonagrioides botanephaga* Lefebvre. Additionally, *Chilo aleniellus* (Strand) is mentioned as a rice stem borer in Ivory Coast.

Distribution and Pest Status of African Sugarcane Stem Borers

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Many subsistence farmers throughout tropical and subtropical Africa grow sugar cane for chewing

Gramineous Lepidopteran Stem Borders in Africa, Table 5 Important stem borers of maize, sorghum and millet in sub-Saharan Africa

Family/species	Area of Africa			
	South	East	West	Central
Noctuidae				
<i>Busseola fusca</i>	+++	+++	++	+++
<i>Sesamia calamistis</i>	+	+	+++	++
<i>Sesamia cretica</i>		+++ ^a		
<i>Sesamia nonagrioides botanephaga</i>			++ ^b	
Crambidae				
<i>Chilo partellus</i>	+++	+++		
<i>Chilo orichalcociliellus</i>		++ ^c		
<i>Chilo aleniellus</i>			+ ^d	
<i>Coniesta ignefusalis</i>			+++ (millet only)	
Pyralidae				
<i>Eldana saccharina</i>	(only sugar cane)	+	+++	++

^aOnly in Northeast Africa (Sudan, Somalia, Egypt)

^bOnly reported as important in Ghana

^cOnly in coastal East Africa

^dOnly in Ghana, Ivory Coast

purposes. Commercial sugar cane production, however, has an interesting history in Africa. Many countries had very strong industries in the early 1900s, which collapsed during various civil wars and for other reasons through the years. Some of these countries now are rehabilitating their industries. A few still have very strong industries, which have withstood the vagaries of time. This section deals only with the commercial sugar industries known to occur in Africa, as it is only from reports and papers emanating from these that pest records are known. Also, for the purposes of this section, Africa is divided into southern, eastern, northern and western regions. The countries known to have, or have had, viable sugar cane industries in southern Africa include South Africa, Swaziland, Zimbabwe, Malawi, Mozambique and Zambia. In east Africa, they are Tanzania, Kenya, Uganda and Ethiopia. In north Africa, these are limited to Egypt, the Sudan and possibly Libya. West African countries producing, or

known to have produced, sugar on a commercial scale include Sierra Leone, Ivory Coast, Burkino Faso, Ghana, Nigeria, Cameroon, Gabon, Mali, Senegal, Guinea Bissau and, more recently, Angola.

In Africa, only lepidopteran larvae have been recorded as borers of sugar cane. These can attack the youngest shoots, causing dead hearts, through to the most mature sugar cane stalks. In severe infestations, the rootstock of ratooning sugar cane can harbor developing larvae, which can severely affect the regrowth of the crop. In addition, larvae of some species of Lepidoptera develop in the whole stalk when the cane is mature, others only in the top third, and still others in the bottom third. In different parts of Africa, the same species may develop in the bottom third of mature sugar cane plants, while in other parts, they may develop in the top third of the stalk.

Oviposition by different species of Lepidoptera attacking sugar cane also may vary. Some

species prefer to oviposit on the green leaves of sugar cane, either on the abaxial and/or adaxial surfaces of leaf blades, and in sugar cane from one month old to maturity, which may be up to 24 or 30 months old. Other species oviposit in cryptic positions, in older sugar cane behind dead leaf sheaths, in folded dead leaf blades, or even in decaying dead leaf material around the bases of mature sugar cane stalks.

Until 1992, fourteen species of Lepidoptera had been recorded as attacking sugar cane in Africa. The majority of these are indigenous to the African continent. In 1999, a fifteenth species, *Chilo sacchariphagus* (Bojer) (Pyralidae), was confirmed as attacking sugar cane in Mozambique. This is the first record of an exotic lepidopteran establishing on sugar cane in economic proportions in Africa. Prior to this, the only other exotic reported to occasionally attack African sugar cane has been *Chilo partellus* (Swinhoe) (Crambidae).

Most of the boring lepidopteran pests of sugar cane belong to the families Crambidae, Pyralidae, and Noctuidae, and a ranking, in 1994, of these species (using the number of citations in Review of Applied Entomology, 1972 to 1992 to each on sugar cane) has revealed that only four are regarded as major pests in Africa. These are *Eldana saccharina* Walker (Pyralidae), *Chilo agamemnon* Bleszynski (Crambidae), *Sesamia cretica* Lederer and *S. calamistis* Hampson (both Noctuidae) (Table 6). More recently, *Busseola fusca* (Fuller) has been recorded occasionally from sugar cane

in West Africa. The following table outlines the distribution of the stem borers regarded as major pests in African sugar cane, and their severity in south, east, north and west Africa.

Eldana saccharina is by far the most injurious stalk boring pest in Africa. It is also one of the few attacking mature (or older) sugar cane stalks. In southern Africa it has been the subject of much research in plant resistance, biological control, insecticide and cultural means in attempts to control it. In southern and coastal eastern Africa, it attacks the lower portion of sugar cane stalks. However, in the Kenyan and Ugandan industries around Lakes Victoria and Albert, respectively, and in West Africa, it attacks the upper third of mature stalks. In many of the more tropical countries, sugar cane is cut at too early a stage for *E. saccharina* to become a pest, although if the cane is not harvested at this early age for some reason, then this borer can affect it seriously.

Chilo agamemnon has received much attention in Egypt, where it is classed as an internode borer, thus attacking the more mature cane stalks. However, it also attacks young plants, causing dead hearts. Researchers in Egypt are working on plant resistance, as well as inoculative biological control using egg parasitoids.

The *Sesamia* species are generally pests of young cane, causing dead hearts. By the time the sugar cane is mature though, these borers have been brought under control by parasitoids, and thus do not become major pests.

Gramineous Lepidopteran Stem Borders in Africa, Table 6 The distribution of stem borers regarded as the major pests of sugar cane in Africa, and a rating of their pest status (+++ = Major Pest; ++ = Occasionally a Pest; + = Present in Low Numbers)

Species	Area of Africa			
	South	East	North	West
<i>Eldana saccharina</i>	+++ Generally ^a +	++ Generally ^b +	+	+
<i>Sesamia cretica</i>			++	
<i>Chilo agamemnon</i>		+	++	
<i>Sesamia calamistis</i>	+	+		+

^aOnly in South Africa and Zimbabwe

^bOnly in Western Uganda

Pest Status of *Mussidia nigrivenella* Ragonot, a Cob-borer of Maize in Western Africa

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and

FRITZ SCHULTHESS

IITA, Cotonou, Republic of Benin,

In West Africa, five borer species are commonly found feeding in maize cobs, but *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae) is by far the most important across all zones. Grain yield losses are relatively low and range from 2 to 25%. Percentage of grain infected by the toxic fungus *Aspergillus flavus* as well as mean aflatoxin content of samples, however, increases exponentially with grain damage. Cob damage by *M. nigrivenella* also promotes the infestation of storage beetles such as *Sitophilus zeamais* Motschulsky, *Carpophilus* spp. and *Cathartus quadricollis* Guérin. Furthermore, damaged cobs cannot be sold as green maize, an important source of cash in the vicinity of centers of population. Thus, in addition to the direct damage, *M. nigrivenella* induces indirect qualitative and quantitative losses in the field and store.

Mussidia nigrivenella is highly polyphagous, and is found on 20 plant species from 11 different plant families, among them cotton, *Phaseolus* bean and cover-crops such as the velvet and Jack-bean. In West Africa, no parasitoids were ever obtained from annual crops, and most alternate host plants. The solitary chalcidid pupal parasitoid, *Antrocephalus crassipes* Masi, was the predominant species with highest and stable parasitism on *Gardenia* spp.

Mussidia nigrivenella has never been described from annual crops in eastern Africa, but according to some anecdotal reports is found on wild host plants. This opens the opportunity of the novel association biological control or expanding the geographic range of a natural enemy species.

Displacement of Native Stem Borers by *Chilo partellus*

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The invasive stem borer, *Chilo partellus*, has proved to be a highly competitive colonizer in many of the areas it has invaded in eastern and southern Africa, often becoming the most injurious stem borer, and displacing native species. In coastal Kenya, there is evidence that *C. partellus* has partially displaced the indigenous borer, *Chilo orichalcociliellus*. Whether the displacement of *C. orichalcociliellus* will proceed toward complete extirpation in the southern coastal area of Kenya seems unlikely. Recent sampling has shown that *C. orichalcociliellus* continues to persist, and laboratory studies have found that *C. orichalcociliellus* was able to complete development in two native grasses in which *C. partellus* could not develop. This difference in niche breadths of the two species may account for the continued occurrence of the native species. Additionally, a parasitoid of *C. partellus* from Asia, *Cotesia flavipes* (Cameron), has been introduced and established in several countries in Africa. Evidence from coastal Kenya suggests that the introduction of *C. flavipes* has resulted in a marked population decrease of *C. partellus*, but that populations of two native borers, *C. orichalcociliellus* and *Sesamia calamistis*, have slightly increased.

In addition to the work in coastal Kenya, there is evidence of displacement of native stem borers in two other areas in Africa. In the Eastern Province of Kenya, work conducted in the 1980s found that *C. partellus* was present, but less abundant than *Busseola fusca*. However, in the same area in the late 1990s, *B. fusca* was rare and *C. partellus* was dominant. Similarly, in the Highveld region of South Africa, *C. partellus* has partially displaced *B. fusca*.

Several factors may be responsible for the competitive superiority of *C. partellus* over the native stem borers. Various studies have shown that *C. partellus* completes a generation in less time

than *C. orichalcociliellus*. As fecundities of both species are similar, the shorter generation time is likely to lead to higher population levels, which may give the alien species a numerical advantage. A more rapid diapause termination compared to both *C. orichalcociliellus* and *B. fusca* has also been shown, which may allow *C. partellus* females to colonize host plants before the two native species, which would be particularly important if the native species avoid previously infested plants.

Damage and Pest Status

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Feeding and tunneling by stem borers can result in serious damage and crop losses. Damage is caused by the larvae, which at first feed on the young leaf funnels at the growing point and then later by tunneling into the stems. Apart from leaf damage, growing points may be killed, leading to stunting and deadhearts or to early senescence of plants. Stem tunneling may cause lodging, but also secondary and insidious effects, such as interference with translocation of metabolites and nutrients, resulting in malformation and loss of grain. There can also be a sharp increase in the incidence of stalk rot. Feeding in ears has been associated with fungal infection and elevated levels of mycotoxins.

Busseola Fusca

In South Africa, crop loss assessments in cereal crops from *B. fusca* attack ranged from 10 to 100%. Although much of this was due to leaf damage in maize, the most severe loss was from stem-boring activity. In Lesotho, seasonal variation in maize yields due to *B. fusca* ranged from 0.4 to 37%.

In Tanzania, 40–100% of the sorghum crop can become infested with *B. fusca*. Together with

Kenya, loss of about 12% maize yield for every 10% of plants infested with *B. fusca* has been documented. In Ethiopia, movement of *B. fusca* larvae into the base of the sorghum panicle resulted in undersized panicles and a 15% yield reduction. In Burundi, using insecticides and exclusion cages, 30–50% of the maize harvest was shown to be lost to *B. fusca*.

In the Northern Guinea savanna of Nigeria, where *B. fusca* is the dominant stem borer, 49% loss of sorghum was reported. Comparative yields on 22 farmers' sorghum fields in Nigeria, sprayed and unsprayed with insecticide, showed a 21% mean loss in yield due to this borer. Losses to *B. fusca* in sorghum crops in Nigeria are very much dependent on the time of initial infestation. Thus, sorghum infested prior to the booting stage suffered the greatest yield losses. The proportion of internodes bored in the lower part of the stalks had a more consistent negative correlation with harvested grain than did the proportion of stalks tunneled. A recent study in Cameroon showed that stem borers, primarily *B. fusca*, were responsible for a 9 g loss in sorghum yield per plant per borer. There was also an 11% crop loss through deadheart.

Chilo Spp

The estimated yield losses in maize and sorghum in South Africa due to *C. partellus* exceeded 50%. A negative correlation between the level of *C. partellus* infestation and yield has been demonstrated. Comparative trials in separate and mixed stem borer populations, using artificial infestation techniques, indicated that *C. partellus* was more injurious to sorghum than *B. fusca*. More damage also was caused by *C. partellus* to long-season sorghum cultivars, mainly due to their longer exposure to stem borer attack while in the susceptible pre-flowering stage.

In Mozambique, the third generation of *C. partellus*, the most important stem borer occurring in the country, was reported to infest 87% of cobs of late planted maize and to cause 70% loss of grain. Infestations of up to 100% of the crop, with

considerable yield losses, were recorded in the Maputo and Gaza Provinces and in the Limpopo Valley, in southern Mozambique.

In Zimbabwe, *C. partellus* caused sorghum yields to drop by 50–60%, while in maize up to 70% damage was reported from the fields of resource-poor farmers. However, in the commercial farming areas, where insecticides are routinely applied, maize damage was less than 30%.

In Kenya, 18% loss of maize was attributed to *C. partellus* and *C. orichalcociliellus*, while 88% loss of sorghum crop to *C. partellus* was reported. Heavy stalk damage to maize, and up to 80% of the sorghum harvest, was lost to the latter borer on 20-day-old crops. *Chilo partellus* infestations caused insignificant crop loss when 60-day-old plants became infested. Similar observations were reported from Uganda.

Sesamia spp

In Ghana, a positive relationship between the number of *Sesamia* sp. larvae and the extent of damage to maize stalks, and a negative relationship between damage to maize stems and maize yields were demonstrated. The calculated losses caused by *Sesamia* sp. to maize in the rain forest, coastal, derived and Guinea ecological zones were 27, 15, 18 and 14%, respectively. Chemical control of stem borers in sorghum in the Southern Guinea savanna of Nigeria, where *S. calamistis* predominates, increased yields by 16–19%.

Eldana Saccharina

In West Africa, natural infestations by *E. saccharina* decreased maize yields by 16, 15 and 28%, respectively, in the dry season and the first and second rainy seasons. Infested maize plots had significantly lower grain weight, indicating that *E. saccharina* damage to the stems affected grain filling.

In Burundi, insecticides and exclusion cage trials indicated diminished maize yields of 12–15%

by *E. saccharina*. Curiously, in southern Africa, *E. saccharina* is not known as a pest of either maize or sorghum, but is a serious pest of sugar cane.

Stem Borer–Fungal Interactions

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Both fungi and insects possess chitin-based exteriors. Also, both are heterotrophic, i.e., acquire nutrients by feeding on other organisms. It is at this nutritional interface where fungi and insects often intersect, giving rise to many different types of insect–fungus relationships, which can be neutral, mutually beneficial, exploitative, or antagonistic. Some relationships are merely opportunistic, while others are co-evolved and have become obligatory. Direct mycophagy, or fungivory, occurs when insects preferentially select fungi as a food source. Alternatively, many fungi require insects as a food source and become pathogens. Insects that feed on plants often encounter fungi that either live within the plant as endophytes or in association with plant tissues, resulting in an indirect effect on insect fitness. Often, insects are the vehicle by which fungi gain ingress into a plant or disperse throughout a habitat.

Fusarium verticillioides is an endophyte of wild and cultivated grasses. It produces mycotoxins such as fumonisin, which promotes esophageal cancer in humans and leucoencephalomalacia in horses. The fungus may attack at all growth stages of the plant and move from seed to stem into the cob. Similarly, variants of *F. moniliforme* have been found to produce the compound beauvericin, which was originally isolated from the entomopathogenic fungus *Beauveria bassiana*. In a survey in southern Benin, *F. verticillioides* was the most common endophytic fungus inhabiting maize stalks. Incidence was higher in plants damaged by insect pests, and was cultured from stems of 71–80% of plants damaged by stem borers. It was found that ovipositing adult

lepidopteran stem and cob borers such as *E. saccharina*, *S. calamistis* and *Mussidia nigrivenella* not only preferred infected plants, but that offspring had higher survival and fecundity. This relationship is completely mutualistic because the insects feeding on infected plants may also vector the fungus from soil to plant and from plant to plant. Furthermore, lepidopteran pests feeding in the ear produce exit holes before pupating, which then are used as entry holes by storage beetles, which may be grain or fungal feeders. They, in turn, vector the mycotoxic fungus *Aspergillus flavus*, which has been shown to be suppressive to *S. calamistis*, *E. saccharina* and *C. partellus*; *M. nigrivenella*, on the other hand, was not sensitive to aflatoxin or *A. flavus* in the diet, which makes it a perfect vector; thus, aflatoxin content in grain increase exponentially with grain damage caused by *M. nigrivenella* or resulting increased beetle infestations. Control programs at the International Institute of Tropical Agriculture in Nigeria aim at both the fungi and the insects, and include biological control (e.g., *Trichoderma* sp.) and seed treatment against *F. verticillioides*, cultural control (sorting of infected ears), host plant resistance, competitive niche displacement (the use of atoxigenic, competitive races) against *A. flavus*, and host plant resistance, biological control and habitat management against stem and ear borers.

Larval Diapause

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Many cereal stem borers undergo a resting period toward the end of the cropping season in response to cold and/or dry conditions. The resting period is spent as mature larvae within dry crop residues and stubble in the fields.

In the elevated regions of southern Africa, *B. fusca* and *C. partellus* pass winter (May to September), which is the cold dry season, in diapause in the lower portions of the dry stalks of their host plants, where they are well protected

from adverse climatic conditions. In West Africa, *B. fusca* also enters a prolonged diapause during the dry season, which takes up to six months to complete. With the start of the rains, the larvae pupate within the stems and 10–12 days later emerge as adult moths.

While *B. fusca* diapauses throughout its distribution range in Africa, the larvae of *C. partellus* do not undergo diapause in the warmer low-lying South African provinces of Kwazulu-Natal and Mpumalanga, Swaziland and southern Mozambique. Likewise, while *C. partellus* is known to diapause in the dry season in India and on several islands off the coast of Africa, non-diapausing larval populations occur along the coast of Kenya. In periods between cropping seasons, some *C. partellus* larvae enter diapause within maize stubble, whereas other larvae remain actively feeding on alternative host plants, such as Napier grass growing in the proximity of the cultivated areas.

Thus, in coastal regions where there is an abundance of host plants and where the climate remains favorable, *C. partellus* normally exhibits continuous development. Whereas inland, on the upland plateau, which experiences a long dry or cold season, larvae enter a diapause. Similarly, *C. ignefusalis* in West Africa exhibits a facultative diapause within dry millet stems.

In the interior of Kenya, the larvae of *C. partellus* and *C. orichalcociliellus*, together with *S. calamistis*, enter diapause for several months in the dry season. However, *S. calamistis* was reported not to enter diapause in Uganda nor in Nigeria.

An increase in carbohydrates and a decrease in protein and water content of the host plant are the principal factors inducing diapause in *B. fusca*. Drying out of the host plant, and a general deterioration in the nutritive environment, were found to induce diapause in *C. partellus* larvae, even when climatic conditions remained favorable for development. Diapause also could be “artificially” induced in non-diapausing larvae by introducing them into aging maize stems.

During diapause, larvae of *B. fusca* and *C. partellus* both showed a progressive decrease in weight and an increase of up to seven additional molts. The

longer the larvae remained in diapause, the smaller the resultant moths became. Such female moths showed impaired ovarian development with fewer oocytes, and also laid fewer eggs. After eight months in diapause, the emerging moths weighed about half as much and produced half as many eggs as those moths emerging from non-diapausing larvae.

Diapausing larvae of *B. fusca* collected in South Africa in the field during winter emerged as moths in mid-October, regardless of the date of collection and the length of time they were kept at 21°C and 60% RH in the laboratory. However, larvae of *C. partellus* collected during April to June from the field emerged in November, while those collected in July emerged as moths in October. Those collected in August emerged in September. Regardless of collection date, *C. partellus* started to emerge from diapause earlier and the emergence period of the moths was up to twice as long as that found for *B. fusca*. In the field, *C. partellus* moths emerged from diapause in the second half of August and continued doing so until the first week of November, emergence thus lasting a total of 12 weeks. In contrast, *B. fusca* only pupated during October to November.

B. fusca hence had an obligatory larval diapause, whereas *C. partellus* had a facultative diapause. These differences in the pattern of moth emergence following diapause explain the distinct annual generations occurring in *B. fusca* and the continuous overlapping generations of *C. partellus* observed in South Africa.

Conditions of continuous moisture during the long rainy season in Kenya played a significant role in the termination of diapause in *B. fusca*. However, rainfall alone did not appear to be the main cause. Contact with free water was of more significance in breaking diapause than water uptake. In Ethiopia, as well as in the Ivory Coast, provision of water played an important role in promoting pupation during post-diapause dormancy of *B. fusca*. Any delay in wetting of larvae after diapause, and access to water early in diapause, had an adverse effect on the larvae. The key factor enabling diapausing *B. fusca* larvae to survive adverse conditions appears to be efficient water conservation.

A combination of temperature and photoperiod also played an important role in termination of diapause of *B. fusca* in South Africa. Water was important in stimulating morphogenesis following larval diapause. Long days accelerated termination of diapause in *C. partellus*, but under a 16 h daylight regime, termination of diapause was faster than under constant illumination. In contrast, temperature, relative humidity and day length did not affect diapause of *C. partellus* and *C. orichalcociliellus* larvae in Kenya.

It appears that *C. partellus* larvae collected in South Africa at 25°38' latitude are more affected by day length than Kenyan borer populations located near the equator. It has been suggested that the right combination of day length and temperature could be used for breaking diapause in order to rear large numbers of larvae for experimental use in plant resistance trials. Simpler and cheaper facilities could hence be used for maintaining continuous laboratory cultures of these stem borers.

Pest Management

Use of Synthetic Sex Pheromones

Pheromone-baited traps are useful devices for monitoring stem borer moth populations. Trap catches of male moths provide useful information for quantifying moth abundance and for alerting and timing of spray applications. From the advances made in the identification and the use of sex pheromones in stem borer monitoring, it was concluded that trapping alone was unlikely to provide effective control; mating disruption was a more likely control option. Synthetic pheromone blends for *Chilo suppressalis*, *C. sacchariphagus*, *C. indicus*, *C. auricilius* and *C. zacconius* have been shown to be attractive to male moths in the field. Sex pheromones for *B. fusca*, *C. partellus*, *S. calamistis*, *S. cretica*, *S. nonagrioides* and *Coniesta ignefusalis* have been identified and are now commercially available.

Several years of monitoring *B. fusca* moths in South Africa with the aid of sex pheromone

traps have revealed that the first flight of moths, emerging from overwintering larvae, peaked about mid-November. A second, larger flight then occurred in the latter half of February, while a third flight peaked around mid-April. No moths were trapped during winter (June to September). In the field, larval peaks of *B. fusca* lagged from 4 to 6 weeks behind the corresponding moth flight peaks. Omni-directional traps were found to be superior to delta traps for quantitative and qualitative estimation of *B. fusca* moth populations. More research into trap design and the correlation between trap catches and subsequent field infestations are required before trapping of *C. partellus* moths can be used in predicting economic threshold levels.

A slow-release pheromone formulation produced high levels of mating disruption in *B. fusca* when applied at 40 g a.i. per hectare at 250–500 release points per hectare. This effect persisted for at least 18 weeks and, based on release rate studies, was predicted to last for six months. In field trials in Kenya, some reduction in damage levels was observed, suggesting that mating disruption had indeed occurred.

Cultural Control

Cultural control is probably still the most relevant and economical method of stem borer control available to farmers in Africa. Other control methods are less practical. For example, pesticides often are unavailable or are too expensive for resource-poor farmers. Resistant cultivars are likewise not easily available, nor can biological control of stem borers be completely relied upon.

Cultural control is amongst the oldest, traditional, farming practice known. It is considered the first line of defense against stem borer pests and includes methods such as removal and destruction of old crop residues, intercropping, crop rotation, manipulation of planting dates and use of different tillage methods. The latter three cultural practices are of particular importance and

can directly benefit crop yields. Though many of these cultural practices are very labor intensive, they do have the advantage of having minimal environmental impact and also can be readily implemented without extra capital investment.

However, adequate knowledge of stem borer biology and phenology, together with a close working relationship with the crop through all its growth stages, are essential for the development of efficient cultural control strategies. The differences found in the behavior of *E. saccharina* in South Africa and in East Africa affords an example of the importance of pest knowledge in making the right control decision. In South Africa, larvae of *E. saccharina* mainly infest the lower part of sugar cane stalks and farmers therefore cut off the tops of the cane, which are simply left lying as crop residues in cane fields. In contrast, the same larvae in East Africa largely occur in the upper cane, and any tops of plants left as residues would therefore provide a further source of infection and exacerbate the carry-over of the pest population.

Although cultural control options for stem borer management appear promising and offer relief, many African farmers have not adopted them. Cultural control is still severely constrained by a lack of management capability of farmers, especially in areas where agricultural extension services are inadequate.

Managing Crop Residues

Crop residues are especially important for the carry-over of stem borer larval populations from one growing season to the next. In Nigeria, larvae of *B. fusca*, *E. saccharina* and *S. calamistis* were found in crop residues below the soil surface, and higher incidences of these borers always occurred in no-tillage plots. In Kenya, *C. orichalcociliellus*, *C. partellus*, *E. saccharina* and *S. calamistis* were observed in stalks after harvest. In Ethiopia, a considerable proportion of *B. fusca* larvae survived in the stubble. In Uganda, untreated crop residues often were used to mulch the next crop. Under

these conditions, moths emerging from the previous crop constantly reinfest newly planted crops.

An effective control option would thus be to reduce the first generation moth populations by destroying the bulk of the mature larvae overwintering in the old stalks. Plowing, in order to bury the maize stubble, proved an effective measure for controlling *B. fusca* infestations as far back as the 1920s in South Africa.

In Zimbabwe, it was observed that *B. fusca* moths experienced difficulty in emerging through 5 cm of soil and that deep burial under 10–15 cm of soil could totally prevent moth emergence. Deep plowing tillage in South Africa, where large areas are under maize or sorghum and where densities of up to 226,000 borer larvae per hectare have been estimated, is thus a viable control option for *B. fusca* and *C. partellus*.

Slashing of maize and sorghum stubble to expose overwintering larvae to the elements and natural enemies destroyed 70% of *C. partellus* and *B. fusca* populations, while additional plowing and disking destroyed a further 24% of the pest population in sorghum and 19% in maize.

However, for these cultural control measures to be really effective, the close cooperation of all farmers in a particular region is required because moths emerging from untreated fields will readily infest neighboring crops. Currently, this cultural control strategy is no longer so widely practiced in South Africa, owing to the advent of minimum tillage and to the importance of providing winter grazing on old maize fields for beef cattle.

In rural Africa, farmers often use the dry stalks of maize, sorghum and millet as building construction material in their houses and fences, in contour terracing and for use as stakes. Stalks also are kept for fuel and for use as bedding for livestock. Farmers often stack the dry stalks in the field, where they are kept until the start of the rainy season, thus creating ideal reservoirs of stem borer infection. To solve this problem, early cutting of stalks and horizontal placement on the soil surface have been recommended. This was found to cause 97% mortality of stem borers in maize and 100% in sorghum in

Ethiopia. This practice also has reduced the residual population of borers in uncut millet stems from 16% to 3%. The high levels of mortality of *C. partellus*, *C. orichalcociliellus* and *S. calamistis* larvae observed in horizontally placed stalks was ascribed to the combined effects of radiant heating and high temperatures on the thermal tolerance of borer larvae. On the other hand, in Nigeria, the control of *S. calamistis*, *B. fusca*, *C. ignefusalis* and *E. saccharina*, through removal of maize stalks and stubble after harvest, did not reduce stem-borer populations significantly, apparently because of immigration of moths into the crop.

Control of *B. fusca* and *C. partellus* by burning old stalks and other crop residues after harvest also has been recommended. For example, almost complete eradication of *C. partellus* was achieved on maize and sorghum in Tanzania after setting fire to old crop residues. However, in Nigeria where the majority of farmers make use of their old sorghum stalks and do not normally burn them after harvest, a partial burn when the leaves were dry and the stalks still green gave up to 95% control of *C. partellus* larvae. The heat generated from burning the leaves apparently killed the larvae inside their tunnels. At the same time this cured the stalks, which not only improved their strength for building purposes, but also made them more resistant to termite attack. On the other hand, crop residues are the only organic matter that is added to the soil on many small scale cultivations in Africa. Burning of old crop residues can thus deprive the soil of organic matter and also result in increased soil degradation due to wind and water erosion.

Manipulation of Sowing Dates and Plant Densities

Planting crops when the pest is least abundant ensures that the more susceptible early growth stages escape becoming infested. In Kenya, an attempt to legislate this principle was made for controlling *B. fusca* on maize during the 1920s and 1930s. The aim was to restrict maize plantings to

the February to May period, a time when moth infestations were normally low. Unfortunately, there is no available information on the efficacy of these measures, and the last attempt at implementing such legislation was in 1937–1938, after which it fell into disuse.

In West and Central Africa, early planting has been found to reduce *B. fusca* and *S. calamistis* infestations. Reports of increased stem borer damage to late maize plantings, as compared to early plantings, have come from Benin, Cameroon, Ghana, Nigeria, Burundi and Zaire. In some areas of West Africa, farmers also do not plant maize during the second rainy season because of the risk of severe infestation. This also influenced the borer populations found in the rain forest zone, where alternative wild host plants in the dry season are scarce.

Early planting of cereals also is practiced in the semi-arid tropics, where rainfall is variable and unpredictable. Late sowing, however, is also unpopular because of poor yields, even in the absence of stem borer damage.

On the Highveld region of South Africa, the second generation of *B. fusca* in mid-summer is larger and causes more damage than the first spring generation. The best control strategy is hence to plant early in the season. Similar conditions apply to Lesotho, Zimbabwe and Ethiopia, where second generation larvae caused crop losses of 23–100% as compared to 0–23% by first generation larvae.

At lower elevations in South Africa, it is recommended that sorghum be planted after mid-October to avoid infestation from the first moth peak of *C. partellus*. In Tanzania, it was shown that maize planted early in the season was more liable to severe infestation by *B. fusca* than later maize plantings. In Malawi, planting date also influenced pest levels of *B. fusca* and *C. partellus* on sorghum. However, the choice of optimum sowing date also depended on the sorghum cultivar planted. In contrast, in the Sahelian region, manipulating the planting dates of millet was not an effective option against infestation by *C. ignefusalis*.

Sowing density may also affect crop growth and thereby influence pest population levels. The behavior of the pest in its search for food or for oviposition sites may well be adversely affected by plant density. Young *C. partellus* larvae need to migrate from their hatching site to the leaf funnels or to reach adjacent plants within their immediate vicinity. During this critical migration period, up to 100% mortality of the first instar larvae may occur. The lowest incidence of deadheart was caused by *B. fusca* at low plant densities of sorghum in South Africa and from maize in Nigeria. Conversely, a reduction in row width increased the number of stem borer larvae infesting adjacent crop rows through migration, and this in turn resulted in greater crop damage. *B. fusca* larvae can migrate up to a distance of 2.4 m from their eclosion site. At the standard 90 cm inter-row planting distance used in commercial maize production in South Africa, lateral transmission over ± 4 rows of maize is thus possible.

Rather than reducing plant densities within individual rows, wider row spacings also have been used in the Ivory Coast in an attempt to reduce *B. fusca* and *E. saccharina* damage to maize. However, studies on *C. partellus* in maize and on *C. ignefusalis* in millet, planted at different crop densities, showed no significant differences in stem borer incidence.

In subsistence farming systems in Africa, where farmers normally intercrop cereals with other crops, and where lack of water is an overriding constraint, manipulation of sowing dates and plant densities is not always possible. Farmers generally must plow and plant after the first rains have fallen, rendering some of these cultural control alternatives impractical.

Fertilizers

Providing fertilizer to cereal crops has been shown to increase stem borer infestation and survival of borer larvae. For example, damage to rice by *Maliarpha separata* in Nigeria increased with

fertilizer application, while sorghum plants with no fertilizer supplied were less preferred for oviposition by *C. partellus* moths in South Africa. However, no such differences were observed in similar oviposition behavior trials with *B. fusca*. However, in South Africa, where *E. saccharina* is a problem on sugar cane, a reduction in nitrogen fertilizer rates from 50 kg to 30 kg per hectare proved beneficial.

Increased survival of *S. calamistis* larvae and accelerated larval development occur with increased nitrogen content of maize resulting from fertilizer treatment. It also was suggested that addition of fertilizer might stimulate additional annual generations of stem borers.

Although nitrogen fertilizer enhanced borer development, it also had a positive effect of increasing host plant tolerance to borer attack. Yield losses decreased linearly from 20% with no fertilizer, to 11% with 120 kg nitrogen added per hectare. It also has been reported that timing of nitrogen fertilizer application influenced the incidence of *C. ignefusalis* on millet. The suggestion has been made that by manipulating the timing and quantity of nitrogen fertilizer, a compromise between using low fertilizer levels to dampen stem borer infestation, and high fertilizer levels to stimulate better yields, might be achievable.

Intercropping and Habitat Management

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Small-scale farmers in Africa practice intercropping or mixed cropping to reduce risk of crop failure, attain higher yields, and improve soil fertility. Although no studies have shown that farmers grow specific intercrops to reduce insect pests, some of these practices also lead to suppression of cereal stem borer populations. Studies in Kenya have concentrated both on the practice of intercropping cowpea with maize and sorghum, and on the ways in which these systems could be adopted by small-scale

farmers in the region. Most studies on intercropping have shown a reduction in the incidence of stem borers. Maize/cassava intercropping systems in Nigeria were found to reduce by half larval numbers of stem borer populations. Unfortunately, many of these intercropping studies did not seek to determine the underlying mechanisms behind the effect of intercropping on stem borer populations. Intercropping maize with cowpea was an effective way of reducing damage caused by *C. partellus*, because 30% of *C. partellus* oviposition was on cowpea.

Planting an outer encircling row of a highly preferred host to act as a trap plant is a useful diversionary tactic to control stem borers. Napier grass, *Pennisetum purpureum*, and Sudan grass, *Sorghum vulgare sudanense*, common fodder plants in Africa, are reported to provide natural control of stem borers by acting as trap plants. Although the stem borers oviposit heavily on the attractive Napier grass, only very few larvae are able to complete their life cycles. In on-farm trials in Kenya, planting Napier grass around maize fields has been shown to significantly increase crop yields by reducing the stem borer population in maize. Sudan grass provided natural control of stem borers by acting as a trap plant, and as a reservoir for its natural enemies.

A recent study from Kenya has reported the effectiveness of intercropping maize with a non-host grass, *Melinis minutiflora*. In field trials, *M. minutiflora* showed no colonization by stem borers, and when used as an intercrop with maize, significantly reduced stem borer infestation in the main crop. A significant increase in parasitism of stem borers by the larval parasitoid *Cotesia sesamiae* was also observed. Volatile agents produced by *M. minutiflora* repelled stem borers but attracted *C. sesamiae*. Female *C. sesamiae* were attracted to (E)-4,8-dimethyl-1,3,7-nonatriene, one of the volatile components released by intact molasses grass. While serving as an effective cover crop, *M. minutiflora* at the same time provides good fodder for livestock. The grass is now being tested in on-farm trials in Kenya to control stem borers on maize.

For the control of stem borers in resource-poor maize farming systems in eastern Africa, “push-pull” or stimulo-deterrent diversionary

tactics have been developed. These strategies involve combined intercropping and trap crops. Stem borers are trapped on highly susceptible trap plants (pull) and are driven away from the maize crop by repellent intercrops (push). The plants that are used as trap or repellent plants in a push-pull strategy are Napier grass, Sudan grass, *M. minutiflora* and silverleaf desmodium, *Desmodium uncinatum*. Napier grass and Sudan grass are used as trap plants, whereas *M. minutiflora* and silverleaf desmodium repel ovipositing stem borers. All four plants are of economic importance to farmers in eastern Africa as livestock fodder.

Before making decisions on the use of intercrops and trap plants for stem borer control, it would be important to assess economic impact as well as the biological effects. The economic gain from the use of intercrops usually depends on the balance between a lowered cost of stem borers control and the increased cost of maintaining an intercropped field, along with any decrease in yield of the main crop from greater plant competition. Net profit can be increased if the intercrop favorably changes the balance between income and costs.

Host Plant Resistance

Host plant resistance as an approach to pest management in gramineous crops confers many advantages. Resistant crop varieties provide an inherent control that involves no environmental problems, and are generally compatible with other insect control methods. Major emphasis on the host plant resistance work in Africa has been on screening maize and sorghum crops against *Chilo partellus* and *Busseola fusca*. Attempts have been made to understand the nature of *C. partellus* and *B. fusca* resistance in maize and sorghum. A general association between plant phenology and resistance to stem borers has been established. A wide range of mechanisms are involved in *C. partellus* and *B. fusca* resistance in maize and sorghum, including non-preference for oviposition, reduced larval settling, reduced larval feeding and food utilization, and reduced larval survival and development. The cause

of ovipositional antixenosis mechanism in maize against *C. partellus* was found to be a high number of trichomes on the lower leaf surface.

Information on the mode of inheritance and the number of genes involved in the resistance of plants to particular insect species, although not essential for breeding plants, has great practical significance for identifying donors for resistance, developing isogenic lines, and breeding broad-based resistant varieties. In maize and sorghum, resistance to *C. partellus*, measured in terms of leaf-feeding, deadhearts and stem-tunneling, is polygenic. Polygenic resistance is moderate, but more stable and longer lasting than monogenic or oligogenic resistance. In sorghum, an additive gene effect was important in the inheritance of *C. partellus* resistance.

Efforts are underway in Africa to identify sources of stem borer resistance in cereal crops, but high levels of resistance have not been found. Crop varieties resistant to one stem borer species are not necessarily resistant to others. Therefore, it is important that sources with multiple resistance to stem borers are selected for breeding for durable resistance. During the last two decades, several national and international programs have been attempting to incorporate resistance to *C. partellus* into a good agronomic background of maize and sorghum, and many genotypes are already in national yield trials. Resistant lines/hybrids with good general combining ability have been identified. Several hybrid sorghums bred in South Africa exhibited tolerance to stem borer damage, and therefore suffered low yield losses.

Introduction of Biological Control of *Chilo partellus* in Africa

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Because *C. partellus* is an exotic stem borer in Africa, there have been several attempts to introduce exotic parasitoids for its control. The first was

in East Africa, where eight species of parasitoids, mostly from India, were released from 1968 to 1972 by the Commonwealth Institute of Biological Control. There were no reports of establishment. In South Africa, there were a series of introductions of 11 parasitoids from various locations from 1980 to 1993, but again, none established.

In 1993, a program was initiated in Kenya to introduce the gregarious larval endoparasitoid, *Cotesia flavipes*, from Pakistan for biological control of *C. partellus*. Releases were made in 1993 at three locations in the southern coastal area of Kenya, and the parasitoid was recovered during the season of release from *C. partellus* and two native stem borers, *C. orichalcociliellus* and *S. calamistis*. *Cotesia flavipes* was released at a fourth site in coastal Kenya during the non-cropping season of 1994 in an area where the vegetation was dominated by a wild grass, *Sorghum arundinaceum* (Desv.) Stapf. Recoveries in the wild habitat, and in a nearby maize field during the following cropping season, indicated that the parasitoid could sustain its population during the dry season in wild grasses and then colonize maize fields during cropping seasons.

Other than recoveries at the wild sorghum site, only one stem borer parasitized by *C. flavipes* was found in 1994, despite intensive sampling. In 1995 and 1996, a few recoveries were made, but parasitism was low. In 1997, the number of recoveries increased dramatically and parasitism at 30 sites averaged about 6%. Parasitism continued to increase during the next two years with average parasitism of about 13% at 67 sites in 1999.

Surveys in other maize growing areas of Kenya in the mid to late 1990s showed that *C. flavipes* was present in the Eastern Province and in the area bordering Lake Victoria in western Kenya. In the Eastern Province, which borders the Coast Province, *C. flavipes* was found in low densities in 1996 and then released at three sites in 1997. Parasitism during the season following the releases was about 14%. Parasitism in western Kenya did not increase to the levels observed in coastal Kenya or the Eastern Province, which may be due to the composition of the stem borer complex. In western Kenya, four

stem borers are common: *C. partellus*, *S. calamistis*, *B. fusca* and *E. saccharina*. All of these are attractive and acceptable hosts for *C. flavipes*, but two of them, *B. fusca* and *E. saccharina*, are not suitable for its development. The presence of acceptable, but unsuitable, hosts in an area appears to act as a sink which depresses population growth of *C. flavipes*.

The impact of *C. flavipes* on stem borer populations in coastal Kenya was recently investigated. A host-parasitoid model was used to estimate the stem borer density with and without the parasitoid. A reduction of 1.1 to 1.6 stem borers/plant, equivalent to a 32–55% decrease in the stem borer density, was shown. As there is not yet any evidence that the *C. flavipes* density has reached an equilibrium, it may continue to increase and provide greater suppression of stem borers in the future.

In addition to the work in Kenya, *C. flavipes* was found in northwestern Tanzania in 1995. Based on surveys conducted prior to 1994, and on electrophoretic evidence, it was concluded that the most likely explanation was that *C. flavipes* moved into Tanzania from Kenya. Likewise, surveys in 1999 and 2000 revealed that *C. flavipes* had moved into Ethiopia.

Releases of *C. flavipes* have now been made in several other countries including Mozambique, Uganda, Somalia, Malawi, Zambia, Zanzibar and Zimbabwe. Establishment has been confirmed in Mozambique, Uganda, Malawi and Zanzibar. In Uganda, *C. flavipes* was found to be the most common larval parasitoid of stem borers one year after its release.

Biological Control of *Chilo sacchariphagus* on the Indian Ocean Islands and Africa

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Over 150 years ago, *C. sacchariphagus* was introduced from Java to the Indian Ocean islands of

Mauritius, Réunion and Madagascar in cane cuttings. The biology of this insect is similar to that of other sugarcane borers like *Eldana saccharina* in Africa or *Diatraea saccharalis* in the Americas. Damage is caused by the larvae, which penetrate into the stalk internodes where they feed until pupation. In terms of economic losses, damage results in a significant lowering of cane tonnage and, to a lesser extent, in a loss of sugar due to the inversion of saccharose, and to impurities in the juice. On a susceptible variety, the loss in cane weight is estimated to range from 10 to 30 tons per hectare, depending on the growing conditions. This pest has been increasing in some cane producing areas of the island due to the adoption of new varieties, and since 1994 it has been the subject of research to devise an integrated control program. Recent results from field experiments suggest new strategies for minimizing borer attack using predators, parasitoids and varietal resistance.

Biological Control Attempts: Lessons from the Past

In the Indian Ocean islands, attempts to control *C. sacchariphagus* with exotic parasitoids started in the 1940s. However, variable results were obtained. In Mauritius and Réunion, introduction and large scale releases of parasitoids, mainly originating from India, did not control *C. sacchariphagus*, despite the successful establishment of species like *Trichogramma chilonis* Ishii and *Cotesia flavipes* in sugar cane fields. In Réunion, several attempts at biological control in the 1970s by introducing and releasing tachinid flies also failed to control the pest.

Paradoxically, during the years of mass-releases, there were few ecological studies on *C. sacchariphagus* and its indigenous parasitoids and predators. Moreover, no accurate information was available concerning the parasitization rate of borer eggs by *Trichogramma* spp. and other egg parasitoids. However, in Réunion,

Mauritius and Madagascar, natural parasitism of *C. sacchariphagus* eggs was generally high and ranged from 80 to 90%.

The Importance of Predation by Ants

Predation of *C. sacchariphagus* eggs in Réunion was assessed on sugar cane fields in 1996–1997 by placing fresh eggs on the top leaves through the cane cycle. In two experiments conducted at different localities, 70–100% of the eggs were attacked by ants when sugar cane was six months old. The level of predation remained very high until the harvesting period (12 months). Trap catches and regular observations in the plots revealed that *Pheidole megacephala* F. (Hymenoptera: Formicidae) was the major predatory species.

However, predation by ants on eggs interfered with a major parasitoid, *Trichogramma* sp. Observations of parasitized eggs in clutches spared by the ants indicated that the ants destroyed the eggs whether they were parasitized or not. Despite this, natural control of the stem borer is a reality in sugar cane fields, and efforts should be focused on conserving natural enemies. This can be done by ceasing certain cultural practices such as burning at harvest, which is totally incompatible with the conservation of predatory insects.

Revised Biological Control with the Use of *Trichogramma* sp

A new biological control program using *Trichogramma* spp. is currently being implemented in Réunion Island. This program encompasses different steps, from field and lab research to technology transfer. It includes the choice of suitable species and the selection of strains to improve field performance (higher fecundity, survivorship and more efficient parasitism). One of the most important steps was to identify the *Trichogramma* strains and set up different studies on biology and population dynamics. Morphological and molecular characterization of

numerous strains collected from different sites around the island led to the identification of *Trichogramma chilonis* Ishii. This species, previously named *T. australicum*, probably originated from Southeast Asia, the native home of *C. sacchariphagus*. All biotypes identified were evaluated for parasitism and the most suitable one will be mass-reared for inundative releases in the field. Further studies on population dynamics of *T. chilonis* are currently being conducted on a susceptible cane variety. The main objective of this study is to investigate the response of *T. chilonis* to different densities of *C. sacchariphagus* eggs. This information is essential to determine the ability of *T. chilonis* to control the borer in the field.

