Fig. 190. A female meadow grasshopper Conocephalus strictus. (From Illinois Nat. Hist. Survey)



Fig. 191. The bush katydid Microcentrum rhombifolium. (From Illinois Nat. Hist. Survey)



Fig. 192. A camel or cave cricket Ceuthophilus maculatus. (From Illinois Nat. Hist. Survey)

fields or in woodland grasses. Other genera frequent shrubs or trees. One of these, *Oecanthus*, containing the tree crickets, has an awl-shaped ovipositor with which it drills holes into pithy stems and deposits its eggs in these holes, fig. 194. In local areas raspberry canes may be injured seriously in this manner by *Oecanthus* females.

The mole crickets represent two other families, the Gryllotalpidae and the Tridactylidae. The Gryllotalpidae, fig. 195, are about an inch (25 mm.) long and have large scooplike front legs used in digging. The species make burrows in fairly light soil and feed on small roots and insects which they encounter underground. The adults rarely emerge





Fig. 193. A field cricket *Nemobius fascialus*. (From Illinois Nat. Hist. Survey) Fig. 194. The snowy tree cricket *Oecanthus niveus*. Egg punctures and eggs exposed to view in a raspberry cane, and adult male. The males are among the most fascinating insect musicians. (From Essig, after Smith, College entomology, by permission of The Macmillan Co.)



Fig. 195. Mole cricket Gyllotalpa hexadactyla. (From Illinois Nat. Hist. Survey)

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Fig. 196. Pygmy mole cricket Tridactylus minutus. (From Illinois Nat. Hist, Survey)

from their burrows and are seen only occasionally. The Tridactylidae, or pygmy mole crickets, are much smaller, at the most 5 mm. long, fig. 196. They occur at the edge of lakes and streams, where they may be found either burrowing in the sand or leaping about near the shore line.

## Suborder Grylloblattodea

The Grylloblattids. This suborder is composed of one family, the Grylloblattidae, which contains only the single genus *Grylloblatta*. These are small wingless elongate insects, fig. 197, the head bearing long antennae, small eyes, and chewing mouthparts of generalized shape. The legs are slender, but well developed, and have five-segmented tarsi. The abdomen of the female bears at its apex a stout ovipositor and in both sexes a pair of eight- or nine-segmented cerci.

These are among the most interesting of all insects. In North America they have been found near the snow line of a few mountains in western Canada, California, Montana, and Washington. They live in soil or rotten wood, or under logs or stones, always in places which are covered with snow for much of the year. They feed on vegetation or dead organic matter. The females deposit black eggs in moss or soil.

Only a very few species of grylloblattids have been described. In addition to North America they have been found in Japan.

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Fig. 197. Grylloblatta campodeiformis. (From Essig, College entomology, by permission of The Macmillan Co.)

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#### Order EMBIOPTERA: Embiids, Web Spinners

Elongate flattened insects, fig. 198, with curious enlarged front tarsi, used for spinning silken webs in which the insects live. Mouthparts are the chewing type, primitive in structure; eyes well developed, ocelli absent; antennae many-segmented and elongate; legs short but stout, the tarsi three-segmented; cerci one- or two-segmented. Females always wingless; males usually with two pairs of long membranous similar wings with reduced venation. Metamorphosis gradual.

To this order belong a small number of peculiar tropical and semitropical insects, which live in silken tunnels on their food supply. They feed on a wide variety of plant materials, especially dried grass leaves. Their tunnels may be found under loose bark, among lichens, or on the ground. The ground nets are often among matted leaves, or under dry cattle droppings or stones. Sometimes these nets are found around the bases of plants. In arid regions the insects may be active at the ground surface during the wet seasons and retire into the soil during the dry season. The embilds themselves are active and rapid in movement. The winged males fly readily and are frequently attracted to lights.

The web spinners live in large colonies, with numerous interlocking tunnels, and are gregarious. Most species have both males and females, but a few are parthenogenetic, and of these only females are known. The eggs are elongate and relatively large. They are laid in clusters attached to the walls of the tunnels. The female exhibits considerable maternal interest in both eggs and newly hatched nymphs, remaining near them and attempting to drive away enemies.

The nymphs are remarkably similar to the adults that are wingless. In those species with winged males, there is a noteworthy phenomenon. In the male nymphs the wing pads develop internally as imaginal buds until the penultimate molt and appear as typical wing pads only in the last nymphal instar. This is what happens in holometabolous insects, so that this last embiid nymphal stage might well be called a pupa.

About seventy species of the order have been found in the Americas, representing seventeen genera and six families. Most of these occur in



Fig. 198. Structures and forms of Embioptera. Letters on male terminalia refer to special parts used in embiid taxonomy. (From Essig, College entomology, by permission of The Macmillan Co.)

the tropical areas, but five species extend north into the southern portion of California, Arizona, Texas, and Florida. Two of these, *Oligotoma saundersii* and *nigra*, are tropicopolitan, and have been transported by commerce to most of the equatorial world. A few additional species are occasionally found by quarantine inspectors in shipments of material to the United States from other countries.

All species of the order are remarkably uniform in general appearance. In fact, to date few characters have been discovered to use for the identification of the females, and almost the entire classification of families, genera, and species is based on males.

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## Order PLECOPTERA: Stoneflies

Moderate-sized to large insects with aquatic nymphs and gradual metamorphosis. The adults, fig. 199, have chewing mouthparts, frequently reduced in size and sclerotization; long many-segmented antennae; distinct eyes and ocelli; cerci ranging from short and one-segmented in some families to long and multisegmented in others. Two pairs of welldeveloped wings are almost always present. These are of similar texture and have only a moderate number of veins but frequently a large number of crossveins; the front pair is usually narrower than the hind pair. Several species have short wings, and in *Allocapnia vivipara* the males have no wings. The nymphs, fig. 199, of all stoneflies are aquatic. They have long antennae and a pair of long multisegmented cerci, chewing-type mouthparts, well-developed eyes and ocelli, and body proportions as in adults.

The nearctic stoneflies include about two hundred and fifty species, comprising about ten families and thirty-five genera. Their generalized mouthparts, antennae, and wings, together with their simple type of metamorphosis, indicate that the order is a primitive one allied to the orthopteroid orders.

The nymphs of this order are one of the abundant and interesting components of stream life. They range in body length from about 5 to over 20 mm. and present a varied appearance, including drab plain forms, spotted patterns, and forms striped with yellow, brown, or black. Many of them breathe by means of external finger-like gills. Sometimes



Fig. 199. A stonefly Isoperla confusa, nymph and adult. (From Illinois Nat. Hist. Survey)

the gills are filamentous. The gills are single in some and arranged in tufts in others. Some nymphs have no external gills and simply use the cuticle for respiration. As a rule, the nymphs are found in cool unpolluted streams; a few species occur also along the wave-washed shore area of some of the colder lakes. The nymphs live in a variety of situations, frequently specific for the species. They are found under stones, in cracks of submerged logs, in masses of leaves which accumulate against stones or around branches trailing in the water, and in mats of debris. The majority of the nymphs are vegetarian, feeding on dead organic matter presumably incrusted with algae and diatoms. A number of species are predaceous, feeding on small insects and other aquatic invertebrates.

The females lay several hundred to several thousand eggs, discharging them in masses into the water. The eggs soon hatch. The smaller species and some large ones mature in 1 year, but other large species

require 2 years to complete their development. When full grown, the nymphs crawl out of the water and take a firm hold on a stone, stick, tree trunk, or other object preparatory to the final molt. At molting a dorsal split occurs in the nymphal skin; then the adult emerges in about a minute or less. After another few minutes the wings have expanded and hardened enough for flight. The adults live for several weeks.

There is a peculiarity about certain groups of stoneflies which is only rarely encountered among insects. Winter signals the end of the active season and the beginning of the quiescent period for most insects. With many of the stoneflies the opposite is the case. Apparently the firstinstar nymphs do not develop further during the warmer months of the year. With the approach of winter, nymphal development becomes accelerated, and the adults emerge during the coldest months of the year, beginning in late November or early December, and continuing through March. The adults are active on the warmer winter days and may be found crawling over stones and tree trunks, mating, and feeding on green algae. They show a decided preference for concrete bridges and may be collected in great numbers there. This group is called the fall and winter stoneflies and includes roughly the families Capniidae, Leuctridae, Nemouridae, and Taeniopterygidae. The latter three have members which appear later in the year, and their emergence overlaps that of the spring and summer species.

This peculiar growth behavior of the fall and winter stoneflies indicates a physiological adjustment to the warm and cold seasons quite different from that in most insects. When discovered, the controls and mechanisms for this adjustment will make an interesting story.

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#### Order ZORAPTERA: Zorapterans

Minute insects, 1.5 to 2.5 mm. long, with both winged and wingless adult forms, fig. 200. In both the head is distinct and oval and has



Fig. 200. Forms of Zorotypus hubbardi. 1, winged adult female; 2, adult female that had shed her wings; 3, nymph of winged form; 4, wingless adult female; 5, antenna of adult wingless Zorotypus snyderi. (After Caudell)

chewing-type mouthparts, long nine-segmented antennae, and onesegmented cerci. The wingless forms are blind, with only occasional vestiges of eyes or ocelli; the winged forms, or alates, have compound eyes and distinct ocelli. The alates have two pairs of delicate membranous wings, each with only one or two veins which may be branched. These wings are shed by the adults much as in the termites, leaving only small stubs attached to the body. Metamorphosis is gradual.

The order is one of the rarest among the insects. It contains one family, the Zorotypidae, in which there is only a single genus, *Zorotypus*. From the entire world less than twenty species are known, most of them found in the tropics. Two occur in North America, *Z. snyderi* described from Jamaica and Florida, and *Z. hubbardi* which has been collected in many localities in the southern states as far north as Washington, D. C.

Zorapterans live in rotten wood or under dead bark and are usually found in colonies of a few to a hundred individuals. Their food, as far as is known, consists mainly of small arthropods, especially mites and small insects. Whether they are scavengers or predators has not been established, but observations on culture specimens indicate the former.

The wingless and winged adults have similar genitalia and reproductive habits. Eggs of only Z. *hubbardi* have been observed, laid without definite anchor lines or matrix in the runways of the colony. The creamy-colored oval eggs hatched in about 3 weeks. Basing his estimate on collection observations over several years, Dr. Gurney believes that it requires several months for the nymphs to become adults.

Although the development of winged and wingless forms might indicate a forerunner of a caste system, no evidence of social life has been observed in the Zoraptera. There is apparently no division of labor, care of young, or social interrelationship between individuals. The gregarious nature of the colonies is very similar to the conditions found in many species of Corrodentia.

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#### Order CORRODENTIA: Psocids, Booklice \*

Small insects, ranging in length from 1.5 to about 5 mm., with chewing mouthparts, long 13- to 50-segmented antennae, small prothorax, and no projecting cerci, fig. 201. Two pairs of wings are well developed in

<sup>\*</sup> The names Psocoptera and Copeognatha are sometimes used for this order.



Fig. 201. A winged psocid Ectopsocus pumilis, and its life history stages. (After Sommerman)

some forms, the front pair much larger than the hind pair, both of similar texture and with a reduced and simple venation. In other forms the wings may be small and scalelike or absent. Metamorphosis is gradual.

Most of the members of this order are small, averaging 2 to 4 mm. in length, and are either inconspicuously colored or exhibit marked

protective coloration. For this reason they are seldom collected by the beginning student, although they occur abundantly in many habitats. Their food is relatively nonspecific, consisting of fungus mycelium, lichens, dead plant tissue, and dead insects, even of their own species. They live in a wide variety of situations out-of-doors—on clumps of dead leaves, dried standing grass, dead or dying leaves of corn plants, bark of tree trunks, in the leaf cover on top of the ground, on shaded rock outcrops, under fence posts, and in bird and rodent nests. Several species live on moldy or partially moldy foods, bookbindings, and almost anything with available starch or fungus mycelium.