The technology for mass rearing of *Galleria* moths to produce high quality *Trichogramma* has been transferred to an organization in Réunion, which has many contacts with farmers. The method will be improved for eventual mass-releases. Nevertheless, small scale production of *Trichogramma* will allow the testing of different factors linked to the methods of release, quantity of *Trichogramma* per hectare, time of releases, packaging of the parasitoids, and indicators to assess efficacy of the releases. These practical studies will be conducted in partnership with farmers.

Predation by ants, as mentioned previously, also should be considered in the timing of *Trichogramma* releases. Therefore, to ensure the highest efficiency, these releases should be conducted during the period when predation is low and sporadic, which is also the egg laying period for *C. sacchariphagus*. After this period and until maturity of the cane, predation should assure the destruction of most of the borer eggs.

***C. sacchariphagus* in Mozambique: a Threat to the South African Sugar Industry**

In 1998, the presence of *C. sacchariphagus* in sugar cane in Mozambique was confirmed. Prior to that, its presence was suspected and was mentioned in various unpublished reports as early as the 1970s.

Subsequent to its positive identification, a biological control program has been initiated with the collaboration of the sugar estate management. An ichneumonid pupal parasitoid, *Xanthopimpla stemmator*, which is a parasitoid of *C. sacchariphagus* in Sri Lanka, and which had been introduced and established in Mauritius and Réunion, was chosen as the first biocontrol candidate.

Methods to detect the presence of *C. sacchariphagus* in the South African sugar industry are already organized. During the last two years, a series of insect pheromones traps have been in operation in strategic locations along the border of South Africa with Mozambique. However, traps cannot detect the presence of borers in sugar cane stalks transported across the border. It is suspected that the first introduction of this pest into the Indian Ocean islands and Mozambique was made in this way. Presently, the risk of invasion of *C. sacchariphagus* is high for countries that have a common border with Mozambique (particularly Zimbabwe and Tanzania). Continued vigilance along the common borders will minimize the possibility of the importation of infested sugar cane stalks. Appropriate control measures can be applied immediately should an infestation in sugar cane farms be detected.

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Graminivory

Eating or feeding on grasses (the plant family Graminae or Poaceae). Arthropods that feed on grasses are said to be graminivorous or graminivores. Grasses are sometimes said not to be particularly well defended biochemically against insect feeding, depending instead on silicification, lignification, trichomes, and a basal meristem for defense against herbivory. However, secondary plant compounds are also abundant in grasses.

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Granary Weevil, *Sitophilus granarius* (Linnaeus) (Coleoptera: Curculionidae)

This is an important pest of Stored grain.

- ▶ [Stored Grain and Flour Insects](#)

Granivory

Seed feeding. Such arthropods are said to be granivorous or granivores. This is distinct from graminivorous (graminivores), or grass feeding,

though animals that feed on grass seeds can be said to be both granivorous and graminivorous.

- ▶ [Food Habits of Insects](#)
- ▶ [Phytophagy](#)
- ▶ [Herbivory](#)

Granular Formulation

A dry formulation of pesticides that is substantially larger and heavier than dust, and applied with a granule applicator, not a duster.

Granule

The individual particles that are used in a granular formulation of pesticide.

Granulocyte

A type of hemocyte that is important in encapsulation of foreign objects found in the hemolymph.

- ▶ [Hemocytes of Insects: their Morphology and Function](#)

Granulosis

A disease of certain insects caused by granulosis virus (granulovirus) and characterized by the presence of minute granular inclusions in infected cells.

- ▶ [Granulovirus](#)

Granulovirus

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There are an increasing number of problems associated with the use of chemical pesticides, including emergence of resistant insects,

elimination of non-target insects, and environmental contamination. Thus, the need for alternative biological insecticides that are cost-effective and environmentally safe is greater than ever. As a result, interest in microbial insecticides is increasing. Microbiological pathogens include various species of bacteria, fungi, nematodes, and viruses. The best-known example of a microbiological insecticide, which is used in large scale against agriculture and forest pests, is the bacterium, *Bacillus thuringiensis* (commercially known as Bt).

Viruses comprise another important class of insect pathogens that are being considered as good alternative biological insecticides due to their specificity for insect hosts. At least eight families of insect viruses are known, but the viruses most commonly used as viral bioinsecticides are those from Baculoviridae family.

Baculoviruses are a group of viruses that are specific to arthropods. Unlike other insect viruses, no morphologically similar counterpart to baculoviruses has been detected in vertebrates. Baculoviruses are characterized by the presence of a large protein matrix or occlusion body which encase the viral particles. Baculoviruses are classified in two genera: the nucleopolyhedroviruses (NPVs), and the granuloviruses (GVs). Safety testing of non-target organisms including mammals, fish, and birds has shown baculoviruses to have a very limited host range and to be safe to non-target organisms. Of the insect viruses, only baculoviruses have been recommended for field use.

Although baculoviruses have been isolated from different orders of insects, they have been used mostly to control pest species from the orders Lepidoptera, Hymenoptera, and Coleoptera. Overall, the most successful examples of baculovirus usage can be found in forestry. For instance, in the U.S.A. and Canada, baculoviruses have been used successfully in large-scale against the Douglas fir tussock moth (*Orgyia pseudosugata*), pine sawfly (*Neodiprion sertifer*), red headed sawfly (*Neodiprion lecontei*) and gypsy moth (*Lymantria dispar*).

Granulovirus Infection (Granulosis)

Granulovirus (GV) infection, known as granulosis, was first detected by Paillot, in 1926, in the larvae of *Pieris brassicae* (the large white butterfly). At that time he called this disease pseudograsserie. Later he described a similar disease in *Agrotis segetum* (a cutworm). In 1947, Steinhaus rediscovered the disease in *Peridroma saucia* (variegated cutworm), and he called the disease granulosis because he observed some tiny granules in affected tissues when observed with light microscopy. In 1948, a similar disease in *Choristoneura muriana* (pine shoot roller) was described by Bergold. Bergold was the first to demonstrate the viral nature of granulosis with electron microscopy; he described the virus as rod-shaped particles.

Infection begins when larvae ingest the occlusion body. Several days after infection, larvae begin to display unusual characteristics such as sluggishness, loss of appetite, followed by color change from the light brown to pink or white. For example, *Choristoneura fumiferana* (spruce budworm) and *Pieris rapae* larvae become pink, and *Cydia pomonella* (codling moth) larvae become white in very late stages of infection. The organ of the insect that is principally affected is the fat body, but virus also replicates in other tissues such as the epidermis, hemocytes, tracheal matrix cells, and Malpighian tubules.

The high pathogenicity of GV's toward different insect pests of agricultural crops and forests make this group of viruses a very attractive candidate to be used as biological insecticides. Since the 1950s, different GV's have been used as a biological insecticide in different parts of the world. One of the first countries to use GV's against *Hadena sordida* and *Trichoplusia ni* was the former Soviet Union. In Canada, GV's are mostly used in forestry against spruce budworm (*C. fumiferana*), and fir budworm (*C. muriana*). In the U.S.A., GV's have been used against *Cydia pomonella* (codling moth) and *Plodia interpunctella* (Indian meal moth).

General Aspects of Granulovirus

GVs are rod-shaped enveloped virions that contain one molecule of circular (super coiled) double stranded DNA. Nucleocapsids, which consist of proteinaceous capsid and DNA-protein core, are relatively large, 200–450 nm long and 30–100 nm in diameter. Nucleocapsids are cylindrical structures in which subunits of capsid are assembled in rings stacked one on top of another. Each turn of the helix consist of 12 copies of the capsid protein. The two ends of the nucleocapsid are different in shape and have been described as “nipple and claw.” One end (nipple end) has the appearance of stacked rings of decreasing diameter.

GVs produce two different phenotypes, termed budded virions and occlusion-derived virions. Distinct viral structures are visible in thin sections of infected tissue. These two phenotypes are produced at different times and locations in the infected larvae. Budded virions are produced in the late phase of the infection cycle, when nucleocapsids bud from the surface of infected cells. Occlusion-derived virions, on the other hand, are produced very late in infection; they become enveloped and subsequently occluded within an occlusion body within the infected cell. Enveloped nucleocapsids are individually encased in occlusion bodies. Occlusion body is a protein matrix, termed granulin, which protect the viral DNA against the UV radiation of sunlight. Each phenotype has different functional roles. Occlusion-derived virion is the phenotype that is released in the environment after the death of the infected insect, it has a great infectious potential toward other susceptible insects.

Molecular Biology of Granulovirus

Genome

Granuloviruses have large genomes (80–180 kbp) that have the potential to encode about 100 genes. On the contrary, other viruses with big genomes like poxvirus that carry an extensive array of enzyme

which are essential for early gene transcription, granuloviruses (like other baculoviruses) carry no virion-associated proteins that are essential for virus early gene transcription on their genome. The genome of granuloviruses is composed almost entirely of unique DNA sequence, though several small repeated sequences known as homologous regions are known in the DNA. The homologous regions have roles as enhancers for early genes, and also as origin of DNA replication. The activation property of an early gene known as *ie-1* is enhanced when the genes are linked to homologous region sequences.

Open reading frames (ORFs) are located on either strand of the DNA. Most ORFs are separated by 2–200 bps of DNA rich in A + T. There are also some overlapping ORFs in granulovirus genome, usually termination codon UAA overlaps with the primary polyadenylation signal AAUAAA. Some promoters are located within the neighboring ORFs.

Frequently, transcripts of one gene initiate within, into, or through neighboring ORFs. Beside partial clustering of genes which have assigned roles in early gene regulation (e.g., *ie-1*, *ie-2*, and *pe-38*), genes in the genome of granulovirus, like other baculoviruses, do not appear to be clustered. Genes encoding structural proteins are distributed throughout the genome with no obvious pattern to the location.

Structural Proteins

Granulin is the major protein in SDS-polyacrylamide gel electrophoresis (SDS-PAGE). Studies on alkaline solubilized granulin of different GV's show that matrix protein of GV's has a molecular weight equal to approximately 30 kDa. Analysis of the nucleotide and amino acid composition of granulin in different GV's show a high degree of similarity. Amino acid sequence analysis of granulin in different granuloviruses showed conserved amino acid residues, which is likely due to “evolutionary memory,” which maintains the secondary structure of granulin in all GV's.

The presence of 12–20 proteins has been shown in enveloped nucleocapsids of different GV by SDS-PAGE analysis. Molecular weight of these polypeptides ranges from 12 to 160 kDa.

Cycle of GV Infection in Susceptible Insects

The infection cycle of granulovirus has two distinct phases: primary and secondary cycle.

Primary Cycle of Infection

The primary phase of infection is initiated by ingestion of virus by larvae, followed by dissolution of granulin (matrix protein of occlusion body) in the midgut of the insect, and liberation of the enveloped nucleocapsids. Granulin dissolved due to the alkaline environment of the insect's midgut. Occlusion-derived virion infectivity is boosted by a protein present in occlusion body, termed Enhancin, which is a proteolytic compound with structural and functional characteristics of metaloproteases. Enhancin seems to have a direct effect on degradation of the peritrophic membrane in insect midgut.

Enveloped nucleocapsids attach to the surface of microvilli of columnar cells, and nucleocapsids enter the cytoplasm of cells following fusion of the viral envelope with plasma membrane. Nucleocapsids move toward the nucleus of the cell by polymerizing the actin filaments and release their DNA into the nucleus.

Replication and transcription of viral DNA take place in the nucleus of infected cells, and progeny nucleocapsids are formed in the nucleus of columnar cells. Nucleocapsids acquire their envelope by budding through the modified plasma membrane. This modification is due to the transportation of virus-made proteins into the plasma membrane of the infected cells. The primary phase of infection terminates when these enveloped nucleocapsids, known as budded virion phenotype, are released from infected cells. Budded

virions are potentially infectious for tissues within the hemocoel. The mechanism by which the budded virion traverses the basal lamina of the midgut epithelium is not completely known. Some researchers suggest this possibility that budded virions may directly traverse the basal lamina of the midgut epithelium during budding. There is also another possibility that budded virions may use the tracheal system as a conduit to cross the basal lamina of the midgut epithelium.

Secondary Cycle of Infection

The secondary phase of granulovirus infection is different from the primary phase in several ways: (i) budded virions enter these cells by a receptor-mediated endocytosis in contrast to the occlusion-derived virion, which enter by fusion, (ii) more cells are infected, (iii) the yield of progeny virus per cell is much higher, (iv) progeny nucleocapsid acquire envelope inside the cell (instead of budding through the plasma membrane), (v) enveloped nucleocapsids encased inside the proteinaceous matrix, and (vi) the occluded progeny (termed occlusion-derived virion phenotype) are released upon cell lysis.

Viral entry by endocytosis is a process that usually consist of six steps: (i) virion attachment to a receptor on the surface of host cell, (ii) invagination of host plasma membrane in the viral attachment site, (iii) formation of a vesicle containing the enveloped virion (endosom), (iv) acidification of the endosom, (v) fusion of the viral envelope and endosomal membrane, and (vi) release of the nucleocapsid into the cytoplasm.

Following the release of nucleocapsid into the cytoplasm, they are transported toward the nucleus. Studies that concentrate on the mechanism of the transportation in NPVs showed that actin cables might play a major role in this movement. These studies also suggest that a structural protein in the nucleocapsid triggers the polymerization of actin cables. After nucleocapsid reach the nucleus, viral DNA is directly released into the

nucleus through the nuclear pores. It seems that a phosphorylated capsid protein (P78/83), which is localized at one end of the nucleocapsid, plays a role in the interaction of nucleocapsid and nuclear pores. The mechanism of uncoating of DNA in another baculovirus genus, NPVs, is different than GVs. Nucleocapsids of NPVs enter host cell nuclei and uncoat within the nucleus.

Upon uncoating of granulovirus DNA in the nucleus, early genes are transcribed by a host RNA polymerase. Early viral products are mostly regulatory proteins that activate transcription from other early genes. The transition from early to late phase is characterized by inhibition of host transcription and replication of viral DNA. Replication of viral DNA seems to be a crucial step prior to late phase transcription. Late genes are transcribed by a viral RNA polymerase. At least 18 baculovirus genes have been shown to control the late gene expression; these genes are identified as late expression factors genes (*lef* genes). All structural proteins are expressed in late and very late gene expression.

Nucleocapsid assembly begins after synthesis of late proteins. Electron microscopy studies demonstrate that initially a virogenic stroma appears within nuclei, and empty capsids assemble within this stroma. These capsids then fill with DNA. A basic DNA binding protein in the capsid (P7/12) may play a role in packaging of viral DNA. This protein has similarity to cellular protamines, the basic proteins that substitute for histones in the packaging of DNA within the sperm of many species. Both proteins (i) are rich in arginine residues which lead to a high basic charge, (ii) have the ability bind zinc (Zn^{+2}), and (iii) are a substrate for kinase activity.

After the process of packaging viral DNA, nucleocapsids are ready for envelopment followed by occlusion. The mechanism for envelopment is not known, but some researchers suggest that budding through the nuclear membrane fragments is a possible way for envelopment. The very late phase of infection starts by hyper-expression of very late genes such as granulin

(the occlusion body protein). Granulin crystallizes around the enveloped nucleocapsids and encases the virions. Following the occlusion process, an envelope-like structure (calyx) covers the occlusion body.

At the final stage of granulovirus infection, cells become packed with occluded virions that cause cell lysis and liberation of virus into the hemocoelum followed by death of the insect.

Use of Baculovirus against Lepidoptera

Baculoviruses have been used to control different lepidopterous pests in agriculture and forestry. Historically, the first attempt to use viruses as a bio-insecticide date back to 1892. In this year, a baculovirus was used to control *Lymantria monacha* population in pine forests in Germany. The United States was the first country in North America to use a baculovirus against *Lymantria dispar*.

There is no record of large scale use of baculoviruses in agriculture in United States before the late 1940s. In this year, aerial application of NPV against *C. eurytheme* (alfalfa caterpillar) were attempted in California. The use of *Helicoverpa zea* NPV in the 1970s showed promising results in soybean and maize agriculture. Between 1975 and 1980, over one million hectares were treated by HzNPV. Introduction of synthetic pyrethroids in the early 1980s decrease the use of HzNPV, but the emergence of a worldwide resistance against pyrethroids during the 1990s promoted the use of the HzNPV. In 1996, HzNPV were again used in large scale in the cotton industry in the United States. Currently, China is one of the countries that use HzNPV and *H. armigera* NPV in cotton industry. Annually, 100,000 ha of cotton fields in China is treated by HaNPV. Thailand and Vietnam are two other countries, among others, that use HaNPV on a large scale.

One of the best examples of using baculovirus in fruit crops is the use of a granulovirus against *Cydia pomonella* (codling moth: a pest of apples,

pears and walnuts). *Cydia pomonella* granulovirus (CpGV) demonstrates a high pathogenicity against the larva and kills the insect very quickly. Field tests with CpGV in North America demonstrated that CpGV is a highly virulent and selective control agent against codling moth. CpGV is currently in use in different European countries. France, Switzerland, Germany, and Russia are the major consumers.

Records of using baculoviruses in forestry show that the following insects were the most important Lepidoptera that were subjected to applications of baculoviruses: *C. fumiferana* (spruce budworm), *C. occidentalis* (western spruce budworm), *C. pinus* (jackpine budworm), *L. dispar* (gypsy moth) and *O. pseudotsugata* (Douglas-fir tussock moth). A NPV for *O. pseudotsugata* was registered and used in United States in 1976. This virus has been used during the last three decades in different parts of the United States and Canada. *Lymantria dispar* NPV is another baculovirus that has been used widely since its registration in 1978.

The first baculovirus used against spruce budworm was CfMNPV. The most important problem related to CfMNPV is its low pathogenicity. The other baculovirus that has a great potential to be used as a microbiological insecticide against spruce budworm is *C. fumiferana* granulovirus (ChfuGV).

A Case Study: Use of *Choristoneura fumiferana* Granulovirus (ChfuGV) in Canada

In eastern North America, spruce budworm is considered the most destructive insect of coniferous trees. The spruce budworm is a huge economic threat to vast forest areas (60 million ha) in Canada and eastern United States. The Maritime Provinces (New Brunswick, Nova Scotia, Newfoundland), Quebec, Ontario, and the Great Lake states are the areas that are affected by spruce budworm outbreaks most extensively. Spruce budworm larvae feed on a number

of conifers, but balsam fir (*Abies balsamea* [L.] Mill.), and white spruce (*Picea glauca* [Moench] Voss) are the major hosts in eastern North America. Species occasionally attacked include black spruce (*Picea mariana* [Mill.] B.S.P.), red spruce (*Picea rubens* Sarg.), eastern hemlock (*Tsuga canadensis* [L.] Carr.), tamarack (*Larix laricina* [Du Roi] K. Koch), and white pine (*Pinus strobus* L.).

In Quebec, Canada the outbreak of *C. fumiferana* usually affects huge forest areas. For example, the infested area in 1999 was estimated more than 23,000 hectares. This figure was twice as large as the infested area in 1998. Defoliation, inhibition of seed production, cone mortality, root mortality and tree mortality are the most important impacts of spruce budworm on trees. Defoliation caused by spruce budworm decreases the growth rates of trees; this decline can last several years. When outbreaks occur, the affected trees usually die after three to four years of heavy defoliation, and most of the trees die between six and ten years after the first attack. Even when the spruce budworm population returns to its endemic level, the damaged trees continue to die.

Chemical insecticides were the most common method of protecting spruce-fir forests from spruce budworm from 1927 up to the 1970s. DDT and Phosphoramidon were used mostly during the period from 1944 to 1970. In the 1970s and 1980s organophosphates and carbamates replaced DDT. Most of these compounds are toxic to humans and other warm-blooded animals. The concern about finding an alternative for chemicals started during the 1960s and among the candidates were biological insecticides. Also, as insects continue to gain resistance to chemical pesticides, industrial interest in commercial development of biological pesticides increases.

Natural predators, parasites, competitors and pathogenic microorganisms like fungi, bacteria and viruses have been used as biological agents. In eastern Canada *Bacillus thuringiensis* var. *kurstaki* (Btk) is used in insect control programs against spruce budworm. No major resistance against Btk in natural population of spruce budworm has been

reported. However, laboratory results demonstrated that several insect species are able to develop resistance against the Btk toxin. The risk of appearance of resistance against Btk obligates the researchers to quest for new alternatives.

ChfuGV has been isolated from infected spruce budworm in several part of eastern Canada. This virus is considered a very attractive and powerful candidate to be used instead of, or along with, Btk in the case of the emergence of resistant spruce budworm larvae.

Laboratory bioassays with ChfuGV demonstrated its high pathogenicity for spruce budworm population ($LD_{50} = 5.72 \times 10^5$ viruses/larvae). The development and implementation of ChfuGV as a microbial insecticide were carried out during a pilot project on 100 ha of forests in Quebec, Canada. The results of these field experiments demonstrated that two weeks after treatment with ChfuGV a considerable reduction (40%) of defoliation was observed in treated areas as compared to control areas. Also, the number of *C. fumiferana* larvae was reduced by over 35% in treated areas. One of the most interesting results, from an economical perspective, is that when ChfuGV was used in a lower rate volume applied per ha, the same level of protection was observed.

Production of Granulovirus-based Insecticides

Currently, most granuloviruses are produced in vivo. The reason is due either to the absence of cell lines for some granuloviruses, or low yield of virus production for the others. One of the most important drawbacks concerning the in vitro production is that the viruses often lose infectivity after several passages through cell culture. The most important aspect of the virus production process is: (i) choice of the host. (ii) rearing conditions. (iii) virus purification. (iv) formulation.

Usually, a natural virus host is the best choice in virus production, but in the cases that the natural host is not suitable for laboratory rearing, and

alternative hosts must be considered. The following cases are examples of unsuitable hosts: (i) when the natural host has a special dietary requirement, or (ii) when long obligatory diapause is required.

Temperature and humidity are the most important aspects in insect rearing. The other key factor for in vivo virus production is the number of larvae per each diet container and the size of container. The use of large containers is not recommended for species with a cannibalistic nature.

Formulation of granulovirus-based insecticides is a very important part in production. For large-scale applications, different aspects such as storage stability and UV protection must be considered in order to have a stable and high quality product. The formulation also must provide good residual activity in field. The formulation must not contain any additive with negative effects on virus activity.

Standardization and Quantification of Granulovirus-based Insecticides

One of the most important requirements for the production and use of GVs is the availability of bioassays. With bioassays, GV producers can determine the potency and virulence of an industrial product or preparation. On the other hand, bioassays can be also used: (i) to determine the biological activity of GVs for different insect species, (ii) to determine the relative biological activity of several viruses against one or more insect hosts.

Bioassays ensure the activity of the product prior to field use. In each bioassay there are some facts that should be respected to ensure the quality of the bioassay: (i) the purity of the virus preparation should be established by electron microscopy or other analytical procedures, (ii) presence of contaminating micro organisms such as bacteria and mycets should be checked, (iii) the assay must be reproducible for the same strain of insect species under similar conditions. Different methods of bioassays, such as bioassays by injection, bioassay

by contaminated leaf disks, and finally bioassays by contaminated artificial diet have been suggested by different workers.

Injection methods have been used for establishment of activity of non-occluded virus obtained from alkaline-dissolved granules (granule: a complete granuloviral particle contain nucleocapsid, envelope and occlusion body). This method is very tedious and time consuming, but the primary advantages of this type of assay are (i) the amount of inoculums per insect is known, and (ii) the time of the beginning of infection is known.

Another time consuming method of bioassay is using leaf disks contaminated by with known quantities of GV preparation. Bioassays using contaminated artificial diets are the most commonly used assays for many insect viruses including GVs. In this method, known quantities of GVs are incorporated into, or layered on, the surface of artificial diets, which allows the evaluation of the LC_{50} . There are two very important advantages related to this method: (i) early stages of insect larvae, which are generally the most susceptible to viral infection, can be used in large numbers, (ii) insect handling is minimized since the stay in the same container throughout the bioassay. The disadvantage of this method is that the dose of the virus ingested by each insect is not known. There are always problems that could arise in different types of bioassays, but these problems can be avoided if certain precautions are taken.

Methods of Application of Granulovirus-based Insecticides

An effective application should distribute virus to the insect's feeding sites in a way that the probability of acquiring a lethal dose of virus is maximized. Granuloviruses, like most other baculoviruses, are applied by spraying the viral product to the target site. Ground application is mostly used for agricultural crops, but aerial application is the common method in forestry. There also are other application techniques that

have been demonstrated, such as release of infected insects, though these have some limitations.

The Future of Granulovirus

Baculoviruses and among them granulovirus, can be considered to be major elements in biological control programs in the next 10 years. On the other hand, considering the fact that a great deal of effort has been directed toward the development of recombinant baculoviruses, it also is probable that recombinant viral insecticides will be used on a large scale against insects pests of forests and crops in near future. The most important issue concerning the use of genetically modified baculoviruses is the safety issue. Therefore, to be safe, it is important to prepare comprehensive risk assessment protocols for genetically modified baculoviruses.

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Grape Berry Moth, *Endopiza viteana Clemens* (Lepidoptera: Tortricidae)

Endopiza viteana is an important grape pest.

► [Small Fruit Pests and their Management](#)

Grape Leafhopper, *Erythroneura* sp. (Hemiptera: Cicadellidae)

Several species of *Erythroneura* are pests of grapes.

► [Small Fruit Pests and their Management](#)

Grape Phylloxera, *Daktulosphaira vitifoliae* (Fitch) (Hemiptera: Aphidoidea: Phylloxeridae)

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Grape phylloxera is a primitive aphid that feeds and develops on grapevines (*Vitis* species). It is notorious for the damage it caused to viticulture first in France, then globally as it was introduced and spread into vineyards in nearly every grape-growing region of the world in the middle to latter part of the nineteenth century. Its native range is North America east of the Rocky Mountains, the southwestern USA, and well into Mexico and Central America to as far south as Venezuela. Grape phylloxera has had a checkered nomenclatural history, and the genus names *Pemphigus*, *Rhizaphis*, *Peritymbia*, *Viteus*, and *Daktulosphaira* as well as *Phylloxera* have been applied to it. For many years, *Phylloxera* was the most commonly applied name so the common name and Latin genus name were one and the same. This name was subsiding from use after 1952, however, and Russell cleared up the nomenclatural mess more than thirty years ago. However, there is no phylogenetic hypothesis for the Phylloxeridae so nothing is known about the relationship of *D. vitifoliae* to the approximately 41 described species of *Phylloxera* and it may still turn out, once such a hypothesis is in hand, that erecting a new genus for grape phylloxera was unjustified. There is an unfortunate prevalence in both entomological and viticultural circles to use the name phylloxera as the common name. Because a large number of other species in the family have this as their Latin name, it is desirable to specify “grape” phylloxera when discussing this insect.

Life Cycle and Biology

Grape phylloxera is a gall forming insect (as are the majority of species in the Phylloxeridae) causing galls on leaves and young roots on native vines and on hardened roots of susceptible cultivars. It has been stated that grape phylloxera may form galls on vine tendrils, but this is not true under natural conditions. Its host range appears to be restricted to about six to eight (depending on taxonomic concepts) of the some 20 or so *Vitis* species in the Americas and a number of cultivars, most notably the wine grape *V. vinifera* L. The distribution of grape phylloxera in Mexico and Central America is uncertain at this time. On leaves, pouch galls are formed that completely enclose the gall-former and her eggs. Galls on young roots (typically called nodosities) have a characteristic hook shape as cells distal to the insect feeding site become hypertrophied. The gall-former may be partially hidden in the elbow of the hook, but is otherwise exposed. Galls on hardened roots (tuberosities) appear as bumps on the surface of the root, with the gall-former and her eggs exposed on the surface. There is currently no evidence to suggest that the mechanism of gall induction differs on the three different plant organs or tissue types attacked; the different morphology is due to the different substrates galled (i.e., a pouch gall cannot form on a cylindrical and hardened root).

The life cycle differs in the native range and under most vineyard conditions and these will be discussed separately:

Native Range

As with the majority of Aphidoidea, grape phylloxera is a cyclic parthenogen in its native range. That is, one to multiple generations pass by apomictic parthenogenesis followed by a single generation of sexual reproduction each year. Sexually produced eggs are cold-resistant and are the overwintering stage. Individuals hatching

in the spring from these zygotic eggs are called fundatrices. As first instar crawlers, fundatrices initiate galls on newly forming leaves in which they will mature in 2–3 weeks, laying upwards of 300 eggs as adults. Galls can only form on the newly expanding leaves. Fundatrices and all subsequent gall mothers (gallicolae) generally do not leave their gall after gall initiation. As eggs hatch, the crawlers leave the galls and move up the shoots to newly forming leaves where they in turn make their galls. A variable number of generations may pass this way. New leaf growth tends to slow or cease as summer progresses, meaning there is no longer any leaf resource for grape phylloxera. In the southwestern USA, and perhaps Mexico and Central America, it appears that this is when sexual forms (sexuales) are induced and overwintering eggs produced, ending the life cycle. There is evidence that gallicolae will sometimes secondarily occupy already-formed galls. There are no winged forms (alatae). In eastern North America the life cycle is prolonged by crawlers moving to the roots where they (called radicolae) form galls on new, unhardened rootlets. Analogous to host alternation in aphids, it is here that alatae are produced that ascend into the canopy to lay a small number of male and female eggs. Induction of alatae may be influenced by density dependence, deterioration of the resource, or temperature. The neotenic sexual morphs have no mouthparts and live only a few days. Following mating these females lay a single zygotic egg each. It is often said that the overwintering eggs are laid in crevices in the bark on the trunks of vines but there have been too few observations to convincingly say how these eggs are distributed.

Vineyards

Vineyards in the eastern part of North America appear to be attacked by the local populations of grape phylloxera, and the life cycle on these

cultivated vines does not differ. Elsewhere, except in cases where rootstocks are allowed to sucker or grow from cut down vines, the life cycle has been modified by elimination of the leaf galling phase, and with it production of sexual forms. Overwintering occurs as first or second instars. There is now good evidence that most populations of grape phylloxera, in vineyards of Australia and California at least, reproduce only asexually. Alate individuals are common, however, and have been observed at various times of the year. Apparently they are either infertile, their eggs are inviable, or sexuales do not survive to adulthood. Both nodosities and tuberosities are formed, with some cultivars resistant to tuberosity formation but susceptible to nodosity formation.

Dispersal of grape phylloxera occurs by flight of alatae and by blowing of crawlers by wind, and may also occur by windblown or water-carried galled leaves that harbor eggs or live individuals. In vineyards, all stages could be moved by agricultural equipment and activities.

Damage and Management

There are no data directly relevant to how damaging grape phylloxera is to wild grapevines and what effect on fitness, if any, is incurred. It has commonly been assumed that these vines are tolerant, but this is not likely to be strictly true because extensive galling must divert resources away from seed production. More study of this plant-insect interaction on wild grapevines is needed and would aid in understanding the evolution of resistance in grapevines.

In vineyards, damage is most severe when tuberosities are formed, vines being able to withstand the damage from nodosity formation. Tuberosities tend to occlude the vascular system, and a heavy infestation high up in the root system will effectively remove a substantial proportion of the translocation to and from the root system. This effect is exacerbated significantly by entrance of fungal pathogens through the

cracked surface of the galled portion of the roots, resulting in necrosis and loss of root area. Ultimately, attacked vines die.

Management tactics have varied over the years and have included spraying of copper bisulphide in the early days to more modern insecticides (especially against leaf galling forms), and even flooding vineyards. The cryptic and protected habitat of root galling individuals makes use of conventional insecticides problematic. Systemic insecticides have found some use, but have not been widely applied. The use of natural enemies has not been thoroughly explored. Because fungal pathogens play an important role in damage, efforts are underway to control these. Finally, grape phylloxera has been effectively excluded from some wine regions in Australia by enforcing strict quarantine measures.

The only effective and durable management tactic has been the development and use of host plant resistance. Resistant cultivars have been developed directly from vine collections from the native range or, more often, from breeding programs, often leading to complex hybrids. The dominant *Vitis* species that have been used in these breeding programs have been *V. riparia*, *V. rupestris*, and *V. berlandieri*. Once developed, these cultivars are used as rootstocks for scions of the wine grape, *V. vinifera* L. The mechanisms of resistance are not well understood but there is evidence for antixenosis (insect avoidance), antibiosis (death or poor development of the insect) as well as tolerance (plant can suffer large numbers of herbivores without succumbing). Phenolic compounds may play a role in inhibiting development, and a hardened periderm beneath the feeding site has been observed, which would inhibit gall formation and isolate the insect from its nourishment.

Host plant resistance has been an effective strategy for managing grape phylloxera since it was introduced in the late 1800s, with only a few examples of failure. A notable example of a failure of what was previously considered to be a resistant rootstock is that of the rootstock AXR#1 in California in the 1980s. This rootstock was widely planted in California vineyards in the

1960s and 1970s but began declining under grape phylloxera attack in the 1980s, leading to large scale replanting to other rootstocks and massive economic outlays. It is likely, however, that this rootstock was never sufficiently resistant to grape phylloxera under California conditions, and the failure of resistance in this case may be more a failure of implementation than a failure of resistance.

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Grape Root Borer, *Vitacea polistiformes* (Harris) (Lepidoptera: Sesiidae)

Vitacea polistiformes is one of the most important grape pests in eastern North America.

► [Small Fruit Pests and their Management](#)

Grapevine Leafhopper Complex (Hemiptera: Cicadellidae) in Cyprus

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Various species of leafhoppers attack grapevines throughout the world. In Cyprus, the grapevine leafhopper complex consists of three species that have been identified by C.A.B. International Institute of Entomology (London) as *Zygina rhamni* (Ferrari), *Jacobiasca lybica* (Bergevin & Zanon), and *Asymmetrasca decedens* (Paoli). Assessment of population density through D-vac samples and insect counts directly on the plants showed an overall prevalence of *Zygina* over the other two. *Zygina* and *Jacobiasca* prevailed in areas with drier microclimatic conditions (Avdhimou and Pakhna) where the overall relevant populations were 52% and 45%, respectively. At Phassouri, though, a much less drier area, 45% of the leafhopper population was *Asymmetrasca*. This pest prevailed from April to early August and then its populations dropped significantly as it moved to other host-plants. Minor differences have so far been found in the within-plant distribution of the two principal species. At low population levels, these cicadellids had the tendency to live on different leaves, but at higher populations they could also be found on a same leaf, almost exclusively on the lower leaf surface. More insects were found on the basal than on the apical half of the vines.

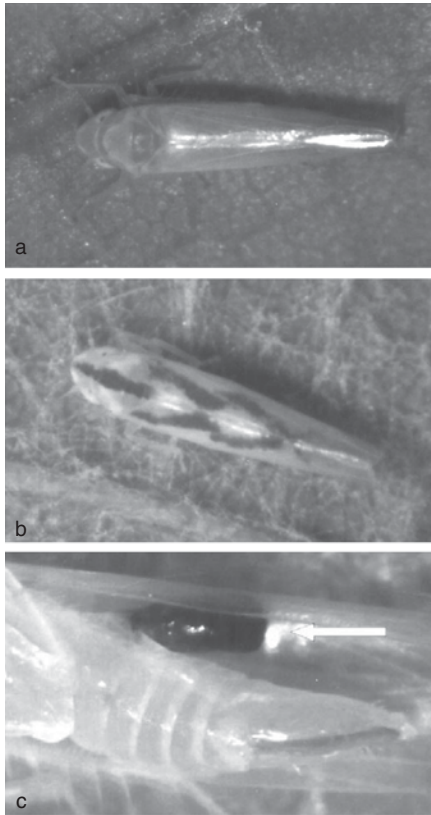
The adult females lay their eggs singly in the epidermal tissue of the leaves and appear like tiny bean-shaped blisters. The young leafhoppers that emerge (nymphs), and the adults, are found almost exclusively on the lower leaf surface. They feed by sucking out the sap from the leaf cells or veins causing discoloration, deformation and in cases of heavy infestation, drying and shedding of leaves. Although *Zygina* is more widespread, it is not so harmful to the plants because it sucks the sap from the leaf cells, causing only leaf discoloration. The

other two leafhopper species are more harmful because they suck the sap from the leaf veins, causing leaf deformation and drying. Yellow sticky trap catches showed increased populations of *Zygina* only from the end of July to the end of November, while those of *Jacobiasca* followed the same trend with about a three-week delay. Considering this population behavior, and the insect count on the grapevine leaves that were much lower than those reported as economically significant elsewhere, the pest status of the leafhopper complex was questionable.

Adults of *Z. rhamni* overwinter on *Rubus* sp. and *Sarcopoterium spinosum* (L.) Spach. They present a reddish pigmentation on their head and front wings, which in grapevines with poor growth starts appearing gradually from mid-August onwards, while in those with rich and tender growth, 15 days later. This gradual change of adult pigmentation is completed generally by mid-November. Adult migration to the winter quarters may start as early as September with a gradual infestation of *Rubus*, which is an evergreen bush. *Sarcopoterium* is available for infestation from around mid-November. This cicadellid develops (Fig. 31) one generation on these plants in early spring, and then it moves to grapevines where it stays for as long as there are green leaves, developing a maximum of 4 more generations.

Jacobiasca lybica overwinters as adult on *Rubus*, and then it develops only on grapevines, completing a maximum of six generations per year. *Asymmetrasca decedens* overwinters on citrus and on several weeds without interrupting its development, although it slows down because of the lower temperatures. In spring it moves to several vegetables and to grapevines where it prevails until the end of July. It then develops on various vegetables until winter, completing a maximum of eight generations per year.

Aphelopus orphanidesi Olmi (Hymenoptera Dryinidae), a new species, was the only parasite of *Z. rhamni* found so far in Cyprus. Adult females oviposit in the body of the leafhopper nymphs



Grapevine Leafhopper Complex (Hemiptera: Cicadellidae) in Cyprus, Figure 31 *Zygina rhamni*: (a) adult of summer generations, (b) adult of overwintering generation, (c) adult female parasitized by *Aphelopus orphanidesi*.

only and larval development extends in the adult stage of the host. The older nymphal stages seem to be preferred. Adult leafhoppers exposed to parasitoid females have never been attacked. The parasitoid female grasps the cicadellid nymph with her mandibles, holds it in position with her legs, and oviposits in its body. Parasitized leafhoppers, noticed by the unaided eye only at the adult stage, bear a sac on either side of the fore parts of the cicadellid gaster in a dorso-lateral position under the wings that contains the parasitoid larva. No leafhopper nymphs have been found to carry any larval sac of the parasitoid. On the overwintering leafhoppers, the sac darkens gradually as the parasitoid larva grows, and

becomes shining black. It then becomes white after the larva abandons it. On adults reared in the laboratory at 25°C and in the field during the summer, the sac remains white throughout the entire larval development. Upon completion of its development, the parasitic larva leaves its moribund host, and drops to the soil where it becomes pupa and then adult.

The parasitoid completes five generations in one year. Emergence of adult parasitoids from the overwintering generation occurs in March and coincides with the appearance of first generation host nymphs, which are available for parasitization. Adults of the following parasitoid generations appear in May, July, August, and September. Parasitization rates are relatively high (75%) only on the overwintering leafhopper generation. In this generation, oviposition starts from September, but parasitized leafhoppers are noticed by the unaided eye from January onwards.

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Grass

A plant with narrow leaves containing parallel veins. A monocotyledonous plant. A common

name for plants in the family Graminae (contrast with broadleaf plant).

Grass Flies

Members of the family Chloropidae (order Diptera).

► Flies

Grasshopper and Locust Pests in Africa

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Africa has an exceedingly rich fauna of Orthoptera, including several families and well over 1,000 species, that could be considered to be grasshoppers or locusts. In Africa (also in Asia, Australia, and South and Central America), some grasshoppers are called “locusts.” This term is applied to species of grasshoppers that display phase polymorphism. Phase polymorphism is largely a behavioral change between different states: gregarious and solitary forms, with intermediate forms called “transiens.” During the gregarious phase, which is induced by high densities, locusts tend to disperse long distances in groups (during the nymphal stage the groups are called bands, during the adult stage they are called swarms). These same species are not very dispersive, nor gregarious, during the solitary phase. Physical changes in appearance may also occur during the change in phase, and of course physiological changes underlie the behavioral and morphological shifts. Transition between the solitary and gregarious phase takes more than one generation. In contrast, grasshoppers tend not to disperse long distances, tend not to aggregate during dispersal, and their appearance remains about the same regardless of density conditions. Thus, “grasshoppers” do not display phase change. Africa suffers from both grasshopper and locust

infestations, but is best known for locust problems. The Arabic phrase for locusts translates to “teeth of the wind,” providing some indication of the severity of the problem. As is the case elsewhere in the world, most of the orthopteran pests are in the family Acrididae, but other families of the order Orthoptera, particularly Pyrgomorphidae, are present as pests.

Locusts and grasshoppers sometimes, but not always, conform to the “typical” phase pattern suggested by the common name of these insects. As expected, when comparing the gregarious and solitary phases of desert locust, *Schistocerca gregaria* (Forskål), and migratory locust, *Locusta migratoria migratorioides* (Reiche & Fairmaire), the different phases can be quite distinctive. The behavior, coloration and size differ markedly between the gregarious and solitary phases. A common measure of the gregarious phase is the ratio of wing length to the width of the head; the gregarious phase has relatively longer wings. However, in some other species such as the Moroccan locust, *Dociastaurus maroccanus* (Thunberg), there is little or no change in color, though the relative size of body parts does change. The Senegalese grasshopper, despite not being called a locust, displays some morphological differences between the swarming and non-swarming populations, including longer wings. Thus, it is a good idea not to dwell on the common name of orthopterans, but to look critically at the biology of species individually. Other species are more typically grasshopper-like. Africa has a few spectacular species of “locusts” that command most of the attention and notoriety (as is largely the case in Australia), but some regions also suffer from a large assemblage of grasshoppers (as is largely the case in North America). Some of the more important species are shown in Table 7 and Fig. 32.