Some of the species are stocky and move slowly, even when disturbed. Many of them are more slender, and a few are quite flat. These usually move with considerable speed, and a few are among the most rapid dodgers to be found among the insects. Studies to date indicate that the entire life span from egg to death of the adult is between 30 and 60 days, of which about half is spent in the adult stage. The eggs are laid on the leaf surface or other spot which the adult frequents. Depending on the species, eggs are deposited singly or in groups up to about 10. After oviposition the female spins strands of silk over the eggs and anchors them to the surface of the support. In some species only a few strands are spun over the eggs; in others a dense web may be spun over each group of eggs. The eggs hatch in a few days, and the nymphs pass through six nymphal stages and become adults in 3 or 4 weeks.

In the more northern states the winter is passed in the egg stage by some species and as nymphs or adults by others. Species inhabiting warm buildings continue to breed throughout the year.

About one hundred and fifty species are known from North America, representing about twelve families and many genera. The group is world-wide in distribution, with an estimated number of species nearing nine hundred.

ECONOMIC STATUS. Several species of psocids cause considerable waste of food and damage to libraries. They cause little loss by actually eating foodstuffs, because they feed chiefly on mold. At times, however, they become extremely abundant, spread through an entire building, and get into every possible hiding place. In this way they may contaminate otherwise merchantable goods to such an extent that quantities of the material must be discarded. Their damage to libraries is more direct. They eat the starch sizing in the bindings of books and along the edges of the pages, defacing titles and necessitating rebinding and repairs. The two most common species are the common booklouse, *Liposcelis divinatorius*, a minute wingless species, fig. 202; and *Trogium pulsatorium*, another small species having the wings reduced to small scales.

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Fig. 202. A wingless booklouse *Liposcelis* divinatorius. (From U.S.D.A., E.R.B.)

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## Order PHTHIRAPTERA: Chewing and Sucking Lice

Small to medium-sized wingless insects, usually somewhat flattened, figs. 203, 206, which live as ectoparasites on birds and mammals. They have various types of mouthparts; only short three- to five-segmented antennae, sometimes hidden in a recess of the head; reduced or no compound eyes; and no ocelli. The thorax is small, the segments sometimes indistinct; the legs short but stout; and the abdomen has from five to eight distinct segments. Metamorphosis is gradual.

The Phthiraptera contain three distinctive suborders with an interesting evolutionary history. Members of the primitive suborder Mallophaga live on sloughed skin, dried blood at wounds, and other organic material on the body of the host. This suborder has a simple, reduced type of chewing mouthparts. One line of the Mallophaga apparently began to break the skin of the host and feed on exuding blood. Concurrently with this development the mouthparts became reduced to only the labium and mandibles, and an oesophageal pump developed, used for sucking up this food. The only known representative of this stage is the elephant louse *Haematomyzus*. From a primitive member of this line arose a branch in which a wholly new set of piercing-sucking stylets, fig. 205, evolved in company with the blood-sucking habit. This branch developed into the suborder Anoplura, the sucking lice.

## Key to Suborders

1.	Mandibles sclerotized, toothed, and functional, situated at end of a beaklike
	projection of the head or on ventral side of head, fig. 204; mouthparts not
	styliform
	Mandibles apparently absent; mouthparts composed of long stylets retractable
	into a cavity in the head, fig. 205 Anoplura
.2.	Front of head produced into a narrow beak longer than the rest of the head.
	Contains only Haematomyzus elephantis, occurring on Indian elephant
	Rhyncophthirina
	Front of head not produced into a beak. On many kinds of mammals and
	birds Mallophaga

## SUBORDER MALLOPHAGA

**Chewing Lice.** The chewing lice average about 3 mm. in length, a few species attaining 10 mm. They vary considerably in shape and habits, some being long and slender, others short and wide; some are active and rapid of movement, others sedentary and sluggish. There is little correlation between speed and shape. Their mouthparts are of the chewing type, but greatly reduced and difficult to interpret without careful study.



Fig. 203. The chicken head louse Cuclotogaster heterographus. A, adult; B, eggs on feather. (A, from Illinois Nat. Hist. Survey; B, from U.S.D.A., E.R.B.)

There are several hundred species of Mallophaga in North America, comprising about six families and many genera. Each species occurs on only one species of host, or on a group of closely related species. The turkey louse, for instance, occurs only on turkeys, but the large poultry louse occurs on many kinds of domestic fowl, such as chickens, turkeys, peacocks, guinea hens, and pigeons. The small family Trichodectidae occurs only on mammals, and the large family Menoponidae occurs only on birds.

All the Mallophaga live entirely on the host body and have continuous and overlapping generations throughout the year. They feed on scaly skin, bits of feather, hair, clotted blood, and surface debris. The eggs are glued to the hair or feathers of the host and thus kept under incubator conditions. The eggs of various species differ in shape; some are long and simple, as in fig. 203B; others are ornamented with tufts of barbs or hair, as in fig. 204B.

#### Key to Families

Maxillary palps present; antennae arising from ventral portion of head and
usually situated in grooves or cavities, fig. 204 (series Amblycera) 2
Maxillary palps absent; antennae arising from or near lateral margin of head
and not situated in grooves, fig. 203 (series Ischnocera)
Tarsus with 1 claw or none. On guinea pigs Gyropidae
Tarsus with 2 claws. On birds
Entire head triangular in outline, fig. 204, the posterolateral areas posterior to
the eyes considerably expanded laterally; antennae in grooves which are
completely open laterally Menoponidae
Head more elongate and the anterior portion comparatively wide; antennae in
nearly circular cavities opening ventrally4
Sides of head with conspicuous swellings anterior to eyes Laemobothriidae
Sides of head straight or nearly so, without such swellings Ricinidae
Tarsus with a single claw. On mammals Trichodectidae
Tarsus with 2 claws. On birds Philopteridae

ECONOMIC STATUS. Many species of Mallophaga infest domestic birds and animals and cause a considerable over-all loss. Poultry are the most important group attacked. Chicken lice, *Menopon gallinae* and *Menacanthus stramineus*, fig. 204, cause loss of weight and reduction of egg laying in chickens, turkeys, and other fowl. The chicken-head louse *Cuclotogaster heterographus*, fig. 203, occasionally occurs in outbreak form and causes the death of broods of young chicks. Several other species infest fowl, but the aforementioned, because of their reproductive capacity, are the most common and destructive.

Domestic animals are attacked by various species of the genus *Trichodectes.* Dogs, cats, horses, cattle, sheep, and goats may suffer considerable



Fig. 204. The chicken body louse *Menacanthus stramineus*. A, adult; B, eggs on feather. (From U.S.D.A., E.R.B.)

loss of condition if badly infested with these lice. There is evidence that the biting sheep louse T. *ovis* injures the base of the wool and causes commercial depreciation by lowering the staple length of the sheared product.

#### Suborder Anoplura

Sucking Lice. The North American species represent about twenty genera and one hundred species ranging in length from 2 to 5 mm. All of them occur normally on mammalian hosts and feed on blood which is sucked through a tube formed by an eversible set of fine stylets, fig. 205. Occasionally poultry may have a small infestation of sucking lice, but all cases on record have been accidental colonizations by a common mammalian species. The entire life cycle is spent on the host. The eggs are glued to a hair and soon hatch into nymphs which are very similar to the adults in both appearance and habits. Breeding occurs continuously throughout the year.

## Key to Families

1. Body with a dense covering of short, stout spines or of spines and scales; parasitic on marine mammals such as seals, sealions, and walrus

Echinophthiriidae

	Body chiefly with discrete rows of spines or hairs, figs. 207, 208, never with
	scales; on land animals 2
2.	Head with no trace of eyes, fig. 206 Haematopinidae
	Head with eyes or eye tubercles present, figs. 207, 208 3
3.	Three pairs of spiracles, forming an oblique row on each side, on what appears
	to be the first abdominal segment (really the fused first three), fig. 207
	(Phthirius) Phthiriidae
	Only one pair of spiracles on first abdominal segment (apparent as well as real),
	fig. 208 (Pediculus) Pediculidae

ECONOMIC STATUS. Sucking lice are a real concern on two counts: (1) losses inflicted on livestock, and (2) their menace to man.

LOSSES TO LIVESTOCK. Horses, cattle, sheep, goats, dogs, and cats are attacked by several species of lice. The loss is due partly to irritation and partly to loss of blood, with resultant poor condition of the animal and failure to gain weight normally. Frequently lice will cause sheep and goats to rub against fences or trees, with heavy damage to the wool. In the main, poorly kept animals are the principal individuals badly attacked, but this is not always the case. An outbreak allowed to go unchecked will usually spread through an entire herd. Most of the lice attacking domestic animals belong to the family Haematopinidae, of which *Haematopinus asini* the horse sucking louse, fig. 206, is a common example.

MENACE TO MAN. Two species of Anoplura are external parasites of man. They are both widespread in distribution and are most abundant under crowded insanitary conditions. They spread from person to person in crowded situations or by clothing and bedding.



Fig. 205. Head and mouthparts of *Pediculus humanus*. (After Metcalf and Flint, Destructive and useful insects, by permission of McGraw-Hill Book Co.)



Fig. 206. The horse sucking louse *Haematopinus asini*. (From Illinois Nat. Hist. Survey)

CRAB LOUSE, *Phthirius pubis*, FIG. 207. A very small crablike species infesting hairy portions of the body, especially the pubic region. It is seldom found on the head. This species inflicts painful bites and causes severe irritation. It has not been incriminated in the dispersal of any disease.

BODY LOUSE OR COOTIE, *Pediculus humanus*, FIG. 208. A larger louse about 4 or 5 mm. long, which occurs on the hairy parts of the body. There are two forms of this species, the head louse which occurs chiefly on the head and glues its eggs to the head hairs, and the body louse which occurs chiefly on the clothes and reaches to the adjacent body areas to feed. The body louse glues its eggs to strands of the clothing. Under



Fig. 207. The crab louse *Phthirius pubis*. (Redrawn from Ferris)



Fig. 208. The cootie or body louse *Pediculus humanus*. (Redrawn from Ferris)

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condition of regular head washing and clothes change cooties are seldom a nuisance. Under insanitary conditions they may develop in tremendous numbers and produce constant irritation.

The cootie has vied with the mosquito in shaping the destiny of history. Cooties transmit typhus fever and trench fever, which until recent years have been the scourges of northern armies, especially in winter. Under insanitary crowded camp or trench conditions, soldiers with heavy clothing provided ideal hosts for cooties. Typhus and trench fever have occurred in outbreak form and with disastrous results throughout many European armies. Napoleon's army in Russia was decimated as much by louse-borne disease as by hunger and exposure. The opposing Russian army suffered fully as much from typhus as the French army. Many claim that the cooties won the campaign, defeating both armies.

In World War II the control of lice by treatment of entire city populations stopped outbreaks of typhus which had reached epidemic proportions. Especially effective results achieved in Naples in 1944 represent one of the most significant modern advances in the annals of preventive medicine.

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#### Order THYSANOPTERA: Thrips\*

Small elongate insects, fig. 210, most of them between 2 and 3 mm. long, with six- to nine-segmented antennae, large compound eyes, and compact mouthparts which form a lacerating-sucking cone. Many forms are wingless; others may have short wings or well-developed wings. In the latter case there are two pairs, both very long and narrow, with only one or two veins or none; the front pair often larger, and both with a long fringe of fine hair along at least the hind margin. The legs are stout, the tarsi ending in a blunt tip containing an eversible pad or bladder. Metamorphosis appears to be gradual, but there is present a definite pupa.

<sup>\*</sup> In the European literature the name Physopoda is often used for this order.

The thrips are an extremely interesting group, quite different from any related forms. They occur commonly in flowers, and they may be found by breaking open almost any blossom and looking around the bases of the stamens or pistils. A large number of diverse forms can be taken by sweeping grasses or sedges in bloom. Many species are destructive to various plants and are found on the leaves of infested hosts. A large number of species, predaceous on mites and small insects, occur under bark of dead trees and in ground cover.

Thrips' mouthparts are of an unusual type, fig. 209. The various parts fit together to form a cone; some of the parts are needle-like stylets, which pierce and lacerate the food tissues; the juices thus released are sucked up into the stomach by a pump in the head capsule which pulls the liquid food through the cone formed by the mouthparts.

The metamorphosis of thrips is as unusual as their morphological features. The early nymphal stages are similar to the adults in structure of legs and mouthparts and in general shape; their feeding habits are also the same as those of the adults. These points are characteristic of insects having gradual metamorphosis. The first two instars have no wing pads, fig. 210,2; the pads appear suddenly in the third instar as fairly large structures, fig. 210,3; in the fourth (last) nymphal instar



Fig. 209. Mouthparts of the flower thrips. (From Metcalf and Flint, Destructive and useful insects, by permission of McGraw-Hill Book Co.)



Fig. 210. The red-banded thrips *Heliothrips rubrocinctus*. 1, adult; 2, nymph or larva; 3, propupa; 4, pupa. (After U.S.D.A., E.R.B.)

the wing pads are greatly enlarged, fig. 210,4. This fourth instar is quite unlike the others in habits. It does no feeding and is completely quiescent, with the antennae held back over the top of the head and pronotum. Certain thrips have an additional fifth nymphal instar. In some species having this, the fourth-instar nymph enters the soil and forms a cocoon, in which the quiescent fifth stage is passed. This feature is similar in so many respects to holometabolous development that the quiescent stage is called a *pupa*, and the first two instars are called larvae. The third-stage form, the active stage with the wing pads, is called a *propupa*. In some groups this form is not developed, the larvae transforming directly to the quiescent pupae.

The order contains several families represented in North America by about five hundred species, some of them measuring 5 or 6 mm. in length. A large number of species occur on only one species of plant, but a few common species, such as the flower thrips, *Frankliniella tritici*, feed on a great variety of plants and frequent blossoms of almost any species of plant. A few species are predaceous, feeding on red spiders and other mites, and minute insects.

#### Key to Common Families

1. Major anal setae of last segment arising from a ring at apex of segment, which forms an undivided tube in both sexes, fig. 211F (suborder TUBULIFERA)

#### Phlaeothripidae



Fig. 211. Structures of Thysanoptera. A, apex of abdomen of Anaphothrips, Thripidae; B, base of antenna of Heterothrips, Heterothripidae; C, same of Acolothrips, Aeolothripidae; D, antenna of Anaphothrips, Thripidae; E, dorsum of apex of abdomen of Oxythrips, Thripidae; F, same of Allothrips, Phlaeothripidae. (Redrawn from various sources)

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3. Apex of third antennal segment having a complete band of small, circular sensoria, fig. 211B; female saw curved down at apex, as in fig. 211A Heterothripidae

Apex of third antennal segment with one or two ovoid or elongate sensoria, fig. 211*C*; female saw curved up at apex ..... Aeolothripidae

ECONOMIC STATUS. Several species of this order inflict considerable damage on commercial crops. The following, all belonging to the family Thripidae, are among the most injurious thrips over the United States as a whole:

The onion or tobacco thrips *Thrips tabaci* is a widespread species varying from lemon yellow to dark brown, which is especially injurious to onions, beans, and tobacco.

The greenhouse thrips *Heliothrips haemorrhoidalis* is a dark species with the body ridged to give it a checked or reticulate surface. The species is cosmopolitan. In the temperate region it is chiefly a greenhouse pest, attacking many kinds of hothouse plants.

The pear thrips *Taeniothrips inconsequens* is brown with gray wings. It attacks pears, plums, and related plants and produces a curious silvery blistered appearance on the injured leaves.

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#### Order HEMIPTERA: Bugs and Their Allies

A large assemblage of diverse insects, characterized chiefly by (1) piercing-sucking mouthparts which form a beak, (2) gradual metamorphosis, and (3) usually the possession of wings, fig. 212. With few exceptions the compound eyes are large, the antennae four- to tensegmented, the individual segments frequently long, two pairs of wings are present and have relatively simple or reduced venation, and the abdomen has no cerci.

The order derives its name from the structure of the front wing in many families, figs. 212 and 214, in which the basal portion is hard and thick, called the *corium*, and the apex is thinner and transparent, called the *membrane*. The corium approaches in texture the hard wing cover or elytron of beetles; hence the name "hemelytron" is often applied to this half and half type of front wing.



Fig. 212. A typical stink bug, illustrating beak and wings. (From Illinois Nat. Hist. Survey)

The Hemiptera are divided into two suborders, the Heteroptera and Homoptera. The families represented in North America fall definitely into one suborder or the other, but a few families occurring in other regions appear to present intergrading conditions between the two groups.

## Key to Common Families

1.	Hind leg without tarsal claws and having both tarsus and pretarsus flattened
	and bearing a dense fringe of long hair down each side, fig. 213A; middle
	tarsus having normal tarsal claws (part of Heteroptera)
	Hind tarsus having tarsal claws similar to those on middle tarsus; hind leg
	usually without a long fringe but occasionally having one, fig. $213C3$
2.	Beak forming a triangular striated piece that appears as a ventral sclerite of
	the head, fig. 213G; middle tarsus having extremely long claws, fig. 213B;
	front tarsus comblike
	Beak cylindrical and rodlike, curving back from the ventral portion of the
	head, as in fig. 213L; front and middle legs usual in shape
	Notonectidae, p. 272
3.	Beak arising from front or venter of head, fig. 213L; the venter of the head
	posterior to beak forming a sclerotized bridge or gula (Heteroptera) 4
	Beak arising from posterior margin of head, fig. 215L; no gula present behind
	it (Homoptera)
4.	Antennae shorter than head, usually recessed in a concavity beneath the eyes
	or under the lateral margin of the head, as in fig. $213G$
	Antennae at least as long as the head, usually extending free from it, fig. 218,
	sometimes fitting into a pronotal groove when at rest
5.	Ocelli present. Small toadlike bugs, fig. 215E, found along the margins of
	lakes and streamsGelastocoridae
	Ocelli absent. Forms living in water, sometimes flying and attracted to
	lights
6.	Tarsi 1-segmented, front tarsus with only a minute claw or none, fig. 213D;
	apex of abdomen with a long or short respiratory tube, fig. 216B, each blade



Fig. 213. Diagnostic characters of Hemiptera. A, and B, hind leg and middle leg of Corixa, Corixidae; C, front and hind tarsi of *Belostoma*, Belostomatidae; D, front and hind tarsi of Nepa, Nepidae; E and F, front tarsus, lateral and dorsal aspect of Gerris, Gerridae; G, head of Corixa; H, head of Nabis, Nabidae; I, head of Lygaeus, Lygaeidae;  $\tilde{J}$ , head of Myodocha, Lygaeidae; K, front leg, inset showing structure of tarsus of Phymata, Phymatidae; L, head of Alydus, Coreidae; M and N, head and antenna of Jalysus, Neididae; O, antenna of Myodocha, Lygaeidae; F, antenna of Lyctocoris, Anthocoridae. f, femur; g, gula; l, labrum; o, ocellus; ta, tarsus; tc, tarsal claws; ti, tibia.

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The	Orders of Insects	بەر	267	
	of which is concave mesally, the two fitting together hind legs slender and without fringes of long hair Tarsi 2-segmented, front tarsus with a stout curved abdomen at most with a pair of short flat respirate and tarsus often flattened, always having fringes of	to make a hol claw, fig. 213 ory filaments; long hair for s <b>Belostomatid</b>	low tube; . <b>Nepidae</b> <i>C;</i> apex of hind tibia swimming <b>ae,</b> p. 273	
7.	Head extremely long and slender, slightly bulbous at the eyes situated at the middle of what appears to body also very slender, fig. 216 <i>C</i>	apex, where be be a long ne <b>Hydr</b> o	eak arises, ck; rest of metridae	
	Head much stouter, fig. 213 <i>I</i> , or eyes not situated on	the neck, fig. 2	137 8	
8.	Front leg having femur and tibia chelate, forming a femur swollen and triangular, tibia curved and cl femur, fig. 213K	a large graspi osing against	ng device, the end of <b>ymatidae</b> 9	
9.	Claws of front tarsus inserted before apex, fig. 213E, I Claws of front tarsus attached at apex, as in fig. 213C	₹	10 11	
10.	Middle pair of legs attached far from front legs, close very long, fig. 218; beak 4-segmented	to hind legs; h	ind femur <b>ae,</b> p. 274	
	femur only moderately long; beak 3-segmented		. Veliidae	
11.	<ul> <li>Scutellum very large, reaching about one-half or more margin of pronotum to end of folded wings, fig. 21</li> <li>5-segmented. (Pentatomidae, p. 279)</li> <li>Scutellum much smaller, reaching about a guarter of several sever</li></ul>	e distance from 5 <i>B-D;</i> antenn	a posterior ae usually 12 from pro-	
12.	notum to tip of body, fig. 215 <i>A</i> ; antennae usually 4 Tibia armed with rows of thick thornlike spines, fig. 2 Tibia having series of short even spines, occasionally w	-segmented 215F	15 13	•
	slender hairs, fig. $215G$	· · · · · · · · · · · · · · · ·	14	
13.	Scutellum triangular and not very large, as in fig. 21 Scutellum large and U-shaped, covering most of ab	5 <i>B</i> domen, fig. 2	<b>Cydninae</b> 15D	
		Thyr	eocorinae	
14.	of scutellum U-shaped and very wide, covering almost a of scutellum curved mesad at extreme base, as in fi Scutellum V-shaped, fig. 215 <i>B</i> , or, if U-shaped, then 215 <i>C</i> and slightly contracted just beyond base	ig. 215 <i>D</i> Scu never larger t	tellerinae han in fig.	
15.	Front wing abbreviated, with no membrane, and rea of abdomen, fig. 220.	iching at most	to middle	
	Front wing normal, with a large apical membrane, middle of abdomen, fig. 214	or reaching w	ell beyond	
16.	Body flat and wide; front wing short, broad, and scaling over base of abdomen; sides of pronotum larg fig. 220; beak 3-segmented; antennae long and sler	lelike, only bar e, round, and nder . <b>Cimicid</b>	ely reach- flangelike, a <b>e,</b> p. 275	
	Body narrower, or otherwise different from foregoin mented beak, different-shaped wing, or short antenn of them rare, difficult to key to family, belonging to <b>Aradidae, Lygaeidae,</b> or <b>Nabidae;</b> and all nymph	g, having eith nae. A few ges <b>Anthocoridae</b> s of Heteropte	er a 4-seg- nera, most <b>, Miridae,</b> ra families	

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Fig. 214. Elytra or forewings of Hemiptera. A, Triphleps; B, Lygus; C, Pselliopus; D, Salda E, Gargaphia; F, Blissus; G, Myodocha; H, Alydus; I, Nabis; J, Euryophthalmus; K, Piesma.

listed beyond this point. The wingless species of this group are keyed no farther here.

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19. Ocelli prominent, two in number; membrane of hemelytron having a long
vein proceeding from top of upper closed cell, fig. 214C. Reduviidae, p. 274
Ocelli absent; membrane with a vein proceeding only from bottom of lower
closed cell, or such a vein lacking, fig. 214 <i>B</i> Miridae, p. 275
20. Antenna having first two segments stout, last two threadlike, forming a slender
terminal filament, fig. 213P; ocelli present but small; hemelytral membrane
with only one or two weak veins, fig. 214AAnthocoridae
Antenna having one or both of the two apical segments as thick as the first or
second, fig. 213N, O
21. Hemelytral corium extending markedly beyond a ridgelike oblique vein near
apex of corium, fig. 214K; corium entirely reticulate
Hemelytral corium not extending beyond an apical oblique vein, fig. 214H-7,
or not having such a vein, fig. $214G$
22. No ocelli present
Two ocelli present
23. Flat wide warty bugs fig 2234 B: tarsus 2-segmented the first segment short:
hemelytra often small the periphery of the abdomen extending considerably
hereord them Aradidae n 278
Stout insects, the body deep: tarsus 3-segmented the first segment long; here-
lytra larger fig 2147 covering all abdomen excent tin and sides near apex
ly the larger, lig. 2143, covering all abdoment except tip and sides hear apex
Pyrmocoridae
24. Hemelytral memorane having four or live large and fairly regular closed cells
and no other venation, ng. 214D, oval lairly hat bugs found on stream and
lake shores
Hemelytral membrane having either an irregular network of cells or only one
or two small ones, fig. $214F-1$
25. Membrane having a series of about 15 irregular veins, at least on apical por-
tion, fig. 214 <i>H</i> , <i>1</i>
Membrane having only five or six veins across it, fig. $214F, G. \ldots 27$
26. First segment of beak short and conelike, thicker than the second, fig. 213H;
front femur thickened, front tibia armed inside with a double row of short
black teethNabidae
First segment of beak cylindrical and long, similar in general shape to second
segment, fig. 213L; front femur usually more slender, front tibia never with
inner rows of black teeth Coreidae, p. 278
27. Each ocellus situated behind an eye, at the base of a distinct swelling, fig.
213M; extremely slender and elongate bugs, with long and slender legs and
antennae; last segment of antenna short and oval, forming a small club,
fig. 213NNeididae
. Ocelli situated closer to or between eyes, and not at the base of a swelling, fig.
2131, 7; chiefly robust short insects or having short legs; antennae either
short, fig. 2130, or not clubbed Lygaeidae, p. 277
28. Having wings, which are sometimes reduced to short scales
Completely wingless species
29. Front femur greatly enlarged in comparison with middle femur. fig. 215K:
three ocelli present
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; ; ;