In Africa, and generally elsewhere in the world, grasshopper and locust populations in arid regions tend to grow in response to increased rainfall, and increased availability of host plants brought about by the precipitation. Annually, favorable habitats result from the belt of rain that

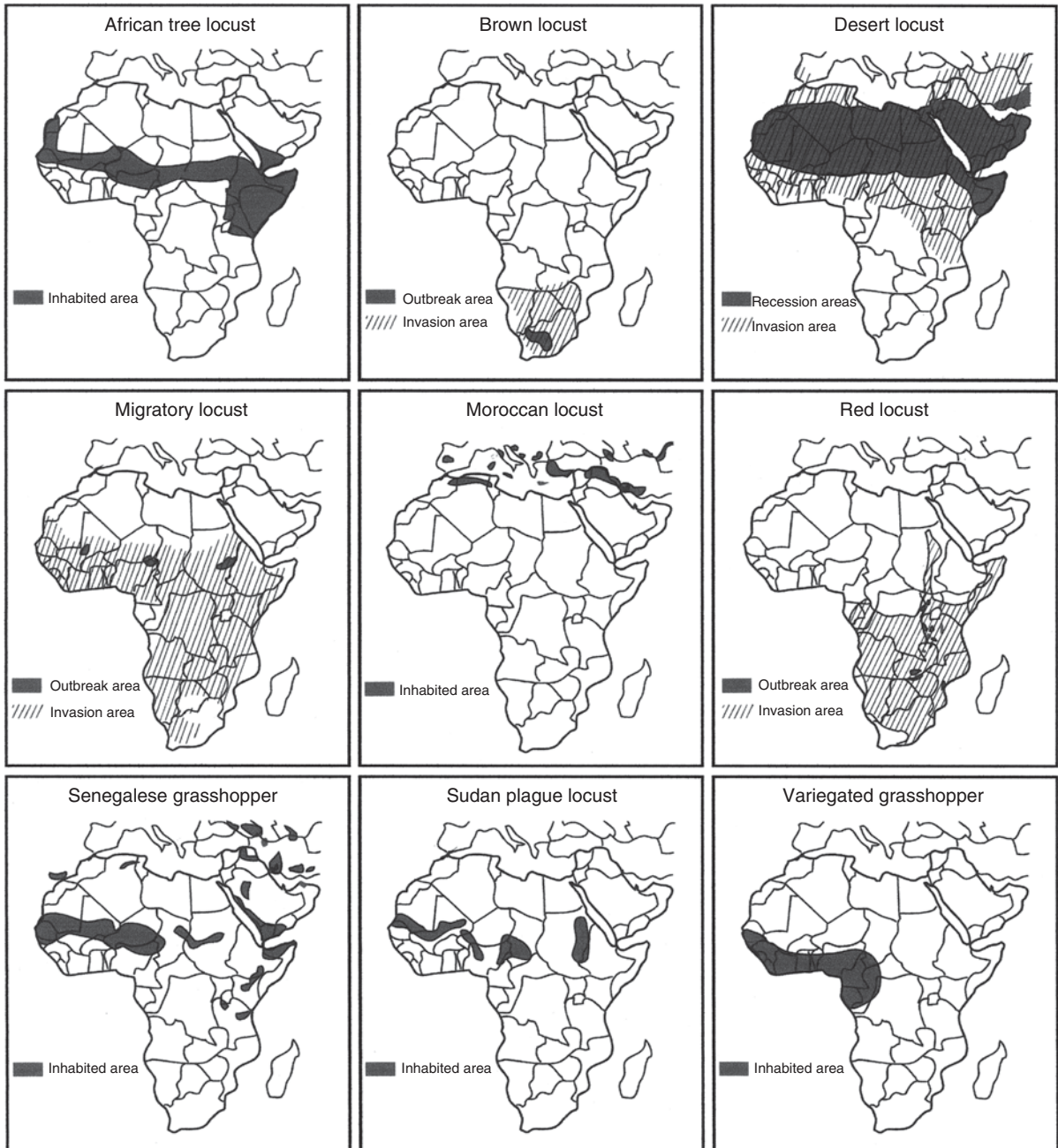
Grasshopper and Locust Pests in Africa, Table 7 Examples of serious and less serious locust and grasshopper pests in Africa, and regions of Africa where they are abundant

Pest status	Scientific name	Common name	Region
Serious	<i>Schistocera gregaria</i> (Forskål)	Desert locust	N, E, W
	<i>Locusta migratoria migratorioides</i> (Reiche & Fairmaire)	Migratory locust	N, S, W
	<i>Nomadacris septemfasciata</i> (Serville)	Red locust	S, E, W
	<i>Locustana pardalina</i> (Walker)	Brown locust	S
	<i>Doclostaurus maroccanus</i> (Thunberg)	Moroccan locust	N
	<i>Anacridium melanorhodon</i> Walker	Tree locust	E
	<i>Oedaleus senegalensis</i> (Krauss)	Senegalese grasshopper	N, W
	<i>Aiolopus simulatrix</i> (Walker)	Sudan plague locust	E, W
	<i>Zonocerus variegatus</i> (Linnaeus)	Variiegated grasshopper	W
	Less serious	<i>Hieroglyphus daganensis</i> Krauss	Rice grasshopper
<i>Kraussaria angulifera</i> (Krauss)			N, E, W
<i>Cataloipus fuscocoeruleipes</i> Sjöstedt			E, W
<i>Cataloipus cymbiferus</i> (Krauss)			N, S, W
<i>Kraussella amabile</i> (Krauss)			
<i>Diaboloatantopx axillaris</i> (Thunberg)			N, W
<i>Ornithacris turbida cavroisi</i> (Finot)		Bird locust	W
<i>Pyrgomorpha</i> spp.			
<i>Acorypha glaucopsis</i> (Walker)			E, W
<i>Acanthacris ruficornis</i> (Fabricius)			W
<i>Zonocerus elegans</i> (Thunberg)			S
<i>Catanops</i> spp.			
<i>Eyprepocnemis plorans</i> (Charpentier)		Bersim grasshopper	N, E, W

N, S, E, and W indicate northern, southern, eastern and western Africa, respectively

follows the movement of the intertropical convergence, the pattern of prevailing winds that sweeps southward toward the equator from the northern hemisphere, and northward to the equator from the southern hemisphere. Higher than normal

levels of precipitation in the arid regions tends to result in population upsurges, but population decrease can be brought about by losses due to dispersal, competition for food, reduction in food due to decrease in precipitation, and the actions of



Grasshopper and Locust Pests in Africa, Figure 32 The distribution of some important grasshoppers and locusts in Africa. The regularly inhabited areas are dark-shaded. For the dispersive species, the areas inhabited occasionally (during periods of outbreak) are shown as cross-hatched.

natural enemies. However, as is often the case in biology, not always does this simple pattern of seasonal rainfall leading to population increase occur. This is due partly to the vagaries of weather, which

are quite complex, and regionally and temporally subject to variation. Also, the different grasshopper and locust species have evolved different survival strategies. Species like the desert locust,

especially when in the gregarious phase, are capable of long distance dispersal, and contrary to expectations, may seemingly disperse against the prevailing winds or disperse to areas where rainfall has not recently occurred.

Temperature is as important as rainfall and food in governing grasshopper and locust populations. Temperature affects nearly all biological activities, and when grasshoppers are outside their relatively narrow optimal temperature zone, they do not thrive. Optimal body temperature for most species is 35–42°C. To some degree, grasshoppers can modify their internal temperatures by changing their behavior, a process called thermoregulation. By basking in the sun, they can raise their body temperature by several degrees, and by moving into the shade or elevating themselves away from the hot soil surface, they can reduce their temperature. However, they remain substantially at the mercy of ambient weather conditions. In northernmost and southernmost Africa, weather is predictably limiting during the cool periods of the year. However, even in the warmer regions, temperature can be limiting, and grasshoppers engage in basking behavior and suffer metabolically during periods of heavy cloud cover or rain.

Desert Locust, *Schistocera gregaria* (Forskål)

Not only is desert locust a devastating pest in Africa, but worldwide it is the most dangerous locust species. It has the capacity to produce very large, long-lasting, and dispersive swarms. This insect is graminivorous, but during outbreaks it feeds on a large number of plants, including all the important grain crops, cotton, and fruit of the region. It occurs in a persistent form within a large area of northern Africa, Saudi Arabia, and east to India. Only small areas of this area of persistence, called a recession area, typically produce the locusts leading to swarms that spread more widely, to regions called invasion areas. Even portions of

Europe and the former Soviet Union are invaded on occasion, and invasion of over 60 nations in the area has been recorded. Within the recession area are sites where locusts feed, breed and become gregarious; these can be called outbreak areas. These outbreak areas are characterized by having sandy or silty soils and being in arid or semi-arid regions. They are not always the same sites, however, because rainfall and vegetation are prerequisites to population increase.

Rainfall is required for oviposition, and females produce 20–100 eggs per pod, and two to three pods per female. On average, the solitary form produces about 95 eggs in the first pod, the gregarious form about 75. Subsequent pods have fewer eggs. The eggs complete their development in 11–75 days, fastest at about 32–34°C. The ensuing nymphs develop in about 38 days (range of 20–66 days), undergoing five instars. The molt to the adult is called fledging, and the young adult a fledgling. The adults require weeks to months to mature reproductively, but once mature persist for only about 30 days. Once they are ready to oviposit, they have only a few days to find a suitable site. Eggs do not undergo diapause. One to three generations are completed per year, depending on conditions.

Crowding for more than one generation is required for development of fully gregarious characteristics. Reduction in plant material within the outbreak sites sometimes forces the insects into closer proximity and stimulates gregarization. Alternately, repeated rains can produce several generations in the same area, allowing population increase and crowding. Sometimes partially gregarized populations move to another site that fosters further gregarization. Hoppers spend most of the day marching, and then roost at night on vegetation. Much of the feeding occurs while roosting. Once hoppers reach the adult stage, they are soon capable of flight, but do not always do so. Solitary locusts fly at night, gregarious locusts during the day. During swarms, locusts can fly for up to 17 hr per day, and travel for 5,000 km

during their lifetime. Breeding can occur in the winter months in the Somali peninsula and along the Red Sea, some of the Saharan summer breeding areas and southeast Africa, and some of Pakistan and India.

Migratory Locust, *Locusta migratoria migratorioides* (Reiche & Fairmaire)

There are several named subspecies of migratory locust found in the eastern hemisphere. In Africa, the *migratorioides* subspecies is by far the dominant race. Migratory locust traditionally has been more of an issue in the southern half of Africa. It occurs in varied habitats, including dunes with open tussock vegetation, man-made habitat including fallow fields, and flooded areas. Its areas of outbreak normally are limited to small areas just south of the Sahara Desert where grass plains flood during summer rains, providing ample food. In more recent times, migratory locust has benefited from the expansion of irrigated agriculture in the Sahara region, and northern Africa is now realizing migratory locust problems. It is gramini-vorous. Migratory locust has two to four generations per year, and females produce one to five egg pods with up to 65 eggs per pod. Eggs normally hatch in 10–50 days, but sometimes persist for up to 100 days. There are five to seven instars, requiring a total of 21–40 days. The adults remain immature for 10–14 days, but persist for up to 70 days.

Unlike most locusts and grasshoppers, migratory locust lacks a stage that can tolerate long periods in unfavorable conditions. They must breed continuously or they die out. On the other hand, favorable conditions allow them to increase in number rapidly. The locusts migrate from the flood plains to the surrounding Sahelian areas where they oviposit, but then migrate back to the flood plain and reproduce further. The offspring of this generation again migrate to the Sahel, and return, as did their parents, to the flood plains.

Red Locust, *Nomadacris septemfasciata* (Serville)

Red locust occurs widely in southern Africa during periods of swarming, but the areas of outbreak are limited to several small regions along the Rift Valley in eastern Africa. Outbreak areas are wet lowland regions dominated by grasses and characterized by extreme conditions of flooding and drought. The outbreak areas comprise only 1/1,000 of the invasion area. This locust has only one generation per year, and eggs complete their development in 30 days. The female deposits about 100 eggs in each pod (more in the solitary form), with up to five pods produced per female at 10–15 day intervals. Six to seven instars are completed in about 60–70 days. The pre-reproductive adults persist through the dry season in regions called retention areas; these are principally in eastern Zimbabwe, southern Malawi, southwest Uganda, and northern Tanzania. They persist in this stage for over eight to nine months, and then at the start of the rainy season they mature and lay eggs, but adults live for only about a month. Eggs are deposited in areas of bare soil or sparse vegetation.

Young hoppers initially remain clumped in family groups, then disperse and re-group in about the second or third instar. The tendency to concentrate is highest in dense vegetation. About the third instar, nymphs begin to form into hopper bands. They shelter at night beneath vegetation and then climb upward to bask in the sun in the morning. As ambient temperatures reach 23°C the nymphs commence feeding and disperse, only to reassemble into bands for evening roosting. This species is graminivorous, and there always seems to be plenty of grass in the outbreak areas, so formation of swarms cannot be ascribed to lack of food. Swarms persist for long periods within their favored habitats, but when they disperse to other areas that are less favorable for reproduction the population declines.

Brown Locust, *Locustana pardalina* (Walker)

Brown locust occurs only in southern Africa, and its outbreak area is found in the southernmost part of the continent. Like most locusts, its preferred habitat is semi-arid and desert. It is graminivorous, feeding on grain crops and pastures. There are two to four generations per year. The female deposits four to five egg pods with about 40 eggs per pod at 7–8 day intervals. Oviposition occurs in dry soil but eggs require moisture to hatch. They can persist for up to 15 months without rain. These locusts tend to oviposit communally. Some eggs display delayed hatch of 1–3 months, even though they may be in the same pod as eggs hatching quickly. The rapidly developing eggs require only about 10 days to develop, and hatch when 10 mm or more of precipitation occurs. The nymphal stage has 4–5 instars, and requires 20–40 days to develop. Solitary hoppers complete development in as few as 20 days whereas gregarious hoppers tend to require 40 days, and transient forms intermediate in development time. The adults are short-lived, persisting for 2–3 weeks in the pre-reproductive stage and then 1–2 months in the reproductive stage.

Moroccan Locust, *Dociostaurus maroccanus* (Thunberg)

Moroccan locust occurs throughout the Mediterranean region on semi-arid steppe and semi-arid desert with grasses, particularly *Poa bulbosa*. It is found in northern Africa in Morocco, Algeria, and Tunisia, but is also found in southern Europe and east to Iran and central Asia in a discontinuous pattern. Formerly a minor pest, it has assumed greater importance due to destruction of forests and overgrazing, which provide additional habitat for this insect. This graminivorous species thrives in regions with winter rains and untilled soil for oviposition. Tilled soil is unsuitable, but

fallow or abandoned crop land becomes suitable again. Moroccan locust has only one generation per year, and persists during the dry season, about nine months, in the egg stage. The female produces 2–5 pods, each containing 20–30 eggs. Pods tend to be grouped in clusters of 5–6 pods with several such clusters in a one meter square area. The nymphs have five instars, and develop in 30–45 days. They form narrow bands when marching, often only 2 m deep, but a single band may extend for several km. Bands usually march during the day, but sometimes extend into the night. The adult persists for 2–4 months. The adult is gregarious, but not migratory.

Tree Locust, *Anacridium melanorhodon* (Walker)

Tree locust generally is considered to be inconsequential except in Sudan, where it defoliates *Acacia senegal*, the tree used to produce gum arabic. It feeds preferentially on trees, and is found in the Sahelian region, south of the Sahara desert, from coast to coast. Despite this preference for *Acacia*, there are reports of it attacking fruit trees, cotton, tobacco, and millet. Outbreaks occur in semi-arid areas, within natural thickets of *Acacia* spp. Normally, a single generation occurs annually, sometimes a second. Egg pods contain about 150 eggs per pod, and the eggs require 1–2 months before hatching. The nymphs undergo 5–8 instars and complete their development in 2–3 months. Immatures are found throughout the dry season, and adulthood is attained with the onset of rains (usually May–June). Oviposition begins in June–July, and young hoppers appear in August–October. Despite numerous attempts to differentiate between swarming and non-swarming populations on the basis of morphometrics, there is little difference to be found. Swarms and bands, when they occur, are relatively small. Both adults and immature forms tend to roost high in trees during the day, descending and feeding at night or early in the morning. They also fly at night.

Senegalese Grasshopper, *Oedaleus senegalensis* (Krauss)

The Senegalese grasshopper is graminivorous, and is associated with sandy soils and open steppe vegetation, predominately grasses. Found mostly in Sahelian central Africa, its distribution also extends to North Africa, the Arabian peninsula, and beyond into southwest Asia. It occurs principally in lightly wooded or open savanna, and steppe or ephemeral prairies with sandy soil. It often is associated with *Aristida pallida*, a perennial tussock grass, and *Cenchrus biflorus*, an annual grass. This species has 2–4 generations per year, and the female produces 1–2 pods with only 20–30 eggs. Eggs are deposited in moist, sandy soil. The eggs resist desiccation, and enter a period of quiescence if adequate moisture is not available. Eggs laid after late August enter obligatory diapause, which can continue for two or more years if adequate moisture is not available. The young hoppers develop quickly, progressing through five instars in 17–20 days. The interval between hatch and first oviposition is about 35 days. The adults can live for 1–4 months. Like some other grasshoppers, this species shows some of the characteristics of locusts, displaying changes in morphology, marching by hoppers, limited swarming by adults, and long distance migration. Flight occurs mostly at night.

Sudan Plague Locust, *Aiolopus simulatrix* (Walker)

Sudan plague locust occurs in a broad band across Central Africa, and also in Asia. It is most abundant, and damaging, in the Nile Valley of Sudan. It is graminivorous and has two generations per year. Breeding begins soon after the start of rains. The female produces 2–3 pods containing 20–30 eggs per pod, which require less than a month for development. The nymphs undergo five instars, and complete their development in less than a month. The adults are long-lived, persisting for 6–9 months. Adults disperse when they are unable to

find suitable breeding sites, which are normally the clay soils of flood plains.

The first generation adults migrate north, where the second generation is produced. In turn, the adults from the second generation migrate southward. Flight occurs at night. Second generation adults survive the dry season hidden deeply within the cracks in the parched soil. As temperatures and humidity rise, signaling the beginning of the rainy season, the adults emerge from the soil cracks, but return during the heat of the day. The populations inhabiting the Nile Valley, which is oriented north and south, generally have higher densities than other inhabited areas, which are smaller and not so oriented. The north-south orientation of the Nile Valley allows the locusts to remain within suitable habitat during their migrations, resulting in lower mortality.

Variegated Grasshopper, *Zonocerus variegatus* (Linnaeus)

Variegated grasshopper is found in west-central Africa. Unlike most African grasshopper and locust pests, it is found in humid and sub-humid area, inhabiting openings in the forest zone. It occupies both natural clearings and deforested, cultivated areas. This species has only one generation per year. In the mid-March to May period, females produce 2–3 pods, each containing 50–60 eggs. Egg pods tend to be clustered, often in groups of hundreds or thousands. The eggs enter diapause, and require 6–7 months for development. Hatch occurs in October or November. The nymphs require a fairly long time, 75–90 days, to undergo 5–6 instars. The nymphs tend to remain clustered into dense groups, and emit foul-smelling liquids from the first abdominal segment. They disperse relative short distances.

The adults emerge in February and persist for 60–90 days. They are dimorphic for wing length, and the long-winged forms are capable of short flights. This species is also unusual in that it prefers broadleaf plants rather than grasses.

It damages herbs, flowers, citrus, and coffee. To a lesser extent it feeds on banana, cassava, and cotton. They are most abundant, and damaging, in the dry season.

Damage

Most of the African grasshopper and locust pests feed on grasses, and it is the cultivated grasses, the grain crops, that are most damaged. The grain seedlings and immature seed heads are most susceptible to damage. Although rangeland grasses are injured, they usually recover quickly, unlike crops. However, many rangelands, particularly in the Sahel region, are being overgrazed by livestock. The additional loss of forage to locusts on such rangelands can have long-term implications for the health of this ecosystem.

Damage to both crops and rangeland is often greatest along the margins of deserts. However, when locusts swarm they can affect crops nearly anywhere. Insect damage, when taken on a regional or national basis, often seems relatively insignificant, or difficult to justify when compared to the costs of pest suppression. However, to an individual farmer or pastoralist, the losses can be devastating, and sometimes fairly large regions suffer severe losses simultaneously. Particularly in Africa, the losses caused by grasshoppers and locusts are not easily rectified due to poor infrastructure for reallocation of food, poor communication, or political turmoil. Thus, locust and grasshopper problems can have surprisingly severe consequences, and suppression programs can provide significant benefit.

The severity of the issue in Africa can be seen by examining Table 8, which shows the frequency and distribution of locust and grasshopper problems in northern Africa and adjacent areas of the Middle East for the 20-year period of 1963–1982. This example shows only countries experiencing large-scale problems that resulted in organized suppression campaigns, not smaller or localized problems. Nevertheless, the scale of the problem is

apparent, and in each year there was need for organized suppression in at least one country. Also, it is apparent that some countries experienced locust or grasshopper problems almost annually, whereas for others it was an infrequent issue. Lastly, an element of area-wide population increase and decrease is evident, with many countries experiencing problems nearly simultaneously, and then release from locust and grasshopper problems at about the same time.

Management

Technologies for population assessment have improved, eliminating some of the element of surprise from locust and grasshopper outbreaks. Weather monitoring and modeling are often very useful for forecasting the potential for problems, and vegetation can be assessed with remote sensing technology. However, insect populations are normally confirmed by ground survey personnel via site visits, although swarming populations are sometimes monitored by observers in aircraft. The most important benefit of newer (remote) assessment technologies is that ground survey personnel are able to focus their visits and insect sampling to areas and times where they are likely to detect the pests. This improved efficiency translates into considerable financial savings. The locust outbreak areas are often targeted for more intensive monitoring and control efforts because costs are greatly reduced by treating pests while they are confined to these relatively small areas.

Although it is possible to recommend cultural and physical management techniques to help suppress grasshoppers and locusts, implementation is often difficult. Over the last 50 years, chemical insecticides have proven to be the management technique of choice, and a considerable amount of effort has been dedicated to improving the application techniques or otherwise affecting the killing power of the insecticides. Generally, application of liquid, residual insecticides to plants, by use of both ground application equipment and aircraft,

Grasshopper and Locust Pests in Africa, Table 8 North African and Middle Eastern countries in which large-scale locust/grasshopper suppression occurred during the 20 year period of 1963–1982 and the total number of years the suppression programs were instituted

COUNTRY	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	No. years	
Somalia					•	•	•			•	•			•						•	•	7
Djibouti						•					•					•					•	4
Ethiopia	•		•	•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•	13
Sudan		•		•	•	•	•		•	•	•	•	•	•	•	•	•	•	•	•	•	17
Saudi Arabia		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	17
Yemen AR			•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	13
PDR Yemen					•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	11
Egypt					•	•	•	•			•							•				6
Oman														•								1
U.A.E.			•											•								3
Kuwait														•								1
Jordan						•																1
Nigeria						•																1
Niger					•	•	•	•				•	•	•	•	•	•	•	•	•	•	11
Mali				•	•	•	•	•	•			•		•	•			•	•	•	•	11
Chad				•	•																	2
Mauritania			•	•		•	•	•	•			•	•						•			8
Western Sahara						•		•														2
Morocco						•	•	•	•			•	•	•								6
Algeria					•	•	•	•					•	•						•	•	8
Libya		•		•						•	•	•	•	•	•	•	•	•	•	•	•	12
No. of countries doing control in any year	1	3	4	7	11	16	11	6	7	7	9	10	9	13	8	9	4	6	7	7	7	

has been effective. On a much more restricted scale, poison bait applications have been used, especially for the treatment of bands of the gregarious, wingless stages of locusts. More recently, flying swarms have been sprayed with insecticides, or even better, swarms that have alighted. For both ground and air application of liquid insecticides, ultra low volume (ULV) techniques are preferred because mixing and dilution with water is unnecessary, and applicators can spray more land area with each load of insecticide.

Bioinsecticides have recently been developed as an alternative to chemical insecticides. In particular, identification of a relatively fast-acting fungal pathogen, *Metarhizium anisopliae* var. *acridum* (formerly known as *M. flavoviridae*), and the formulation of this in oil, have greatly improved the ability to implement non-chemical suppression. Other bioinsecticides, such as *Beauveria bassiana* and *Nosema locustae*, have proven to be less efficacious, as has the botanical insecticide neem. Insect growth regulators have been shown to disrupt the development of grasshoppers, but this requires that the product be applied to the immature stages, and will not protect against winged swarms.

- ▶ [Grasshoppers, Katydid and Crickets \(Orthoptera\)](#)
- ▶ [Diseases of Grasshoppers](#)
- ▶ [Grasshoppers and Locusts as Agricultural Pests](#)
- ▶ [Grasshopper and Locust Pests in Australia](#)
- ▶ [Grasshopper Pests in North America](#)
- ▶ [Grasshoppers of the Argentine Pampas](#)
- ▶ [Desert Locust Plagues](#)

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Grasshopper and Locust Pests in Australia

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In Australia (also in Asia, Africa, and South and Central America), some grasshoppers (Orthoptera: Acrididae) are called “locusts.” This designation is applied to species of grasshoppers that display phase change. Phase change is largely a behavioral change between different states, gregarious and solitary forms. During the gregarious phase, which is induced by high densities, locusts tend to disperse long distances as groups (during the nymphal stage, the aggregations are called bands, during the adult stage, they are called swarms). These same species are not very dispersive or gregarious during the solitary phase. Physical changes in appearance may also occur during the change in phase, and of course physiological changes underlie the behavioral and morphological shifts. Transition between the solitary and gregarious phase takes more than one generation. In contrast, grasshoppers tend not to disperse long distances, tend not to aggregate during dispersal, and their appearance remains about the same regardless of density conditions. Thus, “grasshoppers” do not display phase change.

The distinction between grasshoppers and locusts is not clear-cut. At low densities, locusts are not gregarious, nor highly dispersive, but they are still called locusts. Some species that occasionally form aggregations, even forming bands, are called grasshoppers, not locusts, because they do not disperse long distances. In Australia, migratory locusts have all the features associated with phase change: change in body shape and color, and formation of dense swarms during dispersal. The Australian plague locust displays a tendency to become gregarious and to swarm, but lacks a change in

appearance during the transition between phases. The spur-throated locust rarely forms bands, though it does form swarms. The small plague grasshopper forms aggregations, but does not undergo long distance dispersal in swarms. So the “locusts” of Australia display a wide range of behaviors, from very locust-like to not so typically locust-like.

Australia is known for frequent and severe problems with locusts, but grasshoppers also are implicated. The severity of the problem is due principally to the fact that Australia is largely an arid country (about 80% is arid or semi-arid), and in this environment not only do grasshoppers tend to thrive, but the effects of their herbivory are amplified by the sparse grass and other herbage available to livestock in this climate. During periods of drought, forage plants are especially valuable, and vital for livestock grazing; thus, conflict with humans is inevitable. However, the relationship of grasshoppers with moisture is not simple. In the more arid, ephemeral grasslands, high levels of summer moisture provide an abundance of food, allowing grasshoppers to maximize their reproductive potential and build to high numbers, usually over three to four generations. As the vegetation dries, the grasshoppers disperse (migrate) until they find areas with green vegetation.

In regions with more rainfall during the summer breeding season (formerly forested but cleared by humans for grazing or crops), however, biotic factors that suppress grasshopper numbers are more effective during wet seasons, so population outbreaks are associated with drought. In some areas, clearing of forest, expansion of improved pasture, and the introduction of irrigation have created environments conducive to grasshopper outbreaks. In these areas, species not formerly causing problems have emerged as pests.

Pest Species of Grasshoppers in Australia

Despite that fact that about 275 species of grasshoppers are known from Australia, only a few are

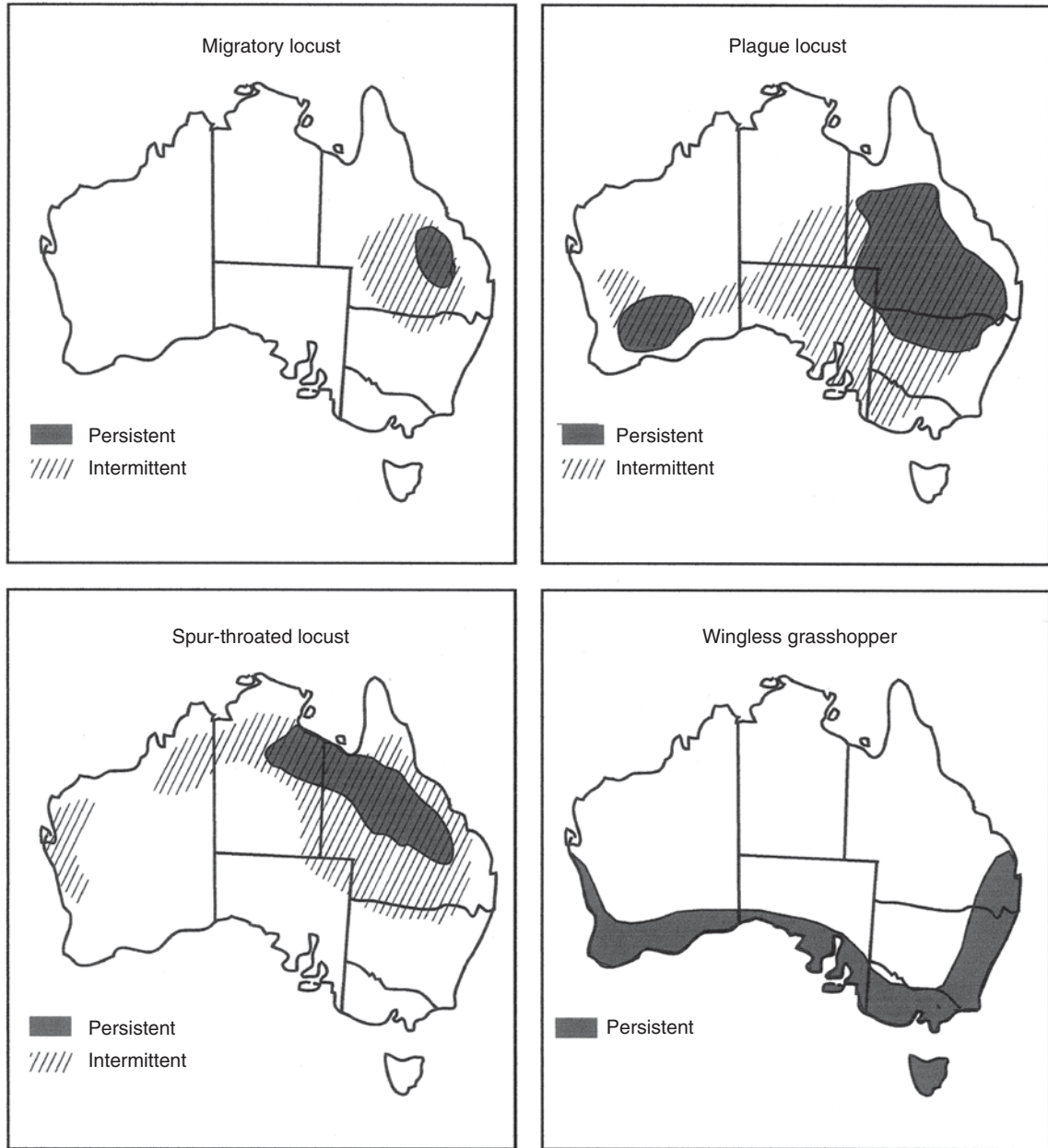
serious pests, and most are indigenous to Australia. However, most of the damage is caused by only four species: Australian plague locust, *Chortoicetes terminifera* (Walker); spur-throated locust, *Austracris guttulosa* (Walker); migratory locust, *Locusta migratoria migratorioides* (Reiche & Fairmaire), and wingless grasshopper, *Phaulacridium vittatum* (Sjöstedt), and of these, two are rather widespread in Southeast Asia (Fig. 33). The important species are given in (Table 9).

Spur-throated locust and migratory locusts sometimes cause severe damage on a localized basis, but the frequency of this is low. Wingless grasshopper has emerged as a chronic pest of improved pastures in southeastern Australia. Small plague grasshopper was formerly a serious pest in Australia during the 1930s and 1940s on cereal crops grown in southern and western Australia, but has diminished in importance. Giant grasshopper is pestiferous only occasionally, and this species is limited to northern and eastern Australia. Yellow-winged locust feeds only on grasses, and though irregularly important, seems to be favored by drought.

Australian Plague Locust, *Chortoicetes terminifera* (Walker)

The Australian plague locust is the most important grasshopper pest in Australia due to the high frequency of outbreaks and the widespread nature of the problem. For example, during the period of 1976–2001, Australian plague locust required control in eastern Australia in 18 of the 27 years. The number of generations ranges from one per year in arid, interior regions, to three per year in the more favorable regions of eastern Australia. Outbreaks normally originate in the arid zone of southeastern Australia, and to a lesser degree southwestern Australia, but they can disperse into adjacent but much larger areas during periods of outbreak.

Australian plague locust normally inhabits areas containing Mitchell grass, *Astrebla* spp., species that remain green for several months after rain, thus providing a relatively constant



Grasshopper and Locust Pests in Australia, Figure 33 The distribution of some important grasshoppers and locusts in Australia. The regularly inhabited areas are dark-shaded. For the dispersive species, the areas inhabited occasionally (during periods of outbreak) are shown as cross-hatched.

food supply. If multiple rainfall events occur, populations build rapidly, and migrate if rain does not continue. The direction of dispersal is determined by the pattern of weather; in eastern Australia, those moving in southerly or easterly

directions pose a serious threat to crops. Long-distance dispersal occurs when nighttime temperatures (above 25°C) are warm, and strong winds are present at high altitudes. These locusts typically remain airborne for 8–9 h, descending

Grasshopper and Locust Pests in Australia, Table 9 The most important grasshopper pests in Australia

Scientific name	Common name	Occurrence
<i>Chortoicetes terminifera</i> (Walker)	Australian plague locust	Semi-arid interior of Australia
<i>Austracris guttulosa</i> (Walker)	Spur-throated locust	Northern and northeastern Australia, and elsewhere in Southeast Asia; adapted to seasonally dry regions
<i>Locusta migratoria migratorioides</i> (Reiche & Fairmaire)	Migratory locust	Adapted to continuous moist tropical and subtropical conditions, especially coastal regions of northern and eastern Australia, but widespread in the Pacific Region
<i>Phaulacridium vittatum</i> (Sjöstedt)	Wingless grasshopper	Moist uplands of temperate regions of Australia
<i>Austroicetes cruciata</i> (Saussure)	Small plague grasshopper	Limited to southern fringe of arid zone in Australia
<i>Gastrimargus musicus</i> (Fabricius)	Yellow-winged locust	Moist subcoastal regions of Australia
<i>Valanga irregularis</i> (Walker)	Giant grasshopper	Eastern Australia
<i>Oedaleus australis</i> Saussure	Eastern plague locust	Eastern interior Australia
<i>Aiolopus thalassinus</i> Fabricius	Clearwinged grasshopper	Coastal and subcoastal eastern Australia
<i>Praxibulus</i> spp.	Yellow-bellied grasshoppers	Southeastern Australia
<i>Fipurga crassa</i> Sjöstedt	Dimorphic grasshopper	Southeastern Australia
<i>Urnesia guttulosa</i> Walker	Salt and pepper grasshopper	Semi-arid interior of Australia

at daybreak. Emigrants may breed successfully and continue the outbreak, but Australian plague locust outbreaks typically dissipate within a few generations. Thus, its notoriety is based more on the frequency of occurrence than the length of the plague. Sometimes migration proves to be deadly for locusts, as their dispersal is largely determined by strong winds associated with weather fronts or low pressure systems. Low pressure is often indicative of rain, which works to the advantage of insects requiring green grass for breeding, but sometimes locusts are deposited in lakes or the ocean, causing massive mortality. Also, though it is less evident, the progeny of some migratory locusts return from the invaded areas to their regions of persistence, helping to re-establish the potential for new outbreaks.

In the south, the cool winters inhibit development and no egg laying occurs for about three months. Egg deposition typically occurs in hard, packed soil or stony areas. In the warmer north, the interruption in reproduction is shorter. Irrespective of location, however, at the start of the spring the majority of the population is usually in the egg stage, and some diapause occurs. This locust has five or six nymphal instars after hatching, which requires (in total) 3–5 weeks. Males of Australian plague locust measure about 25–30 mm long, females 30–42 mm. Adults of this species are distinguished from other common locusts by the presence of a dark spot at the tip of the hind wing. The adult requires only about 2 weeks to mature, and then deposit eggs. Eggs are deposited in the soil at a depth of 6–8 cm. If the weather is favorable and no

diapause occurs, eggs can hatch in as little as 2 weeks. Females deposit two to three egg pods, each containing about 50 eggs. Often females lay large numbers of pods in the same area (egg beds), probably because soil moisture conditions are appropriate. If the rainfall is concentrated into a brief period (typically summer, but winter in some locations) the population is limited to a single generation, but if rainfall continues (e.g., spring and autumn), up to four generations may occur. It is these multiple generations per year that can result in rapid population increase and development of a plague.

Spur-Throated Locust, *Austracris guttulosa* (Walker)

This tropical species occurs widely in Australia and nearby islands, north to the Philippines. Unlike most of Australia's locust and grasshoppers, which survive the inclement periods in the egg stage, this species undergoes reproductive diapause. Thus, it fails to reproduce during the dry season, but commences egg production with the onset of the monsoons in the spring. Additional rain is needed for good egg and nymph survival. As noted previously, the egg stage does not undergo diapause and requires warm conditions in order to develop. A period of quiescence is possible, however, and egg hatch can be delayed for a month if moisture is absent.

This species is distinguished by the presence of a large spine between the front legs, and its large size. Males are 55–65 mm in length, females 70–80 mm long. This species lays up to 160 eggs in a pod, and up to five pods within its life span. It does not favor oviposition in egg beds, though barren areas are favored. Areas along roadways and irrigation ditches often are favored oviposition sites. Eggs require 18–30 days to hatch. Nymphs can be found at high densities, but they do not form marching bands. Duration of the nymphal stage is 1–2 months. There are 6–8 instars. The adults mature at the end of summer. Only one generation develops per year.

Outbreaks of spur-throated locust are infrequent, and initially are quite confined in area. Population dynamics are not well understood, but abnormally high summer rainfall is thought to precede population increases. If vegetation becomes dry, adults are more likely to migrate. After spending the dry winter months in a rather sedentary manner, roosting in trees or other tall vegetation, the adults become active in the spring and may disperse and expand the outbreaks. The populations cannot thrive without wet conditions, however, so except during outbreaks it is largely confined to the wet northern regions. Grasses are the principal host during the early instars. As summer habitats dry up, swarms disperse to winter habitats, which are woodlands and cultivated crops. Because the adult stage persists through the winter until mid summer, it can easily damage a wide range of winter crops (wheat, barley, millet) and summer crops (sunflower, soybean, cotton, sorghum), and others. The adults tend to feed during the day, and roost in trees at night.

Control of this species is directed at the adult stage, which is sedentary in winter and therefore easy to assess and treat with insecticides. Once the adults disperse, egg laying is scattered, so treatment of nymphs is difficult.

Migratory Locust, *Locusta migratoria migratorioides* (Reiche & Fairmaire)

Widely distributed in the Australasian region, this is a diapause-free insect that inhabits the mild, mostly coastal and subcoastal regions of Australia, and cannot survive the colder regions of southern Australia. Two (in temperate areas) to four (in tropical areas) generations are produced per year. They are primarily grass feeders, attacking grass pastures and grass crops such as sugarcane, sorghum, maize, and wheat.

This large, heavy-bodied species measures about 45–55 mm in length for males, and 55–65 mm for females. Females commonly oviposit in groups,

resulting in “egg beds” that contain numerous egg pods. A pod contains about 50–60 eggs, with females producing 3–5 pods. Eggs require 11–15 days to hatch. There are about six instars, and this insect requires approximately 30 days to attain maturity.

Changes in weather precipitate outbreaks of this species, resulting in gregarization. Increases in winter rainfall and decreases in summer rain are the normal triggers. However, forest removal and pasture improvement has fostered winter breeding in some areas, and provided good sites for oviposition. It was not until the extensive clearing of native vegetation of the central highlands of Queensland that migratory locust became a pest, as pastures and crops have become important food resources.

Migratory locust is less dispersive than many other locusts, and nighttime flights are lacking, so development of outbreaks proceeds slowly. The swarms are unusually cohesive, however, and characterized by a low, tumbling or rolling progression. Once the swarms leave habitat suitable for breeding, they collapse. Duration of outbreaks is 10–20 generations over 4–5 years, which is longer than some other locusts but shorter than exhibited by the same species in Africa and the Philippines (7–13 years). A wide range of crops are damaged by migratory locust, and damage can be quite severe, but due to the limited dispersiveness it tends to be a regional concern rather than a national problem.

Control of migratory locust is feasible if properly timed because, during the period of gregarization, the populations are confined to relatively small areas. If detected during the period of gregarization, suppression with chemical insecticides, using aerial or ground application technology, is quite efficient and economical.

Wingless Grasshopper, *Phaulacridium vittatum* (Sjöstedt)

Wingless grasshopper is actually a species complex, consisting of *Phaulacridium crassum* Key

(though much less important and confined to southwestern Australia) in addition to *P. vittatum*, though the presence of *P. crassum* is often overlooked. It is found in the cooler, temperate areas of Australia. Wingless grasshopper has only one generation per year. Eggs are deposited in the fall, undergo diapause and hatch in the spring. Egg pods contain only about 12 eggs per pod, considerably less than the aforementioned locusts, which usually produce pods of 50 or more eggs. However, they may produce 12–16 pods. There are five instars during the summer months.

Males of wingless grasshopper are about 8–12 mm in length; females are 12–18 long. Despite the name given these grasshoppers, wingless grasshopper is short-winged under most pasture conditions and often long-winged in woodland and garden conditions.

Wingless grasshopper problems were not known in Australia until about 1935, and were not recorded as a severe problem until 1979, but are increasing in severity. This grasshopper normally feeds on broadleaf plants in woodlands and pastures, and though present, is not common in natural woodlands, probably due to shortage of suitable food. With European settlement came land clearing and introduction of grazing animals that depleted the native grasses. Accidentally introduced and deliberately introduced broadleaf plants soon replaced native grasses; the broadleaf plants proved to be very suitable food for wingless grasshoppers. However, it was not until about 1945, when subterranean clover (a winter-active plant) was planted into pastureland, and fertilized, that wingless grasshopper became a regular problem. Addition of other legumes (perennial clover in southeastern Australia and alfalfa [lucerne] in southwestern Australia) during the summer exacerbated the grasshopper problem by providing a continuous suitable food supply. It also attacks crops such as sunflowers, sweet corn, potatoes, grapes, ornamentals, and trees. Movement of these grasshoppers is unlike that of most locusts. The dispersing assemblages are described

as streaming, and as formation of loose bands. They occur when food is depleted, which often is associated with hot weather.

The continuous availability of food predisposes improved pastures to wingless grasshopper problems, but outbreaks also involve drought, overgrazing, and insect parasitic nematodes. When droughts occur, the carrying capacity of pastures is exceeded, and overgrazing occurs. Overgrazing, and opening of the canopy, initially favors grasshopper survival, and drought inhibits mermithid nematodes (*Amphimermis acridiorum*, *Agamermis catadecaudata*, *Mermis quirindiensis*, *Hexamermis* spp.) from parasitizing wingless grasshoppers. When rainfall again increases, the activity of the nematodes increases correspondingly, resulting in grasshopper suppression.

Wingless grasshoppers can be managed if continuous vegetative cover is maintained, particularly an increase in grasses at the expense of legumes. Natural enemies, particularly mermithid nematodes, are important and favored by good vegetative cover and high moisture. Reforestation, especially of ridge lines where grasshopper survival is favored, will reduce grasshopper numbers. Overgrazing should be avoided.

Management Strategies

Many of Australia's locust problems result from changes in precipitation, and there is little to be done about weather other than careful weather monitoring. However, it is imperative to understand how different species respond to precipitation, and to be alert for impending problems. Population monitoring can be difficult when dealing with swarming insects, as it is easy to overlook mobile swarms until they move to cultivated areas. Once increasing populations are detected, it is advisable to decrease the threat of economic loss from migrating swarms by eliminating the problem before it fully develops. This usually requires decreasing the pest population by 50% in each generation, even when the pests are limited to

waste areas and not immediately threatening. This is a departure from past practices, when populations were treated primarily when they moved into crop or pasture areas. The reasoning behind not treating locusts until the threat was imminent was that many swarms would collapse due to changes in weather without ever doing damage to crops. However, to allow the populations to develop unimpeded meant that the resultant populations could be quite large and difficult to control. Locust and grasshoppers are treated with liquid insecticides by air and ground; poison baits also are used, especially for wingless grasshopper. As noted above, some species become problems following changes in land management, mostly land clearing for crops or replacing grasses with more susceptible plants. Thus, some problems can be alleviated by wise land use.

- ▶ [Grasshoppers, Katydid and Crickets \(Orthoptera\)](#)
- ▶ [Diseases of Grasshoppers](#)
- ▶ [Grasshoppers and Locusts as Agricultural Pests](#)
- ▶ [Grasshopper and Locust Pests in Africa](#)
- ▶ [Grasshopper Pests in North America](#)
- ▶ [Grasshoppers of the Argentine Pampas](#)

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Grasshopper Pests in North America

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In North America, there is not much effort to label grasshopper species as “locusts,” as is done elsewhere in the world, though the Central American locust, *Schistocerca piceifrons* (Walker), occurring in Mexico and southward into South America, is a notable exception. At least one additional species (*Melanoplus sanguinipes* [Fabricius]), perhaps others, would qualify as locusts using the standards of orthopterists elsewhere (see “Grasshopper and locust pests in Australia” for discussion of this topic). Also, the crop-damaging shieldback katydids or long-horned grasshoppers (Orthoptera: Tettigoniidae) are often called crickets, but functionally affect crops and rangeland like grasshoppers, or maybe even locusts, so they are mentioned below even though they are technically neither grasshoppers nor crickets. With few exceptions, North American grasshoppers considered to be pests are in the order Orthoptera and family Acrididae; the exceptions are lubber grasshoppers (Romaleidae) and the aforementioned tettigoniids.