Fig. 215. Diagnostic characters of Hemiptera. A, outline of Lygus, Miridae; B, outline of Solubia, Pentatomidae; C, outline of Stiretrus, Pentatomidae; D, outline of Corimelaena, Pentatomidae; E, Gelastocoris, Gelastocoridae; F, hind tibia and tarsus of Pangaeus, Pentatomidae; G, hind tibia and tarsus of Thyanta, Pentatomidae; H, hind tibia and tarsus of Aulacizes, Cicadellidae; I, hind tibia and tarsus of Aphrophora, Cercopidae; J, hind tibia and tarsus of Stenocranus, Fulgoridae; K, front femur of Pacarina, Cicadidae; L, head of Gypona, Cicadellidae; M, head, lateral and anterior views, of Poblicia, Fulgoridae; N, wing of Psylla, Psyllidae; O, wing of Aphis, Aphididae. · . ·

	Front femur no larger than middle femur; three, two or no ocelli present 30
30.	Antennae arising from sides of head, situated beneath or behind eyes, fig.
	215 <i>M</i>
	Antennae arising from front of head between eyes, fig. 215L 31
31.	Pronotum enlarged dorsally into a large structure which covers most of head
	and body and may be highly ornamented with spines and processes, fig. 225
	Membracidae, p. 281
	Pronotum small, without dorsal enlargement

32.	Pronotum forming a broad shield which covers the greater part of the meso-
	notum, fig. 228; tarsus 3-segmented, fig. $215H-\mathcal{J}$
	Pronotum forming a narrow collar which does not extend back over the meso-
	notum, fig. 231; tarsus 1- or 2-segmented
33.	Hind tibia bearing a double row of spines down its entire length, its apex
	usually not enlarged, fig. 215H Cicadellidae, p. 282
	Hind tibia with only scattered spines except at apex, which is enlarged and
	armed with a prominent crown of spines, fig. 2151 Cercopidae, p. 281
34.	Having only one pair of wingsmale Coccoidea, p. 284
	Having two pairs of wings
35.	Wings milky-opaque, covered with a fine powdery white wax
	Aleurodidae, p. 283
	Wings transparent or patterned, not covered with a waxy secretion 36
36.	Front wing with $R_s$ very long, arising before stigma, and Cu branched, fig.
	215.N; abdomen never with cornicles
	Front wing with $R_s$ short, arising from some part of the stigma, and Cu un-
	branched, fig. 2150; abdomen in many species having a pair of lateral tubes
	or cornicles, fig. 231
37.	Eyes large, antennae situated at sides of head below or behind eyes, fig. $215M$
	Fulgoridae, p. 281
	Either eyes rudimentary or absent, or antennae situated on front of head be-
	tween eyes, fig. 231
38.	Tarsus 1-segmented; body covered with a hard shell, waxy secretions, or a de-
	tachable scale, fig. 232; abdomen never having cornicles. Coccoidea, p. 284
	Tarsus 2-segmented; body at most with waxy secretions; abdomen often hav-
	ing a pair of conspicuous cornicles or tubes, fig. 231 Aphidoidea, p. 284

SUBORDER HETEROPTERA

**Bugs.** This suborder contains a wide variety of forms ranging from a few millimeters to a few inches in length, and including terrestrial, semiaquatic and aquatic types. The antennae are four- or five-segmented, and the eyes are well developed except in the ectoparasitic family Polyctenidae.

The nymphs of all forms resemble the adults in general outline, but differ uniformly in having dorsal stink glands on the abdomen. In this respect they differ also from the nymphs of the Homoptera.

The eggs are usually laid singly or in groups glued to stems or leaves. In some forms the eggs are inserted into plant stems or, rarely, into damp sand.

The suborder contains about equally predaceous species and plantfeeding species; often both types occur in the same family. The predaceous species feed chiefly on smaller insects. In certain species of the plant bugs, Miridae, the predaceous habit is only partially developed, and insect blood serves merely to supplement the principal diet of plant

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juices. The mixture of food habits in the same families has resulted in some queer anomalies. In the stink bug family Pentatomidae the harlequin bug *Murgantia histrionica* is a serious pest of cabbages; a predatory species *Perillus bioculatus* is one of the most effective natural enemies of the dreaded Colorado potato beetle.

SHORT-HORNED BUGS. The members of this group have short antennae, usually recessed under the head and not visible from the dorsal aspect. The group gets its name from this characteristic. The families represented in North America are either aquatic or shore-inhabiting. Of the nine families recognized in our fauna, the Corixidae, Notonectidae, and Belastomatidae are the most common.

**Corixidae, water boatmen.** These bugs, fig. 216*A*, are characterized by the short stout labium which looks more like the lower sclerite of the head than like a beak, fig. 213*G*. The front legs are short, flattened, or scoop-shaped; the hind legs are long, flattened, and fringed with combs of bristles. Both nymphs and adults are truly aquatic, swimming in the water and incapable of more than clumsy flopping on land. The fringed hind legs are used for swimming; they swim dorsal side up. The adults leave the water for dispersal flights and may be observed in swarms over bodies of water. Sometimes these swarms are attracted to lights. The eggs are attached to solid supports such as stones, sticks, and shells in the water. Certain forms, such as *Ramphocorixa*, more often lay their eggs on the body or appendages of the crayfish *Cambarus*, which in some localities may be literally plastered with corixid eggs.

The water boatmen differ from all other Hemiptera in their feeding habits. They feed in the ooze at the bottom of the water, the stylets of the mouthparts darting in and out in unison like a snake's tongue. These stylets draw into the pharynx an assortment of diatoms, algae, and minute animal organisms which constitute their food.

Notonectidae, backswimmers. In form these aquatic bugs superficially resemble the water boatmen, particularly in the long-fringed oarlike hind legs used for swimming. They are very different, however, in many ways. Most conspicuous is their habit of always swimming on their backs. The coloration of the backswimmers is modified to match this change in swimming position. The ventral side, which is uppermost, is dull brown to match the stream or pond bottom. The dorsal side, which is hidden from above when the insect is swimming, is usually whitish, creamy, or lightly mottled. The beak in the Notonectidae is stout and sharp, used to suck the body contents from small aquatic animals such as Crustacea and small insects on which the backswimmers feed. Many species of backswimmers deposit their eggs on the surface of objects in the water; others insert their eggs into the stems of aquatic plants.



Fig. 216. Heteroptera. A, dorsal aspect of Arctocoriza, Corixidae; B, dorsal aspect of Nepa, Nepidae; C, ventral and partial lateral aspects of Hydrometra, Hydrometridae. (A adapted from Hungerford, B and C from Hemiptera of Connecticut)

Belostomatidae, giant water bugs. Members of this family are wide and stout, with grasping front legs and crawling and swimming middle and hind legs, fig. 217. They include some of the largest North American Hemiptera, for example, *Lethocerus americanus*, which attains a length of 3 to 4 inches. The giant water bugs have strong beaks. They are predaceous, feeding on insects, snails, small frogs, and small fish. Commonly they are attracted to lights where they draw considerable attention, owing to their ungainly movements and large size.

LONG-HORNED BUGS. In this group the antennae are exposed and elongate, projecting well in front of the head. Over thirty families are recognized in North America, including a great variety of shapes and

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Fig. 217. A giant water bug Lethocerus, Belostomatidae. (Original by C. O. Mohr)

habits. The following nine families afford a good cross section of the group.

Gerridae, water striders. These are slender bugs with long legs, fig. 218. They live on the surface of water, inhabiting chiefly ponds, the margins of lakes, and the more sluggish backwaters and edges of rivers and streams. The tarsi are fitted with sets of nonwetting hair which allow the bugs to run and stand on the water surface with amazing speed and ease. All species are predators or scavengers, feeding chiefly on other insects that occur on the water surface. They lay their eggs in masses attached to aquatic plants or thrust them into submerged stalks. Several other closely related families live as striders or skaters on the water surface; from these the Gerridae differ in having very long hind femora, which extend considerably beyond the apex of the abdomen.



Fig. 218. A water strider Gerris rufomaculata, Gerridae. (Original by C. O. Mohr)

**Reduviidae, assassin bugs.** These are sluggish predaceous insects, usually medium-sized to large, that feed on other insects. Most of our species have fully developed wings, fig. 219, and several have wide foli-



Fig. 219. Three Reduviidae. Left to right, Pselliopus barberi, Melanolestes picipes, and Triatoma sanguisuga. (Drawings loaned by R. C. Froeschner)

aceous legs. The nymphs of certain species secrete a sticky substance over the dorsum, on which are carried bits of leaves and debris, providing the animal with very good camouflage. The eggs are laid singly or in clusters, glued to plants or other supports. Assassin bugs sometimes attack man, inflicting a painful burning wound. All the Reduviidae are terrestrial.

**Cimicidae, bed bugs.** This family includes only a few species of wide flat insects that feed on the blood of birds and mammals. The fore wings or hemelytra are represented only by short scalelike pads; the hind wings are completely atrophied. They live in bird or mammal nests and in dwellings. Man is attacked by the common bed bug *Cimex lectularius*, fig. 220, which may become an important pest in living quarters of all kinds. During the day the bed bugs hide in cracks and crevices of woodwork, furniture, and debris, emerging at night to seek a blood meal. The female lays up to two hundred cylindrical whitish eggs, depositing them in crevices.

**Miridae, plant bugs.** This family is a very large one, containing about fifteen hundred species, over a third of all known North American Heteroptera. The plant bugs, fig. 221, belong to the series of families having a four-segmented beak and no ocelli. With few exceptions they possess fully developed wings; the hemelytron usually has a distinctive sclerite or *cuneus* in the sclerotized portion and one or two simple cells in the membrane, fig. 214*B*.

Most of the species are plant feeders, many attacking only one or a very limited number of host species. Plant-bug feeding causes etiolation

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Fig. 220. The common bed bug *Cimex lectularius*. (From Canadian Department of Agriculture)

or blossom blight of the host and frequently results in marked commercial loss of certain crops. Some of the more destructive economic species



Fig. 221. Miridae, plant bugs. A. the tarnished plant bug Lygus lincolaris; B and C, the garden fleahopper Halticus bracteatus, male and female. (From Illinois Nat. Hist. Survey)
are the cotton fleahopper *Psallus seriatus;* the garden fleahopper *Halticus bracteatus,* which damages alfalfa, clover, and garden crops such as beans; and the tarnished plant bug *Lygus lineolaris,* a general feeder and a local pest of many crops. Certain genera, including a few striking ant mimics, are predaceous on aphids and other insects.

The plant bug females insert their eggs into dead herbaceous stalks. Most of the species have only a single generation a year, and the winter is passed in the egg stage. A few species, including the tarnished plant bug, hibernate as adults and deposit their eggs the following spring.

Lygaeidae, chinch bugs, lygaeid bugs. Most North American members of this family are fairly small somber-colored or pale forms. A few genera, such as the milkweed bug Oncopeltus fasciatus, fig. 222A, are strikingly marked with red and black. The diagnostic family characters include the four-segmented beak and a hemelytron with a few irregular veins crossing the membrane, fig. 214F. Most species have distinct ocelli. In North America the most important member of this family is the chinch bug Blissus leucopterus, fig. 222B, which is one of the major insect pests of corn and small grains in the corn-belt states. The chinch bugs hibernate in ground cover as adults. In early spring they feed on grasses and small grains and lay their eggs on the roots and crown of the food plants. The eggs hatch in about 2 weeks, the nymphs feeding on the same plants and maturing in 6 weeks. By the time this brood matures, the original food crop is almost invariably either mature and becoming dry, or it has been overpopulated and offers little in the way of nourishment. When this happens, the entire brood moves out in search of more succulent food. The exodus takes the form of a mass



Fig. 222. Heteroptera. A, the milkweed bug Oncopeltus fasciatus and B, the chinch bug Blissus leucopterus, Lygaeidae; C, the squash bug Anasa tristis, Coreidae. (A after Froeschner, B from Illinois Nat. Hist. Survey, C from U.S.D.A.)

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migration, not by flight but by foot. Mature nymphs and newly emerged adults make up the hurrying mass of insects on the march. The search for a better food supply usually ends in a field of corn, now well established and in prime growth. To protect the corn at this time various types of barriers have been developed to trap and kill these marching hordes. The individuals which reach the corn plants establish themselves and produce the second generation. Both the migrating first generation and the second generation feeding to maturity do extensive damage to the corn crop. When mature, the second generation goes into hibernation until the following spring.

**Coreidae, squash bugs, coreid bugs.** In general characters the Coreidae are like the Lygaeidae, differing chiefly in having many veins in the hemelytron membrane. Many of these bugs resemble the lygaeid bugs in general shape. Others, such as *Acanthocephala*, bear a striking resemblance to the Reduviidae. Coreid bugs feed on plants. The most widely known is the squash bug *Anasa tristis*, fig. 222*C*, which attacks squash, cucumbers, and other cucurbit crops. Its eggs are laid in patches on the leaves and stem of its hosts. There are several generations each year, and winter is passed in the adult stage.

Aradidae, flat bugs. This family includes a group of moderatesized species which are the flattest members of the Heteroptera. They live under the bark of dead trees and are thought to feed on fungi. The tarsi are two-segmented, the antennae and beak four-segmented, and ocelli are lacking. The wings are greatly reduced in size and when folded occupy only a small area of the dorsum, fig. 223*A*, *B*. This illustration depicts two common species in eastern and central North America.

Tingidae, lace bugs. These are small delicate plant-feeding insects,



Fig. 223. Heteroptera. A, B, flat bugs Aradus acutus and Neuroctenus simplex; C, D, lace bugs Atheas exiguus and Corythuca floridanus. (A, B, after Freeschner, C,  $D_7$  after Heidemann)

fig. 223*C*, *D*, usually occurring in large colonies. The pronotum and hemelytron are wide, reticulate, and lacelike, extending well beyond the sides of the body; in certain genera the pronotum has a large bulbous mesal lobe which extends forward above the head, fig. 223*D*. The antennae and beak are four-segmented, ocelli are lacking, and the tarsi are two-segmented. The nymphs differ considerably from the adults in general appearance; some are comparatively smooth and scalelike; others are armed with large numbers of long spines. The eggs are laid in or on the leaves of the host plant. The Tingidae are represented in North America by over two hundred species, most of them specific to a single host genus or species. A colony of lace bugs produces a characteristic white-spotted appearance of the leaves that readily betrays the presence of the colony. Examination of alder, oaks, sycamores, hawthorns, apples, birches, and other trees will net many species of lace bugs. Shrubs and herbs also support a considerable fauna.

**Pentatomidae, stink bugs.** To this family, figs. 215*B*, *C*, and 224, belong many large or medium-sized bugs, most of them broad, many of them mottled with shades of green, gray, or brown. A few are brightly



Fig. 224. Pentatomidae. The harlequin bug, *Murgantia histrionica. a*, adult; *b*, egg mass; *c*, first stage of nymph; *d*, second stage; *e*, third stage: *f*, fourth stage; *g*, fifth stage. (From U.S.D.A., E.R.B.)

patterned. Some species are predaceous, feeding on a wide variety of other insects. Others are entirely phytophagous, of which the harlequin bug *Murgantia histrionica*, fig. 224, is a familiar example. This bug feeds on cruciferous plants and often does serious damage to cabbage. Three subfamilies, the Scutellerinae, Cydninae, and Thyreocorinae, are classed as separate families in some works. The identifying characteristics of these subfamilies, given in the key to families, hold fairly well for the nearctic fauna but break down when considered for the world fauna as a whole.

## Suborder Homoptera

**Cicadas, leafhoppers, aphids, scale insects, etc.** This suborder contains two distinct groups of insects: the needle-horned series, containing the cicadas, leafhoppers, and their allies; and the thread-horned series, to which belong the aphids, scale insects, and their allies.

THE NEEDLE-HORNED SERIES. In these the adult antenna is sometimes large at the base, but the apical portion is always in the shape of a slender bristle or needle, fig. 215L. The series is further characterized by having the tarsi almost invariably three-segmented, front-wing venation which is relatively complete, and the beak appearing to be a definite part of the head. The insects belonging to this group are all plant feeders. With few exceptions the females have a sawlike ovipositor, by means of which punctures for egg reception are cut in plant stems. The North American fauna of the needle-horned series is composed of about a dozen families. Among them are found many forms of bizarre ap-



Fig. 225. Treehoppers, Membracidae. A, Campylenchia latipes; B, Ceresa bubalis; C, Enchenopa binotata. (A, C, from Kansas State College; B from U.S.D.A.)



Fig. 226. A fulgorid Peregrinus maidis. (After Thomas)

pearance. Some of the Membracidae, or treehoppers, fig. 225, have the pronotum greatly enlarged and ornamented with ridges, horns, or prongs. The Fulgoridae are a large family, and many resemble leafhoppers, fig. 226. Some of the fulgorids have large foliaceous wings, and others, such as our native *Scolops* and the South American lantern fly, or peanut bug, *Lanternaria phosphorea*, have bizarre projections of the head. Another oddity is the spittle bug family, Cercopidae. The nymphs of this family produce masses of white froth or spittle-like substance and live hidden beneath it. Two well-known and abundant families of the group are the Cicadidae (cicadas) and the Cicadellidae (leafhoppers).

**Cicadidae, cicadas.** These are large insects, many North American species measuring 2 inches or more. They are distinguished structurally from related families by having three distinct ocelli on the dorsum of the head. The males have highly developed musical organs, and during warm days and summer evenings they make a shrill noise. The nymphs have enlarged front legs, presumably for digging, and are subterranean, feeding on sap from the roots of deciduous trees.

The nymphal period is long, 2 to 5 years for most species. The peri-



Fig. 227. The periodical cicada *Magicicada septendecim.* a and d, adults; b, nymph; c, shed nymphal skin. (From U.S.D.A., E.R.B.)



odic cicada *Magicicada septendecim*, fig. 227, also called the 17-year locust, has a nymphal life of 13 years in the southern states and 17 years in the northern states. This insect has attracted widespread attention because of the periodic nature of its cycles. In some areas only a single brood occurs, and there the adults appear only every 13 or 17 years. On these occasions they usually appear in huge swarms, and the ovipositing females may cause serious damage to the twigs and branches of fruit and hardwood trees.

Cicadellidae, leafhoppers. This family is the largest in the entire order Hemiptera, represented in North America by over twenty-five hundred species. Leafhoppers are not only numerous in species but also extremely abundant in numbers of individuals. They are probably collected in general sweeping more commonly than any other insect group. Most of these are less than 10 mm. long and have long hind tibiae bearing longitudinal rows of spines, but with neither large spurs nor a crown of spines at the tip. Although a few species are broad or angular, most are slender and nearly parallel-sided, fig. 228. Female leafhoppers have strong ovipositors which they use to cut slits for eggs in plant stalks (usually herbs) or leaves. Leafhoppers are often destructive to certain crops, not only by direct damage caused by feeding, but also because they transmit many plant diseases. The beet leafhopper Circulifer tenellus transmits the virus which causes curly top of beets, a most destructive disease to the sugar-beet crop; and the plum leafhopper Macropsis trimaculatus transmits another destructive virus which causes peach yellows.



Fig. 228. A leafhopper *Draeculacephala mollipes*, adult, nymphs, and eggs. (From U.S.D.A., E.R.B.)

THE THREAD-HORNED SERIES. In this series the antennae are either short and stout or long and threadlike, fig. 231, in at least some stage of the life cycle. The wing venation is greatly reduced, and the tarsi have only one or two segments. Various families exhibit extremely interesting phenomena, such as alternation of sexual and parthenogenetic generations and alternation of hosts, as in the aphids, and unique examples of sexual dimorphism and specialization by reduction of locomotor parts, as shown by the scale insects. Because of the occurrence of diverse body forms within the life cycle of a single species, it is difficult to characterize the families with a brief description.

Two families, the jumping plant lice or Psyllidae, fig. 229, and the whiteflies or Aleurodidae, fig. 230, have a simple life cycle in which adults of both sexes are winged and similar in general appearance. In



Fig. 229. The pear psylla *Psylla pyricola. a*, adult; *b*, nymph; *c*, egg. (From Connecticut Agricultural Experiment Station)

many Psyllidae and all Aleurodidae the later nymphal instars are flat, inactive or sluggish, and scalelike in appearance. The members of both families are small.

All the other families of the thread-horned series are segregated into two large groups: (1) the aphids and their allies, the superfamily Aphidoidea, and (2) the mealybugs and scale insects, the superfamily Coccoidea. Each group contains several families differentiated chiefly by biological characteristics and including many species of great economic importance.





Fig. 230. A whitefly Trialeurodes vaporariorum. a, egg; b, larva, first instar; c, puparium dorsal view; d, puparium, lateral view; e, adult. (After Morrill)

The Aphidoidea, fig. 231, are characterized by (1) the presence o several veins and a stigmal area in the fore wings of the winged forms (2) the existence of two-segmented tarsi in most species; and (3) the existence of a complex system of alternating generations including wing less, winged, parthenogenetic, and sexual forms in the life cycle of a single species. This phase is discussed more fully in Chapter 6. The Aphidi dae, or plant lice, is the most important family in the group. Many species of great economic concern are members of this family, for example, the melon aphid *Aphis gossypii*, a pest of cucurbits and cotton; and the green peach aphid *Myzus persicae*, a pest of many crops and the disseminator of many plant diseases.

The Coccoidea, fig. 232, differ in several important respects from the aphids: (1) The females are always wingless, extremely sluggish or completely fixed in position, and are covered by a waxy secretion or a tough scale, or have a hard integument as in the family Coccidae; (2) the males are small and delicate and have a single pair of wings with only one or two simple veins; and (3) the life cycle is relatively simple.

The family Diaspididae, fig. 232, is one of the most important in the scale insect group. The females are the sedentary, small, scalelike or cushion-like insects found on many species of trees. The actual insect is a delicate oval body hidden beneath the scale, which is a protective covering. The appendages are extremely reduced, the body becoming



Fig. 231. The apple aphid *Aphis pomi*. A, alate viviparous female; B, apterous viviparous female; C, nymph of alate; D, oviparous female; E, male. (From U.S.D.A., E.R.B.)

little more than an egg sac at maturity. As the eggs are gradually discharged, the body shrinks, so that the entire egg mass is laid within the protective covering of the scale. The first-instar nymphs are minute and extremely active. They crawl with rapidity in all directions and thus effect the widespread distribution of these scale insect species. After the first molt, the nymphs become sedentary, and each forms a scale. Several species of the family are among the most destructive insects known to commercial agriculture. The San Jose scale *Aspidiotus perniciosus*, fig. 232, is a persistent pest of deciduous fruit trees and many ornamentals; before advent of oil sprays it threatened to wipe out several of the fruit crops in many areas in the United States. The cosmopolitan oystershell scale *Lepidosaphes ulmi*, fig. 233, is a common pest of almost all deciduous trees and shrubs in the United States.

The family Eriococcidae or mealy bugs, fig. 234, are another important group, attacking many hosts, especially greenhouse and household plants in the more northern areas. The mealy bugs make no scale but secrete waxy filaments which are especially noticeable along the periphery of the body.

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Fig. 232. The San Jose scale Aspidiotus perniciosus, infesting apple. A, scale of adult female; B, scale of male; C, first-instar young; D, same more enlarged; E, scale lifted to expose the female body beneath; F, body of the female; G, adult male. (From U.S.D.A., E.R.B.)