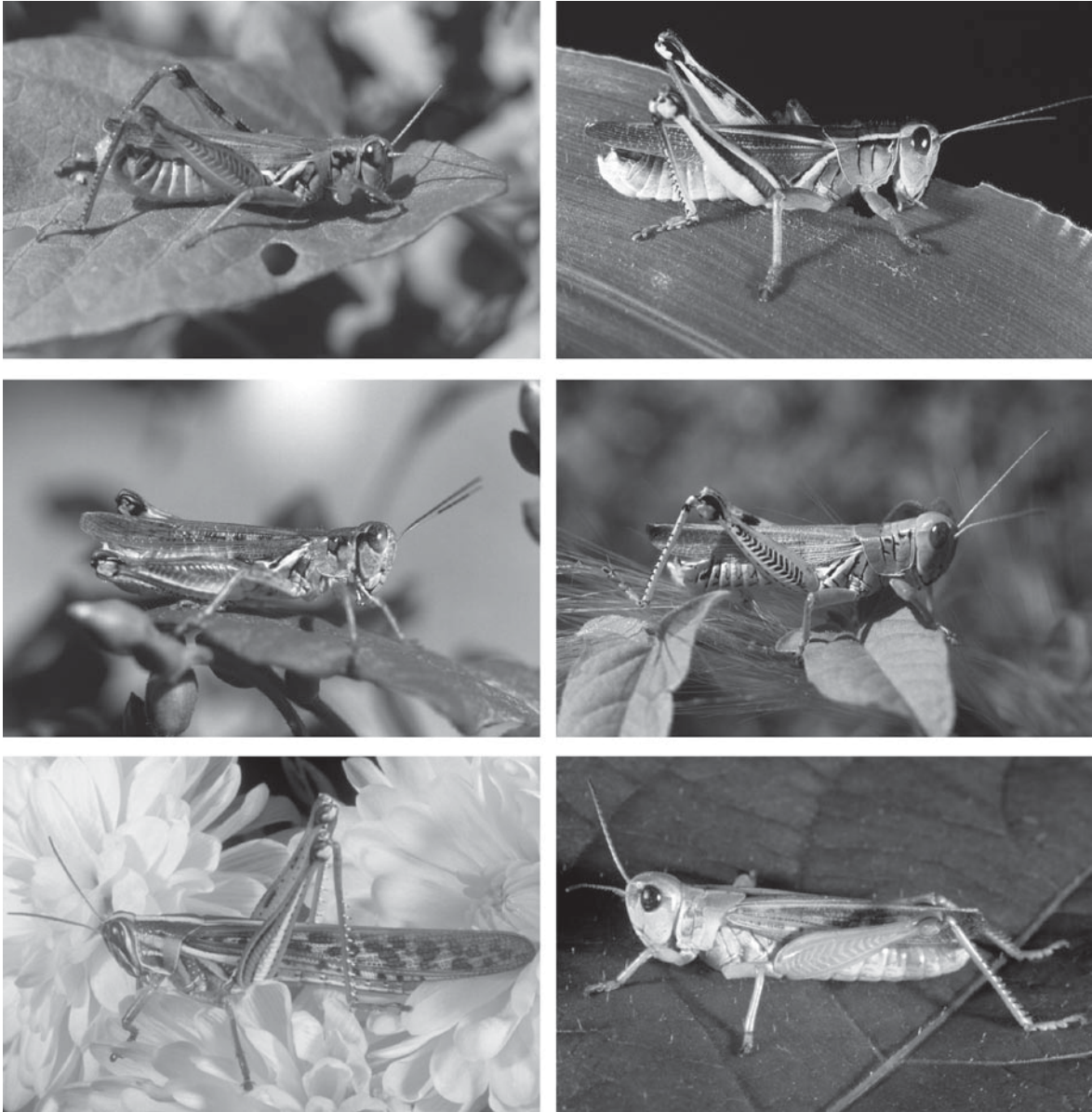
Grasshoppers attack nearly all grain, forage, field, fruit, and vegetable crops. Ornamental plant crops are also damaged in both nurseries and the landscape when grasshoppers are especially abundant, but less often than other crops due to their common location in or near urban and suburban areas, away from habitats conducive to grasshopper outbreaks. Rangeland is the natural habitat of an immense assemblage of grasshoppers, and more than any cultivated crop, it is affected by grasshoppers. Sometimes the grasshoppers cause injury when the plants are quite small and easily defoliated, or stressed by lack of precipitation. However, mature or nearly mature crops are commonly damaged when grasshoppers enter crops along the field margins, feeding on the foliar or reproductive structures. Unhindered, they may eventually spread over the entire field. On rangeland, grasshoppers are

often found throughout the environment, though the elements of the species assemblage vary according to topographic and host plant characteristics.

Ragged leaf tissue or complete defoliation of plants along field margins is suggestive of grasshopper problems. Normally the grasshoppers are readily visible, though the adults of some species sometimes disperse to distant areas with good cover, re-invading the crop daily.

Identity of Crop-Feeding Grasshoppers (Families Acrididae, Romaleidae, Tettigoniidae)

Melanoplus spp. (family Acrididae) grasshoppers are the most important grasshopper pests of crops in North America. The principal pests in North America are two-striped grasshopper, *Melanoplus bivittatus* (Say); differential grasshopper, *M. differentialis* (Thomas); red-legged grasshopper, *M. femurrubrum* (De Geer); and migratory grasshopper, *M. sanguinipes* (Fabricius) (Fig. 34). In northernmost states of the United States and the Prairie Provinces of Canada, Packard’s grasshopper, *M. packardi* Scudder, can be locally important, as can other species including some band-winged species, particularly the clear-winged grasshopper, *Camnula pellucida* (Scudder). In southeastern North America, eastern lubber grasshopper, *Romalea microptera* (Beauvois) (family Romaleidae) and American grasshopper, *Schistocerca americana* (Drury) (Acrididae) are locally important. In Mexico and Central America, the Central American locust, *Schistocerca piceifrons* Walker displays locust-like behavior. Overall, migratory grasshopper is the most damaging species, and though not usually called a “locust,” nonetheless it is a strong flier and has gregarious tendencies. Other species can surpass the abundance of *M. sanguinipes* locally, and others display gregarious and dispersive tendencies, but none compare on a regional basis to this widespread grasshopper. In the mountain and intermountain areas of western North America, certain shieldbacked katydids (family



Grasshopper Pests in North America, Figure 34 Some common crop-feeding grasshoppers: *upper left* – red-legged grasshopper, *M. femurrubrum* (De Geer); *upper right* – two-striped grasshopper, *M. bivittatus* (Say); *center left* – migratory grasshopper, *Melanoplus sanguinipes* (Fabricius); *center right* – differential grasshopper, *M. differentialis* (Thomas); *lower left* – American grasshopper, *Schistocerca americana* Drury; *lower right*, clear-winged grasshopper, *Camnula pellucida* (Scudder) (photos by J.L. Capinera).

Tettigoniidae) are grasshopper- or locust-like, though flightless. The most important is Mormon cricket, *Anabrus simplex* Haldeman, but sometimes coulee cricket, *Peranabrus scabricolis* (Thomas) is abundant enough to be damaging to crops.

Life Cycle of Crop-Feeding Grasshoppers

Most grasshoppers pass the winter in the egg stage and have a single generation per year, but in

southern areas *M. sanguinipes* and *S. americana* may have additional generations, and *S. piceifrons* has two generations. Grasshoppers typically hatch from eggs in the spring or early summer. The species differ slightly in the timing of their hatch, and the hatching is not synchronous, so different stages may be found throughout the summer. Grasshoppers usually molt five or six times and require about 5–6 weeks to reach maturity. About two weeks later they commence egg laying, and continue to deposit eggs, in clusters called pods, containing 20–100 eggs per pod until they are killed by cold weather. Eggs, which are deposited in the soil, are not normally affected by weather, but are susceptible to damage by tillage and certain predatory insects. When the young grasshoppers hatch in the spring they are susceptible to inclement weather (low temperatures and rainfall). Throughout their lives, grasshoppers are attacked by parasitic insects, diseases, and insect and vertebrate predators. These natural enemies can suppress grasshoppers locally, but often only after the grasshoppers attain very high and damaging densities. Plants differ greatly in suitability for grasshopper survival and growth. In general, these pests prefer broad-leaf plants, not grasses, but the cultivated grains, especially wheat and corn, are highly attractive and suitable for grasshopper survival.

Management of Crop-Feeding Grasshoppers

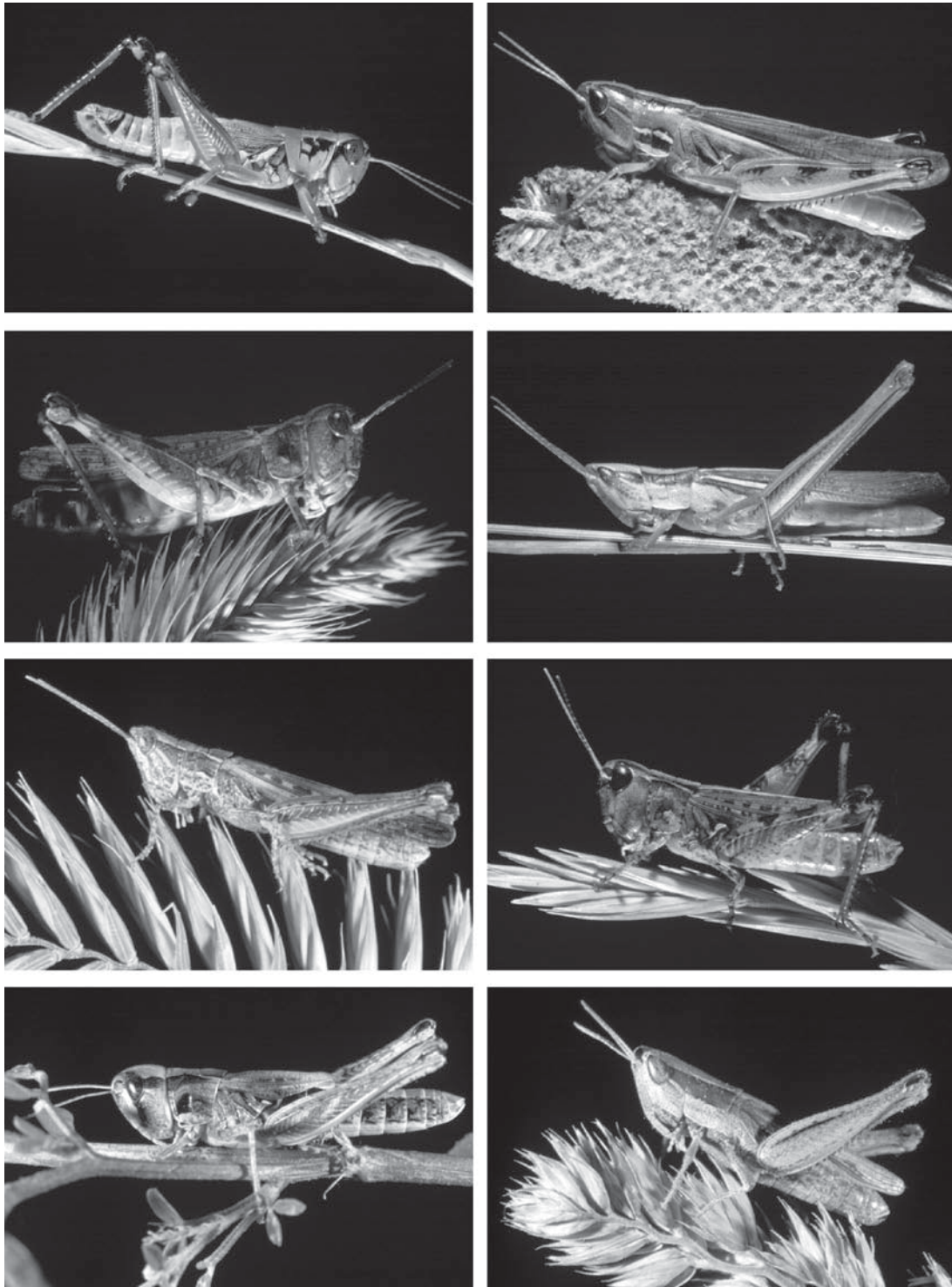
The need for management is most directly related to grasshopper density. As a general rule, when grasshopper densities are 15 or more per square yard (18 per square meter) within a grain field or more than 40 per square yard (48 per square meter) along field borders, economic damage will ensue. With densities of 8–14 per square yard (10–17 per square meter) within a field, or 20–40 per square yard (24–48 per square meter) along field borders, the crop is at risk. These lower densities can prove damaging when the grasshoppers are more mature (larger), the crop is young, or the crop is stressed by lack of soil moisture. Thus, for winter wheat culture

(the crop is planted in the late summer, becomes dormant in the winter, and completes its growth in the spring), the lower thresholds for treatment are used because the grasshoppers are mature in the autumn when the wheat is young.

Grasshopper problems most often originate outside the crop field (though planting into wheat stubble or fields that were previously weedy can be exceptions), so treatment of weedy or waste areas (sometimes rangeland) surrounding a field with an insecticide can be an effective approach to prevent invasion of the crop (Fig. 36). Liquid formulations of contact insecticides are usually used for this approach. Alternatively, treatment of the crop margin (about 150 feet [47 m] of the border areas) will kill most grasshoppers as they disperse into a crop. Fast-acting contact insecticides applied to foliage or soil, contact insecticides applied to wheat bran bait, and systemic insecticides applied to the foliage or seed are some approaches used to deliver toxicants to grasshoppers. In some areas, farmers commonly plant higher densities of grains along the field margins if they anticipate grasshopper problems, to allow for some crop loss.

Identity of Rangeland Grasshoppers

Rangeland occurs mostly in arid and semi-arid regions, which corresponds roughly with the western half of the United States and Canada. This habitat consists of grasses and broadleaf plants (forbs), and sometimes shrubs, but not usually trees. The North American grasshoppers affecting rangeland sometimes are the same as those affecting crops, particularly *Melanoplus sanguinipes*, and to a lesser degree *Camnula pellucida* and *Anabus simplex*, which can be abundant and damaging in both environments. Most often, however, the abundant species on rangeland are not the same as those affecting crops (Fig. 35), even when irrigated crops are surrounded by rangeland, providing good opportunity for rangeland species to disperse into crops. Often when the crop-feeding



Grasshopper Pests in North America, Figure 35 Some common rangeland grasshoppers: *upper left* – *Phoetaliotes nebrascensis* Thomas; *upper right* – *Amphitornus coloradus* Thomas; *second row, left* – *Aulocara elliotti* Thomas; *second row, right* – *Mermiria bivittata* Serville; *third row, left* – *Cordillacris occipitalis* Thomas; *third row, right* – *Ageneotettix deorum* Scudder; *bottom left* – *Aeropedellus clavatus* (Thomas); *bottom right* – *Opeia obscura* Thomas (photos by J.L. Capinera).



Grasshopper Pests in North America, Figure 36 Damage to the edge of a winter wheat field caused by grasshoppers. Grasshoppers dispersed from the residue of a previous weedy wheat crop (designated “a”), to the margin of a young wheat crop, where they destroyed the seedlings (location “b”). The undamaged wheat is in the foreground (location “c”).

species are present on rangeland, it is due to disturbance and growth of weedy vegetation instead of native grasses or forbs. Floral disturbance can occur following overgrazing, excessive trampling of the soil (a common occurrence around livestock water tanks), or other factors such as outbreaks of white grubs (Coleoptera: Scarabaeidae) which kill the grasses, allowing weeds to invade. The species most commonly associated with rangeland damage are listed in the table.

North America has a surprisingly rich fauna on rangeland, with a large number of species contributing to “grasshopper” population outbreaks (Table 10). About 375 species of grasshoppers are found inhabiting North American rangeland. About a third are considered to be pests, but nearly all the rest are innocuous, either due to their dietary habits or their lack of abundance. Most outbreaks on rangeland consist of an assemblage of species, with the species varying from place to place, and some peaking early in the outbreak cycle, and others later. Another interesting aspect of rangeland grasshopper problems is that some species have proven to be destructive at one time or another, only to fade into oblivion for many years (e.g., high plains grasshopper, *Dissosteira longipennis* Thomas).

Interestingly, not all rangeland-dwelling grasshoppers are pests. Many species do not feed on grasses or other important livestock food (the “grass” hopper designation, like many common

names, is not entirely accurate). More importantly, some species feed selectively on rangeland plants that are considered to be toxic to livestock (e.g., *Hesperotettix viridis* [Scudder] on snakeweed, *Gutierrezia sarothrae* and *microcephala*) or competitors for moisture or light with more nutritious species (e.g., *Hypochlora alba* Dodge on sagebrush, *Artemisia* spp.). Even *Anabrus simplex*, long viewed as a scourge of farmers and ranchers in the Rocky Mountain region, has been shown to be relatively innocuous on rangeland under normal conditions. It avoids grasses, except for seed heads, preferring to feed on flowers and foliage of low-value broad-leaf weeds. Only under severe drought conditions, when there is almost no forage available for livestock, is this insect a pest of rangeland.

Life Cycle of Rangeland Grasshoppers

The biology of rangeland grasshoppers and crop-feeding grasshoppers is, in most cases, about the same. However, a few rangeland species overwinter as nymphs, and in southernmost areas adults are sometimes found in the winter. Natural enemies are more important in the survival of rangeland grasshoppers because insecticides are rarely used, and therefore beneficial insects are more abundant. Tillage is not normally practiced on

Grasshopper Pests in North America, Table 10 Grasshoppers commonly damaging to rangeland in North America

Family	Subfamily	Scientific name	
Acrididae	Melanoplinae	<i>Melanoplus sanguinipes</i> Fabricius	
		<i>Melanoplus infantilis</i> Scudder	
		<i>Melanoplus devastator</i> Scudder	
		<i>Melanoplus occidentalis</i> Thomas	
		<i>Oedaleonotus enigma</i> Scudder	
		<i>Phoetaliotes nebrascensis</i> Thomas	
		Gomphocerinae	<i>Aulocara elliotti</i> Thomas
			<i>Aulocara femoratum</i> Scudder
			<i>Ageneotettix deorum</i> Scudder
			<i>Aeropedellus clavatus</i> (Thomas)
	<i>Amphitornus coloradus</i> Thomas		
	<i>Phlibostroma quadrimaculatum</i> Thomas		
	<i>Opeia obscura</i> Thomas		
	<i>Cordillacris occipitalis</i> Thomas		
	<i>Mermiria bivittata</i> Serville		
	<i>Chorthippus curtipennis</i> Harris		
	<i>Psoelessa delicatula</i> Scudder		
	<i>Eritettix simplex</i> Scudder		
	Oedopodinae	<i>Camnula pellucida</i> Scudder	
		<i>Trachyrhachys kiowa</i> Thomas	
<i>Dissosteira longipennis</i> Thomas			
<i>Dissosteira spurcata</i> Saussure			
<i>Encoptolophus costalis</i> (Scudder)			
<i>Metator pardalinus</i> Saussure			
<i>Trimerotropis pallidipennis</i> Burmeister			
Tettigoniidae	Tettigoniinae	<i>Anabrus simplex</i> Haldeman	

rangeland, so there is less soil disturbance that might result in destruction of egg pods. In contrast to crop environments, egg pods in rangeland are less likely to be concentrated along field margins, as often occurs with crops that have weedy margins along fences and irrigation ditches, which are favored by grasshoppers for oviposition.

A notable aspect of rangeland grasshopper biology is the relatively synchronous increase or decrease in abundance of different species in the grasshopper species assemblage. Population cycles

are related to weather, host plant abundance, and natural enemy abundance. Generally, hot and dry weather are responsible for increase in population density in northern areas, where grasshoppers are limited by inadequate daily warmth during the summer days, or a short summer season. In southern regions, however, warmth is not so limiting, and the lack of abundant nutritious vegetation is more constraining, so rainfall during the spring (which determines the availability of host plants) is a controlling variable.

Grasshoppers need to control their body temperature if they are to feed, develop, and reproduce optimally. Patches of bare soil allow grasshoppers a site to elevate their body temperatures by basking in the sunshine, and so many species thrive where the vegetation density is low enough to allow basking. However, if there is too much vegetation-free space they cannot meet their nutritional needs. Thus, there are trade-offs between not enough and too much vegetation, and this is made more complex by the differing dietary needs (different host preferences and amount of vegetation required) of different species of grasshoppers. Competition for the most suitable food resources is more frequent and important than generally acknowledged. Many observers fail to recognize that grasshopper populations can be under nutritional stress when there is still relatively abundant vegetation on rangeland because it may be difficult to discern that the most favored plant species have already been consumed.

Rangeland differs greatly in suitability for plants and grasshoppers. Precipitation is the major determinant of plant species occurrence and in plant size, but temperature effects, due both to altitude and latitude, are important. The dominant species of grasses, and their biomass, change with location. For example, the dominant grasses are various *Adropogon*, *Agropyron*, *Stipa*, *Panicum*, and *Calamovilfa* spp. in the eastern areas of the Great Plains of North America, but are replaced by *Bouteloua* and *Stipa* spp., *Koleria scoparius*, and *Agropyron smithii* centrally, and *Bouteloua gracilis*, *Agropyron smithii*, and *Buchloe dactyloides* in more western regions. There is also a general decrease in the average height of vegetation as one moves from east to west in the Plains region, so these regions are denoted as tallgrass, mixedgrass and shortgrass regions, respectively. In the intermountain region, bunchgrasses such as *Agropyron spicatum* and *Bromus* spp. predominate. As noted in the table, species from three subfamilies, Melanoplineae, Gomphocerinae, and Oedopodinae, are important

rangeland grasshoppers. Generally, members of each subfamily occur together, but the proportion in each subfamily is not constant among different localities. Though tallgrass and mixedgrass environments are dominated by grasshoppers in the subfamily Melanoplineae (spurthroated grasshoppers), shortgrass sites are dominated by grasshoppers in the subfamily Gomphocerinae (stridulating slantfaced grasshoppers).

Management of Rangeland Grasshoppers

The principal challenges confronting rangeland grasshopper management are the extensive areas to be managed, and the low value of the forage. Both factors limit the amount of money that can be expended per unit area, and preclude using anything but the most economic pest suppression measures in most instances.

Insecticides are generally used for suppression of grasshoppers, and usually area-wide campaigns are instituted with the help of government agencies because when a problem develops, it normally occurs over a large geographic area. Large, specially equipped aircraft often are used to treat large land areas with liquid insecticide, and sometimes ultra low volume (ULV) insecticides are applied because they are applied undiluted and at very low application rates, which means that more land area can be treated between refills of the spray tanks. This reduces time and labor costs considerably. A common alternative to liquid insecticide application is to apply insecticide-treated bran bait using aircraft. This has the advantage of being more selective, because although many species of grasshoppers will feed on bait and perish, many other insects are unaffected.

When initiating grasshopper suppression on rangeland, the common biological considerations are the grasshopper species involved, their density, and the stage of development. Not all grasshoppers are damaging, and some are quite a lot more damaging than others. A density of 10–15

grasshoppers per square yard (12–18 per square meter) is normally needed to justify treatment (hopefully adjusted for the species involved). Not all grasshoppers hatch synchronously, and applications are timed to allow for all, or at least most, of the hoppers to hatch and thus come into contact with the insecticide. Waiting too long, however, is counterproductive because they will have already consumed a significant amount of livestock forage.

Grasshopper suppression operational considerations are as important as biological considerations in determining the feasibility of area-wide grasshopper suppression. Operational considerations usually involve population sampling to delineate areas that need treatment over an extensive area, including areas that are “sensitive” and cannot be treated; obtaining and scheduling the aircraft and toxicants; organizing ranchers to obtain funds and permission for treatment; and establishing a mechanism of effective mapping, communication, and rancher and public information, including news releases.

Livestock grazing pressure is often suggested as an element that affects grasshopper abundance. Historically, overgrazing by livestock disrupted the native flora, especially in the eastern regions of the Great Plains, allowing invasion of weeds more suitable for grasshoppers. Also, grazing can result in more barren soil, which is attractive to grasshoppers for thermoregulation and oviposition. Thus, grasshopper problems are sometimes attributed to overstocking of livestock. While overgrazing should be avoided for several reasons, including the ability to cause grasshopper problems under certain conditions, some rangeland can tolerate quite a lot of grazing pressure, and even benefit from grazing by livestock. Extensive research has demonstrated a positive correlation between vegetation abundance and grasshopper abundance in the arid regions of the Great Plains where vegetation is shorter or less abundant, and grasshoppers tend to be food-limited. As noted previously, these areas are dominated by gomphocerine species, whereas other areas have

proportionally more melanoplinae and oedopodinae. Where gomphocerine grasshoppers predominate, moderate or heavy grazing can reduce the abundance of grasshoppers relative to ungrazed or lightly grazed areas.

- ▶ [Grasshoppers, Katydid and Crickets \(Orthoptera\)](#)
- ▶ [Diseases of Grasshoppers](#)
- ▶ [Grasshoppers and Locusts as Agricultural Pests](#)
- ▶ [Grasshopper and Locust Pests in Africa](#)
- ▶ [Grasshopper and Locust Pests in Australia](#)
- ▶ [Grasshoppers of the Argentine Pampas](#)
- ▶ [Migratory Grasshopper](#)
- ▶ [Red-Legged Grasshopper](#)
- ▶ [Two-Striped Grasshopper](#)
- ▶ [Differential Grasshopper](#)
- ▶ [American Grasshopper](#)
- ▶ [Mormon Cricket](#)

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Grasshoppers

The suborder Caelifera of the order Orthoptera.

- ▶ [Grasshoppers, Katydid and Crickets](#)

Grasshoppers and Locusts as Agricultural Pests

STEVEN ARTHURS

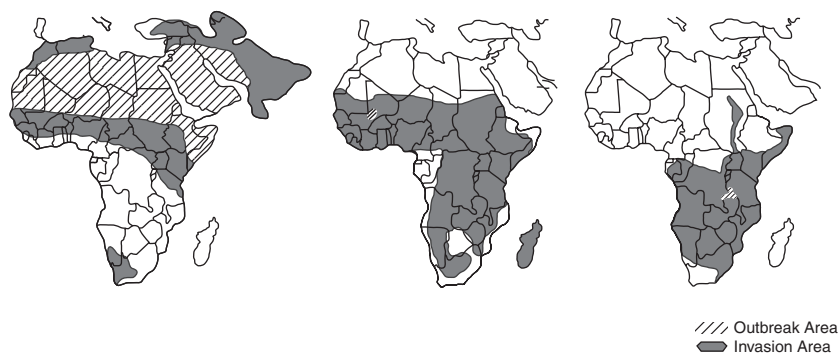
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Orthoptera represent a large insect order with a worldwide distribution. Taxa in the superfamily Acridoidea are commonly either called grasshoppers or locusts. This division separates insects that readily aggregate in persistent bands or swarms in response to increases in intra-specific density (“locusts”) from those that show no such change in behavior (“grasshoppers”).

Economically, socially and historically, locusts and grasshoppers are one of the most destructive pests. This century alone, there have been eight major plagues of the desert locust *Schistocerca gregaria* Forskål. Agricultural production across 29 million km² in Africa and south-western Asia is threatened during plague periods.

Although the desert locust is probably the most infamous of all acridoid pests, a suite of other locust and grasshopper species and species assemblages cause more frequent and cumulatively far more significant damage (Fig. 37) throughout Africa,

Australia, the middle East and parts of Asia and North and South America. In Southern Africa, the Brown Locust, *Locustana pardalina* Walker, has necessitated frequent widespread control measures over the last 45 years. In central and southern Africa, the Red locust, *Nomadacris septemfasciata* Serville; in Sudan, the tree locust, *Anacridium melanorhodon* Walker; in Madagascar, the migratory locust, *Locusta migratoria migratorioides* Reiche and Fairmaire; and in semi-arid territories around the Mediterranean, the Moroccan locust, *Dociostaurus maroccanus* Thunburg, all require regular control measures to prevent the formation of migratory swarms. Although less mobile, grasshoppers such as *Melanoplus sanguinipes* Fabricius within North America, and *Phaulacridium vittatum* eastern Sjöstedt within Australian grasslands also require frequent control measures. Grasshopper complexes within the semi-arid African Sahelian belt such as *Aiolopus simulatrix* Walker, *Kraussaria angulifera* Krauss, *Acrotylus* spp. and *Oedaleus senegalensis* Krauss, as well as those from the more humid West Africa zone, notably *Hieroglyphus daganensis* Krauss and *Zonocerus variegatus* L., represent a continuing threat to the food security of many rural communities. Even today, locusts and grasshopper outbreaks cause problems in every major continent of the world.



Grasshoppers and Locusts as Agricultural Pests, Figure 37 Outbreak and invasion areas of some African locusts. The locusts tend to persist in the outbreak areas, and when conditions for reproduction are favorable the locusts multiply and spread to invasion areas. Desert locust, *Schistocerca gregaria* (left map), has a relatively large area of persistent habitation, consisting of most of northern Africa and the Arabian Peninsula, whereas African migratory locust, *Locusta migratoria migratorioides* (center map), and red locust, *Nomadacris septemfasciata* (right map) have small areas of origin in northwest and south central Africa, respectively.

Grasshopper and Locust Control

The task of combating locust and grasshopper plagues usually falls to the national crop protection services in cooperation with regional control organizations such as the Desert Locust Control Organisation for Eastern Africa (DLCO-EA). In recent years, this challenge has largely relied on the application of synthetic chemical insecticides applied as baits or dusts, and more recently and more commonly, sprayed as ultra low volume (ULV) oil formulations. The adoption of recent environmental monitoring technologies means the breeding habitats of some migratory locusts and grasshoppers can be monitored using satellite imagery as well as aerial and ground surveys. Prevention of upsurges by early intervention is now normally the preferred approach. Modeling and recent improvements in forecasting have helped some governments, donors, researchers and locust officers predict potential outbreak periods and contain the problem of outbreaks at the source level. For example, the goal of the FAO's Emergency Prevention System (EMPRES) for Transboundary Animals and Plant Pests and Diseases is to minimize the risk of locust plagues emanating from the central region of the desert locust distribution area through timely, environmentally sound interventions. However, in many rural areas, such as the Sahel, where access to pesticides is limited, traditional methods such as using smoke to repel arriving swarms or driving migrating hopper bands (immature locusts) into steep-sided ditches from which they cannot escape continue to be employed.

Chemical Control

Locust and grasshopper control has evolved since the middle of the twentieth century. Until the 1970s, most control operations used persistent organochlorine insecticides, with dieldrin favored for desert locust control due to its effectiveness at low doses and in barrier sprays. There is circumstantial evidence supporting the effectiveness of such

insecticides in suppressing plagues, with the period 1930 to 1960 representing the longest known inter-plague period for the desert locust. Dieldrin, however, is now banned in most countries due to environmental damage, negative effects on human and animal health and legislation originating in the USA concerning the stockpiling of toxic wastes. The use of carbamate and organophosphorous such as bendiocarb, malathion and fenitrothion began in the 80s, and more recently pyrethroid insecticide compounds such as deltamethrin have been used. However, although these products have a lower mammalian toxicity (most insecticides currently used for locust control are classified as "moderately hazardous" to human health based on acute oral and dermal toxicity studies in rats) their reduced persistence makes them less effective than dieldrin, and repeated applications are often necessary to achieve the same level of control. This is of particular importance in recession (permanent sites of locust breeding) areas where the requirements for repeat applications have resulted in increased control costs and amounts of pesticides used. Most recently, the phenylpyrazole compound fipronil has been promoted as a significant break-through in locust control, since it is effective and persistent at low doses. Fipronil was largely used in the half-million hectares treated against migratory locusts in Madagascar in recent years.

The most recent desert locust upsurge (1986–1989) and a simultaneous grasshopper outbreak in the West African Sahel triggered a massive emergency response from the international community. The problem was again countered by large-scale spraying of swarms as well as feeding and breeding sites. Nearly 14 million hectares in Africa alone were sprayed for locusts while additional millions of hectares were sprayed in the Sahel for grasshopper control. Total donor assistance was approximately \$250 million (U.S. dollars) and total costs including contributions from afflicted countries exceeded \$295 million (U.S. dollars). However, the value of recent desert locust control campaigns has been called into question. While crop losses caused by swarms during plague conditions may be high

(national pre-harvest losses due to grasshoppers in the Sahel have been estimated at 30% or more), overall yields may not be affected, as plague years are normally rainy and thus associated with better than average harvests.

As well as concerns over economic viability, the environmental and human health consequences of large-scale control campaigns using synthetic broad-spectrum insecticides in sensitive ecological areas (often representing breeding sources for many migratory acridid pests) has come under increasing scrutiny. For example, at the recommended rates for locusts and grasshoppers, fenitrothion is near the threshold where it can cause immediate death among birds. Chlorpyrifos and pyrethroids may reduce the biodiversity of honeybees, spiders and aquatic insects. Fipronil is highly toxic to certain birds, fish, terrestrial and freshwater invertebrates. Human exposure to pesticides during control operations can present problems during handling, or as a result of spray drift from operations, especially where protective clothing is not available or there is an unwillingness to wear it under hot field conditions. Local residents and nomadic pastoralists may also be affected directly through spray drift or through contamination of livestock, water or foodstocks.

Biological Control

There are numerous reports of natural enemies of grasshoppers and locusts. The principle groups consist of vertebrate and invertebrate predators which attack eggs, nymphs and adult insect, as well as insect parasitoids, parasitic nematodes and pathogens. In addition to natural control, recent research has led to the development of biopesticides based on entomopathogenic fungi.

Most locusts and grasshopper predators are generalists, and will attack a range of species, rather than any single host. Both nymphs and adults are attacked by various arthropods such as scorpions, spiders and solifugids and predaceous

insects like asilid flies, sphecid wasps, ants, mantids and ant lions, and also by many species of lizards, snakes and birds. Eggs are also attacked by larvae of bombyliid flies and various Coleoptera, chiefly tenebrionid larvae. Additionally, a number of naturally occurring diseases also suppress locust and grasshopper populations worldwide, including descriptions of spectacular epizootics by the *Entomophaga grylli* complex of fungal pathogens. There are, however, relatively few in-depth studies on the impact of grasshopper and locust natural enemies, especially for tropical species.

Although they merit conservation, indigenous natural enemies are often killed by non-selective chemical insecticides. This aspect, plus the concerns over the human health consequences of large-scale applications of chemical pesticides during recent locust campaigns, has led to recommendations by the World Bank and others to place locust and grasshopper control within the context of integrated pest management (IPM) programs. This has increased pressures to introduce biological control.

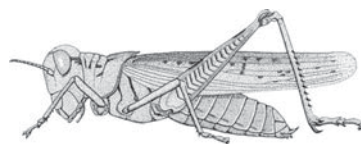
Although arthropod predators and parasitoids may hasten the end of plagues, apart from possibly controlling static grasshopper populations they cannot be manipulated, and migratory pests such as the desert locust are poor targets for classical biological control. However, pathogens can be manipulated for use as biological pesticides. Many locusts and grasshoppers are migratory pests and have characteristics amenable for control with microbial agents, (i) feeding and breeding take place outside the crop, often in conservation areas where high natural mortality can be expected to occur; (ii) as there is often public funding for control, high environmental values are involved in the purchasing decisions.

The major pathogen groups that have received interest as biological control agents of locusts and grasshoppers are bacteria, protozoa, entomopox viruses and fungi. The characteristics needed for a good agent include cheap and easy production, toxicological safety, host specificity and (given the existence of highly developed application technology)

the ability to be formulated and applied using currently available equipment. Commercial formulations of entomophilic nematodes are available, but their high cost and water requirements during application and infection restrict their use in most regions against locusts and grasshoppers.

The use of entomopathogenic bacteria against locusts and grasshoppers has received some attention. The non-sporeforming *Serratia marcescens* Bizio and *Pseudomonas aeruginosa* (Schroeter) Migula have high pathogenicity in laboratory cultures. However, disappointing field results and concerns over mammalian safety have precluded further investigation. Though it has a well-developed production technology, efforts to find strains of *Bacillus thuringiensis* that produce endotoxins with pathogenicity against locusts or grasshoppers have not yet been successful. Various protozoa are known to infect locusts or grasshoppers. Among the Microsporidia (Phylum Microspora), *Nosema locusta* Canning has received the most attention, possibly due to its easy and efficient *in vivo* production characteristics. *N. locusta* has been the subject of a number of inundative field trials against grasshoppers where its spores are typically incorporated into bait carriers. However, the release of such pathogens generally only causes modest reductions. Nevertheless, because *N. locusta* may reduce the rates of host development, fecundity and feeding, it is considered by some to be a candidate for long-term population suppression and low impact maintenance in IPM strategies. *N. locusta* is registered for grasshopper control within conservation rangeland areas in the USA.

The use of entomopox viruses (EPVs) against locusts and grasshoppers is also receiving attention. The most extensively studied is the rangeland grasshopper *Melanoplus sanguinipes* (Fig. 38) virus (MsEPV), which is considered to have some potential as a biocontrol agent on Canadian rangelands. However, field studies demonstrating effective control are limited and restrictions to their production *in vitro* and ability to be formulated in spray carriers suggest that using EPVs against locusts and grasshoppers currently



Grasshoppers and Locusts as Agricultural Pests, Figure 38 Migratory grasshopper, *Melanoplus sanguinipes* (Fabricius), an American grasshopper with locust-like dispersive behavior. (artwork, J. Mottern)

remains unlikely. Further investigations into the infectivity of the baculoviruses, such as the nuclear polyhedrosis viruses (NPVs), which have better production characteristics, may open up new opportunities.

Among pathogens, the entomopathogenic fungi are the easiest to be manipulated as biopesticides. They have the advantage over other pathogens because they are able to infect through the insect cuticle, thus avoiding the necessity of providing bait. Spores (conidia) of fungal pathogens are also lipophilic, favoring their formulation in the oil-based carriers that are typically applied as a low volume spray in locust and grasshopper control campaigns.

Over 700 species of fungi from approximately 90 genera are pathogenic to insects; however, only the deuteromycetes *Metarhizium* spp. and *Beauveria* spp. (class Hyphomycetes) currently fulfill the criteria required for a successful inundative biological control agent. The entomophthorean fungi, in particular members of the *Entomophaga grylli* (Fres.) Batko species complex, represent a group of obligate pathogens found in most areas of the world that have frequently been recorded decimating populations following epizootics. Although species in the *E. grylli* complex have been used successfully in some classical biocontrol introductions in the USA, difficulties with host specificity and *in vitro* mass production limit their application for inundative release.

Recent research programs have developed the fungal pathogen *Metarhizium anisopliae* var. *acridum* for the control of locusts and grasshoppers in Africa and Australia, and *Beauveria bassiana*

for grasshopper control in Canada. Currently the development of microbial-based pesticides follows the same procedures of testing and registration as the chemical ones. Ongoing technological research in these programs has resulted in significant advances in the *in vitro* production, storage and formulation characteristics of such pathogens and recently has been the focus of commercial scale efforts to produce available mycopesticide products. Accordingly, applied using conventional spraying equipment at rates of 0.5–5 l per hectare, mycopesticides have proven at least as effective as chemical insecticides against locusts and grasshoppers in a variety of ecological zones.

- ▶ [Grasshoppers, Katydid and Crickets](#)
- ▶ [Diseases of Grasshoppers and Locusts](#)
- ▶ [Desert Locust Plagues](#)

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Grasshoppers, Katydid and Crickets (Orthoptera)

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Members of the order Orthoptera are found at nearly all latitudes, though they are primarily tropical insects as judged by species diversity, which is greatest in warm areas. Most are known for their

well-developed hind legs and jumping abilities, but many are noteworthy because they “sing,” particularly at night. Orthopterans, or at least the grasshoppers and locusts, are often considered synonymous with “plagues” due to the devastating damage they inflict during periods of abundance.

Orthopterans are usually medium-sized to large insects. Not surprising for a large taxon, the wing condition varies considerably. They may be apterous (wingless), micropterous (short-winged and incapable of flight), or macropterous (long-winged and capable of flight). When bearing wings, which is the usual condition, they usually bear two pairs, and sometimes are capable of very strong flight. The name Orthoptera means “straight-winged” and refers to the thickened front wings or tegmina. The front wings bear numerous veins, and function more for protection than as an aid for flight. The front wings often are pigmented with a color or pattern that provides camouflage. Sometimes the front wings are quite broad and modified to resemble leaves. The hind wings usually are broader, folded like a fan, and though sometimes brightly colored, often are unpigmented. The wings, even if short, are often involved in sound production. Species inhabiting open desert and grasslands tend to be strong fliers, those inhabiting woodlands, islands and mountaintops tend to be flightless. In a few taxa, the second pair of wings is absent. In several groups, including many crickets, katydids and pygmy grasshoppers, the front wings are shorter than the hind wings.

Orthopterans possess chewing mouthparts. Their eyes are large, and ocelli are usually present and three in number. The antennae usually are narrow, but vary in length: short in suborder Caelifera and long in suborder Ensifera. The thorax is large, and the saddle-shaped pronotum bears large lateral lobes that serve as the sides of the thorax. The legs are long. The hind legs are most often enlarged, especially the hind femora, and allow the insects to jump when alarmed. The tarsi have 1–4 segments and normally end with a pair of claws. Contrary to popular belief, normal locomotion is by walking, not jumping. Sometimes the front legs

are enlarged, either for digging or for prey capture. The abdomen consists of about 11 segments and usually is free of notable structures other than the cerci and the ovipositor. Tympana, or hearing organs, are commonly present in these insects. In the suborder Caelifera, they are located on the side of the first abdominal segment. In the suborder Ensifera, they are found on the front tibiae.

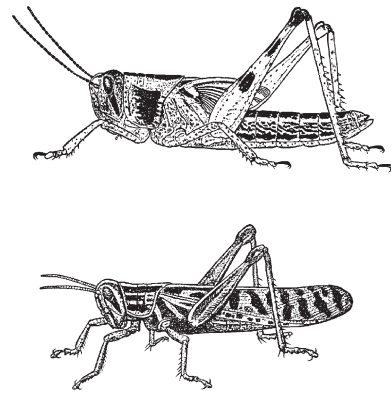
Orthopterans display gradual metamorphosis. After hatching from the egg, the immature stage (nymph) feeds and grows, molting four or more times before reaching the adult stage. The number of molts varies considerably among taxa, and is commonly 4 or 5 in grasshoppers, but generally more than 10 in crickets. As in all exopterygote (wings developing externally) insects, the nymphs greatly resemble the adults, both in appearance and in mode of life. There is an exception, however. Grasshoppers and katydids hatching in the soil actually have a pronymphal stage preceding the first instar. This initial form is called the vermiform (worm-like) larva, and consists of the young nymph encased in a cuticular covering. The vermiform larva wriggles through the soil to the surface, and then the nymph escapes the covering, beginning its above-ground existence as a young hopper. The vermiform stage is not counted in the instar numbering system because it is just the first instar within a sheath.

Nymphs and adults can be difficult to distinguish (Fig. 39). The principal differences in appearance are the imperfectly developed wings and genitalia of nymphs. Nymphs have external wing pads that enlarge with each molt. Their shape is useful for determining the instar. In Acrididae, Tettigoniidae and Gryllidae, the wing pads initially point downward, but part-way through nymphal development, the orientation switches and the wing pads point upward or backward. With wingless or short-winged species, distinguishing the instar is more difficult. At maturity, the males court the females (rarely the roles are reversed) and copulate. In the suborder Caelifera, the male deposits the sperm internally. In the suborder Ensifera, the males of some taxa attach a

spermatophore (packet containing sperm) externally at the female's genital opening, whereas others display the internal sperm deposition system. In both cases, the female stores sperm until oviposition (egg deposition), when fertilization occurs.

Insects with gradual metamorphosis have the ability to regenerate lost limbs. If a grasshopper loses an antenna or leg as a young nymph, the missing appendage is regrown, in part, at the next molt. If the damage occurs early enough in the development of the insect, the lost appendages may be completely regenerated. These insects also shed limbs readily, a process called autonomy. If a leg is grasped by a predator or caught in a spider web, the leg may be shed, allowing the insect to escape.

The order Orthoptera is usually divided into two suborders: Caelifera and Ensifera. The suborder Caelifera consists of the grasshoppers and locusts (including the deceptively named pygmy



Grasshoppers, Katydid and Crickets (Orthoptera), Figure 39 Typical nymphal and adult stages of a grasshopper, *Schistocerca americana* (Thomas). Note that they are similar in body form, with the primary distinguishing factor the abbreviated wings of the nymph (top). Shown is the sixth instar, which bears the largest wings prior to the molt to the adult. Unfortunately, many grasshopper species possess such abbreviated wings as adults, making age determination difficult. Some possess both short-winged and long-winged forms. A few species show no development of wings. (images from United States Department of Agriculture).

mole “crickets,” which are now recognized to be derived from grasshoppers, not crickets). The suborder Ensifera consists of the katydids and crickets (including the true crickets, mole crickets, camel crickets and Jerusalem crickets). There are many easily-recognizable groups within the order, and there is little dispute about most of these divisions and their phylogenetic relationships. However, there is considerable disagreement over the placement of the groups within the taxonomic hierarchy, i.e., whether or not they should be regarded as superfamilies, families or subfamilies. There are more than 25,000 species of Orthoptera in the world and, depending on the author of the classification system, up to about 35 families within the order.

Suborder Caelifera

The Caelifera usually have enlarged hind femora, short antennae, and tarsi with three or fewer segments. The antennae are normally threadlike, sometimes flattened, and occasionally enlarged at the tip. Tympana are often present, and are located on the sides of the first abdominal segment. Wing length is variable, but the cerci and the ovipositor are always short. Most species are diurnal, and phytophagous. Some primitive caeliferans, such as Eumastacidae, Tetrigidae and Tridactylidae, feed on more primitive plants, such as ferns and algae. Some Caelifera species inhabit areas of bare soil, many are associated specifically with grasses or broadleaf plants, while others dwell in trees. Visual and acoustic displays are part of the mating ritual of many species, and one or both sexes may produce sound. Sound production usually results from rubbing the hind legs against the front wings (called stridulation), although some groups stridulate by rubbing the front wings against the hind wings. Wing snapping in flight (called crepitation) also can occur. Eggs are normally deposited in the soil in clusters, and usually within a protective foamy structure called an egg pod. Univoltine and multivoltine species occur, with a tendency for greater multivoltinism in the warmer latitudes.

Following is one possible classification system for Caelifera, which basically follows Otte's Orthoptera Species File. Subfamilies are not given in the following list except in the case of Acrididae, the largest and most important family.