Fig. 234. A mealy bug. The inset shows natural size. (Original by C. O. Mohr)

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#### NEUROPTEROID ORDERS

The ten neuropteroid orders all have a complete metamorphosis and because of this are frequently termed the Holometabola. Their relationships are outlined in fig. 163, p. 204, and on p. 206.

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hall

### Order MEGALOPTERA: Dobsonflies and Alderflies

Large insects having complete metamorphosis, aquatic larvae, and terrestrial pupae. The adults, fig. 235, have long antennae, chewingtype mouthparts, large eyes, and two pairs of wings. The wings are similar in texture and venation and have all the major veins plus some additional terminal branches and a large number of crossveins. The pronotum is large and wide, the abdomen without projecting cerci. The larvae, fig. 235, have strong biting mouthparts; distinct, segmented antennae; large eyespots each composed of a group of about six facets; well-developed thoracic legs, and paired abdominal processes or gills. The apex of the abdomen has a long mesal process in Sialidae, and a pair of stout hooked larvapods in Corydalidae.

### Key to Families

Head with three ocelli; tarsi with all segments cylindrical. Dobsonflies



Fig. 235. An alderfly Sialis sp., larva and adult. (From Illinois Nat. Hist. Survey)

Both families together are represented in North America by only five genera and less than fifty species. The adults range in color from black to mottled or yellow, and in one genus (*Nigronia*) the wings are banded with black and white.

The larvae are aquatic, occurring in both lakes and streams. They are predaceous on small aquatic animals. The mature larvae of *Corydalus* may attain a length of 80 mm. They are ferocious larvae, highly prized for bait by fishermen, and called hellgrammites. The smaller species of the order mature in a year and have an annual life cycle. The hell-grammites require 2 or 3 years to reach full growth.

When mature, the larvae leave the water and make a pupal cell in damp earth or rotten wood near by. Here the larvae transform to pupae. Megalopteran pupae are active if irritated and capable of considerable locomotion. The pupal stage usually lasts about 2 weeks.

The adults are good fliers, but not agile compared to some of the flies and moths. Some *Corydalus* adults may have a wing span of 5 inches and are among our largest North American insects. The females lay their eggs in large clusters of several hundred each on stones and other objects overhanging the water. These hatch soon after deposition, and the minute larvae fall or twist their way into the water.

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#### Order NEUROPTERA: Lacewings, Mantispids

The adults are minute to large insects, usually with two pairs of clear wings having many veins and crossveins, with chewing-type mouthparts, long and multisegmented antennae, and large eyes, fig. 238*A*. The larvae are varied: Most of them are terrestrial and predaceous; one family (Sisyridae) is aquatic, and the larvae feed in fresh-water sponges. All the larvae have thoracic legs, but no abdominal ones, well-developed heads, and mandibulate mouthparts.

#### Key to Families

1.	Front legs with apical segments enlarged for grasping, fig. 237 Mantispidae
	Front legs with apical segments slender, same as other legs, fig. 238 2
2.	Wings with very few veins or crossveins, fig. 236B. Minute insects covered with
	a waxy bloom and gray in appearance Coniopterygidae
	Wings with veins and crossveins numerous, fig. 236C-G. Larger insects never
	covered with waxy bloom



Fig. 236. Front wings of Neuroptera. A, Nallachius, Dilaridae; B, Semidalis, Coniopterygidae; C, Climacia, Sisyridae; D, Hemerobius, Hemerobiidae; E, Chrysopa, Chrysopidae; F, Lomamyia, Berothidae; G, Polystoechotes, Polystoechotidae. b, basal vein; g, gradate vein. (From various sources)

3. Front wings with a regular, fencelike series of 12 or more crossveins (gradate
veins) between $R_1$ and $R_s$ , fig. $236E$
Front wings either with only 1-5 well-separated crossveins between $R_1$ and $R_3$ ,
fig. 236C, G, or $R_1$ and stem of $R_s$ fused, fig. 236D $\ldots \ldots \ldots \ldots \ldots 6$
4. Antennae long and slender, fig. 238, tapering to apex Chrysopidae
Antennae either short and clavate or knobbed at apex
5. Antennae short, gradually thickened towards apex Myrmeleontidae
Antennae long, knobbed at apex Ascalaphidae
6. Front wings with 2 or more branches of $R_s$ arising from fused $R_1$ and $R_2$ , fig.
236DHemerobiidae

	Front wings with all branches of $R_s$ arising from a separate $R_s$ stem, fig. 236C
	<i>F</i> , <i>G</i>
7.	Front wings with almost all costal crossveins forked, fig. 236F, G 8
	Front wings with few or no costal crossveins forked and with apical margin
	evenly rounded, as in fig. 236A, C
8.	Front wings only slightly incised and with recurrent costal vein, fig. 236G
	Polystoechotidae
	Front wings markedly incised and with no recurrent costal vein, fig. 236F

Berothidae 9. Front wings with Sc and  $R_1$  not fused before apex; basal vein (b) present; fig. 236A ..... Dilaridae Front wings with Sc and  $R_1$  fused some distance before apex; basal vein absent; fig. 236C ..... Sisyridae

**Sponge feeders.** The spongeflies are a small family comprising the Sisyridae. The adults look like typical lacewings, but the larvae are robust creatures that live in and eat fresh-water sponges. Their mouth-parts form a long beak which sticks out in front of the larva, fig. 238C. Only a few species are known to occur in the nearctic region.

Sedentary predators. The mantispids, fig. 237, are another small family, Mantispidae. The adults have a striking resemblance to praying mantids. The front legs are greatly enlarged and fitted for grasping insect prey and are attached at the anterior end of the very long pronotum. The larvae feed on egg sacs of spiders or contents of wasp nests. The first-instar larvae are slender and active, and hunt for a suitable food reservoir. Once this is found, the larvae enter a parasitoid stage, and succeeding instars are grublike and have degenerate legs.

Active predators. The larvae of all the other families are active predators. The adults have transparent and abundantly veined wings, which give them the name "lacewings," fig. 238*A*. Most of these insects are relatively slow on the wing. The eggs are laid either attached directly to foliage or at the end of a long hairlike stalk, which is attached to a leaf, fig. 137*N*. This latter method is used only by the Chrysopidae. The larvae are active, but sluggish and soft-bodied, and frequently bear warts, tubercles, and long hair. The mouthparts are modified for sucking body juices from the prey. The mandibles and ends of the maxillae are long, bladelike, and sickle-shaped, and a maxillary blade fits beneath each mandible; each of these opposing pieces has a groove, the two fitting together to form a canal from near the tip of the mandible into the mouth opening. The two mandibular-maxillary blades are thrust into the body of the prey from opposite sides, and its body juices are sucked out through the canals.

The larvae of Chrysopidae, fig. 238B and Hemerobiidae crawl freely



Fig. 237. A mantispid *Mantispa brunnea*. (From Essig, College entomology, by permission of The Macmillan Co.)

about on plants and feed on aphids, other small insects, and insect eggs. Their frequent attacks on aphids have earned them the name "aphidlions." When full grown, the larvae spin a woolly ovoid cocoon under a leaf or in some sheltered spot, and pupation ensues. The larvae of Myrmeleontidae live in sandy soil and dig cone-shaped pits that trap ants and other prey which fall into them. These larvae, called "antlions," differ from the aphidlions only in being more robust. The antlion digs the pit by throwing out sand from the center by upward jerks of the head, using the long mandibles as shovels. The pitfalls may be an inch deep, with sides sloping as much as the texture of the loose sand will allow. The antlion stays in the soil with its head just below the bottom of the crater, constantly in wait for unwary prey. These curious larvae are known to most people by the name "doodlebug." When mature, the larva forms a cocoon in the soil and pupates in it.

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## Order RAPHIDIODEA: Snakeflies

Large insects, with two pairs of transparent net-veined wings, similar in many features to the Megaloptera but distinguished by the long serpentine neck, fig. 239. They have long antennae, chewing mouthparts, large eyes, and two pairs of very similar wings. The female has a conspicuous terminal ovipositor. The larvae are terrestrial. They have segmented antennae, faceted eyes, well-developed thoracic legs, but no processes or appendages on the abdomen. The entire known world



Fig. 238. Neuroptera. *A*, *B*, adult and larva of a lacowing *Chrisopa* sp.; *C*, larva of a spongefeeder *Sisyra* sp. (*A*, *B*, from Illinois Nat. Hist. Survey; *C*, after Townsend)

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Fig. 239. A European snakefly *Raphidia ratzeburgi*. (From Essig, College entomology, by permission of The Macmillan Co.)

fauna of five genera and about a hundred species is divided into two families, the Raphidiidae (having ocelli) and the Inocelliidae (lacking ocelli). Two genera occur in North America, both confined to the West, *Agulla* (Raphidiidae) and *Inocellia* (Inocelliidae). The larvae occur under loose bark of conifers and are predaceous on other insects. When mature, the larvae do not spin cocoons but form an oval retreat in a sheltered position, and here the pupal stage is passed. The adults are also predaceous. They are occasionally swept from foliage and are indeed strange-appearing creatures to find in the net.

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## Order HYMENOPTERA: Sawflies, Ants, Bees, and Wasps

A large order, including many different body shapes and with a size range from 0.1 mm. in minute parasitic forms to at least 50 mm. in some of the wasps. Integument heavily sclerotized, the pleural sclerites considerably coalesced. Mouthparts are of the chewing type, in many forms modified for lapping or sucking. Wings well developed, reduced, or absent; if well developed, they are transparent, the two pairs similar in texture, and without scales; they have a great range in venation. Generalized forms, fig. 240, have a considerable reduction and coalescence of veins, but there are a moderate number of crossveins. Antennae range from 3- to about 60-segmented, and are of many shapes. Larvae

are caterpillar-like or grublike, all having a distinct head and chewing mouthparts, some with thoracic or abdominal legs or both, and others without any legs.

The Hymenoptera include leaf-feeding forms, parasites, predators, gall makers, and pollen feeders. In one group of families, the Apocrita, social life has been developed, carried to its highest level in the ants.

#### Key to Suborders and Common Families

1.	First abdominal segment solidly joined with second, at most a shallow constric-
	tion between them, first tergite forming a distinct plate or pair of plates,
	fig. 241 <i>A</i> , <i>B</i> (suborder Symphyta, p. 300)
	Juncture of first and second abdominal segments constricted to form a ball-
	and-socket joint, fig. 241D; the first tergite is fused solidly to the thorax.
	and the remainder of the abdomen forms an articulating unit called the
	gaster (suborder Apocrita p 302)
2	Antenna 3 segmented for 2424 the third sometimes solit longitudinally to
2.	form a lure shared prong for 242R
	Antenno at least 6 common ted the end common traver eleft for 242C I
•	Third enter also exert at last as last as such is die with the set of the set
э.	I nird antennal segment at least as long as combined length of the succeeding
	9 segments, the segments beyond the third forming a slender terminal hla-
	ment, fig. $242E$ Xyelidae
	Third antennal segment not longer than the combined length of the next 3 or
	4 segments, or antenna clavate, fig. 242C
4.	Antenna capitate, fig. 242C; lateral edge of abdomen sharp and angular; large
	robust species, fig. 245Cimbicidae
	Antenna pectinate, serrate, filiform, or in a few species as clavate as fig. 242G;
	lateral edge of abdomen round 5
5.	A shallow but distinct constriction between first and second abdominal tergites,
	and cenchri absent, fig. 241B Cephidae
	No constriction between first and second abdominal tergites, and cenchri $(c)$
	well developed, forming a pair of velvety pads on the metanotum, fig.
	241 <i>A</i> 6



Fig. 240. Diagram of hymenopterous wing, combining primitive veins of several archaic families.



Fig. 241. Diagnostic characters of Hymenoptera. A, thorax of Arge, Argidae; B, thorax of Janus, Cephidae; C, venter of abdomen of Chrysis, Chrysididae; D, thorax of Eremotylus, Ichneumonidae; E, head and thorax of Chalcis, Chalcididae; F, thorax of Proctotrupes, Proctotrupidae; G, thorax of Ancistrocerus, Vespidae; H, thorax of Sceliphron, Sphecidae. c, cenchrus; j, basal articulation of gaster; me, metaepimeron; mp, metapleuron; ms, metaepisternum; pl, mesopleuron; pn, pronotum; pr, pronotal lobe; s, first abdominal spiracle; t, tegula. III, metanotum. 1, 2, 3, segments of abdomen.