Suborder: Caelifera

Superfamily: Acridoidea

Family: Acrididae

Subfamily: Acridinae

Subfamily: Calliptaminae

Subfamily: Catantopinae

Subfamily: Conophyminae

Subfamily: Coptacridinae

Subfamily: Cyrtacanthacridinae

Subfamily: Dericorythinae

Subfamily: Egnatiinae

Subfamily: Eremogryllinae

Subfamily: Euryphyminae

Subfamily: Eyprepocnemidinae

Subfamily: Gomphocerinae

Subfamily: Hemiacridinae

Subfamily: Illapeliinae

Subfamily: Lithidiinae

Subfamily: Melanoplinae

Subfamily: Oedopodinae

Subfamily: Ommatolampinae

Subfamily: Oxyinae

Subfamily: Podisminae

Subfamily: Proctolabinae

Subfamily: Rhytidochrotinae

Subfamily: Spathosterninae

Subfamily: Teratodinae

Subfamily: Tropidopolinae

Subfamily: Trybliophorinae

Family: Charilaidae

Family: Lathiceridae

Family: Lentulidae

Family: Ommexechidae

Family: Pamphagidae

Family: Pauliniidae

Family: Pyrgomorphae

Family: Romaleidae

Family: Tristiridae

Superfamily: Eumastacoidea

Family: Eumastacidae

Family: Proscopiidae
 Superfamily: Pneumoroidea
 Family: Pneumoridae
 Family: Tanaoceridae
 Family: Xyronotidae
 Superfamily: Trigonopterygoidea
 Family: Trigonopterygidae
 Superfamily: Tetrigoidea
 Family: Tetrigidae
 Superfamily: Tridactyloidea
 Family: Cylindrachetidae
 Family: Regiatidae
 Family: Ripipterygidae
 Family: Tridactylidae

Following is information on some of the important families and subfamilies within the suborder Caelifera:

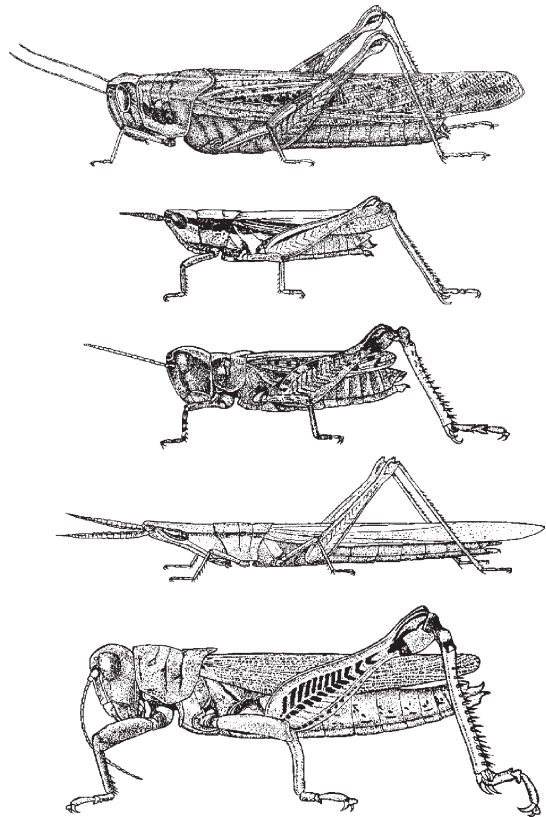
Family Acrididae

This is the largest family of the Orthoptera, and consists of the “true” grasshoppers and locusts. It is not uncommon to see other approaches to the classification of this family. The acridids are small to large in size, and stout to slender in general appearance. Their color is variable, but green and brown are common. The antennae and the pronotum are elongate and distinct. The legs are long, the hind legs are especially long and the femora is stout. The wings are variable in length, but often long. Acridids possess tympana, and sometimes produce sound. They are found in nearly all habitats. They are generally phytophagous, but vary in specificity. Eggs are deposited within pods in the soil; pods may contain three to 200 eggs, depending on the species.

Some subfamilies, such as Catantopinae, Gomphocerinae, Melanopliinae and Oedopodinae, are large and contain 500 or more species. Other subfamilies possess as few as one to five species. Some subfamilies are quite limited geographically and are found only on a single continent. Other taxa are found across Africa, Europe, Asia and Australia, or even more broadly (though they are absent from Antarctica).

Subfamily Acridinae (Silent Slantfaced Grasshoppers)

Grasshoppers in this subfamily have a slanted face and flattened, sword-shaped antennae (Fig. 40). Acridines lack a spine (the prosternal spine) between the front legs. The hind wings are colorless or nearly so. Acridinae are very similar in appearance to the



Grasshoppers, Katydid and Crickets (Orthoptera), Figure 40 Representative grasshoppers in the family Acrididae (top to bottom): a birdwing grasshopper, *Schistocerca nitens* Thunberg (subfamily Cyrtacanthacridinae); stridulating slantfaced grasshoppers, *Opeia obscura* (Thomas), *Psoloessa texana* (Scudder), and *Achurum sumichrasti* Saussure (subfamily Gomphocerinae); a New World spurthroated grasshopper, *Melanoplus differentialis* Thomas (subfamily Melanopliinae). (images from Arizona Agricultural Experiment Station).

stridulating slantfaced grasshoppers (subfamily Gomphocerinae), but as the common name suggests, members of this subfamily lack stridulatory pegs on the hind femora of males and thus do not produce sound. This subfamily is most abundant in Africa and Eurasia, though it occurs widely. Over 400 species are known.

Subfamily Calliptamine

These small to medium-sized grasshoppers are fairly typical in most respects, but the males are distinguished by their large, forceps-like cerci. The antennae are threadlike. The face is vertical or curved, but not strongly angled. The wing length is variable. Tympana are present, though sound production is limited to mandibular stridulation. They occur in Europe, Africa and Southeast Asia. About 100 species are known.

Subfamily Catantopinae (Old World Spurthroated Grasshoppers)

These typical-appearing grasshoppers vary considerably in size, and in wing structure. Their antennae are threadlike. The tympana generally are present though sound production is unknown. A prosternal spine is present. They greatly resemble Melanoplinae, and are separated mostly on the basis of geography. Catantopines occur in Europe, Asia and Africa. Over 1,000 species are known.

Subfamily Cyrtacanthacridinae

The treatment of this subfamily varies greatly among authors. Sometimes the subfamily name Cyrtacanthacridinae is used to include a great number of genera and species. Here, it is restricted to about 75 genera, the most important of which is *Schistocerca*, the birdwing grasshoppers.

These grasshoppers bear a prosternal spine ventrally between the front legs (on the proster-

num). The antennae usually are threadlike. The head is not especially large in size, and these grasshoppers do not appear to be especially heavy-bodied. In most genera, the head has a vertical orientation. These grasshoppers generally have long wings. The genus *Schistocerca* contains especially long-winged, strong fliers. Cyrtacanthacridine grasshoppers do not make sounds during flight; nor do they stridulate.

The habitat preferences of these grasshoppers are highly variable. Dietary habits also vary, but generally these insects are polyphagous. This group contains many important pests. Many of the grasshoppers are called "locusts" because of the swarming behavior found in this group. These grasshoppers are found throughout the world, but the greatest diversity occurs in Africa. In *Schistocerca*, however, the greatest diversity is in Central and South America.

Subfamily Eyprepocnemidinae

These insects are fairly typical in appearance, and variable in size. The antennal shape also varies. They possess a prosternal spine. The wing length is variable. The typana are present, though sound production is limited to mandibular stridulation. These insects are found principally in Africa, but also in southern Europe and Southeast Asia. About 175 species are known.

Subfamily Gomphocerinae (Stridulating Slantfaced Grasshoppers)

Grasshoppers in this subfamily tend to have slender bodies and long, slender legs. Their heads are elongate and often cone-shaped, usually with a highly slanted face. The hindwings are not colorful. Gomphocerines often have relatively short wings, rendering them incapable of sustained flight. When disturbed, these grasshoppers leap and use their wings, but their wings often do little

more than increase the distance jumped. They do not make sounds during flight. This does not mean that these grasshoppers are silent. They can stridulate by rubbing the inner surface of the hind femur on the edges of the forewing while resting. Because the males of this subfamily usually have a row of stridulatory pegs on the inner surface of the hind femora, they are also known as toothlegged grasshoppers.

The habitat of gomphocerines tends to be tall grasses in open fields. The form and color of many species allows them to blend in with stems and blades of grass, making them difficult to detect until they move. Most species feed predominantly on grasses. They are found throughout the world, and species number nearly 1,000.

Subfamily Melanoplinae (New World Spurthroated Grasshoppers)

These grasshoppers bear a prosternal spine, the basis for their common name. For this reason, they are often grouped into the Cyrtacanthacridinae. The antennae usually are threadlike. The head is not especially large, and they do not appear to be especially heavy-bodied. In most genera, the head has a vertical orientation. The wing length is variable. Melanoplinae do not make sounds during flight; nor do they stridulate. The habitat of these grasshoppers is highly variable. Thus, their dietary habits vary. This group contains many important crop and pasture pests. During periods of drought, they often attain high densities and cause considerable damage. They are found in North, Central and South America. Over 600 species are known.

Subfamily Oedipodinae (Bandwinged Grasshoppers)

The bandwinged grasshoppers are usually heavy bodied, and bear enlarged hind legs. The head of these grasshoppers often appears enlarged and

broadly rounded. The orientation of the face is nearly vertical. Bandwinged grasshoppers lack a spine between the front legs. The bandwinged grasshoppers tend to be gray or brown in color, and often are mottled with darker spots. The forewings frequently bear distinct or indistinct transverse bands. The bandwinged grasshoppers usually bear bright colors, but this may not be obvious. The hindwings are often yellow, orange, or reddish basally, with a broad black band crossing near the center of the wing. The colorful hindwings are hidden by the front wings except when in flight. The males produce sound in flight.

The oedipodine grasshoppers normally are associated with open, sunny areas, and particularly with bare soil where their coloration provides excellent camouflage. About 800 species are known throughout the world.

Subfamily Oxyinae

These are small to medium-sized grasshoppers, and their body has a smooth integument. They do not stridulate, and they lack tympana. The wing length is variable. The antennae are threadlike. An interesting characteristic of these grasshoppers is that the hind tibiae usually are expanded distally, which is thought to be an adaptation for swimming. The female's ovipositor valves are serrate or spined. Oxyinids are found in Africa, Europe, Southeast Asia and Australia, but are most abundant in humid, tropical habitats, especially wet environments. About 175 species are known.

Family Eumastacidae

This is one of the more primitive forms of grasshoppers, and they are sometimes referred to as monkey grasshoppers. The common name is derived from their agility when moving through vegetation. They tend to be small to medium in size. These insects lack tympana. They may bear wings, or be wingless. The legs, when the insect is

at rest, are often held away from the body. The tarsi are three-segmented. The antennae usually are variable in shape, unusually short, and often bear a small tubercle on an apical segment, called the antennal organ. They lack a prosternal spine. These are tropical insects, and are absent from Europe and northern Asia. In North America, they are found only in the warm-weather Southwest. They feed on ferns, algae and gymnosperms. Most of the approximately 750 known species occur in the Old World.

Family Pamphagidae

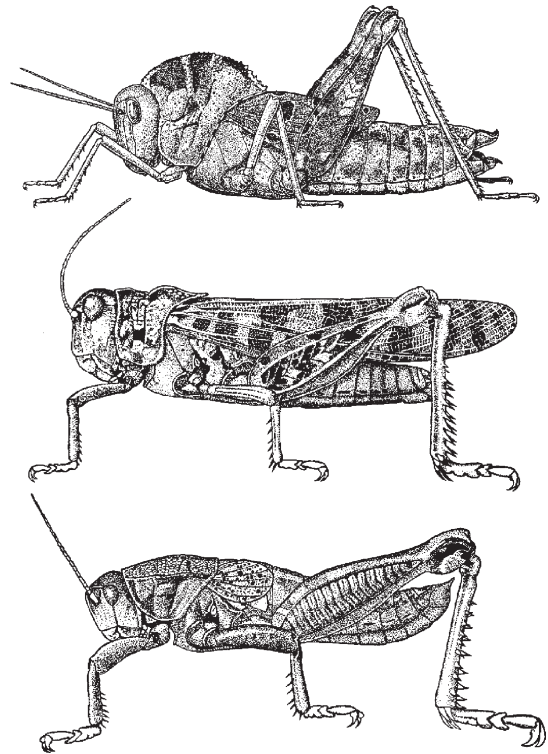
Generally medium or large in size, these grasshoppers possess a prosternal spine or elevated process. The pronotum is often elevated, sometimes forming a distinct crest. The wing development is variable. The tympana are either present or absent, and stridulation occurs. These grasshoppers often are cryptically colored, allowing them to blend with rocky soil and sand. These grasshoppers are found in Africa, southern Europe and Asia. Over 300 species are known.

Family Pyrgomorphidae

These insects have a conical head, usually with a very slanted face. They have a relatively soft body and weak integument. The antennae are threadlike or flattened. A prosternal spine or elevated process on the prosternum is present. Often brightly colored, they also excrete body fluids from between the first and second abdominal segments that provides a form of chemical protection that is variously repellent or poisonous. Wing length varies in this group. These grasshoppers usually are associated with grass vegetation in tropical and subtropical areas. They are known mostly from eastern Africa, Southeast Asia, Australia, and Central and northern South America – basically everywhere except North America. Over 400 species are known in this family.

Family Romaleidae

This group, also known as lubber grasshoppers, is sometimes considered to be a subfamily of Acrididae. It is distinguished, in part, by having a spine on both the inner and outer surface at the tip of the hind tibiae. Other grasshoppers (Fig. 41) may have moveable spurs, which resemble spines, but lubbers also have immovable spines at this location. Lubber grasshoppers also bear a prosternal spine. Lubber grasshoppers often are large, robust, colorful and usually bear short wings. The name “lubber” is derived from the heavy-bodied appearance and clumsy behavior of these insects. The shape of the



Grasshoppers, Katydid and Crickets (Orthoptera), Figure 41 Representative grasshoppers in the family Acrididae (*top to bottom*): bandwinged grasshopper, *Tropidolophus formosus* (Say) and *Xanthippus corallipes* Haldeman (subfamily Oedipodinae). Representative grasshopper in the family Romaleidae: a lubber grasshopper, *Brachystola magna* Girard. (images from Arizona Agricultural Experiment Station).

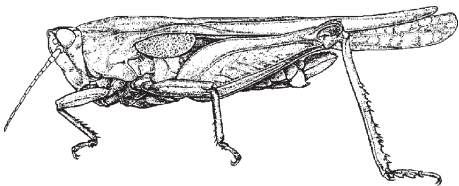
head, though variable, is usually broadly rounded. The hind femora are enlarged. When disturbed, lubber grasshoppers may hiss and spread their wings. The males also may use their wings to stridulate. The forewings and hindwings sometimes are brightly colored. The lubber grasshoppers are found in North, Central and South America, with their abundance greater in the southern latitudes. About 500 species of Romaleidae are known.

Family Tanoceridae

These grasshoppers, known also as desert long-horned grasshoppers, are medium in size and wingless. The threadlike antennae are relatively long in males and shorter in females. They are nocturnal, and are not often found by collectors. They are known only in the southwestern region of North America. Only four species from this family have been described thus far.

Family Tetrigidae

The pygmy grasshoppers (Fig. 42) are also known as groundhoppers and grouse grasshoppers. They are distinguished by their small size, usually 6–16 mm in length; their dull, cryptic coloration, usually brownish gray, gray, or black or mottled, but never green; their prominent eyes; and especially their greatly elongated pronotum, which often extends backward to the tip of the abdomen and ends in a sharp point. The antennae are relatively short. They may be long- or short-winged, or



Grasshoppers, Katydid and Crickets (Orthoptera), Figure 42 Representative of the family Tetrigidae: (top) a pygmy grasshopper, *Tetrix subulata* (Linnaeus).

wingless. Like other grasshoppers, their hind femora are enlarged. Both sexes stridulate, and mating is a very brief process. They apparently feed on algae and possibly other organic matter in the soil. They often are found in marshy areas and at the margins of water, or in moss covered habitats. Some can descend into water, carrying an air bubble with them. They deposit loose clusters of eggs in wet soil. They tend to live in small groups in a more or less gregarious condition. They are difficult to collect unless special effort is made to sweep close to the soil. In some environments, they may be common. Tetrigids are found throughout the world, but they are most abundant in Southeast Asia. About 1,200 species are known.

Family Tridactylidae

These very small insects, usually measuring only 4–10 mm in length, are grasshoppers despite their common name: pygmy mole crickets. The antennae are relatively short, as with acridid grasshoppers. However, they possess some unusual features that differentiate them from other grasshoppers. They resemble mole crickets because they have front legs that are adapted for digging in soil and an arched pronotum. The tip of the abdomen bears a set of bristly appendages that resemble cerci, so they appear to have two sets of cerci. The hind tarsi possess plates that help them move on water, an important feature because they frequent the sandy edges of streams and ponds. They are quite good at walking on the water surface. Their diet consists mostly of organic material such as algae, possibly fungi, nematodes and bacteria, often ingested along with sand particles. Tridactylids are found throughout the world, but seem to flourish in tropical and subtropical locations. Nearly 200 species are known.

Suborder Ensifera

The ensiferans, like the caeliferans, are jumping insects. However, their legs tend to be longer, and the

hind femora less enlarged, than the caeliferans. Their most distinctive feature is their long, threadlike antennae, which normally exceed the length of the body. The tarsi are three or four-segmented. The tympana, when present, are located on the front tibiae. Stridulation is common, and normally is caused by rubbing one front wing against the other. Sometimes the wings are slightly elevated when singing, but this behavior varies among taxa. Females bear a long sword-shaped or cylindrical ovipositor. The wing length is variable, but often even the long-winged species are weak fliers. Most species are nocturnal, and dietary habits vary from carnivory to phytophagy, but omnivory is common. Ensiferans often are associated with thick vegetation, and are most common in mesic areas. The superfamily Tettigonioidae, in particular, frequent vegetation almost exclusively. The Gryllacridoidea and Grylloidea, in contrast, often seek shelter in crevices, tunnels beneath the soil, or tree holes. Acoustic displays are an important part of the mating ritual of many species. Eggs are deposited singly, though several may be laid at the same location. Unlike grasshoppers, katydids and crickets do not produce egg pods. Some crickets and katydids deposit eggs on or in vegetation, others in soil.

Following is one possible classification system for Ensifera, based on that found in Otte's Orthoptera Species File. Subfamilies are not given, except in the case of the Tettigoniidae and Gryllidae, the most important groups.

Suborder: Ensifera

Superfamily: Tettigonioidae

Family: Haglidae

Family: Tettigoniidae

Subfamily: Austrosaginae

Subfamily: Bradyporinae

Subfamily: Conocephalinae

Subfamily: Hetrodinae

Subfamily: Lipotactinae

Subfamily: Listroscelidinae

Subfamily: Meconematinae

Subfamily: Microtettigoniinae

Subfamily: Phaneropterinae

Subfamily: Phasmodinae

Subfamily: Phyllophorinae

Subfamily: Pseudophyllinae

Subfamily: Saginae

Subfamily: Tettigoniinae

Subfamily: Tympanophrinae

Subfamily: Zaprochilinae

Family: Prophalangopsidae

Superfamily: Gryllacridoidea

Family: Gryllacrididae

Family: Cooloolidae

Family: Anostomatidae

Family: Stenopelmatidae

Family: Schizodactylidae

Family: Rhaphidophoridae

Superfamily: Grylloidea

Family: Gryllidae

Subfamily: Brachytrupinae

Subfamily: Cachoplistinae

Subfamily: Eneopterinae

Subfamily: Euscyrtinae

Subfamily: Gryllinae

Subfamily: Gryllomiminae

Subfamily: Itarinae

Subfamily: Malgasiinae

Subfamily: Nemobiinae

Subfamily: Oecanthinae

Subfamily: Pentacentrinae

Subfamily: Podoscirtinae

Subfamily: Pteroplistinae

Subfamily: Sclerogryllinae

Subfamily: Trigonidiinae

Family: Gryllotalpidae

Family: Mogoplistidae

Family: Myrmecophilidae

Following is information on some of the important families and subfamilies within the suborder Ensifera.

Family Anostomatidae

This unusual group is known as king crickets and wetas. They are large, stout, and have oversized heads. Nearly all are wingless, but a few have fully formed wings. The mandibles and hind legs are

sometimes enlarged. they are nocturnal. King crickets seem to be omnivores, though wetas are herbivores. To deter avian and reptilian predation, wetas raise their hind legs, exposing long spines. However, hiding below-ground is the principal defense. Wetas possess large tympana on their front legs. wetas and king crickets stridulate, though their sound production is a relatively primitive, intermediate stage in the evolution of acoustic signaling. They also transmit vibratory signals through their substrate. Tree wetas, but not king crickets, maintain harems of females and possess enormous mandibles that they use for fighting with competing males, whereas giant weta males freely compete for females without aggression. The king crickets and wetas occur in a variety of habitats. About 40 king crickets are known from southern africa, and 60 from australia and New Zealand. Wetas occur in Australia and New Zealand. Wetas are at risk of extinction because they are relatively defenseless against imported animals such as rats.

Family Cooloolidae

The cooloolids are called cooloola monsters due to their unusual appearance. These insects, though considered to be ensiferans, have short (10-segmented) antennae. They possess a large abdomen, and relatively short legs and with a muscular, hump-backed appearance. They resemble king crickets and wetas (Anastostomatidae) and to a lesser degree Jerusalem crickets (Stenopelmatidae). These are not leaping insects. Also, they do not tunnel, rather, living below ground where they “swim” through sandy soil. This very small (three species) and unusual family is known only in Australia.

Family Gryllacrididae

Some gryllacridids are known as leaf-rolling crickets, but not all species exhibit this behavior. They produce silk from glands in their mouthparts, and

use it to tie leaves. The leaf rolls provide daytime shelters, but some species inhabit burrows in soil. The common name raspy crickets has also been suggested. This name stems from a raspy sound produced during defense. These are robust crickets, and can be fairly large, attaining 15 cm in length. They may be winged or wingless. The antennae are as long as or longer than the body. They are distinguished by the lateral lobes of the tarsi, and the presence of pegs on the inner surface of the hind femora that rub against the abdomen. They are not as long-legged as the cave and camel crickets (Rhaphidophoridae), and are soft bodied as compared to the king crickets and wetas (Anastostomatidae). This group is not well known, but all are thought to be nocturnal. They occupy varied habitats, and their dietary habits include herbivory, omnivory and carnivory. They are found widely in southern Africa, southwestern Asia, Australia, the Pacific region and South America. Few species are known from the northern hemisphere. Over 600 species are known around the world.

Family Gryllidae

Most crickets are compact and large-headed insects. Their antennae are long, usually reaching the tip of the abdomen or beyond. The forewings, when fully formed, are relatively broad, and flattened over the abdomen. Many species are wingless or short-winged. The front wings may be shorter than the hind wings, and in males, may function principally as acoustic devices. Many species can only be recognized by their calling behavior. Some species are mute. Tympana are found on the front tibiae. The ovipositor is long, thin and tubular. The body color is dull, usually pale, brownish or black. Long cerci are found near the tip of the abdomen and are similar in both sexes. Gryllids are often considered to be omnivorous, which is largely true, though individual species vary from herbivorous to nearly carnivorous. About 3,000 species occur in this large family.

Subfamily Eneopterinae (Bush Crickets)

The bush crickets are medium sized and slender. The body usually has a fine covering of hairs. They frequent vegetation rather than soil. About 200 species are known from this subfamily.

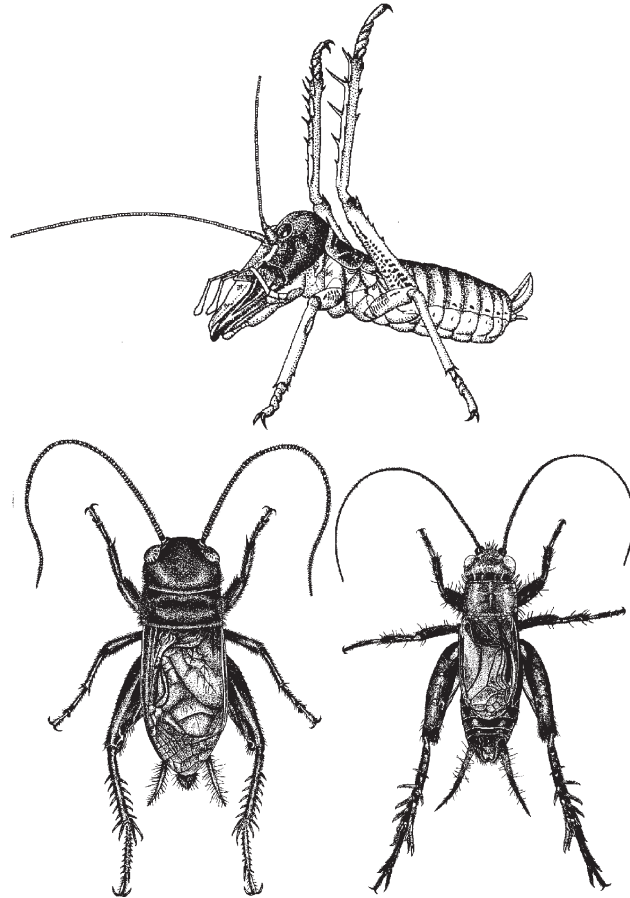
wing length varies considerably. They can call during the day and night, and tend to dwell below-ground. Many species are similar morphologically and are distinguished by their calling behavior. They are omnivorous. About 500 species are known and are distributed widely in the world. A few species are considered to be crop pests.

Subfamily Gryllinae (Field Crickets)

These common crickets (Fig. 43) are similar to the ground crickets (Nemobiinae), but usually are medium in size rather than small. They tend to be heavy-bodied and brown or black in color. Their

Subfamily Nemobiinae (Ground Crickets)

The ground crickets tend to be small, and often bear a sparse covering of hairs. Tympana are present on the front tibiae. The wing length is variable. They often are uniformly brown, which



Grasshoppers, Katydid and Crickets (Orthoptera), Figure 43 Representative of the family Anostomatidae (*top*) a weta, *Hemideina crassidens* (Blanchard) (image from Larry Field); the family Gryllidae: (*bottom left*) a field cricket, *Gryllus veletis* (Alexander and Bigelow) (subfamily Gryllinae); and (*bottom right*) a ground cricket, *Allonemobius griseus* E.M. Walker (subfamily Nemobiinae) (images from Lyman Entomological Museum).

allows them to blend in well with their terrestrial environment. These insects can be quite numerous in pastures and woodlands, and can be active during the daylight hours. They are omnivorous. About 200 species are known around the world.

Subfamily Oecanthinae (Tree Crickets)

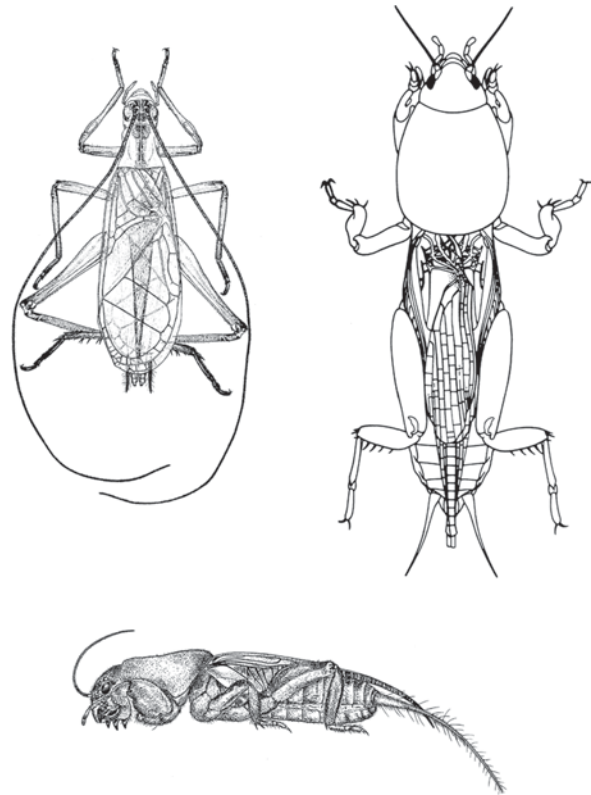
The tree crickets (Fig. 44) are slender and pale colored, often greenish or whitish. The males tend to have broad front wings. Most are quite vocal. They inhabit trees, shrubs and weedy fields. Some cause injury to trees and shrubs by depositing their eggs within twigs. Tree crickets tend to be predatory. They are found throughout the world, but are most numerous in Africa and South America. About 175 species occur in this subfamily.

Subfamily Trigoninae (Sword-Tail Crickets)

These insects tend to be small, and pale in color. The wing length is variable, though the wings can be quite long when present. Tympana are present. Sword-tail crickets often are found in vegetation adjacent to water, and do not normally frequent the soil surface. About 275 species are known throughout the world.

Family Gryllotalpidae

Among the most easily distinguished orthopterans, the mole crickets bear wide forelegs modified for digging. Both the femora and tibiae are flattened, with the tibiae bearing enlarged teeth or “dactyls.” The hind legs are not markedly enlarged. The antennae are shorter and thicker than in many ensiferans. The oval pronotum is disproportionately large and sturdy. They are often, but not always, long-winged. The ovipositor is not apparent. These insects dwell below-ground during the day, often



Grasshoppers, Katydid and Crickets (Orthoptera), Figure 44 Representative of the family Gryllidae, (top left) a tree cricket, *Oecanthus nigricornis* (subfamily Oecanthinae); the family Gryllotalpidae, (top right) a mole cricket, *Scapteriscus* sp.; and (bottom) a mole cricket, *Neocurtilla hexadactyla* (images Lyman Entomological Museum except *Scapteriscus* from Florida Division of Plant Industry).

emerging in the evening to sing or eat. They sing from specially constructed acoustical chambers, constructed in the soil, that expand as they open to the outside like the end of a trumpet. This design serves to amplify their call. Some species are mute. Mole crickets create deep permanent burrows, but also superficial foraging tunnels. The eggs are deposited in special egg chambers within the burrows. Their dietary habits range from carnivorous to phytophagous, but some are important vegetable and pasture pests. Three species of *Scapteriscus* from South America were accidentally introduced into southeastern North America and have caused

considerable damage. Less than 100 species are known from this family.

Family Mogopistinae

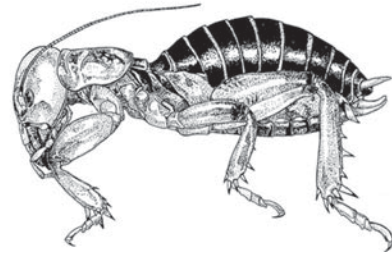
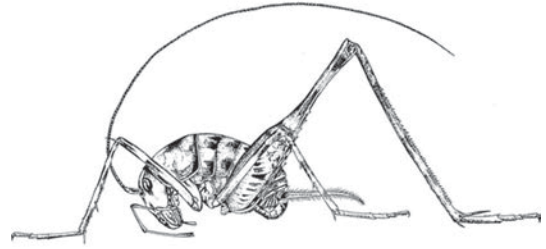
These insects are called scaly crickets. Resembling silverfish, these small crickets tend to be short-winged, flat and slender. Their name is derived from the presence of translucent scales covering most of their body. They are mostly tropical in distribution and seem to favor areas near water. Over 350 species are known.

Family Myrmecophilidae

This is a small family of very small, wingless, oval and flattened crickets that inhabit ant nests. They cannot live independently from the ants. The eyes are reduced, though the cerci are pronounced. The tympana are lacking. The ovipositor is shortened and stout. The hind femora are broad. These unusual insects feed on secretions produced by ants. Apparently, they are taken to be ants by their hosts. Some species are parthenogenetic. Only about 50 species are known.

Family Rhabdophoridae

The camel crickets (Fig. 45) are similar to the Tettigoniidae, but wingless. They bear long, thread-like antennae, usually longer than in Tettigoniidae. Their legs also are quite long. The pronotum is smoothly rounded and lacks ridges. Unlike most of their close relatives, they do not have a hearing organ on the front tibia. They are not usually considered to be singers, though some are capable of making some sounds, and some species have stridulatory pegs. Because they lack wings, it is difficult to distinguish adults from nymphs except by the developing ovipositor, or fully developed male genitalia. They are dull colored insects, usually some shade of brown or gray. Camel crickets are



Grasshoppers, Katydid and Crickets (Orthoptera), Figure 45 Representatives of the family Myrmecophilidae, (top) an ant nest-inhabiting cricket, *Myrmecophilus oregonensis* Bruner; the family Rhabdophoridae, (center) a camel cricket, *Tachycines asynamorus* Adelung; and the family Stenopelmatidae, (bottom) a Jerusalem cricket, *Stenopelmatus fuscus* Haldeman (images from Lyman Entomological Museum).

nocturnal. About 250 species are known around the world.

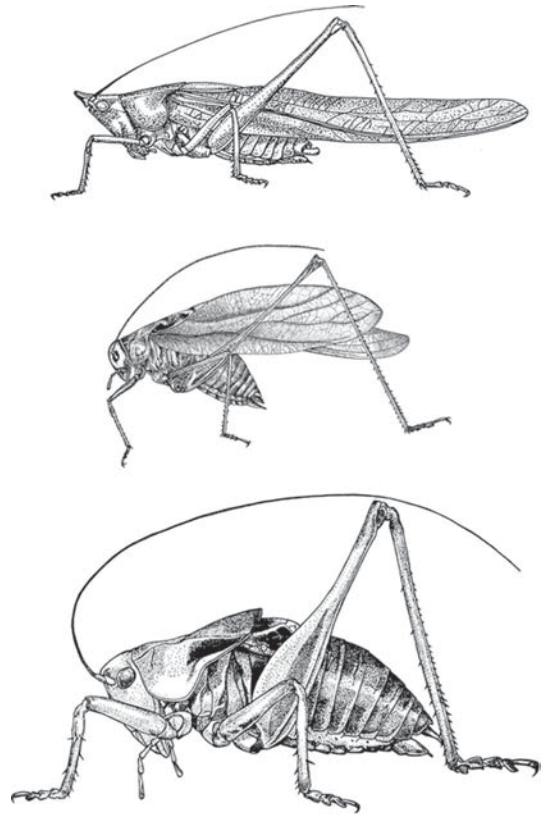
Family Stenopelmatidae

This group consists of cricket-like insects known as Jerusalem crickets. They are flightless, nocturnal and infrequently encountered. Thus, they are poorly known. Jerusalem crickets are large,

somewhat hump-backed, with large heads resembling anastostomatids. Their legs bear stout spines. They have large mandibles and bite readily. When disturbed, Jerusalem crickets will flip onto their backs, exposing their mandibles in a defensive posture. They seem to be omnivores, and they benefit from animal protein. Most occupy arid western North America, often resting below-ground or beneath objects, but surfacing at night to feed. In Central America, however, some inhabit rotting logs and stumps. Jerusalem crickets can be large, some species weighing as much as 8 g, but others weigh less than 1 g. They transmit vibratory signals through the substrate. The males are sometimes eaten by the females after copulating. At least 80 species are known to occur in North America, but most are undescribed.

Family Tettigoniidae

This is a large and important family that is variously known as katydids in North America and Australia, or bush crickets in other English-speaking areas. These species tend to be medium-sized or large in size, often 35–50 mm in length. The antennae are longer than the body. These insects bear tympana on the front tibiae. The pronotum only rarely bears a ridge. A large, sword-shaped ovipositor is usually present in the females. Although some katydids oviposit in soil, they also deposit eggs in leaf tissue, stem tissue and even bark crevices. Some oviposit flattened, overlapping eggs like roof shingles on leaf and stem tissue. A small number construct “nests” of chewed plant material and mud. Katydid (Fig. 46) are usually green or brown in color, and though some species are active during the day, most are largely nocturnal. The males stridulate freely, and in many environments, these insects are an important element of night-time sounds. They are largely phytophagous, but are also omnivorous and a few feed on other insects. They prefer proteinaceous food, and even the



Grasshoppers, Katydid and Crickets (Orthoptera), Figure 46 Representatives of the family Tettigoniidae: (top) a coneheaded katydid, *Neoconocephalus ensiger* (Harris) (subfamily Conocephalinae); (center) a false katydid, *Amblycorypha oblongifolia* (De Geer) (subfamily Phanopterinae); and (bottom) a shield-backed katydid, *Atlanticus monticola* Davis (subfamily Tettigoniinae) (images from Lyman Entomological Museum).

phytophagous species often select blossoms and fruit for their higher protein content. The males tend to produce a large edible spermatophylax, a structure containing the spermatophore. The spermatophylax is passed on to the female as a nuptial gift, and is also a means of providing a protein supplement to the female when she is producing eggs. Tettigoniids are found throughout the world, and number nearly 400 species.

Subfamily Conocephalinae (Meadow and Coneheaded Katydids)

These katydids are small to medium in size. They are long, thin insects and some have a conical head. The ovipositor may be long and sword-shaped. The antennae are long. They are green or brown, blending well with vegetation. The preferred habitat is short or tall grasses and broadleaf plants, normally in fields and swamps, but sometimes in forests. They sing mostly at night, and are found throughout most of the world. Nearly 1,000 species are known. One tribe, the copiphorini, is sometimes treated as a subfamily.

Subfamily Meconematinae (Quiet-Calling Katydids)

These are small, diurnal insects. They are found in Africa, Europe and northern Asia. Over 400 species are known in the subfamily.

Subfamily Phaneropterinae (False Katydids)

This group of katydids is distinguished by the absence of spines on the prosternum and by the wing length; the hind wings are longer than the front wings. These insects are noted songsters, and they vocalize late in the day and during the evening. They normally are brown, but pink forms are known. About 2,000 species are known.

Subfamily Phyllophorinae (Giant Leaf Katydids)

These leaf feeders are the largest of the tettigoniids. Their wing spans attain 25 cm. They bear a very heavy pronotum, and the males have lost the ability to stridulate using the tegmina. There are about 70 known species, all from Australia and nearby areas.

Subfamily Pseudophyllinae (True Katydids)

These are broad-winged insects that commonly inhabit trees and shrubs. The subfamily is quite diverse in the tropics of both the New World and the Old World, and different species often mimic different natural elements of their habitat such as leaves and bark. About 1,000 species are known.

Subfamily Saginae (Stick Katydids)

These flightless insects occur in Africa, Europe and Asia. One species, of European origin, has established in North America. This flightless species, *Saga pedo*, reproduces parthenogenetically, a rare occurrence among katydids. Sagines are predators, and quite aggressive about grasping prey with their spined forelegs. About 50 species are known.

Subfamily Tettigoniinae (Shield-Backed Katydids)

Many large, ground-dwelling, flightless species are found in this subfamily. They tend to be shortwinged, and are sometimes dark in color, often brown or black. Other species in this same subfamily are long-winged and good fliers. They occupy a diversity of habitats. Some, such as the Mormon cricket, *Anabrus simplex* Haldeman, are crop pests in western North America. Omnivory and carnivory are common in this group. Nearly 900 species are known from this group. They are found throughout the world.

Evolution of Orthoptera

The evolution of Orthoptera can be traced back to the Protorthoptera of the Upper Carboniferous-Permian period some 300 million years ago. The

Protorthoptera gave rise to several primitive groups that eventually gave rise to the ancestors of the most recent orthopteroid orders. The order Orthoptera probably underwent an early split to give rise to the two major lines of evolution now recognized as Caelifera and Ensifera. Ensifera is considered to be more primitive than Caelifera.

The orthopterans are closely related to the mantids, walkingsticks, cockroaches and rock crawlers. They are less closely related to earwigs, webspinners and termites. Collectively, these taxa are referred to as the orthopteroid orders. All are thought to be descended from a common neopteran ancestor that predated the Protorthoptera.

Not everyone agrees with this interpretation, however. It is also possible that Caelifera and Ensifera evolved independently from different protorthopteran ancestors. It has even been suggested that the Orthoptera could be an artificial group (Caelifera plus Ensifera) that appears united mostly because they have enlarged hind legs for leaping. Consider that although the orthopterans produce sound, the two suborders differ in how they produce and hear sound. However, most available evidence, and most orthopterists, support the idea of a single order.

Natural Enemies of Orthoptera

There are numerous natural enemies of orthopterans, and the same types of natural enemies generally affect the several taxa of Orthoptera. However, the relative importance of the natural enemies varies among orthopterans, among different periods of the orthopteran population cycle, in different regions of the world, according to the weather and according to the soil type.

Natural enemies of orthopterans include predators (which kill and eat their prey), parasitoids (parasitic insects that develop in or on the host orthopteran and kill the host only when the parasite reaches maturity), and pathogens (microbial diseases that kill the host after the host's nutrients are exhausted).

Important egg predators include bee flies (Diptera: Bombyliidae), ground beetles (Coleoptera: Carabidae) and blister beetles (Coleoptera: Meloidae). Nymphs and adults are captured and eaten by spiders, birds, small mammals and rodents, ants (Hymenoptera: Formicidae), sphecids (Hymenoptera: Sphecidae) and robber flies (Diptera: Assilidae). Among the important parasitoids of nymphs and adults are blow flies (Diptera: Calliphoridae), sarcophagids (Diptera: Sarcophagidae), nemestrinids (Diptera: Nemestrinidae) and tachinids (Diptera: Tachinidae). Mites (Acari) are commonly found clinging to orthopterans, and some feed on the blood of their host. Although mites weaken their host, they are not thought to be important mortality agents. Pathogens affect all stages of orthopteran development, and among the most important are nematodes, fungi, viruses and microsporidians. Nematodes and fungi are readily affected by soil and weather conditions, so their occurrence is inconsistent. However, these pathogens can have dramatic effects on orthopteran populations when conditions favor their virulence. Viruses and microsporidians are found widely, though they often are not especially virulent. The impact of pathogens is often overlooked relative to predators and parasitoids because their effect may be expressed as a shortening of the life span or as a reduction in reproduction, rather than in direct mortality.

The importance of natural enemies is difficult to measure, and the action of these beneficial organisms may come too late in a population outbreak to prevent damage. Sometimes they may interfere with one another, as when robber flies capture insect parasitoids as well as grasshoppers, or when fungal diseases kill a host insect prematurely, causing the death of the parasitoid contained in the host orthopteran. Nevertheless, there are many striking examples of natural enemies suppressing orthopteran populations. Examples of natural enemy effects include: parasitism of grasshoppers by the nematode *Mermis nigrescens* killed 71% of *Melanoplus femurrubrum* grasshoppers in Michigan, USA; mermithids infected 69% of

Locusta migratoria in wet areas of Papua New Guinea, but only 15% in dry areas; 30–70% of field crickets were infected with microsporidians in Michigan, USA; grasshoppers comprised 94% of the diet of the robber fly *Proctacanthus milbertii*, a generalist predator, in studies conducted in Montana, USA, and this fly consumed about 25% of all hoppers present; birds ate about 27% of adult grasshoppers during the summer in Nebraska, USA; over 200 species of birds in Nebraska feed on grasshoppers, and during the summer months, the average bird's stomach contains at least 25 grasshoppers at any time; parasitism of *Zonocerus locusts* exceeded 40% by a calliphorid in Africa; and the combined effects of natural enemies accounted for about 50% mortality in desert locust, *Schistocerca gregaria*, populations in Africa.

Importance of Orthoptera to Humans

Grasshoppers, katydids, crickets and other orthopterans vary considerably in their importance to humans. In some societies, grasshoppers are a minor source of food, and katydids and crickets are kept as pets for their acoustical abilities. However, these beneficial aspects are minor compared to their destructive attributes. Grasshoppers are widely recognized to be serious pests of arid-land or prairie agriculture, and to a lesser degree, in mesic areas. Katydid, crickets and allied insects usually have minor effects on agriculture, though a few species are quite damaging. Grasshoppers, katydids and sometimes other orthopterans consume considerable amounts of foliage during their nymphal development, and also as adults. Occasionally, other insect activities such as tunneling (by mole crickets) or oviposition (by tree crickets) may be the basis for injury. Pasture, forage, grain, vegetable, and even fruit and ornamental crops can be affected. Historically, grasshoppers and locusts have been very disruptive to civilizations in Africa, the Middle East, India, China and North America. However,

Australia, Europe and South America also have witnessed serious problems, so, virtually no area of the globe is immune to attack by grasshoppers. However, except in areas where access to technology and funds are limited, the tools are now available to manage these pests and to prevent them from excessive destruction.

Abnormally high densities of grasshoppers are called outbreaks or plagues. Regardless of the terminology applied, the phenomenon occurs throughout the world, and its origin is invariably related to food and weather. Grasshoppers that tend to attain high densities periodically, especially those that tend to become gregarious and move together as groups or swarms, are sometimes called locusts. Locusts do not really differ from grasshoppers, other than displaying a greater degree of gregarious behavior. Even species known as locusts periodically experience periods when they are not numerous, not gregarious, and do not cause much injury.

Grasshoppers require warm and sunny conditions for optimal growth and reproduction. Warmth alone seems to be inadequate, and grasshoppers often bask in the sun to raise their body temperatures. Thus, drought stimulates grasshopper population increase, apparently because there is less rainfall and cloudy weather to interfere with grasshopper activity. A single season of such weather is not adequate to stimulate massive population increase; rather, 2–3 years of drought usually precede grasshopper plagues. Warm winter temperatures also seem to be beneficial, because less mortality occurs by overwintering nymphs and adults. This scenario explains outbreaks that occur in temperate climates, where food is not limited, but heat may be inadequate. However, it does not explain all grasshopper outbreaks.

Food is a necessary prerequisite for grasshopper success, and optimal weather alone, in the absence of adequate food supply, will prove insufficient for rapid grasshopper population growth. For outbreaks or plagues to occur, both requisites must be satisfied. Thus, some precipitation must be present at the appropriate time to stimulate plant

growth, but an over-abundance results in too much cloud cover. In tropical or subtropical climates, especially warm but arid regions, precipitation is an important stimulus that increases grasshopper breeding and causes outbreaks to develop.

Management of Orthoptera Pests

The ideal way to manage orthopteran pests is to manage the environment to prevent them from attaining pest status. One example of how this can be accomplished is with weed management in fallow fields, and along roadsides and irrigation ditches. Luxurious growth of weedy vegetation often favors the survival of grasshoppers, which then can spread to adjacent crops. If this land is instead tilled or planted with short grass, fewer grasshoppers will breed there and the damage potential is greatly reduced. Unfortunately, many environments cannot be manipulated easily, and when weather or other factors favor population increase, a suppressive action must be initiated. Another example of how problems can be prevented is by introducing natural enemies of grasshoppers that have invaded a new area, and have therefore left their natural enemies behind. The introduction of a parasitic fly, *Ormia depleta*, and an entomopathogenic nematode, *Steinernema scapterisci*, for the suppression of *Scapteriscus* mole crickets in Florida, illustrates how this method can be applied effectively to invaders. However, most orthopteran pests are native, and there is little opportunity to identify natural enemies from elsewhere.

Biological suppression of orthopteran populations is difficult to achieve once they have attained damaging levels. Natural enemies sometimes eventually build to high enough levels to help decrease pest abundance. For example, wild birds will sometimes switch their feeding to take advantage of an abundance of grasshoppers, but this is effective only on a local scale, not a regional scale. Domestic fowl, especially turkeys, readily consume vast quantities of grasshoppers, and can be used for small-scale

suppression. There also are grasshopper disease agents that are under investigation, and even some that are sold commercially, but so far, none has been shown to provide adequate suppression. Entomopathogenic nematodes are used for mole cricket suppression in some environments. Biological control remains a promising area for research, and the search continues for more effective products, but thus far, there are few practical options. For some people, neem products are attractive. Neem products are botanical derivatives that, when applied to plants, act as a feeding deterrent, reducing damage. Also, if applied to grasshopper nymphs, neem can act as a growth regulator, disrupting the normal growth and development, and sometimes resulting in the death or sterilization of grasshoppers. Although neem products are chemicals, many people take comfort in knowing that they are derived from plants, and are therefore somewhat “natural.” Like many natural controls, effectiveness is not always consistent.

In some situations, physical barriers can provide some protection from damage. It is possible to screen or cover valuable plants with netting, floating row cover, or similar material to deny grasshoppers access to susceptible plants. This is suitable for small gardens, and is even applied commercially for ornamental plant production, wherein shade houses are sealed tightly to deny access to orthopterans. The potential for this approach is limited in scale due to the cost. For flightless species such as lubber grasshoppers or Mormon crickets, physical barriers such as a ditch with steep sides, or a short metal or plastic “wall,” can prove to be effective impediments to grasshopper dispersal. If such a wall is contemplated, however, consider that orthopterans have sharp claws and can ascend vertical surfaces with amazing agility, so the top of a barrier should end in a 45 degree angle, forcing the insects to fall back.

As mentioned above, cultural management of crop- and pasture-land can sometimes be used to manipulate orthopteran abundance. The habitats most favorable for grasshopper population growth and survival are open, sunny habitats containing mixed, early to mid-successional plants. Land with

trees providing moderate to deep shade rarely produce large numbers of grasshoppers. Also, land that is kept mowed, either mechanically or by livestock grazing, tends not to produce grasshoppers unless grass pasture-land is damaged by overgrazing and broadleaf weeds invade.

If natural enemies and cultural manipulations have failed to keep orthopteran pests in check, chemical insecticides are most often used to prevent excessive damage. Chemical insecticides can be applied in liquid form, by application directly to the grasshoppers, or to the plants they will walk or feed upon. Insecticides can also be applied to food bait, usually bran flakes, and distributed in the pest's environment. If insecticides are to be used, it is advisable to apply the chemicals when the pests are young. Small insects are much easier to kill than large ones, and grasshoppers and crickets are notoriously difficult to kill under any conditions. Also, because the grasshoppers usually develop in surrounding vegetation, it is usually best to take the "battle" there, and apply insecticides to the young grasshoppers before they disperse into crops and cause damage.

- ▶ [Grasshoppers of the Argentine Pampas](#)
- ▶ [African Pine-Feeding Grasshopper](#)
- ▶ [Diseases of Grasshoppers and Locusts](#)
- ▶ [Grasshoppers and Locusts as Agricultural Pests](#)
- ▶ [Desert Locust Plagues](#)
- ▶ [Rhammatocercus schistocercoides](#)
- ▶ [Weta](#)
- ▶ [Katydid](#)
- ▶ [Jerusalem Crickets](#)

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Grasshoppers of the Argentine Pampas

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The Pampas, which occupies the Province of Buenos Aires and parts of the Provinces of Entre Ríos, Santa Fe, Córdoba, La Pampa and San Luis, are temperate subhumid grasslands. Mesothermic grasses dominate in this region of mild climate with mean annual temperature ranging from 10 to 20°C, and annual rainfall between 400 and 1600 mm. There is a general decrease south-westward in annual precipitation, soil organic matter and grassland productivity.

The landscape has been altered markedly during the last century due to agricultural and grazing activities, and pristine grasslands have been drastically modified. Most of the land has been converted to cropland, mainly soybean, corn, sunflower and wheat.

Among the most important native herbivores are grasshoppers, which are a recurrent pest of the agro ecosystems of this area. These insects may cause, in some years, forage and crop losses of considerable magnitude.

The Pampas and the Great Plains of North America have some ecological similarities in grasshopper fauna. However, species richness and diversity are higher in the US grasslands, while the Pampas have a greater diversity of higher acridid taxa, three families (Acrididae, Romaleidae and Ommexechidae) and nine subfamilies (Melanoplinae, Gomphocerinae, Copiocerinae, Leptysminae, Cyrtacanthacridinae, Acridinae, Romaleinae, Ommexechinae and Aucacrinae)

Grasshoppers of the Argentine Pampas, Table 11 Grasshopper species composition of the Argentine pampas

Acrididae		Romaleidae
Acridinae	Melanoplinae	Romaleinae
<i>Allotruxalis strigata</i> (Bruner)	<i>Atrachelacris gramineus</i> G.Tos	<i>Diponthus argentinus</i> Pictet & Saus
<i>Covasacris albitarsis</i> Liebermann	<i>Baeacris punctulatus</i> (Thunberg)	<i>Elaeochlora viridicata</i> Serville
<i>Laplatacris dispar</i> Rehn	<i>Baeacris pseudopunctulatus</i> Ronderos	<i>Xyleus laevipes</i> Stål
<i>Parorphula graminea</i> Bruner	<i>Dichroplus conspersus</i> Bruner	<i>Zoniopoda omnicolor</i> Bruner
Copiocerinae	<i>Dichroplus elongatus</i> (G.Tos)	<i>Zoniopoda tarsata</i> Serville
<i>Aleuas linneatus</i> Stål	<i>Dichroplus maculipennis</i> (Blanchard)	
<i>Aleuas viticolis</i> Stål	<i>Dichroplus obscurus</i> Bruner	
Leptysmiinae	<i>Dichroplus patruelis</i> Stål	
<i>Leptyσμα argentina</i> Bruner	<i>Dichroplus pratensis</i> Bruner	
Gomphocerinae	<i>Dichroplus schulzi</i> Bruner	
<i>Amblytropidia australis</i> Bruner	<i>Dichroplus vittatus</i> Bruner	
<i>Borellia brunneri</i> (Rehn)	<i>Leiotettix pulcher</i> (Rehn)	
<i>Euplectrotettix ferrugineus</i> Bruner	<i>Neopedies brunneri</i> G.Tos	
<i>Orphulella punctata</i> De Geer	<i>Ronderosia bergii</i> (Stål)	
<i>Rhammatocerus pictus</i> Bruner	<i>Ronderosia forcipatus</i> (Rehn)	
<i>Scyllina signatipennis</i> Blanchard	<i>Scotussa cliens</i> Stål	
<i>Scyllina variabilis</i> Bruner	<i>Scotussa daguerrei</i> Liebermann	
<i>Sinipta dalmani</i> Stål	<i>Scotussa lemniscata</i> (Stål)	
<i>Staurorhectus longicornis</i> G.Tos		

versus two families (Acrididae and Romaleidae) and six subfamilies (Oedipodinae, Melanoplinae, Gomphocerinae, Acridinae, Cyrtacanthacridinae and Romaleinae). The Melanoplinae is the main subfamily in both regions and the genus *Melanoplus* of North American is considered to be the ecological equivalent to the South American genus *Dichroplus* (Table 11).

There exists a large-scale association between grasshopper and plant communities along the Pampas. Indeed, assemblages may differ in density, dominance, and species composition because of differences in vegetation and climatic conditions. Total species richness is thirty nine, ranging from four to sixteen at different sites. *Dichroplus pratensis* and *D. elongatus* (Fig. 47) are clearly the most common and widely distributed species in this region. Both are polyphagous species, eating grasses

and forbs. Eggs hatch in November and, after passing through 5 nymphal instars, reach the adult stage in January. They have an obligatory embryonic diapause and one generation a year.



Grasshoppers of the Argentine Pampas, Figure 47 *Dichroplus elongatus* G. Tos. Another species of this genus, *D. maculipennis*, one of the most harmful species of this area thirty years ago, has exhibited very low populations during the last decade.

In relation to damage, a population of *D. pratensis* with a peak of 22.19 individual/m² may cause a forage loss of approximately 274.32 kg/ha.

Another species of this genus, *D. maculipennis*, one of the most harmful species of this area thirty years ago, has exhibited very low populations during the last decade.

Other common species are *Laplatacris dispar*, *Amblytropidia australis*, and *Scotussa lemniscata* in the humid northeastern grasslands. The central grasslands are dominated by *D. pratensis*, *D. elongates*, *Staurorhectus longicornis*, *Leiotettix pulcher* and *D. vittatus*. *Borellia brunneri*, *Covasacris albitarsis* and *S. lemniscata* are common in the southeastern habitats. Grasshopper assemblages of the xeric western grasslands are dominated by *D. pratensis* and *Neopedies brunneri*, and among common species are *Rhammatocerus pictus*, *S. longicornis*, *D. vittatus* and the Romaleidae *Zoniopoda tarsata*.

Most species in the Pampas are rare. Some are registered every year from most sites, but in low numbers (e.g., *Baeacris punctulatus*), whereas others are found in many years but only in some sites (e.g., *Xyleus laevipes* and *Z. omnicolor*).

At present, the only control measure against these insects is the use of chemical pesticides. The microsporidian pathogen *Nosema locustae* Canning was introduced between 1978 and 1982 to control pest grasshoppers, and became established in some areas. However, no surveys to evaluate the effectiveness as a biological control agent has been conducted. Only one native microsporidian pathogen, *Perezia dichroplusae* Lange, is currently known in Argentine grasshoppers. Other pathogens, like the amoeba *Malameba locustae* King & Taylor (Protozoa: Rhizopoda), the virus *Entomopox* (Poxviridae: Entomopoxvirinae) and the fungus *Entomophaga grylli* (Fresenius) (Zygomycetes: Entomophthorales) also are recorded.

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Grassi, Giovanni Battista

Giovanni Grassi (Fig. 48) was born in the province of Como, Italy, on March 27, 1854. He was educated at the universities of Pavia and Messina (Italy) and Heidelberg and Würzburg (Germany). In 1883 he was appointed professor of zoology, anatomy, and comparative zoology at Università di Catania, and in 1895 he was appointed to a similar position at Università di Roma. His works began on intestinal worms, proceeded to Protozoa (especially of termites), continued with flies (1883, “Malefizi delle mosche”) as vectors of eggs of nematodes and spores of fungi, on embryology of the honey bee, morphology and phylogeny of arthropods, the biology of termites, the transmission of malaria by *Anopheles* mosquitoes, the life history of *Phlebotomus*, on the grapevine pest *Phylloxera*, and on chaetognaths, marine eels, and development of the vertebral column. In 1908 he was made a member of the Italian senate. In 1884–1889 he studied Thysanura, *Scolopendrella*, and *Koenema mirabilis*, the last being an arachnid that he discovered. For his collaborative work with Sandias on termites, and for his studies of muraenoid eels, he was awarded the Darwin gold medal of The Royal Society. In 1898–1900, he concentrated on malaria, finding that all Italian species of *Anopheles* can transmit *Plasmodium*, and that *Plasmodium* is the same parasite that Ross described under the name



Grassi, Giovanni Battista, Figure 48 Giovanni Batista.

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Grass Miner Moths (Lepidoptera: Elachistidae)

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Grass miner moths, family Elachistidae, comprise about 723 species worldwide, but most are Palearctic (472 sp.), and many are in the genus *Elachista*. Two subfamilies are used, or only tribes: Perittiinae and Elachistinae. The family is part of the superfamily Gelechioidea in the section Tineina, subsection Tineina, of the division Ditrysia. Adults small (5–23 mm wingspan), with head smooth-scaled; haustellum scaled; labial palpi upcurved but sometimes porrect; maxillary palpi minute, 1 to 2-segmented. Wings narrow and lanceolate, with reduced venation, but with large hindwing fringes (Fig. 49). Maculation often white with various markings or



Grass Miner Moths (Lepidoptera: Elachistidae), Figure 49 Example of grass miner moths (Elachistidae), *Biselachista cucullata* (Braun) from Florida, USA.

bands, or darker, sometimes with iridescence. Adults are often crepuscular or nocturnal, but some are diurnal. Larvae are leafminers (sometimes gregarious) or stem miners, especially on grasses (Gramineae) and related plant groups like Juncaceae and Cyperaceae, but other plant families are also utilized.

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Grass Moths

Some members of the family Pyralidae (order Lepidoptera) also known as snout moths.

- ▶ Snout Moths
- ▶ Butterflies and Moths

Gravenhorst, Johan Ludwig Christian

Johan Ludwig Gravenhorst was born in Braunschweig [Brunswick], Germany, on November 14, 1777. He was educated at the Katharinen Gymnasium in Braunschweig. Despite an early interest in natural history, he decided on a career in law, and entered Universität Helmstadt to study law. However, in 1790 he entered Universität Göttingen to study zoology, mineralogy, and botany. In 1801 he returned to Helmstadt and defended his dissertation “*Conspectus historiae entomologiae*” and was awarded the title of “*Doctor philosophiae et magister liberalium artium*.” Then he returned to Braunschweig and spent all his time on entomology. His first major publication (1802) was “*Coleoptera Microptera Brunsvicensia*,” after which he journeyed to Paris to study insect collections, and meet entomologists. On return to Braunschweig, he bought entomological collections, became a “*Privatdozent*” at Universität Göttingen, and published (1906) “*Monographia Coleopterorum Microptero-*” which expanded his recognition among entomologists. He worked on an expanded edition of this work until Erichson’s (1840) “*Genera et species Staphylinorum*” made it redundant. In 1810 he accepted a position of professor of natural history and second director of the botanical garden at Frankfurt an der Oder. In 1811, this university was transferred to Breslau (now Wrocław in Poland), and Gravenhorst followed. In 1814 he sold his insect collection to the university in return for a guaranteed annual income transferable to his widow, and he founded the zoological museum there. He began to work on Ichneumonidae (Hymenoptera) on which he published intensively to 1829. In 1830 he travelled to Prague, Vienna, and Trieste to study marine animals, on which he published. He was a member of at least 21 natural history societies in Germany, France, Italy and England. He died in Breslau on January 17, 1857, after a very lengthy illness.

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Gravid

This refers to a female that is full of eggs, or is ready to deposit her eggs.

Gray Mold of Grapes

This is a serious fungal disease of grape.

► [Transmission of Plant Diseases by Insects](#)

Graybacks

A family of dragonflies in the order Odonata: *Petaluridae*.

► [Dragonflies and Damselflies](#)

Greater Date Moth, *Arenipses sabella* Hmps. (Lepidoptera: Pyralidae)

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The importance of the greater date moth as a date pest seems to be increasing. It is known from India, Iran, Iraq, Saudi Arabia, Oman, Egypt and Algeria.

Description

The adult greater date moth is 18–22 mm long, with a wing span of 33–35 mm in males and 40–42 mm in females. They are light brown to yellowish. The head and thorax are light brown and the abdomen is silvery white, the front wings are brownish to yellowish with black scales and the hind wings

are light brown. The eggs generally are laid singly, but also have been observed in clusters. They are creamy-white in color and spherical in shape. The larvae of the greater date moth are 28–35 mm in length and are dark pink in color. The pupae are elongated, about 18 mm in length, and are light brown.

Behavior

The adult greater date moths are nocturnal, but attracted to artificial light. They hide in the inner side of the bases of the palm petioles during the daytime. The larvae are also nocturnal at high temperatures, but have been seen active during the daytime at moderate temperatures. The hiding places of the larvae are at the inner bases of the split spathes, between the base of strands, in the inner base of the palm petioles. The larvae are quite mobile and can hide easily when threatened.

Biology and Damage

The biology of this pest is not well understood. The adults are active most of the year in warm areas and are not seen in the winter months in cold areas. The pest spends the winter in the larval stage in cocoons under the fibers of the tree cabbage (head of the tree). The number of generations per year is uncertain, but there are at least two generations per year. In February in warm areas, larvae feed on the inner base of the petioles. The females lay eggs on the external tips of the unopened spathes, on strands and on fruit clusters. Hatched larvae feed on the tips of unopened spathes, which become black because of the clustering of black frass and silken threads. The larvae penetrate the sheath of the unopened spathes and feed on the strand mainly on tips. The tips of the strands become light gray to silver in color and devoid of flowers. When the spathes open, the larvae may remove the flowers and young fruits from the strands. The larvae also feed on the base of the

main axis of the fruit cluster and make longitudinal tunnels and holes, both filled with black frass, coarse silks and plant fragments. The larvae feed in September on the ripened fruits. The infested dates become filled with black frass tied by silks. The infested dates may be inadvertently harvested and transferred to stores where consumers unfortunately encounter the larvae and adults.

Control

No definitive studies have been done to control this pest. The adult greater date moths were observed to be attracted to light traps with high rates of attracting from March to May. Pruning of the palm fronds may eliminate the hiding places of the larvae and adults. The current general practices to control this pest are dusting the cabbage of the tree with organophosphorus or pyrethroid insecticides in the autumn after harvesting, and dusting the strands and the bases of the fruit clusters with an insecticide at the time of pollination. If the problem persists, sprays also should be applied on the young fruits. No active and promising natural enemies have been recorded for this pest. The pheromone of this pest has not yet been identified, therefore, it is important that new research focus on this aspect.

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Greater Fritillaries or Silverspots, *Speyeria* [= *Argynnis*] (Lepidoptera: Nymphalidae)

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Speyeria scudder (Nymphalidae: Heliconiinae: Argynnini), commonly known as greater fritillaries or silverspots, are medium to large butterflies (wingspans of 40–90 mm) that represent conspicuous members of North American Lepidoptera. The genus was named in honor of a German entomologist, Adolph Speyer, who specialized in butterfly studies. The origin of the common name “fritillaries” is obscure, and one explanation is that these butterflies resemble the lily genus *Fritillaria*. Typically orange and black or brown in color, most are recognized by distinctive black spots and bars on the dorsal wing surface and silvery or cream-colored spots located on the ventral surface of the hind wings.

Speyeria fritillaries are restricted to North America (absent in southeastern regions of the United States and all but northern Mexico), although morphologically similar genera exist in other temperate parts of the world and together may be considered the temperate-zone counterpart to tropical Heliconiini (i.e., passion-vine butterflies). Long included in the Old World genus *Argynnis* Fabricius, they differ from their Eurasian relatives primarily in genitalic structure and were thus considered generically distinct from *Argynnis* by dos Passos and Grey; all North American taxa named since that time have been described within *Speyeria*. Recent workers, however, have treated *Speyeria* as a subgenus of the primarily Palearctic *Argynnis* fritillaries.

Speyeria species and associated geographical forms have been collected and examined in great detail in the past and continue to be a target for professional and amateur butterfly enthusiasts. The early works on *Speyeria* listed over 100 “species” names, but subsequent workers realized that most of these “species” were no more than geographical forms or races associated with a few

polytypic species. Since then, several additional subspecies have been described, three subspecies have been elevated to full species status, and some taxon names have been declared synonyms.

Speyeria is presently comprised of 16 species (Table 12), and according to some authors, over 100 subspecific, geographical forms. *Speyeria cybele* (Fabricius), *S. aphrodite* (Fabricius), *S. idalia* (Drury), and *S. atlantis* (Edwards) occur east of the Mississippi River, each with distributions or subspecies occurring in western North America, while *S. diana* (Cramer) is restricted to the eastern United States (in Appalachian and Ozark Mountain ecosystems). The remaining species occur in the western regions of North America, some as far north as Alaska. All but three *Speyeria* species are extremely variable [exceptions include *S. diana*, *S. idalia*, and *S. edwardsii* (Reakirt)], with the western North American species, in particular, fragmenting into numerous geographic forms that are often clinally joined with considerable intergradation occurring.

Species and subspecies determinations are made primarily using wing patterns, wing coloration, and geographical location; because of this, specific and subspecific identification is difficult in many taxa due to subtle pattern (Fig. 50) and color variations. Generally, adult morphological variation between species and subspecies is based on overall size, varying degrees of sexual dimorphism, and the wings. Important wing characteristics found dorsally are ground color, intensity of black markings, degree of dark basal suffusion, prominence of marginal band, and thickness of veins on the wings. Ventrally the important characteristics are the general ground color of the discal area on the hindwings, the size, shape, color and position of spots on the hindwings, and color and width of the submarginal band between the two outer rows of spots on the hindwings (Fig. 52).

Life History

Adults frequent open fields, moist meadows, and open woodlands near streams, or are restricted

Greater Fritillaries or Silverspots, *Speyeria* [=Argynnis] (Lepidoptera: Nymphalidae), Table 12 The known species of Fritillary butterflies

Speyeria species and associated common names
<i>Speyeria diana</i> (Cramer) – Diana Fritillary, Great Smokies Fritillary
<i>Speyeria cybele</i> (Fabricius) – Cybele Fritillary, Great Spangled Fritillary
<i>Speyeria aphrodite</i> (Fabricius) – Aphrodite Fritillary
<i>Speyeria idalia</i> (Drury) – Regal Fritillary, Eastern Regal Fritillary, Prairie Regal Fritillary
<i>Speyeria nokomis</i> (Edwards) – Nokomis Fritillary, Western Seep Fritillary
<i>Speyeria edwardsii</i> (Reakirt) – Edward's Fritillary
<i>Speyeria coronis</i> (Behr) – Coronis Fritillary
<i>Speyeria carolae</i> (dos Passos and Grey) – Carol's Fritillary
<i>Speyeria zerene</i> (Boisduval) – Zerene Fritillary
<i>Speyeria callippe</i> (Boisduval) – Callippe Fritillary
<i>Speyeria egleis</i> (Behr) – Egleis Fritillary, Great Basin Fritillary
<i>Speyeria adiaeste</i> (Edwards) – Unsilvered Fritillary
<i>Speyeria atlantis</i> (Edwards) – Atlantis Fritillary
<i>Speyeria hesperis</i> (Edwards) – Hesperis Fritillary, Western Fritillary
<i>Speyeria hydaspe</i> (Boisduval) – Hydaspe Fritillary
<i>Speyeria mormonia</i> (Boisduval) – Mormon Fritillary

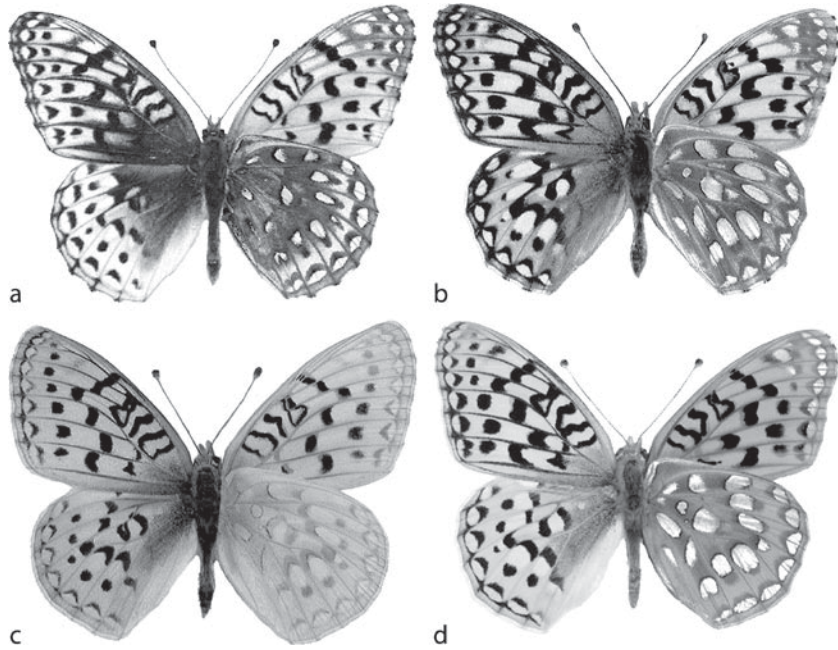
to coastal dunes, tallgrass prairies, or mountains. During the summer months they may be abundant in forest clearings, by roadsides, and along flower rich slopes and meadows in mountainous regions. *Speyeria* often prefer tall nectar sources such as thistles, wild asters, sunflowers, penstemons, mint, and dogbane. Males are often found congregating in large numbers at seeps and roadside puddles. Adults are strong fliers and can fly many kms, especially in late summer. They are rather long lived (several weeks to 2–3 months from May–September) and all members of the genus are univoltine.

Adult males typically emerge a week before females and patrol for potential mates. Courtship is rather elaborate, and pheromone cues from both sexes may be a reproductive barrier between species. *Speyeria* adults (Fig. 51) bear scent scales that lie along the veins on the upper side of the wings. Males pursue females, draw their forewings forward, and flick the closed wings slightly open in quick bursts. Each burst of two to five flicks lasts less than a second, wafting pheromones up to the female's antennae. The tips of the abdomens of male Argynnini

(including *Speyeria*) contain paired glands normally hidden in the abdomen that aid in courtship. Courting males keep their forewings in a forward position and open and close them near the resting female to waft pheromones. Unreceptive females will flutter their wings to reject males.

Fritillaries are fecund butterflies, with some species laying over 2,000 eggs. Females delay egg-laying until late summer and usually oviposit rather haphazardly near their host plants rather than carefully placing them on the plant as most butterflies do. They are known to deposit eggs on twigs, leaves, stones and other debris. Eggs bear a tannish, camouflage coloration and are slightly rounded, tapering toward the apex. They are highly sculptured and likely adapted to withstand considerable environmental pressures including submergence, frost, and ground dwelling predators and microbes.

Larvae usually pass through six instars, overwintering as first instars and breaking diapause to complete development the following season. They are generally secretive and feed primarily at night, returning to hiding places under host leaves or



Greater Fritillaries or Silverspots, *Speyeria* [= *Argynnis*] (Lepidoptera: Nymphalidae), Figure 50 Dorsal (left) and ventral (right) wing patterning of some *Speyeria* species: (a) *Speyeria hesperis* (New Mexico); (b) *Speyeria callippe* (Nevada); (c) *Speyeria mormonia* (Nevada); (d) *Speyeria zerene* (Nevada) (images by James C. Dunford).

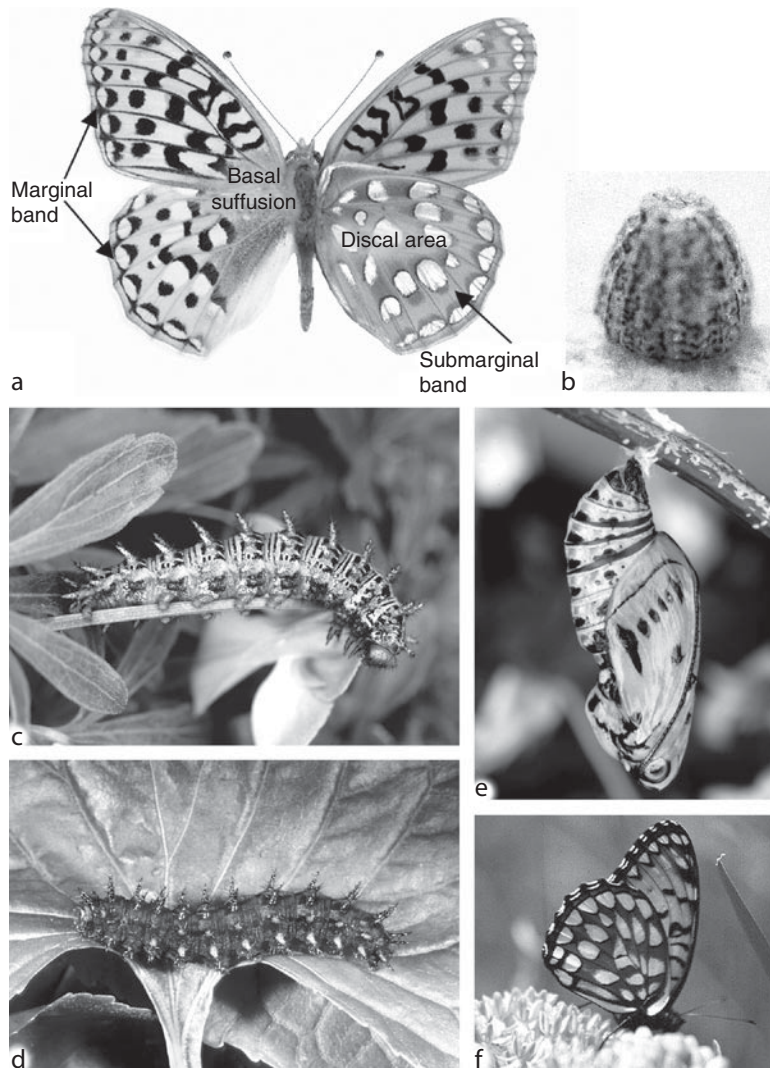
nearby vegetation during the day. Most species are black with lighter markings and bear three rows of branching spines on either side of the body. Some species exhibit spots of red/orange or other colors. Larvae feed on various violet species (*Viola*), and in laboratory conditions they are known to feed on every American violet species tested. *Viola* species range widely across temperate habitats of the Northern Hemisphere and into higher elevations of mountain systems towards the equator. *Speyeria* pupae are generally tan or brown with a few markings and hang freely from the cremastral end.

Speyeria individuals likely gain protection from potential predators in a variety of ways. *Speyeria diana* females (Fig. 52) are sexually dimorphic from *S. diana* males and, unlike the typical orange and black patterning of most *Speyeria* species, have been implicated in a Batesian mimicry complex with the distasteful, similarly colored pipevine swallowtail butterfly. In some *Speyeria* species, an eversible gland, capable of producing an unpleasant odor, is located on the dorsum of the

female abdomen. Larvae also bear a gland located ventrally just behind the head that is likely used for defense against predators. Other avoidance measures during the larval stages include taking refuge under leaves during the day and feeding at night. First instars will also often hibernate inside grass stems. Eggs in some species may also contain phytochemicals used to deter potential predators.

Conservation

A few *Speyeria* species have been declining over the past 200 years and have been listed as either federally/state endangered or threatened [e.g., *S. idalia*, *S. diana*, *S. zerene hippolyta* (Edwards)]. *Speyeria* and their larval host plants (*Viola*) are among the best indicator organisms of native, undisturbed ecological communities in North America. They are also among the first organisms to be eliminated from such communities as a result of human-caused disturbances.



Greater Fritillaries or Silverspots, *Speyeria* [= *Argynnis*] (Lepidoptera: Nymphalidae), Figure 51 *Speyeria* (a) general wing features; (b) *Speyeria idalia* egg; (c) *Speyeria idalia* larva; (d) *Speyeria aphrodite* larva; (e) *Speyeria idalia* pupa; (f) *Speyeria idalia* (Regal Fritillary) nectaring on butterflyweed (Wisconsin) (images b-e by David L. Wagner; images a and f by James C. Dunford).

Speyeria idalia populations have been extirpated in much of the northeastern United States and have declined precipitously in other parts of its range. They inhabit native tallgrass prairies in the Midwest, an ecosystem that is shrinking due to development and agricultural activities. *Speyeria diana* disappeared from southeastern Virginia in about 1951 and is considered uncommon or extirpated in many other parts of its range. Historical populations in the Midwest and the Virginia

Piedmont were extirpated in the 1800s, and most occurrence records (except in the Appalachians and Ozarks) are more than 50 years old. Coastal subspecies, such as the Oregon Silverspot (*S. z. hippolyta*), have been federally listed and depend on vanishing salt-spray meadows along the Oregon coast. Research on *Speyeria* butterflies continues to focus on various conservation and management measures required to maintain and protect threatened or endangered species.



a



b

Greater Fritillaries or Silverspots, *Speyeria* [=Argynnis] (Lepidoptera: Nymphalidae), Figure 52 *Speyeria diana* (a) male and (b) female (Tennessee). In each image, the left side is the dorsal wing surfaces and right side is the ventral wing surfaces (images by James C. Dunford).

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Greenbottle Flies

Members of the family Calliphoridae (order Diptera).

► Flies

Greenbug, *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae)

Greenbug is an important aphid pest of grass crops.

► Wheat Pests and their Management

Green-Eyed Skimmers

A family of dragonflies in the order Odonata: Corduliidae.

► Dragonflies and Damselflies

Green Flies

Members of the family Aphididae (order Hemiptera).

► Bugs

Greenheads

Some members of the family Tabanidae (order Diptera).

► Flies

Greenhouse Whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae)

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Greenhouse whitefly is found widely around the world, including most of the temperate and subtropical regions of North America, South America, Europe, Central Asia and India, northern and eastern Africa, New Zealand and southern Australia. It does not thrive in most tropical locations, and occurs in colder regions only by virtue of its ability to survive winter in greenhouses. It often overwinters only in such protected locations, but in mild-winter areas it survives outdoors throughout the year. The origin of this species is not certain, but is thought to be Mexico or the southwestern United States.

Life History

The development period from egg to adult requires about 25–30 days at 21°C, and 22–25 days at 24°C. Thus, because the preoviposition period of adults also is short, less than two days above 20°C, a complete life cycle is possible within a month. Greenhouse whitefly can live for months, and oviposition time can exceed the development time of immatures; this results in overlapping generations. Optimal relative humidity is 75–80%. The developmental threshold for all stages is about 8.5°C.

Eggs are oval in shape, and suspended from the leaf by a short, narrow stalk. The eggs initially are green in color and dusted with white powdery wax, but turn brown or black as they mature. The eggs are about 0.24 mm long and 0.07 mm wide. Eggs are deposited on the youngest plant tissue, usually on the underside of leaves in an incomplete circular pattern. Up to 15 eggs may be deposited in a circle measuring about 1.5 mm in diameter. This pattern results from the female

moving in a circle while she remains with her mouthparts inserted into the plant. This pattern is less likely on plants with a high density of trichomes because plant hairs interfere with the oviposition behavior. Duration of the eggs stage is often 10–12 days, but eggs may persist for over 100 days under cool conditions. When cultured at 18, 22.5, and 27°C, egg development requires an average of 15, 9.8, and 7.6 days, respectively. Maximum fecundity varies according to temperature; optimal temperature is 20–25°C regardless of host plant. When feeding on eggplant, greenhouse whitefly produces over 500 eggs, on cucumber and tomato about 175–200 eggs.

The newly hatched whitefly nymph is flattened, oval in outline, and bears functional legs and antennae. The perimeter is equipped with waxy filaments. The first instar measures about 0.3 mm in length. It is translucent, usually appearing to be pale green in color but with red eyes. After crawling one cm or so from the egg, it settles to feed and molt. Development in the first instar requires 6.5, 4.2, and 2.9 days, respectively, when cultured at 18, 22.5, and 27°C. The second and

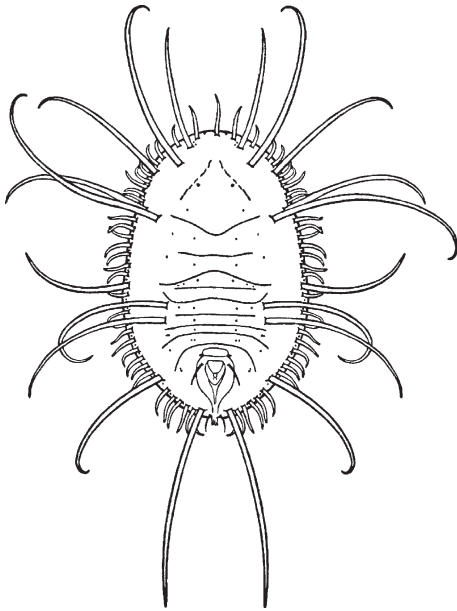


Greenhouse Whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae),

Figure 53 Adult of greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood).

third nymphal stages are similar in form and larger in size, though the legs and antennae become reduced and nonfunctional. They measure about 0.38 and 0.52 mm in length, respectively. Duration of the second instar requires about 4.3, 3.2, and 1.9 days whereas third instars require 4.5, 3.2, and 2.5 days, respectively, when cultured at 18, 22.5, and 27°C. The fourth nymphal stage, which is usually called the “pupa,” differs in appearance from the preceding stages. The fourth instar measures about 0.75 mm in length, is thicker and more opaque in appearance, and is equipped with long waxy filaments. The pupal stage actually consists of the fourth nymphal instar period, which is a period of feeding, plus the period of pupation, which is a time of transformation to the adult stage. Thus, pupation occurs within the cuticle of the fourth instar. Duration of the fourth instar period and pupal period are 8.7 and 5.9, 5.9 and 4.0, and 4.5 and 2.8 days, respectively, at 18, 22.5, and 27°C.

The form of the pupa is used to distinguish among whitefly species (Fig. 54), and can be used to separate greenhouse whitefly from the similar-



Greenhouse Whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae),
Figure 54 Pupa of greenhouse whitefly,
***Trialeurodes vaporariorum* (Westwood).**

appearing *Bemisia* spp. Greenhouse whitefly is straight-sided when viewed laterally, ovoid, and lacks a distinct groove near the anal end of the body. In contrast, the *Bemisia* spp. are oblique-sided, irregularly oval, and possess a distinct groove in the anal region.

Individuals of greenhouse whitefly which develop on lightly or moderately pubescent leaves tend to be relatively large and to have four pairs of well developed dorsal waxy filaments. In contrast, whiteflies developing on densely pubescent leaves tend to be smaller, and to bear more than four pairs of dorsal filaments. These morphological variations are not entirely consistent, and have led to considerable taxonomic confusion.

Adults (Fig. 53), are small, measuring 1.0–2.0 mm long. They are white in color, with the color derived from the presence of white waxy or mealy material, and have reddish eyes. They bear four wings, with the hind wings nearly as long as the forewings. The antennae are evident. In general form, viewed from above, this insect is triangular in shape because the distal portions of the wings are wider than the basal sections. The wings are held horizontally when at rest; this characteristic is useful for distinguishing this species from the similar-appearing *Bemisia* spp. whiteflies, which hold their wings angled or roof-like when at rest. Mating may occur repeatedly, though females can also produce eggs without mating.

This species has a very wide host range, with over 300 species recorded as hosts. However, some hosts are more suitable. Vegetable plants often serving as good hosts are bean, cantaloupe, cucumber, lettuce, squash, tomato, eggplant, and occasionally cabbage, sweet potato, pepper, and potato. Among greenhouse-grown vegetables, the most common hosts are tomato, eggplant, and cucumber. Many ornamental plants serve as good hosts, including ageratum, aster, chrysanthemum, coleus, gardenia, gerbera, lantana, poinsettia, salvia, verbena, zinnia and many others.

Natural enemies of greenhouse whitefly are numerous, but few are consistently effective, especially under greenhouse conditions. Greenhouse whitefly

is attacked by the common predators of small insects, including minute pirate bugs (Hemiptera: Anthocoridae), some plant bugs (Hemiptera: Miridae), green lacewings (Neuroptera: Chrysopidae), brown lacewings (Neuroptera: Hemerobiidae), and ladybirds (Coleoptera: Coccinellidae). Parasitic wasps attacking greenhouse whitefly are largely confined to the family Aphelinidae, but many species are involved and they vary regionally. Some of the important parasitoids are *Encarsia formosa* Gahan, *Aleurodophilus pergandiella* (Howard), *Eretmocerus haldemani* Howard, *Prospaltella transvena* Timberlake, and *Aphidencyrthus aphidivorus* (Mayr). Although these agents exercise considerable control on whitefly populations in weedy areas or on crops where insecticide use is minimal or absent, they do not survive well in the presence of most insecticides. *Encarsia formosa* has been used successfully under greenhouse conditions, and to a lesser extent field conditions, to affect biological suppression.

The pathogens of greenhouse whitefly are principally fungi, particularly *Aschersonia aleyrodinis*, *Paecilomyces fumosoroseus*, and *Verticillium lecanii*. All occur naturally and can cause epizootics in greenhouses and fields, and also have been promoted for use in greenhouses as bioinsecticides. *Aschersonia* is specific to whiteflies, *Verticillium* has a moderately wide host range, and *Paecilomyces* has a broad host range. For optimal development of disease, high humidity is required. *Aschersonia* is spread principally by rainfall, so often fares poorly in greenhouse environments.

Damage

Adult and nymphal whiteflies use their piercing-sucking mouthparts to feed on the phloem of host plants. This results in direct damage, resulting in localized spotting, yellowing, or leaf drop. Under heavy feeding pressure, wilting and severe growth reduction may occur. Whiteflies also secrete large amounts of sugary honeydew, which coats the plants with sticky material, and must be removed

from fruit before it is marketed. The honeydew also provides a substrate for growth of sooty mold, a black fungus that interferes with the photosynthesis and transpiration of plants.

Greenhouse whitefly is, as the common name suggests, primarily a pest in greenhouses, and is a serious limitation to the production of vegetables grown in such structures. However, it can also be a field pest, often in warmer climates but also in cool climates when seedlings contaminated with whiteflies are transplanted into the field.

Greenhouse whitefly is capable of transmitting viruses to plants, but is not considered to be a serious vector, particularly relative to the *Bemisia* spp. However, greenhouse whitefly transmits beet pseudo-yellow virus to cucumber in greenhouse culture.

Management

Although whitefly nymphs and adults can be detected readily by visual examination of foliage, most monitoring systems take advantage of the attraction of adults to yellow, and use yellow sticky traps to capture flying insects. Sticky cards or ribbons are suspended at about the height of the crop for optimal monitoring. Traps must be placed close to plants or close to the ground or population densities will be underestimated. Traps should be dispersed widely because whitefly distribution is not uniform within a crop. Whitefly flight peaks at about noon, but under greenhouse conditions is independent of temperature if the basal flight temperature of 16–17°C is exceeded.

Applications of insecticides are often made to minimize the effects of whitefly feeding on crops in greenhouses. Greenhouse whitefly feeds on the lower surface of foliage and is sessile throughout most of its life, habits that minimize contact with insecticides, and resulting in frequent applications and effectiveness mostly against the adult stage. In greenhouse culture, application intervals of only 4–5 days are common,

and systemic insecticides are often used to increase the likelihood of insect contact with toxins. Thus, whitefly resistance to nearly all classes of insecticides is known, and rotation of insecticide classes is encouraged. Mixtures of insecticides are often used, which is indicative of high levels of resistance among whiteflies to insecticides. Field populations of greenhouse whitefly invariably are derived from greenhouse populations, and possess similar resistance to many insecticides. Applications of petroleum oils and biological control agents help to avoid difficulties with insecticide resistance.

Some insecticidal materials can be integrated into biologically based whitefly management systems. Selective materials that affect only adult and nymphal whiteflies, insect growth regulators, and insecticidal soaps are somewhat compatible with parasitoids and can be used when parasitoids are failing.

Few cultural practices are available, but disruption of the whitefly population with host-free periods is important. Continuous culture of plants allows whiteflies to move from older to younger plants. Similarly, weeds may allow whiteflies to bridge crop-free periods, and should be eliminated. Culture of plants over white reflective mulch also reduces whitefly densities. Yellow sticky traps can be hung in greenhouses to capture adult whiteflies, thereby reducing whitefly density.

Seasonal inoculative release of the parasitoid *Encarsia formosa* Gahan into crops infested with greenhouse whitefly has been used extensively for suppression of whiteflies on greenhouse-grown vegetable crops. Excellent suppression of whiteflies is attainable, but on host plants such as cucumber and eggplant, which are very favorable for whitefly reproduction and have hairy leaves that interfere with parasitoid searching, frequent releases must be made. Alternatively, cucumber varieties with reduced trichome density have been developed, and which favor parasitism. Another critical factor is temperature, because low greenhouse temperatures are more suitable for whitefly activity than parasitoid activity.

Daytime temperatures of about 24°C seem to be optimal; temperatures of 18°C or less suppress parasitoid searching. A cold-tolerant *Encarsia* strain that is active at 13–17°C has also been used to overcome this temperature problem. Interference from pesticides can markedly affect parasitoid survival, so other pests such as mites must be managed biologically also. Lastly, release rates are important because if too many parasitoids are released the host whiteflies are driven nearly to extinction, leading to disappearance of the parasitoids; this is most likely to occur in small greenhouses. Alternatively, parasitoid releases can be made throughout the season, irrespective of whitefly presence. Although the protocols and technologies for whitefly management using *E. formosa* have been perfected for use in greenhouses, management under outdoor conditions awaits further research.

The fungus *Verticillium lecanii* is sometimes used commercially in Europe for whitefly and thrips suppression in greenhouses, though its success is strongly affected by humidity. Where humidity can be raised to a high level, epizootics can be induced in 1–2 weeks. Both young and adult stages are susceptible to infection.