Front tibia having only one apical spurSiricidae, p. 302
Front tibia having two apical spurs
Antenna 7- to 9-segmented, fig. 242F-H Tenthredinidae, p. 302
Antenna having 10 or more segments, figs. 242D, I
Antenna narrow and filiform, proportioned as in fig. $242H$
Tenthredinidae, p. 302
Antenna serrate in females, fig. 242 $D$ , pectinate in males, fig. 242 $I$
Diprionidae, p. 302
Petiole composed of two segments, usually one or both bearing a dorsal hump
or node, fig. 256 Formicidae, p. 310
Petiole consisting of only one segment, figs. 257, 258 10
First segment of gaster forming an isolated petiole bearing a dorsal node or
projection, fig. 257; includes winged and wingless forms. Formicidae, p. 310
First segment of gaster either expanded posteriorly or not bearing a dorsal
node

11.	Wings completely atrophied or reduced to small pads
12.	Body fuzzy with dense hair, fig. 253
	Body smooth or with only inconspicuous hair. A few species in each of sev-
	eral families of parasitic habit, keyed no further here.
13.	Front wing without a stigma (a thickened area along the anterior margin of
	the wing), and with sclerotized venation reduced to a single anterior vein,
	sometimes with a "tail" at its tip, fig. 243D, sometimes completely atro-
	phied
	Front wing either having a definite stigma or having a more extensive vena-
	tion, fig. 243 <i>F</i>
14.	Lateral corner of pronotum extending to the tegula, fig. 241F. Several fam-
	ilies of small parasitic wasps, chiefly Proctotrupoidea
	Lateral corner of pronotum not extending to the tegula, fig. 241E
	Chalcidoidea, p. 305
15.	Pronotum having each posterolateral corner forming a round earlike or
	epaulet-like lobe, fig. 241H 16
	Pronotum having posterolateral corner truncate or angulate, fig. 241G, or

16. Hind basitarsus no wider than succeeding segments, the plantar surface clothed only with dense, short pile; body and appendages without branched hairs, each hair simple, neither branched nor fringed (Sphecoidea)

#### Sphecidae, p. 312

Hind basitarsus slightly wider (in numerous forms many times wider) than succeeding segments, the plantar surface with moderately long and abundant hair; body and appendages having branched or spiral hairs: each hair



Fig. 242. Antennae of Hymenoptera. A, Sofus female, Argidae; B, Sphacophilus male, Argidae; C, Trichiosoma, Cimbicidae; D, Augomonoctenus female, Diprionidae; E, Pleroneura, Xyelidae; F, Cladius, Tenthredinidae; G, Tenthredo, Tenthredinidae; H, Pseudodineura, Tenthredinidae; I, Monoctenus male, Diprionidae.

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•\*•



Fig. 243. Wings of Hymenoptera. A, Ichneumonidae; B, Vespa, Vespidae; C, Myzine, Tiphiidae; D, Tetrastichus, Chalcididae; E and F, two types of Cynipidae.

	has many branches or whorls and may appear fringed, fig. 260 (Apoidea,
	p. 314)
17.	Head having two sutures below each antenna, delimiting a large subantennal
	sclerite, fig. 244H Andrenidae
	Head having only one suture below each antenna, fig. $244G$ 18
18.	Labium with mentum and submentum virtually absent; front wing with free
	basal part of $M$ (basal vein) usually strongly curved Halictidae
	Labium with mentum and submentum present, fig. 244E, F; front wing with
	basal vein straight
19.	Labium with glossa short and its apex either rounded, truncate, or incised,
	fig. 244 <i>E</i> Colletidae
\ \	Labium with glossa elongate and narrow or pointed at apex, fig. 244F 20
20.	Labial palp with segments similar and cylindrical, as in fig. $244E$ . Melittidae
	Labial palp with first two segments elongate and sheath-like. fig. $244F21$
21.	Front wing with 3 submarginal cells (crossveins 2r-m and 3r-m both present,
	as in fig. 243C)Apidae
	Front wing with 1 or 2 submarginal cells (one or both of these crossveins
	lacking)
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22.	Labrum longer than wide and widened at extreme base Megachilidae
	Labrum wider than long or narrowed at extreme baseApidae
23.	Front wing having costa and stem of radius united, obliterating the costal cell,
	fig. 243A, and antenna with more than 16 segments
	Either front wing with an open costal cell between radius and costa, fig. 243B,
	C, or antenna with no more than 14 segments
24.	Front wing having crossvein 2m-cu, fig. 243A Ichneumonidae, p. 304
	Front wing lacking crossvein 2m-cuBraconidae, p. 305



Fig. 244. Parts of wasps and bees. A, mesopleuron of Ceropales, Pompilidae; B, mesosternum of Myzine, Tiphiidae; C, outline of Pelecinus, Pelecinidae; D, thoracic sterna of Scolia, Scoliidae; E, labium of Colletes, Colletidae; F, same of Anthidium, Megachilidae; G, head of Halictus, Halictidae; H, head of Andrena, Andrenidae. as, antennal sutures; c, coxa; es, mesopleural suture; f, flaplike processes of mesosternum; g, glossa; gs, base of gaster; m, mentum; p, palpus; pm, prementum; pr, pronotum; s, sternite; sm, submentum; t, tegula; w, wing base. (E-H after Michener)

25. Gaster with only three apparent dorsal segments, the tergites heavily sclerotized;
the three large sternites each divided longitudinally into a pair of concave armored plates fig 241C. Robust hard shiping metallic bees capable of
curling up into a hall Cuckoo wasps
Gaster with at least five apparent dorsal segments
<b>36</b> Front wings having no definite stigma, but instead a clear, triangular area
bounded posteriorly by a vein fig. $243E F$ but without an anterior vein
Cynipoidea, p. 306
Front wings having a thickened stigma, or an anterior vein, fig. 243B, $C_{\perp}$ 27
27. Gaster extremely elongate and slender, fig. 244C; head and thorax black and
shining. Females only (males are rare) of <i>Pelecinus polyturator</i> . Pelecinidae
Gaster much shorter and thicker; texture and color of various sorts 28
28. Corner of pronotum ending below level of wing and not in vicinity of tegula;
mesopleuron almost always having a straight, fine transverse suture at about
its midpoint, fig. 244A, although in some species it is difficult to detect
Pompilidae, p. 312
Corner of pronotum ending at or above level of wing and usually abutting
against the tegula, fig. 241G; mesopleuron with a crooked suture or none. 29
<b>29.</b> Front wing having cell $1M$ longer than cell $M$ -Cu, fig. 243B; either wings pleated
lengthwise when folded or antennae clublike Vespidae, p. 308
Front wing having cell $IM$ shorter than cell $M$ -Cu, fig. 243C, or former cell
open due to atrophy of 1st $m-cu$
30. Metasternum large and rectangular, fused with the mesosternum, the two
forming a large, level plate overlying the bases of the four posterior coxae;
hind coxae wide apart, fig. 244D
sternum: hind coxae close together fig. 2448
31 Hind margin of mesosternum produced into a pair of triangular plates partially
overlapping the bases of the middle coxae, fig. 244B Tiphiidae, p. 308
Hind margin of mesosternum without such lobes
32. Second segment of gaster large and bulbous compared with third segment
fig. 253: body often conspicuously hairy
Second segment of gaster not markedly wider than third segment: body never
conspicuously hairy

# SUBORDER SYMPHYTA

Sawflies and Horntails. The symphyta, with the exception of the small parasitic family Orussidae, are a plant-feeding group. The larvae either feed externally on foliage or mine in leaves, leaf petioles, or stems. The adults of many groups feed on the pubescence of the host plant, cropping it by means of their sickle-shaped mandibles as a cow does grass; in other groups they may be predaceous on smaller insects or feed on nectar and pollen. The group is a large one; the North American

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Fig. 245. A large sawfly *Cimbex americana*. a, willow leaves showing location of eggs; b, twig showing incisions made by adult; c, egg; d, newly hatched larva; e, e, mature larvae; f, cocoon; g, open cocoon showing pupa; h, pupa, side view; i, mature sawfly; j, k, saw of female. (After Riley)

forms represent twelve families and include in their host selection a great diversity of plant groups.

Distinguishing features of sawfly larvae are: a distinct head, with simple chewing mouthparts; antennae slender or platelike with one to seven segments; eyes with only a single lens; and abdominal legs (when present) without hooks or crochets.

The adults of most sawflies are compact and fairly robust. Of the leaf-feeding families, the largest common species is *Cimbex americana*, fig. 245, in which the antennae are capitate; the males and females are dif-

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Fig. 246. The feeding stage larva of the imported currantworm *Nematus ribesii*. (From Connecticut Agricultural Experiment Station)

ferently colored. The females of all but a few species have a welldeveloped saw used to cut egg slits in leaves or petioles.

The Tenthredinidae is the largest family, characterized chiefly by the simple 9- to 16-segmented antennae. Most of the species are external leaf feeders, and among them are several of economic importance, such as the rose-slug *Endelomyia aethiops;* the imported <u>currant worm</u> *Nematus ribesii,* fig. 246; and the larch sawfly *Pristiphora erichsonii.* In certain species the larvae mine in the leaf tissue, for example, *Heterarthrus nemorata,* one of the birch leaf miners. Species of other genera, including *Euura,* produce true galls.

The Diprionidae is another economically important family. In this family the antennae are at least 13-segmented, serrate in the female and pectinate in the male, fig. 247. All the species are stout and more or less drab in color. The larvae are caterpillar-like and external feeders on coniferous needles. Many species are among the worst defoliators of spruce and pine forests. Of special note are the ravages caused to spruce in northeastern America by the European spruce sawfly *Diprion hercyniae*. Especially injurious to young pines is the red-headed pine sawfly *Neodiprion lecontei*, fig. 247.

The Siricidae contain some of the largest members of the suborder. They are elongate, sometimes attaining a body length of 40 mm. The larvae bore in tree trunks and are cylindrical and almost legless. Both adults and larvae have a horny spikelike projection at the posterior end of the body, the character which gives them the name "horntails." *Tremex columba*, fig. 248, is a common species attacking maple, elm, beech, oak, and some other deciduous trees.

#### SUBORDER APOCRITA

Ants, Bees, and Wasps. In general the Apocrita are more graceful, active, and more rapid of movement than the Symphyta. The larvae are chiefly internal or external parasites, or are fed by the adults, or make plant galls. They are legless, have a distinct exposed head capsule

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Fig. 248. A horntail wasp *Tremex columba.* a, larva; b, larval head, ventral aspect; c, d, female and male pupa;  $\epsilon$ , adult. Note small parasite larva attached to horntail larva. (After Riley)

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bearing greatly reduced mouthparts and antennae, and frequently exhibit hypermetamorphosis.

In the Apocrita the first segment belonging to the abdomen is fused solidly with the thorax, so that what appears to be the abdomen really has lost its anterior segment. This body region which appears to be the abdomen is termed the *gaster*.

Ichneumonidae, the ichneumon flies. Usually slender wasps, having long and many-segmented antennae, fig. 249, and having subcosta fused with the stem of radius in the front wings. All members of this family are parasites on insects or spiders. Their favorite hosts are the larvae of Lepidoptera, for example, *Glypta rufiscutellaris*, a parasite of the oriental peach moth. In addition, a number of ichneumon flies parasitize the larvae of Coleoptera, Hymenoptera, and Diptera, and a few other insects. The adult ichneumon fly female deposits its eggs on or inside the body of the host. If the eggs are laid on the epidermis of the host, the newly hatched larvae may bore into the body. The larvae



Fig. 249. An ichneumon wasp *Glypta rufiscutellaris*. A, male: B. female: C. tip of ovipositor. (From Connecticut Agricultural Experiment Station)

develop into legless grubs which either attach to the outside of the host or develop within the body of the host. When mature, the larvae spin pupal cocoons near the host; the grubs may pupate within the host or leave it to spin cocoons. Ichneumon flies have a wide range in size. Many of the small forms only a few millimeters long parasitize small moth larvae.