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Green June Beetle, *Cotnius nitida* (Linnaeus) (Coleoptera: Scarabaeidae)

► Turfgrass Insects and their Management

Green Lacewings

Members of the family Chrysopidae (order Neuroptera).

► [Lacewings, Antlions, and Mantidflies](#)

Green Muscardine

A mycosis of various larval, pupal, and adult insects, caused by the fungus *Metarrhizium*.

► [Muscardine](#)

Green Peach Aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae)

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Green peach aphid is found throughout the world, including both tropics and temperate latitudes. It is considered to be a pest nearly everywhere, often due to its ability to transmit plant viruses. In addition to attacking plants in the field, green peach aphid readily infests vegetables and ornamental plants grown in greenhouses. This allows high levels of survival in areas with inclement weather, and favors ready transport on plant material. When young plants are infested in the greenhouse and then transplanted into the field, fields will not only be inoculated with aphids but insecticide resistance may be introduced. These aphids are also reported to be transported long distances by wind and storms.

Life History

The life cycle varies considerably, depending on the presence of cold winters. Development can be rapid, often 10–12 days for a complete generation, and with over 20 annual generations reported in mild climates. Where suitable host plants cannot

persist, the aphid overwinters in the egg stage. In the spring, soon after the plant breaks dormancy and begins to grow, the eggs hatch and the nymphs feed on flowers, young foliage, and stems. After several generations on *Prunus* spp., dispersants from overwintering hosts deposit nymphs on summer hosts. In cold climates, adults return to *Prunus* spp. in the autumn, where mating occurs, and eggs are deposited. All generations except the autumn generation culminating in egg production are parthenogenetic.

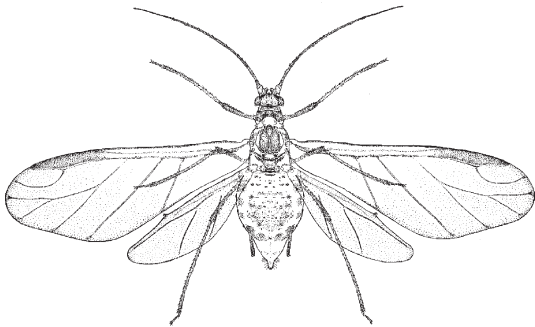
Eggs are deposited on *Prunus* spp. trees. The eggs measure about 0.6 mm long and 0.3 mm wide, and are elliptical in shape. Eggs initially are yellow or green, but soon turn black. Mortality in the egg stage sometimes is quite high.

Nymphs initially are greenish, but soon turn yellowish, greatly resembling viviparous adults. There may be four instars in this aphid, with the duration of each averaging 2.0, 2.1, 2.3, and 2.0 days, respectively. Alternatively, five instars also have been reported, with a mean development time of 2.4, 1.8, 2.0, 2.1, and 0.7 days, respectively. Parthenogenetic females give birth to offspring 6–17 days after birth, with an average age of 10.8 days at first birth. The length of reproduction varies considerably, but averages 14.8 days. The average length of life is about 23 days under caged conditions where predators are excluded. The daily rate of reproduction averages 1.6 nymphs per female, with about 75 offspring produced. The maximum number of generations occurring annually is 20–21, depending on the year.

Up to eight generations may occur on *Prunus*, but as aphid densities increase winged forms are produced, which then disperse to summer hosts. Winged (alate) aphids have a black head and thorax, and a yellowish green abdomen with a large dark patch dorsally. They measure 1.8–2.1 mm in length. Winged green peach aphids seemingly attempt to colonize nearly all plants available. They often deposit a few young and then again take flight. This highly dispersive nature contributes significantly to their effectiveness as vectors of plant viruses.

The offspring of the dispersants from the overwintering hosts are wingless, and each produce 30–80 young. The wingless (apterous) aphids are yellowish or greenish in color. They measure about 1.7–2.0 mm in long. A medial and lateral green stripes may be present. The cornicles are moderately long, unevenly swollen along their length, and match the body in color. The appendages are pale. The rate of reproduction is positively correlated with temperature, with the developmental threshold estimated to be about 4.3°C. As aphid densities increase or plant condition deteriorates, winged forms are again produced to aid dispersal. The nymphs that give rise to winged females may be pinkish. The dispersants typically produce about 20 offspring, which are always wingless. This cycle is repeated throughout the period of favorable weather.

In the autumn, in response to change in day length or temperature, winged male and female aphids are produced which disperse in search of *Prunus* (Fig. 55). Timing is important, as foliage on the *Prunus* hosts is physiologically optimal as leaves begin to senesce. Females arrive first, and give birth to wingless (apterous) egg-laying forms (oviparae). Males are attracted to oviparae by a pheromone, capable of mating with several females, and eggs are produced. The oviparous female deposits 4–13 eggs, usually in crevices in and near buds of *Prunus* spp. The oviparous female is 1.5–2.0 mm long, and pinkish.



Green Peach Aphid, *Myzus persicae* (Sulzer)
(Hemiptera: Aphididae), Figure 55 Adult of green peach aphid, *Myzus persicae* (Sulzer).

Parthenogenic reproduction is favored in the many parts of the world where continuous production of crops provides suitable host plants throughout the year, or where weather allows survival on natural (noncrop) hosts. The average temperature necessary for survival of active forms of green peach aphid is estimated at 4–10°C. Plants in the families Cruciferae and Chenopodiaceae, both crops and weeds, readily support aphids through the winter months.

Green peach aphid feeds on hundreds of host plants in over 40 plant families. However, it is only the viviparous summer stages that feed so widely; the oviparous winter stages are much more restrictive in their diet choice. In temperate latitudes the primary or overwintering hosts are trees of the genus *Prunus*, particularly peach and peach hybrids, but also apricot and plum. During the summer months the aphids abandon their woody hosts for secondary or herbaceous hosts, including ornamental, vegetable and field crops. Crops differ in their susceptibility to green peach aphid, but it is actively growing plants, or the youngest plant tissue, that most often harbors large aphid populations. In warmer climates the aphids do not seek out overwintering hosts, but persist as active nymphs and adults on hardy crops and weeds.

Broadleaf weeds can be very suitable host plants for green peach aphid, thereby creating pest problems in nearby crops. Common and widespread weeds such as field bindweed, *Convolvulus arvensis*; lambsquarters, *Chenopodium album*; and redroot pigweed, *Amaranthus retroflexus*, are often cited as important aphid hosts, and plant viruses may be acquired from these hosts.

Natural Enemies

Hundreds of natural enemies have been recorded, principally ladybirds (Coleoptera: Coccinellidae), flower flies (Diptera: Syrphidae), lacewings (Neuroptera: mainly Chrysopidae), parasitic wasps (Hymenoptera: Braconidae), and entomopathogenic fungi (mainly Entomophthorales). Most are

general predators, moving freely among green peach aphid, other aphids, and even other insects. Quantitative data generally are lacking for the influence of most natural enemies. Weather also reportedly contributes to significant change in aphid numbers, including direct mortality, but this also is poorly documented.

The ephemeral nature of aphid infestation in many crops is believed to prevent the beneficial organisms from consistently locating the aphids and reproducing in a timely manner. Nevertheless, anyone who has frequently observed green peach aphid at high densities probably has observed sudden population decreases following the appearance of ladybirds, wasp parasitoids, or entomopathogenic fungi such as *Erynia neoaphidis*. Unfortunately, the disease epizootic often occurs too late to keep aphids from attaining high numbers. Various studies that selectively excluded or killed beneficial organisms have demonstrated the explosive reproductive potential of these aphids in the absence of biological control agents, thus demonstrating their value in reducing damage potential. In greenhouse crops, where environmental conditions and predator, parasitoid, and pathogen densities can be manipulated, biological suppression can be effective and consistent.

Damage

Green peach aphids can attain very high densities on young plant tissue, causing water stress, wilting, and reduced growth rate of the plant. Prolonged aphid infestation can cause appreciable reduction in yield of root crops and foliage crops. Contamination of harvestable plant material with aphids, or with aphid honeydew, also causes loss. Where mild winters allow good overwintering survival of green peach aphid on spinach, crop value is affected by insect presence. Blemishes to the plant tissue, usually in the form of yellow spots, may result from aphid feeding. Leaf distortions are not common except on the primary host.

Contamination of vegetables by aphids sometimes presents quarantine problems and fumigation techniques have been developed that kill the insects without causing harm to the vegetables.

The major damage caused by green peach aphid is through transmission of plant viruses. Indeed, this aphid is considered by many to be the most important vector of plant viruses throughout the world. Nymphs and adults are equally capable of virus transmission, but adults, by virtue of being so mobile, probably have greater opportunity for transmission. Both persistent viruses, which move through the feeding secretions of the aphid, and non-persistent viruses, which are only temporary contaminants of aphid mouthparts, are effectively transmitted. Over 100 viruses are transmitted by this species. Some of the particularly damaging diseases include potato leafroll virus and potato virus Y to Solanaceae, beet western yellows and beet yellows viruses to Chenopodiaceae, lettuce mosaic virus to Compositae, cauliflower mosaic and turnip mosaic viruses to Cruciferae, and cucumber mosaic and watermelon mosaic viruses to Cucurbitaceae. A discoloration in potato tubers, called net necrosis, occurs in some potato varieties following transmission of potato leafroll.

Management

Day-degree models using a developmental threshold of 4°C can be used to predict various phenological events such as egg hatch and immigration of alate aphids. Yellow traps, particularly water pan traps, are commonly used for population monitoring.

Despite the numerous options potentially available, many crop producers are dependent on insecticides for suppression of green peach aphid abundance. Systemic insecticide applications are especially popular at planting time, most of which provide long-lasting protection against aphid population buildup during the critical and susceptible early stages of plant growth, and some of which provide protection for months.

Green peach aphid is able to develop at lower temperatures than its parasitoids, so the wasps are beneficial only in benign climates or where temperature can be controlled, as in some greenhouses. Indeed, there has been considerable success using parasitoids, the entomopathogenic fungus *Verticillium lecanii*, and the predatory midge *Aphidolutes aphidimyza* (Diptera: Cecidomyiidae) for greenhouse-grown vegetables in Europe.

The overwintering behavior of green peach aphid, which in many areas is restricted to *Prunus* or other relatively restricted sites, has fostered research on techniques to reduce aphid abundance and disease transmission to other crops, by either removing the overwintering site or by eliminating the aphids before they disperse. Destruction of peach and apricot trees, and treatment of trees with dormant oil and insecticide, have been used effectively to disrupt aphid population increase. Similarly, vegetable and flower plants grown in greenhouses during the winter months have been shown to be an excellent source of infestation during the following spring, and incidence of leafroll in potatoes can be directly related to the abundance of aphids in home gardens. Inspection of garden centers and treatment of seedlings found infested with aphids can be important elements of the overall potato leafroll reduction effort. As is usually the case with aphids, green peach aphid populations tend to be higher when plants are fertilized liberally with nitrogen fertilizers.

Because some of the virus diseases transmitted by green peach aphid are persistent viruses, which typically require considerable time for acquisition and transmission, insecticides can be effective in preventing disease spread in some crops. For example, potato leafroll virus is transmitted within the potato crop principally by wingless aphids moving from plant to plant. Infected seed potatoes are the principal source of leafroll in most potato crops, so planting disease-free seed is obviously an important step in minimizing the incidence of the disease. Insecticides may not keep winged aphids from alighting in a crop and quickly transmitting non-persistent virus, but they can certainly prevent the

secondary spread of virus within a crop by colonizing aphids. However, insecticide resistance is a severe problem in many areas. Application of mineral oil and use of aluminum or white plastic mulch reduces virus transmission. Aphids that are not effectively repelled by reflective mulch seem to thrive on mulched crops and exhibit high rates of reproduction. Therefore, even in mulched crops some aphid control is necessary.

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Green Stoneflies

Members of the stonefly family Chloroperlidae (order Plecoptera).

► [Stoneflies](#)

Green Vegetable Bug

This is *Nezara viridula* (Linnaeus) (Hemiptera: Pentatomidae), and is also known as southern green stink bug. The latter name is based on its distribution in the USA, but it now occurs on most continents.

► [Southern Green Stink Bug](#)

Gregarines of Insects

The subclass Gregarinasina currently encompasses about 220 genera and 1,500 named species. The modern day gregarines are a monophyletic group associated with invertebrates, including various

polychaetes (marine worms), oligochaetes (earthworms), and arthropods. The majority of the gregarines have been described from insect hosts, including a wide variety of aquatic insects and many coleopterans. Normally, these organisms are capable of infecting a certain group of hosts without the involvement of a vector or secondary host. It is likely that the current list of gregarine species represents only a small percentage of the gregarines existing in nature. Gregarines display a high degree of host specificity, and may be restricted to a particular tissue (or site) of a specific life stage of a single insect species. However, certain neogregarines (*Mattesia* spp.) have been experimentally transmitted to insects of different orders. In many cases, insects may harbor a gregarine complex. Gregarines, lacking the virulence of other insect disease agents and not possessing a vertebrate counterpart, have not received much attention from pathologists during the past several decades.

Morphologically, the gregarines produce mature gamonts which have the conoid structure modified into an epimerite or mucron. The epimerite, often containing attachment hooks, mediates gregarine attachment to the host cell. This anucleated segment, separated from the main cell by a septum, often is lost when the gamont detaches from the host cell. The mucron, unlike the epimerite, lacks the septal structure. Gregarines are divided into four major groups: the Archigregarines, Blastogregarines, septate Eugregarines, and Neogregarines. The primitive archigregarines and blastogregarines are parasites of the digestive tracts of marine worms and annelids. The life cycle of these latter gregarines includes three schizogonies: merogony, gametogony, and sporogony.

The Eugregarine group, believed to arise from an ancestral archigregarine, contains the vast majority of the described gregarines (1,300 species). Most eugregarines that are detrimental to the host insect are found within the genus *Ascogregarina*. The life cycle of the eugregarines, unlike the archigregarines or neogregarines, lacks the merogony phase. Host insects ingest the dormant oocyst stage that is activated to release infectious sporozoites that exit through the

polar canals. Excystation is a pH-sensitive event and, therefore, may be regulated by the pH gradient existing in the insect's digestive tract. Excysted sporozoites (4–8 per oocyst) migrate to the midgut epithelium and undergo both intracellular and extracellular growth phases. Upon attaching to the midgut epithelia, sporozoites differentiate and produce either epimerite (septate gregarine) or mucron (aseptate gregarines) attachment structures. These cells, referred to as trophozoites or gamonts (Fig. 56), may penetrate the midgut or remain attached to the microvillar surface. Individual gamonts undergo extensive growth, reaching a size that may be measured in millimeters. Normally, the fully mature detached gamont is the stage that is detected in infected insects. Mature gamonts detach themselves from the midgut and pair off in the lumen, forming a prenuptial association known as syzygy. A membrane is formed around the paired gamonts, forming the gametocysts that are expelled in feces. Within the gametocyst one of the gamonts produces microgametes and the second gamont develops macrogametes. Alternatively, both gamonts may produce isogametes. The gametes fuse, producing a diploid zygote that undergoes successive meiotic and mitotic divisions, resulting in a thick-walled oocyst filled with haploid sporozoites.



Gregarines of Insects, Figure 56 Light micrograph of septate gamonts of *Gregarina blatteria* attached to cockroach midgut surface.

Eugregarines lacking the merogonic cycle are unable to multiply and spread within host insects. The number of gamonts found in the host is a direct reflection of the number of sporozoites released from the ingested oocysts. The impact of gregarines inhabiting the digestive tract is often negligible; damaged host cells are replaced without a noticeable impact on the host insect. For example, the mealworm *Tenebrio molitor* is host to *Gregarina polymorpha*, and can harbor up to 6,000 gamonts in its digestive tract without any pathological effect. In certain cases, these organisms are considered commensals. However, in other cases, the presence of these gregarines results in a measurable impact on the host. Large numbers of gregarines often damage the gut barrier and allow opportunistic microbes to invade and kill the host. This is especially true for the coelomic gregarines that penetrate the midgut and develop in the hemocoel. Normally, the impact of these organisms is subtle and cannot be measured simply in terms of insect mortality. For example, *Ascogregarina barretti* does not kill infected *Aedes triseriatus*, but results in the production of short winged adults. Similarly, under appropriate environmental conditions, infection by the aseptate gregarine *Ascogregarina culicis* alters the developmental kinetics and reduces the survival fitness of the host mosquito *Aedes aegypti*. A second aseptate gregarine, *Ascogregarina chagasi*, has been reported to cause population declines in laboratory colonies of the dipteran *Lutzomyia longipalpus*.

The order Neogregarinida includes the neogregarines characterized by their additional merogonic life stage. Neogregarines are found commonly in members in the orders Lepidoptera, Coleoptera, Hemiptera, Diptera, and Orthoptera and include the well-studied genus *Mattesia*. Neogregarines are transmitted orally and display a high level of host specificity. These gregarines usually are smaller than the eugregarines and possess a nonsegmented body plan. The oocyst stage of neogregarines is ingested and the digestive fluids act on polar caps (plugs), allowing for the release

of the infectious sporozoites. The sporozoite penetrates the midgut and invades the fat body. Within this tissue, the sporozoites develop and give rise to micronucleate meronts. These meronts grow, producing multinucleate cells that measure 20–30 μm in length, and contain 30–200 nuclei. The nuclei move to the peripheral region and bud from the meront, releasing motile, elongate merozoites. These motile merozoites, released from infected cells, infect other healthy cells, spreading the infection through the target tissue(s). The merozoites, after undergoing one or more cycles, eventually undergo macronuclear merogony. The exocellular budded macronuclear merozoites round up and transform into gamonts, thus initiating the sexual phase. The gametocytes form pairs that synthesize an envelope and transform into the gametocyst. The gamonts within the cyst each produce a set of gametes that fuse to form the zygote. The zygotes develop a spore wall forming the oocyst. The zygote undergoes division, producing a set of sporozoites within the oocyst or spore.

The best-studied genus of insect neogregarines is *Mattesia*. The species *M. grandis*, pathogenic to the cotton boll weevil, *Anthonomous grandis*, has been examined as a microbial control agent. Under insectary conditions, *M. grandis* was found to cause epizootics and to decimate laboratory colonies. In the mid-1960s, this pathogen was mass-produced in host weevils. Spores harvested from infected adults were bait formulated and tested against weevil populations. Field-cage experiments demonstrated that spores delivered as baits could infect weevils. The high cost of production and erratic field performance has limited subsequent interest in this pathogen.

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Gregarious Behavior

The tendency of organisms to stay in groups.

Gregarious Behavior in Insects

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Many insects spend time in a group of conspecifics at some point during their lives. Insect groups can form passively, for example, through the common use of feeding, mating, oviposition, basking or shelter sites. Alternatively, insect aggregations may arise through the detection and active movement toward conspecifics or their associated cues. Cues used to detect the presence of conspecifics can be tactile, visual, auditory, olfactory or pheromonal, and may act alone or in combination.

Gregarious behavior is commonly associated with social insects that live in communal colonies (see *Sociality of Insects*), but it is also widespread among the non-social insects considered here. In these cases, insect groups of various sizes form under a myriad of conditions and are often interchangeably referred to as aggregations, associations, clumps and other such terms. Importantly, gregariousness is not limited solely to insects, but rather is widespread throughout the animal kingdom (e.g., fish schools and bird flocks). As such, the study of group living and its population level consequences are active areas of behavioral, ecological and evolutionary research.

Entomological studies have played important roles in all of these disciplines.

In general terms, insect groups are considered as associations among multiple conspecifics at some point in space and time. Although a precise definition of groups and their respective sizes that might be appropriate for all non-social insects is lacking, this omission is largely irrelevant to the study of gregariousness. The conditions under which insects aggregate, the developmental stages during which aggregation occurs, as well as the physiological and behavioral mechanisms that underlie their formation have all been found to vary among and even within species (Fig. 57).

The evolution and maintenance of gregariousness necessarily requires the benefits of group formation to outweigh the corresponding costs in terms of individual fitness consequences. Empirical and theoretical studies investigating the benefits of grouping have historically outnumbered those concerned with measuring its costs. Even more rare are integrative empirical studies that have attempted to examine both the costs and benefits of gregariousness within single species. Comparative phylogenetic analyses that seek to examine the evolutionary relationships between gregariousness and other ecological, morphological and behavioral traits are similarly rare, but have provided important insights and will likely increase as phylogenetic frameworks become available for a variety of different insect lineages.

Some of the many examples of the costs and benefits of gregariousness in insects are provided below. When considering these examples, it is important to keep in mind that they are by no means mutually exclusive. Multiple benefits, as well as costs, may be at play and those benefits that initially favor the evolution of gregariousness need not be the same ones responsible for its maintenance. Indeed, a broad consensus has emerged that no single factor likely serves as a general explanation for the evolution and maintenance of gregarious behavior, or the lack thereof, among insect species.



Gregarious Behavior in Insects, Figure 57 A dense aggregation of *Doratifera casta* caterpillars. *Doratifera casta* expresses ontogenetic variation in gregariousness. Larvae are gregarious during the early instars, but become solitary in later stages. Gregariousness confers at least two advantages during early stages of development, facilitation of feeding and functioning as part of an aposematic anti-predator strategy. Their subsequent switch to a solitary lifestyle suggests that these advantages disappear or are outweighed by costs associated with intraspecific competition during the final instars. (Photo by Dieter Hochuli.)

Benefits of Gregarious Behavior

Mate Finding

Many insects that are otherwise solitary-living form groups during the process of finding a mate. In acoustically signalling insects such as crickets and some grasshoppers, males can be attracted to the calls of conspecific males, resulting in local aggregations. Males in these groups often have a higher probability of securing a mate than their solitary counterparts. Among desert clicker grasshoppers, *Ligurotettix coquilletti*, which tend to aggregate in this manner, males selectively chose the highest quality food plants from which to call. Thus, a male's call may also serve as an indicator of host plant quality to females. Insects in a variety of orders also form leks in which males aggregate

and display to attract mates. Females visit these sites only to mate and typically gain no other resources. The advantage to females afforded by leks appears to be the choice of a large number of potential mates and the opportunity to simultaneously assess the quality of multiple males. The advantage to males of participating in leks is less clear, but is likely related to the prediction that the rates of female visiting and mating should increase with lek size, thereby increasing the average number of matings per male participant in the lek.

Facilitation of Feeding

Gregarious insects are often able to obtain food resources that they would otherwise be unable to consume as solitary individuals. Nymphs of the

two-spotted stinkbug, *Perillus bioculatus*, feed together on caterpillars and beetle larvae. Older and larger nymphs are better able to overcome prey defenses than are the smaller and younger nymphs that often join them in feeding. Older nymphs likely benefit from the assistance provided by younger nymphs in subduing larger prey, whereas the younger nymphs gain access to otherwise unobtainable prey items.

Among herbivorous insects, there are many examples in which individuals in larger groups develop at an increased rate compared to smaller groups or lone individuals. Grouped larvae of the neotropical nymphalid *Chlosyne janais* achieve this benefit either by inducing a nutrient sink in the damaged leaf or by overcoming an induced defensive response on the part of their host plant. In the eucalyptus-feeding beetle *Chrysophtharta agricola*, neonate survivorship increases with group size because feeding sites on tough leaves initiated by larvae with larger mandibles provide smaller individuals with access to feeding sites. Milkweed bugs, *Oncopeltus fasciata*, feed on seedpods and also survive better in larger groups. In this case, the joint secretion of lytic enzymes by multiple individuals facilitates the ingestion of nutrients from the seeds within the pod.

Microhabitat Modification

Insect aggregations can serve to buffer group members from harsh environmental conditions. Aggregations of *Blattella germanica* cockroach nymphs enable group members to better survive under dry conditions. The diffusion fields of water vapor overlap among group members and reduce individual evaporative water loss to the air. Anti-desiccant effects have also been observed in aggregations of other insects such as woodlice, stinkbugs and beetles. Clustering of eggs by ovipositing females similarly functions to prevent water loss by reducing the amount of exposed surface area. Importantly, this strategy of egg clustering may serve as one of the principle

mechanisms underlying the initial formation of many larval insect groups.

Grouping has also been shown to play an important role in thermoregulation. Higher body temperatures in grouped versus solitary caterpillars have been observed in a number of different lepidopterans. These higher temperatures result in faster growth rates and reduced development times that in turn can reduce the risk of exposure to predators, parasitoids or pathogens, and possibly allow the insects to outpace a decline in host plant quality. Some gregarious insects even build structures within which their microhabitat is modified. For example, temperatures inside the tent shelters constructed by eastern tent caterpillars, *Malacosoma americanum*, have been shown to be higher than outside air temperatures.

Protection from Natural Enemies

By far the most commonly invoked benefit of gregarious behavior is protection from natural enemies such as predators and parasitoids. The notion that individual attack risk declines as group size increases has been widely referred to as the “selfish herd” effect. In other words, the reduction in attack risk provides individuals with a selfish motive to join a group. However, a number of different underlying mechanisms, both passive and active, may be responsible for conferring protection to individual group members. Similarly, as evidenced by the other benefits described above, instances in which the improved survivorship of insects in groups was assumed to be due to protection from natural enemies may actually have been due to other unrecognized benefits of group living.

The simplest scenario for protection in a group is a dilution effect in which the risk of attack to an individual group member is inversely proportional to the size of the group. However, few if any insects rely solely on a dilution effect for protection. They often also have some means of active defense such as early detection, evasion, chemical defense and warning coloration (aposematism).

Groups of sea-skaters, *Halobates robustus*, detect and respond to predators from a greater distance than do solitary individuals. Once a predator attack has been initiated, insects in dense groups will often flee in erratic patterns that are assumed to either startle or confuse predators, or reduce the predictability of prey locations.

Given that individual predators have an upper limit to the number of prey they can consume, sufficiently high numbers of insects in aggregations may effectively swamp or satiate local predators and confer the benefit of reduced predation on surviving group members. Predator swamping has been proposed for mass emerging insects such as mayflies and periodical cicadas, and likely operates during outbreak periods in insects such as locusts (e.g., *Schistocerca* spp.) and Mormon crickets (*Anabrus simplex*) that exhibit widely fluctuating local population dynamics.

Many gregarious insects are also aposematic. These insects utilize conspicuous warning coloration as a signal to potential predators that they are deterrent or unpalatable by virtue of possessing some form of defense, usually chemical. The relationship between insect gregariousness and the evolution of both unpalatability and warning coloration has been the source of long running debate. Theoretical and empirical evidence suggest that grouping can facilitate the evolution of chemical defenses, as well as enhance predator learning of warning coloration. Based on this, it has been hypothesized that gregariousness initially promotes the evolution of unpalatability, followed by the evolution of conspicuous warning coloration. Despite the seeming logic behind this argument, a series of phylogenetic analyses using lepidopteran larvae suggest a different polarity for the evolution of these traits. These analyses indicate that gregariousness has repeatedly evolved after, rather than before, unpalatability and warning coloration. Thus, although it seems likely that defenses have evolved prior to warning coloration and gregariousness, the precise polarity of events could feasibly vary among taxa depending on the specific

ecological circumstances. Additional phylogenetic analyses in other insect lineages will be critical in resolving this issue.

Costs of Gregarious Behavior

Intraspecific Competition

One of the most obvious and widely documented costs of gregariousness is intraspecific competition. As more individuals share a limited resource, the amount available per individual decreases. Food, mates, and sites for shelter, basking or oviposition can all be limiting resources. Some insects such as bark beetle larvae may deplete their food sources and die before reaching the more mobile adult stage. In others such as aphids, the effects of competition may be less severe but still result in restricted access to nutrients, smaller adult size and reduced fecundity. Perhaps the most extreme form of intraspecific competition is cannibalism, the threat of which can be particularly severe among larval forms of insects that feed in enclosed environments such seeds, fruit, stems, and stored products. Cannibalism can also serve as an important mechanism by which individual insects redress nutritional imbalances brought on by increased competition for resources at high population densities.

Pathogen Transmission

Another clear cost of living in a group is the increased risk of becoming infected with a pathogen or parasite. An increased probability of fungal pathogen infection among group members has been shown in a variety of insects such as aphids, cicadas, caterpillars, and beetle larvae. Both pathogens and parasites can be spread by direct contact with infected individuals as well as their excrement and saliva. Alternatively, propagules from infected individuals may be rapidly dispersed locally among group members through the air or

across the substrate surface where they can be secondarily encountered. Some insects have evolved an elegant solution to the increased risk of pathogen infection in crowds by incurring the metabolic cost associated with pathogen resistance only under high population density conditions. This form of density-dependent pathogen resistance or prophylaxis has been demonstrated across insect orders in taxa such as *Tenebrio molitor* beetles, *Spodoptera exempta* caterpillars, and *Schistocerca gregaria* locusts.

Increased Conspicuousness to Predators

A group of insects should simultaneously be more apparent to predators and more worthwhile as a source of potential food than solitary prey. The cost of increased conspicuousness in a group should be even greater for aposematic insects that are themselves conspicuously colored. That so many gregarious insects exist in the first place suggests that this cost is routinely surmounted by at least one of the benefits described above. In addition to providing a larger visual stimulus to predators, aggregations may also result in the local concentration of other cues used by natural enemies to find insect prey. Predators and parasitoids can locate their prey directly by orientation toward cues such as aggregation pheromones or the sound of calling males, as well as indirectly through cues such as volatile compounds emanating from frass or plant tissues exposed by feeding damage.

Physiological Costs

Among insects that use aggregation pheromones for group formation, pheromone production necessarily involves a metabolic cost. For example, these costs may range from minimal when pheromones are by-products of existing metabolic pathways and structures as they appear to be in *Phylotretta cruciferae* flea beetles, to more substantial when pheromone production requires the development

and maintenance of specialized glands or organs as in the triatomine bugs. Furthermore, aggregation pheromone production has been shown in some beetles to be regulated and can be reduced under crowded conditions. However, it is not yet known if this facultative response serves to reduce metabolic costs or is perhaps an adaptation that reduces some other cost associated with crowding.

Population Level Consequences of Gregarious Behavior

Gregariousness not only affects the performance and survivorship of individual insects, but can also have important population level consequences. The expression of gregarious behavior can interact with other ecological processes to influence a species' population dynamics, dispersal or migration, and spatial distribution patterns. Gregarious behavior in insects can sometimes lead to devastating consequences for humans, as evidenced by its central role in the biology of two major pest species, the desert locust, *Schistocerca gregaria*, and the Mormon cricket, *Anabrus simplex*.

The Desert Locust

Under outbreak conditions, locusts form huge groups in which millions of insects can travel en masse on the ground in migratory bands as juveniles and in the air as characteristic swarms of flying adults. Unlike other grasshoppers, locusts can express an extreme form of density-dependent phenotypic plasticity known as “phase polyphenism.” Individuals reared under low population densities (the harmless, non-migratory “solitarious” phase) differ markedly in behavior, physiology, color and morphology from locusts reared under crowded conditions during outbreaks (the migratory swarming “gregarious” phase) (Fig. 58). A shift to the expression of gregarious behavior at high population density is central to the process of locust phase change. This form of behavioral phenotypic



Gregarious Behavior in Insects, Figure 58 Gregarious behavior in locusts is environmentally determined and mediated by changes in local population density. Examples of the alternative density-dependent phenotypes of final instar desert locust nymphs, *Schistocerca gregaria*, are pictured. The non-migratory and cryptic “solitarious” phase produced at low population density is on the left. The migratory and aposematic “gregarious” phase induced by high population density is on the right. (Photo by Greg Sword.)

plasticity suggests that natural selection has favored, within the same individual, the ability to lead a solitary lifestyle when it is advantageous at low population densities, as well as the ability to take advantage of gregariousness under high population density conditions.

At the heart of locust swarm formation and migration is the shift from the shy, cryptic behavior of solitary phase locusts, which are relatively sedentary and avoid one another, to the highly active behavior and tendency to aggregate typical of gregarious phase insects. Nymphs of the desert locust, *Schistocerca gregaria*, can become behaviorally gregarious after just 1 h of crowding. This behavioral transition to gregariousness is soon followed by changes in other traits. One such change is a shift in feeding behavior in which the newly crowded insects become willing to feed on noxious plants that cause the locusts to be toxic to their predators. In turn, these behavioral changes are followed at the next

nymphal molt by a density-dependent change in coloration from crypsis to warning coloration that enables the nymphs to advertise their recently acquired unpalatability to predators. Predator learning and subsequent avoidance of aposematic gregarious phase locust nymphs can reduce the per capita predation risk and facilitate additional population growth.

In addition to functioning as part of an aposematic anti-predator strategy, gregariousness in desert locusts also interacts with local habitat structure resulting in some habitats being more likely than others to generate locust swarms. Individual locusts are more likely to come in contact with each other and change into the migratory gregarious phase when the resources they utilize, such as host plants or roosting sites, are distributed in an aggregated as opposed to dispersed manner. As more and more locusts become gregarious, they also become locally concentrated,

and once a critical population density is reached, mass migration is triggered. Recent evidence suggests that mass movement among juvenile locusts in migratory bands is mechanistically linked to the risk of cannibalism in high-density groups, a process first identified in Mormon crickets and described below.

The Mormon Cricket

Mormon crickets are flightless tettigoniids from western North America that also form huge migratory bands during outbreaks. Although Mormon cricket and locust migratory bands share many similar characteristics, Mormon crickets do not appear to express the density-dependent phase changes in gregariousness or other traits as do locusts. Thus, the phenomenon of migratory band formation (Fig. 59) and movement appears to have convergently evolved in

these two groups via different underlying behavioral mechanisms.

Mormon crickets constitute a unique model system in which understanding the costs and benefits of gregariousness has provided a unifying framework that explains both how and why inter-individual interactions can lead to landscape-scale mass movement. In terms of benefits, a radiotelemetry-based mark recapture study revealed that migratory bands form as part of an anti-predator strategy. Individual band members are much less likely to be killed by predators than are insects that have been separated from the group. As predicted, once migratory bands have formed, individual band members are subject to increased intraspecific competition for nutritional resources. Individual crickets within migratory bands have been shown to be deprived of specific nutritional resources, namely protein and salt. When provided with augmented dietary protein, individual crickets spent less time walking, a response that was not



Gregarious Behavior in Insects, Figure 59 A migratory band of Mormon crickets, *Anabrus simplex*, crossing a dirt road in NE Utah, USA. Migratory bands can contain millions of insects that walk up to 2 km/day. Gregariousness confers protection from predators. However, band members suffer from intraspecific competition and must keep moving to encounter new nutritional resources as well as to avoid being cannibalized by other hungry insects in the band. (Photo by Greg Sword.)

found when crickets had ample carbohydrate. Thus, group movement results in part from locomotion induced by protein deprivation and should act to increase the probability that individual band members will encounter new resources and redress their nutritional imbalances.

An additional cost of group formation is that Mormon crickets are notoriously cannibalistic. Their propensity to cannibalize is a function of the extent to which they are nutritionally deprived. Given that Mormon crickets are walking packages of protein and salt, the insects themselves are often the most abundant source of these nutrients in the habitat. As a result, individuals within the band that fail to move risk being attacked and cannibalized by nutritionally deprived insects approaching from the rear. Thus, the mass movement of individuals in migratory bands is a forced march driven by cannibalism due to individuals responding to their endogenous nutritional state. The fact that migratory bands are maintained as cohesive groups despite these conditions suggests that the risk of predation upon leaving the band must outweigh the combined costs of intraspecific competition for resources and cannibalism.

- ▶ Cycloalexy
- ▶ Sociality of Insects
- ▶ Aposematism
- ▶ Phase Polymorphism in Locusts
- ▶ Phase Polyphenism in Insects
- ▶ Juvenile Hormone

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Gregarious Parasitoid

Parasitoids than can co-exist with others of the same species within the body of a host insect.

Gressitt, Judson Linsley

Judson Linsley Gressitt was born in Tokyo in 1914 to an American family. He grew up in Tokyo and was educated at an American school. On finishing school, he traveled alone at age 18 to Taiwan and collected insects in much of the island, including the highest mountains. His first degrees were in entomology at the University of California, after which he accepted a position at Lingnan University in Guangzhou, China. He continued fieldwork, and he married Margaret Kriete. The family was interned in 1941–1943 by Japanese forces in China. After the war, Lin returned to Berkeley and earned a doctorate in entomology. Then he returned to Lingnan University as Associate Professor until 1951. In 1949 the family was interned again, this time by Chinese forces as the Chinese revolution raged and the Korean War was imminent. His involvement with Pacific entomology and especially with the Bernice

P. Bishop Museum in Honolulu followed. In 1955, he began an association with New Guinea, which led in 1961 to establishment of what is now the Wau Ecology Institute. His research interests covered biogeographic and ecological questions in plants, vertebrates, and invertebrates. His particular taxonomic interests were in the beetle families Cerambycidae and Chrysomelidae. But his work included many other projects such as insect disease carriers, Antarctic entomology, transoceanic dispersal, and insect conservation. He was editor of four serial publications. He and his wife, Margaret, died in an air crash in China on April 26, 1982.

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Grid Mapping

Mapping the locations of pests in a field using coordinates.

Gripopterygidae

A family of stoneflies (order Plecoptera).

► [Stoneflies](#)

Grooming

Cleaning of the body using the mouthparts or legs. In solitary insects, it is a self-cleaning process, but in social insects individuals groom one another.

Grote, Augustus Radcliffe

Augustus Grote (Fig. 60) was born in Liverpool, England on February 7, 1841, of a Welsh mother and German father who moved with him to a

farm in New York when he was seven. As a schoolboy he spent much time collecting insects. His hopes of attending Harvard University were dashed when his father's investments failed and the family was left in straitened circumstances. He did, however, receive an A.M. degree from Lafayette College, Pennsylvania, after studies in Europe. In Alabama in the early 1870s, he studied the cottonworm, *Alabama argillacea*, eventually publishing five papers on it. On the death of his wife in 1873, he moved to Buffalo, New York, and worked as museum director. He was publisher of the *Bulletin of the Buffalo Society of Natural History* and of a short-lived journal called "The North American Entomologist." He wrote many articles on Lepidoptera, and produced with Coleman Robinson "A synonymical catalog of North American Sphingidae, with notes and descriptions" and a "List of the Lepidoptera of North America." In 1884 he moved to Germany, first to Bremen and then to Hildesheim, but continued writing for North American journals. For the last nine years of his life, he was honorary assistant at the Roemer Museum in Hildesheim, in which city he died on September 12, 1903. His large insect collection was offered



Grote, Augustus Radcliffe, Figure 60 Augustus Grote.

for sale in the USA, but when there were no buyers it was sold to the British Museum (Natural History).

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Ground Beetle (Coleoptera: Carabidae) Feeding Ecology

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The Carabidae, or ground beetles, represent approximately 40,000 described species found throughout the world, with most species present in the tropics. There are nearly 2,700 described species in Europe and over 2,000 species in North America. Detailed biological descriptions are available for fewer than 100 species (mostly western European species). Many carabids are easily recognized at the family level. Adults are well-proportioned beetles with pronounced mandibles and palps, long slender legs, striate elytra, and sets of punctures with tactile setae. Many possess an antenna-cleaning organ and mostly pubescent antennae. Many are dark colored, shiny or dull. Some have bright or metallic colors and some are pubescent.

Although carabids possess an easy-to-recognize general body form, they have undergone morphological adaptations to suit the habitat in which they are found. Such modifications have permitted running, burrowing in soil and sand, living under tree bark, climbing plants, and swimming in water. Consequently, some species are found in very unique places. For example, some inhabit the edges of ice glaciers, others live in caves, others along stream banks. Others are found in woodlands, or are found in deserts. Most species reside on the

ground (epigeic), but some species are plant-dwelling (arboreal) during the adult stage. Others live in self-constructed tunnels in sand or fine soil.

Based upon research in Britain (in Europe), carabid genera are found typically in certain habitats: species of *Bembidion* are common amongst vegetation alongside rivers and lakes; species of *Acupalpus*, *Agonum*, *Stenolophus*, and smaller-sized *Pterostichus* are present in litter on the soil surface in marshy (fresh water) habitats. The genera *Dicheirotichus*, *Dyschirius*, and *Pogonus* are found in salt marshes. Larger-bodied genera such as *Calathus*, *Carabus*, *Harpalus*, *Nebria*, or *Pterostichus* can be found in rough grass, or in gardens. In drier habitats, especially exposed to sun, *Amara*, *Badister*, some *Harpalus* and *Notiophilus* can be found. The location of the preferred habitat (and microhabitat) can be influenced by season, temperature and humidity extremes, life history pattern, competitors, and food availability.

General Feeding Ecology

Feeding Preferences

Carabid beetles can be categorized as carnivores, herbivores, or omnivores. A recent survey of 1,290 literature references indicated that 775 species were partially or exclusively carnivorous, 85 species were exclusively herbivorous, and 206 species were omnivorous. Some carnivorous species opportunistically feed on a diversity of prey. For example, the diet of numerous species in the genera *Agonum*, *Calathus*, *Chlaenius*, *Poecilus*, or *Pterostichus* is most often dependent on the season and availability of specific prey. Other carnivorous species are more selective. Some oligophagous species such as those in the genera *Cychrus* and *Scaphinotus* are predators of snails and slugs. Others in the genus *Calosoma* prey upon caterpillars. Species of *Loricera* and *Notiophilus* are predators of springtails (Collembola). Species in the genus *Promecognathus* specialize upon millipedes. Some species are parasitoids in the larval stage,

but are predators in the adult stage. For example, the larvae of *Lebia* spp. are ectoparasitoids of pupae of leaf beetles (Chrysomelidae), whereas the adults attack egg and larval stages. The larvae of *Brachinus* spp. (bombardier beetles) are ectoparasitoids of pupae of water scavenger beetles (Hydrophilidae) and whirligig beetles (Gyrinidae).

Herbivorous carabids may consume plant seeds, ripe fruit, and foliage. *Zabrus* adults and larvae consume ripe grains and sprouting leaves of cereal plants. Many *Harpalus* and *Amara* adults feed on germinating weed seeds. The diet of the larvae, however, is unknown for the majority of species. Several *Harpalus* species collect and cache seeds of grasses in burrows.

Omnivorous carabids are apparently opportunists that feed upon the food items most readily available in their immediate habitat. Many carabid species are likely omnivorous. In fact, predominantly carnivorous species probably consume pollen, fungi, and other plant materials during periods of prey shortage to avoid starvation.

Searching for Food

Carabid beetles are known to search actively for food by means of random search, vision, or chemical cues. Most adults rely on random search, in which the beetle contacts the prey with its mouthparts, antennae, or setae on some body part or appendage. This strategy is common to nocturnal species. Very little is known about the searching behavior of carabid larvae. Presumably, the larvae of most nocturnal species rely on random search and then physical contact with prey. Some carabid larvae do not actively search for prey. Instead, they deploy an ambush strategy. They remain concealed inside burrows or tunnels and only attack prey that come too close to their burrows. This strategy is typical of tiger beetle larvae (tribe Cicindelini; e.g., *Amblycheila*, *Cicindela*, *Megacephala*, and *Omus*).

Diurnal species rely upon short-range vision to locate prey. For example, *Notiophilus biguttatus* adults and larvae feed extensively on springtails

(Collembola). Adults are aided by their large compound eyes to hunt their prey. This predator may intensify its search for prey in relation to light intensity. Greater light intensity usually results in an increased search rate. The *N. biguttatus* larvae rely more on physical contact for detection of prey.

Several carabids respond to the odor of their prey to facilitate detection. Adults of *Pterostichus melanarius* and *Harpalus rufipes* were attracted to an aphid alarm substance released by aphids under attack by predators, such as ladybird beetles. In contrast, *Nebria brevicollis* adults were attracted to the odor of live springtails, but not to aphid alarm substance. Note that *P. melanarius* was also attracted to the odor of live aphids, but the other two species were not. Larvae of *N. biguttatus* are guided by chemical cues to the aggregation sites of springtails. Reliance upon chemical cues from prey (or hosts in the case of parasitoids searching for concealed prey) is probably more widespread than currently reported.

Although most carabids search for prey on the ground, some species seek prey on plants. *Calleida*, *Cymindis*, *Dromius*, *Lebia*, *Parena*, *Pinacodera*, and *Plochionus* adults have been found foraging on plants during the day. More than 30% of tropical carabid species (e.g., *Agra*, *Lebia*) forage on plants. Adults of a few species of *Agonum*, *Amara*, *Chlaenius*, *Harpalus*, and *Pterostichus* are occasionally found foraging on plants. Both adults and larvae of *Calosoma sycophanta* (and other species of *Calosoma*) forage for prey on the trunks of forest trees.

Prey Capture

Once prey is located, some species lunge toward it with their mandibles agape. Most adult carabids use their well-developed mandibles to subdue and kill prey. Morphological and behavioral adaptations can be involved in capturing prey, particularly for the species with specialized feeding habits. *Cychrus caraboides* and *Carabus violaceus* successfully subdue slugs (gastropods) by biting them at specific

locations on the body, which may paralyze prey. This could prevent the production and secretion of mucus by the slugs, a mechanism of defense against predation.

Species that specialize on snails are not deterred by the shell. Some *Cychrus* and *Scaphinotus* adults readily capture and consume large-sized snails by inserting their slender, elongate head and prothorax into the opening, then proceed to kill and consume the prey. *Cychrus* larvae crawl inside the shell and feed, in spite of the mucus secretions of the prey. Some generalists such as *Pterostichus* species can crush shells with their mandibles. Shell thickness could influence the vulnerability of snails to attack from generalist carabids.

Prey capture behavior has been described for several species that hunt springtails. Adults and larvae of *N. biguttatus* rely on vision to capture elusive springtails. Prey capture occurs when the predator rapidly lunges toward the springtail and grasps it within the mandibles. Adults of *Loricera pilicornis* capture springtails at night. Physical contact, rather than sight, is a prerequisite to prey capture. Adults lunge toward prey during the attack and bring their antennae together to entrap the springtail. Long, strong setae on the antennae enclose the prey and draw it toward the gaping mandibles. The prey capture behavior of *L. pilicornis* larvae differs from that of adults. Although prey are located by physical contact, the larvae do not lunge toward prey. Instead, larvae turn in the direction of contact while opening their mouthparts. The setae on the maxillae and an adhesive secretion coating the proximal end of each maxilla function to entrap the prey. The springtail is ultimately grasped by the mandibles.

Digestion

The adults of most carabids ingest and digest prey fragments, after mastication, with little or no extra-intestinal (i.e., pre-oral) digestion. The mandibles are used for crushing or tearing off fragments of food, which then are ingested. Enzymes involved

in digestion are copious once food enters the foregut. In contrast, the adults of other species, particularly in tribes Carabini (e.g., *Calosoma*, *Carabus*), Cicindelini (e.g., *Cicindela*, *Omus*), and Cychrini (e.g., *Cychrus*, *Scaphinotus*, *Sphaeroderus*) masticate their prey only to lubricate it and extract the fluid contents from it. Extra-intestinal digestion commences after adults discharge a fluid from their buccal cavity (mouth) onto the prey or prey fragments. This fluid contains enzymes (proteases, carboxylases, amylases, etc.) that liquefy tissues. These enzymes are synthesized in the midgut, but are stored in the crop, from whence they are regurgitated onto the food prior to feeding. Only very fine particles and liquefied remains of prey are ingested. Digestion proceeds within the foregut, including the crop. Absorption of nutrients occurs primarily in the midgut. As far as is known, carabid larvae digest their food extra-intestinally. Once liquified food is ingested, the digestion process continues in the foregut, with absorption occurring primarily in the midgut. Carabid larvae that are ectoparasitoids (e.g., *Brachinus*, *Graphipterus*, *Lebia*) may rely almost exclusively on extra-intestinal digestion of host tissues.

Applied Feeding Ecology

Predation of Aphids and Leafhoppers

In sugar beet fields, carabid adults (especially *Pterostichus dorsalis*) were capable of reducing aphid (*Aphis fabae*) population densities in field cages. Carabids, even when at relatively low densities, were able to locate low density populations of aphids.

The impact of carabids and wolf spiders (Class Arachnida, Order Araneae, Lycosidae) on leafhopper (Cicadellidae) and aphid populations was assessed in maize fields. The abundance of both predator groups was manipulated by removing or adding individuals within field enclosures during mid-season and end-of-season. Although the impact of carabid predation could not be differentiated from spider predation, the combined

action of both predator groups reduced populations of leafhoppers. In addition, the combined predators were capable of reducing aphid populations during mid-season.

Research in cereal fields indicated that the rate at which aphids (*Sitobion avenae*) dropped from plants to escape predators on the plants was critical to the efficacy of carabid predation on the ground. Carabids intercepted many aphids before they could climb back up on the plants. The effect of generalist predators functioning in-concert to impact aphid populations was investigated in experiments deploying carabids and lady beetles (Coccinellidae) in alfalfa fields. Positive predator-predator interactions occurred between the lady beetle *Coccinella septempunctata*, and the carabid *Harpalus pensylvanicus*. In laboratory arenas and in field cages, both predators fed on pea aphids, *Acyrtosiphon pisum*. Predation rates were greater than expected for the combined action of both predators. Thus, synergism occurred as *C. septempunctata* foraged on plants and *H. pensylvanicus* foraged at the base of the plants.

Predation of Flies

Predation of gall midge (Cecidomyiidae) larvae on the soil surface was found to be considerable, since polyphagous predators were responsible for 43–58% reduction of wheat gall midges (*Contarinia tritici*). Predation caused an 81% decrease in adult emergence of the midge *Sitodiplosis mossellana*. Feeding bioassays in the laboratory indicated that the carabids *P. melanarius* and *Platynus dorsalis* were primarily responsible for the decline of *S. mossellana* populations.

Carabid predation of the cabbage root fly (*Delia radicum*) and other anthomyiid species has been examined. Carabids (especially *Bembidion lampros* and *Trechus quadristriatus*) caused approximately 30% mortality of *D. radicum* by predation of eggs and first instar larvae in the soil. In a greenhouse experiment, a predator density of two *Bembidion tetracolum* adults per plant

prevented an infestation of *D. radicum* in the spring season. Carabid predation caused an 82% reduction of the pest population, when *D. radicum* eggs were exposed on the soil surface. But, other carabid species (*B. tetracolum*) had difficulty locating eggs that were buried just beneath the surface.

Bembidion quadrimaculatum adults located onion maggot (*Delia antiqua*) eggs that were buried 1 cm deep in the soil. Up to 25 eggs were consumed daily under laboratory conditions and onion maggot numbers were reduced by up to 57% in field cages. Another study investigated the impact of predation on *D. antiqua* pupae exposed on the soil surface in corn fields. Carabid beetle abundance was manipulated so that the rate of removal of pupae from field enclosures (excluding vertebrates but not invertebrates) was determined during the growing season. Significantly more onion maggot pupae were removed from the cages that excluded vertebrates than from the cages that excluded both vertebrates and invertebrates. Carabid abundance correlated positively with predation rates. Feeding trials in the laboratory indicated that the four most abundant carabids (*Pterostichus* and *Poecilus* species) in corn fields readily consumed *D. antiqua* pupae.

Predation of Beetles

Carabids can be significant predators of the Colorado potato beetle *Leptinotarsa decemlineata* (Chrysomelidae), a pest of cultivated potato. In Bavaria (Germany), predation of larvae by *Carabus* spp. reduced the yield damage from this pest by approximately 33% in experimental plots compared to infested control plots that did not contain *Carabus* adults. *Carabus* consumed from 8 to 10 *L. decemlineata* larvae (third and fourth instars) per day in the laboratory.

In the United States, *Lebia grandis* larvae are confirmed ectoparasitoids and adults are specialist predators of *L. decemlineata* on cultivated potato. In the late 1930s, several years after the inadvertent introduction of *L. decemlineata* into

France, *L. grandis* was imported from the United States and a mass rearing program was initiated. The rearing technique was capable of generating large quantities of *L. grandis*, but was too labor intensive. Released adults had little demonstrable impact on *L. decemlineata* populations and failed to become established in France.

Carabid predation of weevils (Curculionidae) was documented. One study revealed that 28% of *Sitona hispidulus* eggs were removed by carabids when placed in experimental cages in alfalfa fields. Of the carabid species tested, *Amara aenea* was the most efficient predator. Carabid predation resulted in greater than 30% reduction of larvae and overwintering adults of *Sitona lineatus* in field beans. *Bembidion properans* adults consumed *S. lineatus* eggs and young larvae.

Predation of the rape blossom beetle, *Meligethes aeneus* (Nitidulidae) by the carabid *Clivina fossor* was documented. In a two-week period *C. fossor* adults consumed 65% of *M. aeneus* larvae and pupae that had been introduced into an arena containing soil at a depth of 6–7 cm. Another investigation indicated that *M. aeneus* experienced a 39% population decline, perhaps, during the time that mature larvae had left the crop plants (rape) and wandered on the soil surface, prior to pupation. Predation by polyphagous predators was thought to be responsible for the decline of the pest population. Research is ongoing to determine the contribution of different species to the mortality of *Meligethes* spp.

Predation of Moths

In the early 1900s, *Calosoma sycophanta* was introduced into northeastern United States to control the gypsy moth *Lymantria dispar* (Lymantriidae), an inadvertently introduced pest of forest and shade trees. The beetle is well-established in most areas where gypsy moth is distributed, and is an important arthropod natural enemy of larval and pupal stages. Adult *C. sycophanta* are long-lived

(2–4 yr) and even a low density of beetles can have considerable impact on *L. dispar* populations. A single *C. sycophanta* larva can kill more than 50 late instar *L. dispar* larvae during a two-week time span, whereas, an adult can kill an average of 150 late instar larvae. Unfortunately, this carabid has a slow numerical response to pest population densities and has not been able to prevent gypsy moth outbreaks.

In apple orchards, carabids are important predators of codling moth, *Cydia pomonella* (Tortricidae), a worldwide pest of pome fruit, including apple. Carabids can forage on the ground during the season when mature larvae are wandering on the soil surface before pupation in leaf litter or under loose tree bark. Several carabid species from an apple orchard in Canada gave positive serological reactions to antiserum against *C. pomonella* larvae. *Pterostichus* species consumed *C. pomonella* mature larvae in experimental arenas in the laboratory. In the field, tethered mature larvae were located and then killed by carabids; 60% predation by carabids per night was estimated during the first generation of codling moth in the spring in an apple orchard in northern California, USA. *Pterostichus californicus*, *Pterostichus cursor*, and *Pterostichus lustrans* dominated the carabid assemblage in an unsprayed orchard in northern California.

Maize plants suffered significantly less damage from armyworms *Pseudaletia unipuncta* (Noctuidae) when ground-foraging predators were included in experimental arenas rather than excluded from arenas. Carabid predation of armyworms was thought to be responsible for the reduction. *Pterostichus chalcites*, *Pterostichus lucublandus*, and *Scarites subterraneus* adults readily consumed second and fourth instar *P. unipuncta* larvae in the laboratory.

A laboratory and field investigation assessed the impact of carabid predation on diamondback moth *Plutella xylostella* (Yponomeutidae) larvae on seedling cabbage plants in Japan. The highest consumption rate (of 24 carabid species tested) was 23 larvae (fourth instars) per day by *Chlaenius*

posticalis adults. Note that *C. posticalis* and *Chlaenius micans* larvae consumed approximately 92 and 191 early fourth instar *P. xylostella* larvae, respectively.

Conclusion

Despite their generally accepted role as natural enemies, detailed information on the feeding ecology of carabids is not available for many species. More research is needed to clarify the trophic relations of carabid larvae. Carabids appear to affect the populations of some crop pests. Carabids may have their greatest impact when operating in concurrence with other natural enemies.

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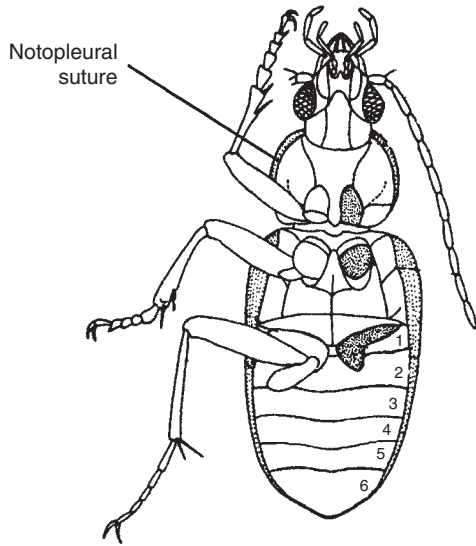
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Ground Beetle (Coleoptera: Carabidae) Taxonomy

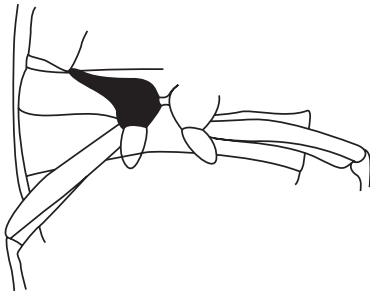
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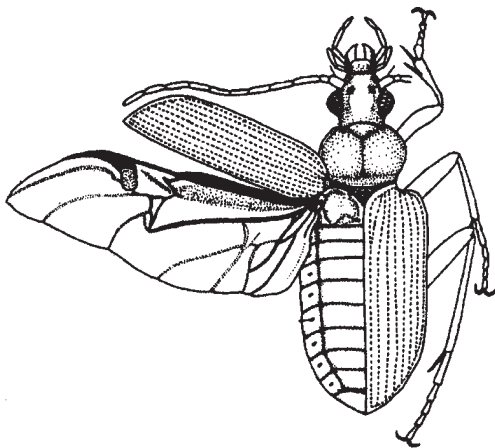
There are approximately 110 families of beetles found worldwide. The order Coleoptera is subdivided into two major sub-orders, Adephaga and Polyphaga. Polyphaga contains most beetle species. Ground beetles are placed in the sub-order Adephaga. This sub-order contains relatively few families of beetles, most families belonging to the much larger sub-order Polyphaga. As now defined, Adephaga contains the families Gyrinidae, Haliplidae, Trachypachidae, Noteridae, Amphizoidae, Dytiscidae, Hygrobiidae, and Carabidae. Adult Adephaga are separated from all other beetle families by the presence of a visible notopleural suture on the prothorax; six visible abdominal sterna; with the first 3 segments fused and divided by hind coxae (Figs. 61–64). Many species are capable of flight and possess fully developed flight wings. Ground beetles range in size from less than 1 mm to more than 60 mm in length. Most ground beetles are uniformly dark in color, but some species are brightly colored (especially tropical species). Carabids occur throughout the world, and may be found from sea level to altitudes of above 5,000 m in the Himalayas. Although there is diversity of form among carabid tribes (Figs. 65–74), the large number of species in



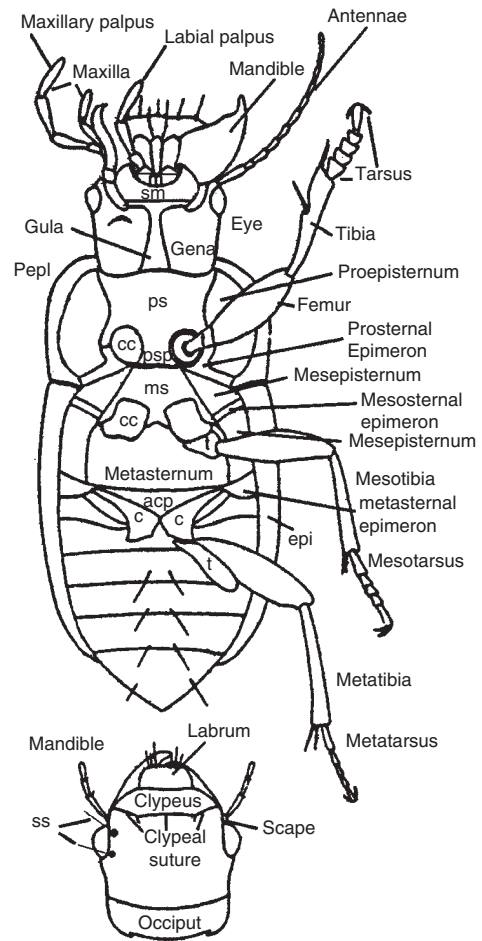
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 61 Ventral view of adult ground beetle.



Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 62 Hind coxa (shaded) fused to and dividing sternite 1.

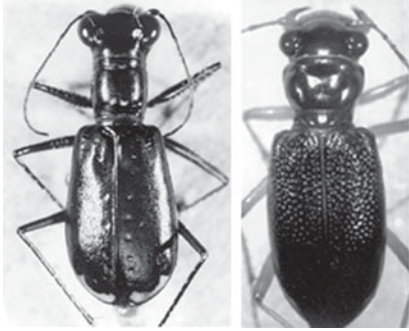


Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 63 Dorsal view of ground beetle adult, showing exposed flight wing.

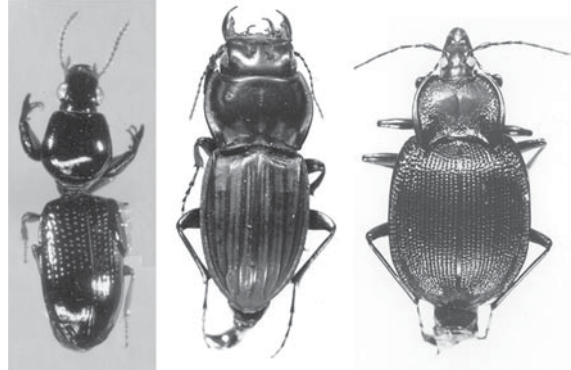


Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 64 Ventral view of a ground beetle showing major sclerites, followed by dorsal view of head. Abbreviations: ps = prosternum; psp = prosternal process; cc = coxal cavity; c = coxa; t = trochanter; epl = epipleuron; pepl = proepipleuron; ss = supraorbital setae; acp = anterior coxal process.

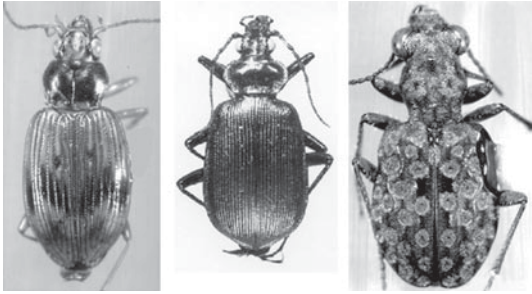
some genera makes separation of specimens difficult at the species level. In spite of the abundant number of species, the tribal classification is fairly well established. Because there are no rules for assignment of categories above the species level, grouping of taxa above tribes is very much unsettled, and vary according to author and region. What follows here is a current arrangement of the higher taxa of ground beetles with representative illustrations of adults of several tribes.



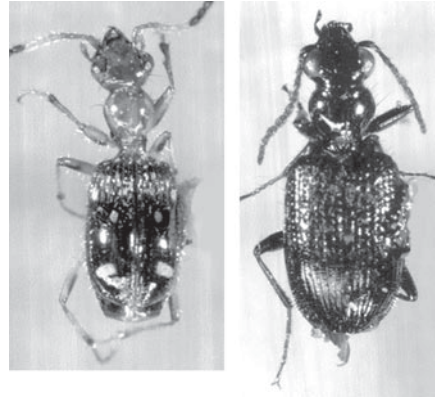
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 65 Representative figures of ground beetle tribes: tiger beetles, (left) Cicindelini, *Cicindela*; (right) Megacephalini (*Megacephala*).



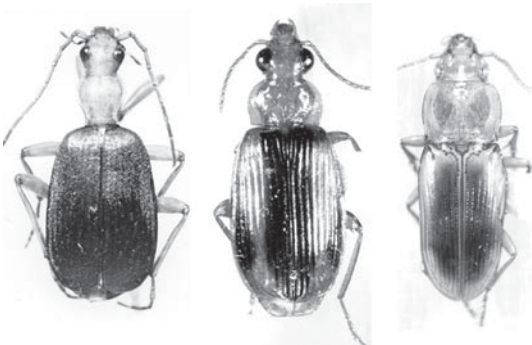
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 68 Representative figures of ground beetle tribes: (left) Dyschirini, *Dyschirius*; (middle) Scaritini, *Pasimachus*; (right) Cychrini, *Scaphinotus*.



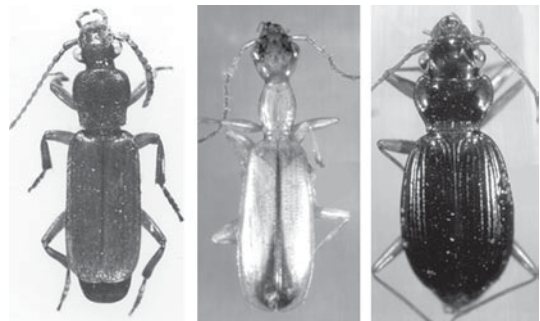
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 66 Representative figures of ground beetle tribes: (left) Bembidiini, *Bembidion*; (middle) Carabini, *Calosoma*; (right) Elaphrini, *Elaphrus*.



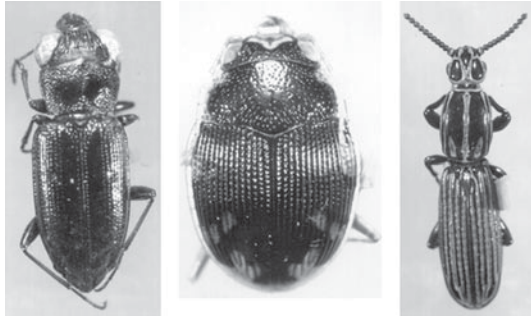
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 69 Representative figures of ground beetle tribes: (left) Lachnophorini, *Calybe*; (right) Lachnophorini, *Euphorticus*.



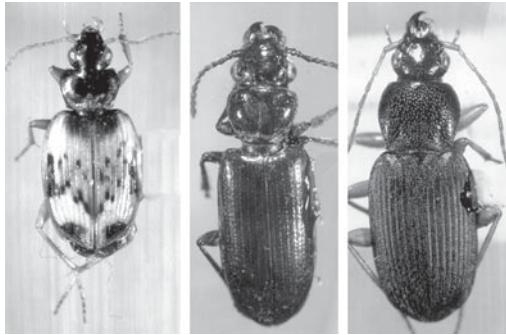
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 67 Representative figures of ground beetle tribes: (left) Brachinini, *Brachinus*; (middle) Lebiini, *Plochionus*; (right) Pogonini, *Diplochaetus*.



Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 70 Representative figures of ground beetle tribes: (left) Helluonini, *Helluomorphoides*; (middle) Ctenodactylini, *Leptotrachelus*; (right) Nebriini, *Nebria*.



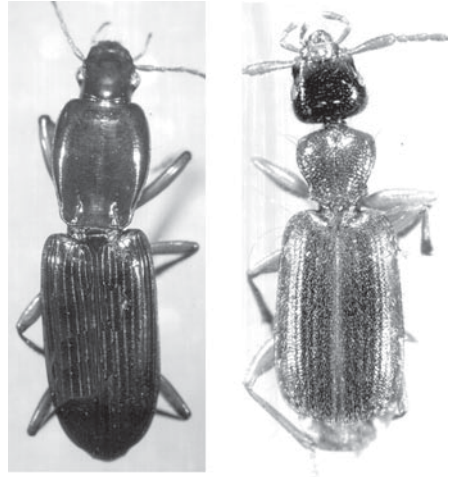
Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 71 Representative figures of ground beetle tribes: (left) Notiophilini, *Notiophilus*; (middle) Omophronini, *Omophron*; (right) Rhysodini, *Omoglymmius*.



Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 72 Representative figures of ground beetle tribes: (left) Cyclosomini, *Tetragonoderus*; (middle) Psydriini, *Nomius*; (right) Chlaeniini, *Chlaenius*.



Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 73 Representative figures of ground beetle tribes: (left) Platynini, *Olisthopus*; (middle) Panagaeini, *Panagaeus*; (right) Pentagonalini, *Pentagonica*.



Ground Beetle (Coleoptera: Carabidae) Taxonomy, Figure 74 Representative figures of ground beetle tribes: (left) Harpalini, *Stenomorphus*; (right) Zuphiini, *Zuphium*.

Identification of ground beetles includes analysis of external morphological characters, and frequently comparison of genitalic structures. The latter requires dissection of specimens and is used less commonly than external morphological characters. Species definitions for ground beetles are varied, dependent upon the group and diagnostic characters defined by that group's expert.

Literature dealing with the identification of ground beetle species is voluminous. Maddison (1995) listed the world higher classification of ground beetles. His classification differed somewhat from Ball and Bousquet (2001), who presented a comprehensive outline of higher classification of the Nearctic ground beetles based on the classification scheme of Lawrence and Newton (1995). In their classification scheme the wrinkled bark beetles are treated as the family Rhysodidae. Madison (1995) cited disagreement over placement of several Adephaga families, namely the tiger beetles (family Cicindelidae or supertribe Cicindelitae) and the wrinkled bark beetles (family Rhysodidae or tribe Rhysodini). I follow the classification scheme of Lawrence and Newton (1995) here. Tribes are listed in phylogenetic order (according to degree

of relatedness) beginning with what are considered the most primitive groups.

The following abbreviations are used in the listing of ground beetle taxa (f = family; s.f. = subfamily; t = tribe; ** = with representatives in North America). Approximate distributions are listed for those taxa that are sufficiently well known and defined.

Family: Carabidae

Subfamily: Paussinae

Tribe: Metriini ** – 2 species restricted to western North America

Tribe: Ozaenini ** – Pantropical, occurring in Oriental, Afrotropical, Australian, and Neotropical regions

Tribe: Paussini – myrmecophilous, restricted to tropics in southern Hemisphere

Subfamily: Gehringiinae

Tribe: Gehringiini** – a single Pacific Northwest species in North America

Subfamily: Nebriinae

Tribe: Notiophilini** – Palearctic, Oriental, Nearctic, Neotropical regions

Tribe: Notiokasini – Neotropical

Tribe: Pelophilini** – Arctic and subarctic regions

Tribe: Opisthini** – Nearctic and China, India, Bhutan, Nepal, and Taiwan

Tribe: Nebriini** – Holarctic and north Oriental

Subfamily: Carabinae –

Tribe: Carabini** – worldwide distribution

Tribe: Ceroglossini – Chile

Tribe: Pamborini – Australia

Tribe: Cychrini** – Holarctic, and China, Tibet, and Sikkim, Himalaya

Subfamily: Cicindelinae (tiger beetles)

Tribe: Omini** – western US

Tribe: Collyridini – Pantropical

Tribe: Megacephalini** – Nearctic, Palearctic

Tribe: Ctenostomatini – Neotropical

Tribe: Manticorini – South Africa

Tribe: Cicindelini** – worldwide

Subfamily: Loricarinae –

Tribe: Loricerini** – Holarctic – Oriental regions

Subfamily: Omophroninae – found in all major zoogeographical regions except Australia

Tribe: Omophronini**

Subfamily: Elaphrini – Holarctic

Tribe: Cicindini – Kuwait

Tribe: Elaphrini** – Holarctic

Tribe: Migadopini – Chile

Tribe: Amarotypini – distribution uncertain

Subfamily: Promecognathinae –

Tribe: Promecognathini** – Nearctic and South Africa

Subfamily: Scaritini – all major zoogeographical regions

Tribe: Siagonini – Palearctic

Tribe: Hiletini – Peru, tropical Africa, Southeast Asia, Indonesia

Tribe: Clivinini** – all major zoogeographical regions

Tribe: Scaritini** – all major zoogeographical regions

Subfamily: Rhysodinae – worldwide

Tribe: Rhysodini** – wrinkled bark beetles, sometimes placed in family Rhysodidae

Subfamily: Trechinae – worldwide, mostly in temperate regions

Tribe: Psydrini** – Holarctic and Australia

Tribe: Melaenini – South India

Tribe: Cymbionotini – South India

Tribe: Broscini** – temperature portions of all major zoogeographical regions

Tribe: Apotomini – South India

Tribe: Trechini** – worldwide distribution

Tribe: Zolini – Chile

Tribe: Pogonini** – all zoogeographical regions

Tribe: Bembidiini** – all zoogeographical regions

Tribe: Patrobini** – Oriental, Palearctic, and Nearctic regions

Tribe: Amblytelini – Australia

Subfamily: Harpalinae

Tribe: Pterostichini** – all major regions

Tribe: Morionini** – Nearctic and pantropical regions

Tribe: Cnemalobini – Argentina

Tribe: Catapieseini – Neotropics

Tribe: Platynini** – all major zoogeographical regions

Tribe: Zabrinini** – Holarctic, Oriental, Ethiopian, and Neotropical regions

Tribe: Bascanini – sub-Saharan Africa

- Tribe: Peleciini – Neotropics, Oriental, Afrotropical regions
- Tribe: Cuneiptectini – western Australia
- Tribe: Chaetogenyini – distribution uncertain
- Tribe: Licinini** – all major zoogeographical regions
- Tribe: Oodini** – all major zoogeographical regions
- Tribe: Panagaeini** – Nearctic, Neotropics
- Tribe: Chlaeniini** – worldwide
- Tribe: Harpalini** – all major zoogeographical regions
- Tribe: Dryptini** – all major zoogeographical regions
- Tribe: Zuphiini** – all major zoogeographical regions
- Tribe: Galeritini** – Pantropical, Holarctic
- Tribe: Physocrotaphini – distribution uncertain
- Tribe: Anthiini – eastern Hemisphere tropics
- Tribe: Helluonini** – most zoogeographic region
- Tribe: Idiomorhini – India
- Tribe: Orthogoniini – eastern Hemisphere
- Tribe: Hexagoniini – Afrotropical, Oriental regions
- Tribe: Ctenodactylini** – Neotropical
- Tribe: Amorphomerini – distribution uncertain
- Tribe: Lachnophorini** – Western hemisphere
- Tribe: Pentagoncini** – all major zoogeographical regions
- Tribe: Odacanthini** – all major zoogeographical regions
- Tribe: Calophaenini – distribution uncertain
- Tribe: Perigonini** – Pantropical
- Tribe: Graphipterini – Afrotropical
- Tribe: Cyclosomini** – primarily tropical, Oriental, Afrotropical, Neotropical
- Tribe: Masoreini – Afrotropical
- Tribe: Lebiini** – all major zoogeographical regions
- Subfamily: Pseudomorphinae
- Tribe: Pseudomorphini** – Nearctic, Neotropical, and Australian regions
- Subfamily: Brachininae (bombardier beetles) – all major zoogeographical regions
- Tribe: Crepidogastrini – eastern Hemisphere
- Tribe: Brachinini** – all major zoogeographical regions, largely tropical

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Ground Beetles

Members of the family Carabidae (order Coleoptera).

- ▶ [Ground Beetle Taxonomy](#)
- ▶ [Ground Beetle Feeding Ecology](#)
- ▶ [Beetles](#)

Ground Crickets

A subfamily of crickets (Nemobiinae) in the order Orthoptera: Gryllidae.

- ▶ [Grasshoppers, Katydid and Crickets](#)

Ground Pearls

Some members of the family Margarodidae, superfamily Coccoidea (order Hemiptera).

- ▶ [Bugs](#)
- ▶ [Turfgrass Insects and their Management](#)

Group Predation

Hunting and retrieving of prey by groups of cooperating individuals. Among insects, this is well developed in ants.

Group Selection

An evolutionary process functioning through the effects of different numbers of descendents left by groups rather than by individuals.

Grouse Locusts

A family of grasshoppers (Tetrigidae) in the order Orthoptera.

▶ [Grasshoppers, Katydid and Crickets](#)

Grub

A thick-bodied larva with well-developed head and thoracic legs, but without abdominal prolegs. At rest, the body is curved, and often is described as C-shaped. A scarabaeiform larva (Scarabaeidae). This term also is sometimes applied to larval wasps (Hymenoptera).

- ▶ [Beetles](#)
- ▶ [Scarab Beetles](#)
- ▶ [Hymenoptera](#)

Gryllacrididae

A family of crickets (order Orthoptera). They commonly are known as leaf-rolling crickets.

▶ [Grasshoppers, Katydid and Crickets](#)

Gryllacridoids

Certain members (suborder Ensifera, superfamily Gryllacridoidae) of the order Orthoptera.

▶ [Grasshoppers, Katydid and Crickets](#)

Gryllidae

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

▶ [Grasshoppers, Katydid and Crickets](#)

Grylloblattodea

An order of insects. They commonly are known as rock crawlers.

▶ [Rock Crawlers](#)

Gryllotalpidae

A family of crickets (order Orthoptera). They commonly are known as mole crickets.

▶ [Grasshoppers, Katydid and Crickets](#)

Grypopidae

A family of chewing lice (order Phthiraptera). They sometimes are called guinea pig lice.

▶ [Chewing and Sucking Lice](#)

Guenée, Achille

Achille Guenée was born in Chartres, France, on January 1, 1809. He began to study Lepidoptera as a boy. His first university education was at Chartres, and then he studied law in Paris. Of a wealthy family, he married and had a son and two daughters, of whom the son died young. He lived at his country residence at Châteaudun for the remainder of his life and contributed 63 papers on Lepidoptera. A major contribution was his six volumes in the series "Suites à Buffon" [a supplement to Buffon's series on "Histoire naturelle"], "Spécies général des lepidoptères" (1852–1857). Another was "Essai sur une nouvelle classification des microlepidoptères" (1845), a major classificatory work. He died at Châteaudun on December 30, 1880.

Reference

Essig EO (1931) Guenée, Achille. In: A history of entomology. The Macmillan Company, New York, NY, pp 640–642

Guérin-Méneville, Félix Edouard

Félix Guérin-Méneville was born in Toulon, France, on October 12, 1799, named Félix Edouard Guérin. He produced taxonomic works on most orders of insects, but later wrote on applied entomology, including sericulture and pests of grapevines. In 1836 he changed his surname to Guérin-Méneville. In 1831 he founded and edited “Magasin de Zoologie,” and when it was merged with “Revue Zoologique” in 1849 as “Revue et Magasin de Zoologie,” he continued as editor until 1873. His own output of publications was over 400, of which his encyclopedic “Iconographie de règne animal de G. Cuvier” in seven volumes brought him the most recognition. France’s “Legion d’Honneur” was the most prestigious of his many awards. He died in Paris on January 26, 1874.

Reference

Herman LH (2001) Guérin-[Méneville], Félix Edouard. Bulletin of the American Museum of Natural History 265:72–73.

Guest

Among social insects, this term is used to indicate a social symbiont.

Guild

A group of species that exploits the same resource in a similar manner. Examples of a guild are the various insects that are responsible for decomposition of cow dung, or the various insects that attack the flower head of sunflower.

Guinea Pig Lice

Members of the family Grypopidae (order Phthiraptera).

► [Chewing and Sucking Lice](#)

Gula

A sclerite found centrally beneath the head, in the position of the “throat.” It also is called the gular plate.

Gundlach, Johannes (Juan) Christopher

Johannes Gundlach was born in Marburg, Germany, on July 17, 1810. His father, a university professor there, died young, leaving his widow and their five children with inadequate income. Johannes became interested in natural history, and began to collect birds by shooting them in preparation for taxidermy. An early accident with a gun left him with an injured palate and nose, and loss of his senses of smell and taste. His mother wanted him to study religion, and he began to do so, but he obtained a job as conservator of the university museum and put aside his religious training to study zoology. He obtained free tuition as son of a faculty member, a master of arts degree in 1837, and a doctorate in philosophy in 1838. He was offered accommodation in Surinam by a friend who was a military doctor there, and began to seek funding for his trip, the funds to be repaid by the sale of specimens collected. While organizing this funding, he spent six months studying specimens in the zoological museum at Frankfurt am Main, southern Germany. His sea voyage to Surinam took him first to Cuba, where he spent from Christmas 1838 through early January 1839 collecting before learning that his friend in Surinam had died. Johannes decided to remain in Cuba and to repay his loan with specimens collected in Cuba. He received much hospitality in Cuba from

landowners, even to the extent in 1846 of establishing a museum of his collections at a farm called “El Refugio” near to Cárdenas. This museum received thousands of visitors. In 1864 the collection was moved to a building on the farm of the Cárdenas family. He collected in all parts of Cuba with enthusiasts and sponsors or alone. The Cuban insurrection against Spanish rule began in 1868 and made fieldwork dangerous because of roving bands of rebels and Spanish soldiers, so Johannes collected intensively on the Cárdenas farm and made three visits to Puerto Rico, in 1873, 1875–1876, and 1881. His hosts, the Cárdenas family, had meanwhile encountered great financial difficulty. In 1892, after approval from Spain, Johannes sold his collections to the Instituto de Segunda Enseñanza de la Habana (“Institute of Havana”), and gave all the proceeds to the Cárdenas family. However, the transaction also allowed a small salary as curator to Johannes. The collections were installed in Havana in 1895, and Johannes (known in Cuba as Juan) died on March 17, 1896. He published on numerous aspects of Cuban and Puerto Rican zoology. His major works on insects were (1881, 1886, 1891) “Contribución a la entomología cubana” in three volumes, and (1887, 1891, 1893) “Apuntes para la fauna puerto-riqueña” (a series published in *Anales de la Sociedad Española de Historia Natural*, of which the parts in volumes 16, 20 and 22 of that journal concern insects). He never married, lived very frugally, and dedicated his life to Cuban zoology.

Reference

Ramsden CT (1915) Juan Gundlach [with bibliography]. *Entomol News* 26:241–260

Gustatory

This is used to describe features related to the sense of taste such as gustatory sensilla or gustatory behavior.

Gut pH

The pH of the insect gut is variable, and has significant influence on the actions of enzymes secreted in the midgut, and solubility of the food. Different enzymes function optimally at different pH levels. Though the gut tends to be slightly acidic in most species (about pH 4–6), the gut pH is related to host plant chemistry. Insects that feed on trees, which typically possess high levels of tannins, have higher pH levels, around 8.6, apparently because this reduces the effects of ingested tannins. The hindgut regions of insects ingesting cellulose, such as termites and crickets, tend to be acidic due to anaerobic fermentation of glucose derived from cellulose digestion.

► [Alimentary Canal and Digestion](#)

Gyllenhal, Leonhard

Leonhard Gyllenhal was born in Algusthorp, Sweden, on December 3, 1752. At the age of 17 he entered the University of Uppsala, and studied natural history with Linnaeus, being influenced by the latter to specialize in entomology. However, after three years he entered the Swedish army and served for 27 years. Upon retirement as a major from the army, he met Gustav Paykull and helped the latter with his “Fauna svecica” (1798–1800), and collaborated with Carl Johann Schönherr in production of the latter’s “*Synonymia insectorum*” (1806, 1808). Only then did he start his own work, “*Insecta Svecica*,” of which four volumes were published (1810–1827) on Coleoptera. In the 1830s he also contributed heavily to Schönherr’s “*Genera et species curculionidum*” He died on May 13, 1840, in Hoeberg, Sweden.

Reference

Herman LH (2001) Gyllenhal, Leonhard. *Bull Am Mus Nat Hist* 265:73–74

Gynandromorph

An individual that contains structural characteristics of both sexes, often with one sex on one side and the other sex on the other side. This is an abnormal condition in insects, occurring infrequently.

Gyne

A female of the reproductive caste in social Hymenoptera. It is applied to potential or actual queens of ants, bees and wasps.

Gynopara (pl. gynoparae)

In aphids, viviparous females that are produced on the secondary host in the autumn, and then fly to the primary host to produce new females that mate and deposit eggs.

► Aphids

Gypsy Moth, *Lymantria dispar* Linnaeus (Lepidoptera: Lymantriidae)

WAYNE BREWER

Auburn University, Auburn, AL, USA

The gypsy moth, *Lymantria dispar* L., is recognized as one of the most serious insect defoliators of North American forests and urban landscapes. Since its introduction, the gypsy moth has spread to all or part of 17 states and the District of Columbia. Yearly defoliation often reaches into the millions of acres, and the costs of damage and control run into tens of millions of dollars. The moth is a native of Europe and Asia where it is a sporadic pest. It was introduced into the U.S. in 1869 by a French naturalist, Etienne Leopold Trouvelot (Fig. 75), who brought the moths to his home in Medford, Massachusetts. He apparently intended to cross them with other moths to create a prolific and hardy



Gypsy Moth, *Lymantria dispar* Linnaeus (Lepidoptera: Lymantriidae), Figure 75 Etienne Leopold Trouvelot, a French naturalist who accidentally introduced gypsy moth into the field at Medford, Massachusetts, in 1869 (courtesy of USDA).

strain of silkworms. The experiment failed, the moths escaped and spread to the surrounding area.

The first outbreaks of the gypsy moth began in Trouvelot's neighborhood about 10 years after their introduction and, in 1890, the State and Federal Government began attempts to eradicate the moth. These efforts ultimately failed and the gypsy moth has continued to spread since that time. Currently established populations occur throughout the northeastern U.S. and the moth is spreading south and west across the U.S. The moth often "hitchhikes" to new areas on the camper trailers and motor homes of northern residents vacationing in uninfested areas. The result is that every year isolated

populations are discovered beyond the contiguous range of the gypsy moth, but these are usually eradicated or disappear without intervention. However, it is inevitable that the gypsy moth will continue to expand its range in the future.

Biology

The gypsy moth (Fig. 76) has one generation per year. The adults emerge in midsummer, usually in July but variations occur depending on local or regional conditions. Although winged, the females cannot fly and usually remain near the pupal case from which they emerged. Soon after emerging, the females release a sex pheromone that attracts the males, which do fly; they mate and she begins to lay eggs. The females normally produce one egg mass in which the number of eggs may range from fewer than 100 to over 1,000. The eggs are covered by a dense coating of hairs that are sloughed from the abdomen of the female as she oviposits. It is thought that these hairs provide a form of insulation that helps protect them from low temperatures. Gypsy moths overwinter in the egg stage which lasts 8–9 months. The following spring, the eggs hatch and the larvae emerge. The date of larval emergence is strongly influenced by temperature. Larval feeding continues through four instars with the last instar doing most of the damage to foliage. It has been estimated that a single larva consumes about one square meter of foliage during its development. Pupation occurs about eight weeks after egg hatch. The pupae are usually located in cryptic locations such as cracks or crevices of the bark, in the leaf litter, or in other protected places. This stage lasts about two weeks and then adults emerge to continue the cycle.

Dispersal

The newly hatched, small and hairy larvae move to the tops of trees and feed on new foliage. Some may be blown by the wind to new locations. The long larval hairs of the early instars and the strands



Gypsy Moth, *Lymantria dispar* Linnaeus (Lepidoptera: Lymantriidae), Figure 76 Some stages of the gypsy moth life cycle: *top*, a mature larva; *center*, female moths (adults) with egg masses protruding from beneath; *bottom*, a male moth (adult photos courtesy of John Ghent, U.S. Forest Service).

of silk they produce from special glands in their heads are conducive to this type of transport. This “ballooning” is a major means of natural dispersal. However, most long distance spread to new locations occurs as result of the transport of infested items by humans. The larvae may pupate, or females may lay egg masses, on almost any object left outside. These include campers, mobile homes, packing crates, pallets and other items. If infested

items are moved to a new location, a new infestation may become established.

Hosts

The gypsy moth is known to feed on the foliage of over 300 species of trees and shrubs with species of oaks ranked among the most preferred hosts. Oaks are common in much of the forested and urban areas of the U.S. and their wide distribution will be a major factor in the ultimate distribution of the moth. Where oaks are less common, however, the gypsy moth has maintained populations on other tree species including aspen and other hardwoods. A few species, including tulip poplar and dogwood, appear to be immune to feeding and other species, especially conifers, are not acceptable to very young gypsy moth larvae, but older instars feed readily on them.

Damage

When the gypsy moth first moves into a new area, tree mortality is often extensive. Species of oaks, especially white and chestnut oaks, appear to be most susceptible with mortality often exceeding 50%. The effects of repeated defoliation can be very serious. Coniferous trees often die after a single defoliation. Deciduous trees can withstand one or two defoliations but the mortality level rises sharply after the third. Other stresses, such as drought or poor site conditions, may increase the risk of mortality. Much tree mortality is actually caused by pathogens or insects, such as wood borers that attack and kill weakened trees. In areas where the gypsy moth has existed for some time, such as New England, the moth is more notorious as a nuisance rather than for killing large numbers of trees. This may be a result of gypsy moth populations eventually coming under control by natural enemies, or the change in forest composition due to favored hosts being killed and the remaining trees being less suitable as sources of nutrition.

Nuisance Factors

At low population levels, gypsy moth larvae remain inactive and secluded in resting places during the day, but when populations are high, their behavior changes dramatically. Larvae in dense populations become hyperactive during the day. Infested areas are literally crawling with larvae as they move incessantly up and down trees and travel along the ground. These larvae are attracted to and climb any object in their path including trees, telephone poles, cars and people. They are not harmful, but the presence and activity of such large numbers of these larvae create a nuisance. In addition, when outbreaks occur, many larvae die from various mortality factors. The unpleasant odor of decaying larvae is often evident throughout the defoliated area. Outdoor activities, such as picnics and barbecues, are often disrupted by larvae, or their frass (excrement) dropping from infested trees onto patios, decks and picnic tables.

Natural Enemies

Various biological control agents have been collected from Asia and Europe and introduced into infested areas of the U.S. over the last 100 years. These include over 20 insect parasitoids and predators that are natural enemies of the gypsy moth. Small mammals, like the white-footed mouse, and other rodents such as shrews, are perhaps the most important gypsy moth predators, especially at low population densities. Birds are also known to prey on gypsy moths, but do not seem to cause any substantial reduction in moth populations. A nucleopolyhedrosis virus usually causes the collapse of outbreak populations, and recently an entomopathogenic fungus species has caused considerable mortality of gypsy moth populations in North America.

Control

In addition to the introduction of natural enemies, several million acres of forest land have been aeri-ally

sprayed with pesticides over the last 20 years to suppress gypsy moth populations. Though some areas are treated by private companies under contract with land owners, most areas are sprayed under joint programs of state governments and the USDA Forest Service. The USDA, state and local governments also jointly participate in programs to identify and eradicate new gypsy moth populations in currently uninfested areas. These survey programs involve the use of small triangular-shaped traps baited with a synthesized female sex pheromone. In addition, the USDA Forest Service, working with state and federal cooperators, began a Gypsy Moth Slow the Spread (STS) project in 1999. The project covers the 1,200 mile gypsy moth frontier from North Carolina through the Upper Peninsula of Michigan. The project goal is to use novel integrated pest management strategies to reduce the rate of moth spread.

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Gyrinidae

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

► [Beetles](#)

Gyropidae

A family of chewing lice (order Mallophaga). They sometimes are called guinea pig lice.

► [Chewing Lice](#)