**Braconidae.** This is a large family closely related to the ichneumon flies. The species average smaller than the ichneumon flies, and many braconids have reduced wing venation. A number of species are important as parasites of economic pests. One of these, *Apanteles melanoscelus*, fig. 150, has been imported for biological control of gypsy-moth larvae. This small parasite exhibits the interesting hypermetamorphosis prevalent among most of the parasitic families of Hymenoptera. In fig. 150 are illustrated the different shapes of the larva in various stages of development; the anal vescicle (a) may be used to identify the posterior end of the larva.

**Superfamily Chalcidoidea, the chalcid flies.** Small wasps, sometimes less than a millimeter in length, having a greatly reduced wing venation, fig. 250, and usually having elbowed antennae. These wasps are largely internal parasites, especially of larval Lepidoptera and of the larvae of other parasitic Hymenoptera, which they attack within the body of the primary host. These parasites of parasites are called hyperparasites. The few chalcids which are not parasitic develop in various seeds, or in plant stems, especially grasses. To this nonparasitic group belongs the clover-seed chalcid *Bruchophagus gibbus*, whose larva develops in the seeds of clover and alfalfa; the wheat jointworm *Harmolita tritici*, whose larva bores in the stems of wheat; and the wheat straw-worm *Harmolita grandis*, fig. 250. Locally and sporadically the wheat jointworm causes serious damage to the crop.

Of unique interest is the specialized life history of certain tiny chalcid flies belonging to the family Agaontidae. These develop in the seeds of



Fig. 250. A, the wheat jointworm *Harmolita tritici*, and *B*, wingless and winged forms of the wheat straw-worm *Harmolita grandis*. (From U.S.D.A., E.R.B.)

figs. The males are wingless and live only within the fig fruit in which they develop, fertilizing the females even before the latter emerge from the fig seed. The females are winged and fly from flower to flower in search of suitable seeds for oviposition, carrying the pollen on their bodies and pollinating each flower visited. This is the only method by which figs are pollinated. Many commercial varieties of figs do not require pollination to develop their fruits, but the fruit of the choice Smyrna fig will not develop without pollination. In order to grow these in North America it was necessary to introduce the European fig chalcid *Blastophaga psenes* to effect pollination.

**Superfamily Cynipoidea, the gall wasps.** These are small wasps, most of them characterized by the large triangular cell near the apex of the front wing, fig. 243*E*, and by the deep but bilaterally compressed abdomen. Many groups of the superfamily are parasitic on dipterous larvae, aphids, and other insects, but the best-known group produces galls on plants. As a matter of fact, the gall wasps themselves are seldom seen, but every naturalist is familiar with some of the many different types of galls that are produced on the leaves, stems, or roots of oak, roses, and other plants by the larvae of these insects. One of these is shown in fig. 251. There are hundreds of species of gall wasps, nearly every species producing a different type of gall. Some species which live on oaks have an alternation of generations, with one generation producing a gall on the roots and the alternate generation making a gall on the leaves or twigs.

PROVISIONING AND SOCIAL WASPS AND BEES. These insects are of special interest because social life has been developed independently in three groups. An account of the development of the social habit is given in Chapter 6. Most of the families, however, are solitary, and parasitic, predatory, or pollen feeding in habit.

Most of the nonsocial wasps secrete a remarkable substance that is discharged with their sting. When injected into their prey, this secretion causes complete motor paralysis without death resulting. Such a paralysis is used by wasps that lay an egg on the prey or provision a nest with prey. The induced paralysis has a triple advantage: It keeps the prey edible until the wasp larva hatches and begins feeding, it insures that the prey will not move away from the legless wasp larva, and it prevents the attraction of scavenger insects to the odor of dead insects.

Scoliidae, the scoliid or digger wasps. These fairly large insects have wings in both sexes, and most of the species are black or are banded or spotted with black and yellow, such as *Scolia dubia*, fig. 252. The female wasps dig through the soil in search of their prey, white grubs (larvae of the beetle family Scarabeidae). When the female encounters

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Fig. 251. A cynipid, C, and its gall; A, immature gall, and B, a section of mature gall showing cells and exits. (From Essig, College entomology, by permission of The Macmillan Co.)

a suitable host larva, she stings it, thereby paralyzing it; digs a crude cell around it; lays an egg on the doomed larva; and then moves on in search of another victim. The egg soon hatches into a legless grub which attaches to the paralyzed beetle larva and begins eating it. Within a period of about 2 weeks, the wasp larva has consumed the host and is full grown. It then spins a cocoon in the earthen cell and usually passes the winter in this stage. The next spring or summer the larva pupates, and later the adult chews its way out of the cocoon and digs to the surface.

Closely related to the scoliid wasps are many families of somewhat similar habits. Species of the family Mutillidae are parasites of wasps and bees. In many mutillids the females are wingless and have a close



Fig. 252. A digger wasp *Scolia dubia*. *a*, female wasp; *b*, antenna of male: *c*, cocoon showing escape opening. (From U.S.D.A., E.R.B.)

resemblance to ants. The Mutillidae females, however, lack the "node" on the petiole of the gaster, fig. 253, and in addition are covered with dense velvety or silky pile. From this latter character the family has received the name velvet ants. These velvet ants have a powerful sting and use it freely if interfered with.



Fig. 253. A mutillid wasp female Dasymutilla bioculata. (After Washburn) -

Many oriental species of *Tiphia*, of the related family Tiphiidae, have been brought to the United States and propagated for parasitizing grubs of the Japanese beetle, and a few have shown definite promise of assisting in the control of the beetle.

Vespidae, yellow jackets and hornets, wasps. This family contains species varying from 10 to about 30 mm. in length, many of them having elaborate yellow and black or white and black markings, fig. 254. In all subfamilies except the Masarinae the wings in repose are folded longitudinally like a fan. In the Masarinae the antennae are capitate. Most of the Vespidae are solitary in habit. The adults make a burrow in wood or soil or construct a pottery container for the abode of the grub. The nest is usually stocked by the adult with paralyzed caterpillars or with pollen and honey. Certain of the Vespidae arc social in habit. By masticating wood fibers with an oral secretion, they produce a paper which they fashion into a platelike or baglike nest. The most familiar of these are the platelike nests of *Polistes*, fig. 235, which are made up of a single horizontal comb of larval cells. These are commonly found hanging from eaves of buildings and in similar sheltered places. Colonies of Polistes rarely have over a few dozen members. The largest colonies of vespids found in North America are made by the bald-faced hornet Vespula maculata. These colonial nests, oval in shape and with an opening at the bottom, are most often attached to



Fig. 254. The bald-faced hornet Vespula maculata. (From Illinois Nat. Hist. Surv



Fig. 255. Adult queen and nest of *Polistes.* (From U.S.D.A., E.R.B.)

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tree branches. Each contains several layers of larval cells, or combs, arranged one above the other. The workers in a colony forage for insect prey, such as flies and caterpillars. These are crushed and mangled by the wasps and fed to the maggot-like larvae in the cells of the nest.

In temperate regions of North America the colonies die out at the end of autumn. In late summer a brood of males and females is produced. At frost the workers and males die; the autumn brood of females, by this time fertilized, hibernate in rotten logs or stumps. These females emerge the following spring and begin new colonies.

**Formicidae, ants.** In these insects the first segment of the gaster forms a petiole or stalk and bears a dorsal projection or node, figs. 256, 257. This structure differentiates ants from other antlike wasps. In addition to the normal males and females, ant species usually have a third form, the nonreproductive workers, which are always wingless. These workers are the ants we usually see scurrying about. They perform most of the work of the colony, such as building the nest, excavating the subterranean chambers, and gathering food for the colony.



Fig. 256. The little black ant *Monomorium minimum*, showing several stages and activities. (After Marlatt, U.S.D.A., E.R.B.)



Fig. 257. Lateral aspect of three ant genera to illustrate the dorsal node on the petiole. Note that in A and C this node is small but distinct.

A typical colony starts with the swarming flights of the winged reproductive males and females. At periodic intervals (frequently once a year) large numbers of winged males and females are produced in an established colony. When weather conditions are favorable, the sexual forms leave the nest as a swarm, embark on their nuptial flight, and mate in flight. The male dies soon after mating. The fertilized female seeks a suitable nest site in the ground, an old log, or other situation, bites off her wings, and seals up a small hollow, which becomes the first nest chamber. The female remains in this chamber for several weeks, during which time the eggs are laid and the grublike larvae are fed to maturity by the female. The food is produced apparently from the histolysis of the wing muscles and the fat body of the female. It is extruded from her mouth as a secretion. The mature larvae pupate and soon emerge as small workers. These break out of the nest chamber, seek food, and henceforth keep the female, or queen, and the next brood of workers provided with food. Subsequent broods help with the task of keeping the colony provisioned. The female continues to lay eggs, without further fertilization, for several years.

Colonies of many species contain only a few dozen or a few hundred individuals, whereas those of other species may attain a population of many thousands. The small colonies are usually situated under stones, in stumps, logs, or in galleries in the soil. Many of the large colonies build large mounds of earth, sticks, and debris, interspersed with a complex system of galleries and chambers.

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In the main, ants are omnivorous, feeding on living or dead animal matter (especially other insects), vegetable substances such as fungi, and sweet exudates or secretions of plants, such as honeydew, nectar, wound discharges, and glandular products. Certain insects such as aphids and some scale insects produce honeydew or other secretions; the ants tend these insects with great care and "harvest" the sweet substances produced. Some ant species are extremely savage and live almost entirely by the capture of live insect prey. Others live almost entirely on sweets, fats, or dead insects.

Several ant species invade houses or stores and are among the most persistent domestic pests. In the northern states the thief ant *Solenopsis* molesta, Pharaoh ant Monomorium pharaonis, and the odorous house ant Tapinoma sessile are common household species. In the southern states the introduced Argentine ant Iridomyrmex humilis is an exceedingly common household pest and has almost replaced the native ant population in many localities.

Some of the ants feed primarily on plant seeds. Of these ants, various species of the genus *Pogonomyrmex*, known as "agricultural ants," have become abundant and are destructive in the grain and grass areas of the Great Plains and westward.

Other Vespoid Wasps. Several small families of wasps are closely related to the Scoliidae and Vespidae. Many of these families are rare or their members are small and secretive, and seldom collected. Two are frequently seen: the green, metallic cuckoo wasps or Chrysididae, which lay their eggs in the burrows of other wasps, and the spider wasps or Pompilidae (sometimes called Psammocharidae), which provision their nests with spiders.

Superfamily Sphecoidea, the solitary wasps. These insects are characterized by the shape of the pronotum: Each corner ends in a small round lobe that is situated beneath but does not touch the tegula, fig. 241*H*. In addition, the hair is simple and undivided, in contrast to that of the bees, and the hind tibiae and tarsi are not modified for pollen gathering. The group is a large one and includes a great diversity of sizes, shapes, and colors. As currently defined it comprises the rare family Ampulicidae and the heterogeneous and large family Sphecidae. The habits of all Sphecidae are essentially the same. The female wasp makes a mud nest or a nest excavated in pith, wood, or soil and provisions it with a particular kind of paralyzed prey. An egg is deposited in each stocked compartment of the nest, this egg hatching into a legless grub which feeds on the provender stored for it by the parent. In temperate climates the larva overwinters in its cocoon, pupating the following year in early summer.

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The various wasp groups are usually specific in the prey they choose for provisioning the larval cells. The Pemphredoninae (often only 2 or 3 mm. long) capture aphids, the Sphecinae usually use caterpillars, the Trypoxylinae use spiders, and so on. One of the most interesting and showy species in the central and eastern states is the cicada killer *Sphecius speciosus*. This is a large black and yellow species which attains a length of 40 or 50 mm. It commonly captures and paralyzes the common cicada *Tibicen linnei* and carries it to a burrow in the ground, provisioning each burrow with one cicada. When attacked by the wasp, the cicada makes a loud piercing noise, but this subsides in a moment as the cicada is stung and becomes paralyzed.

The most familiar of the solitary wasps are the thread-waisted mud daubers, especially species of *Sceliphron*, fig. 258. These mud daubers build a mud nest of several cells. The nests are common under bridges, eaves of houses, or other sheltered places. The wasps gather the mud at the edge of near-by pools or puddles, flying back and forth from water's edge to nest with mouthfuls of "plaster." The cells are provisioned with spiders.



Fig. 258. The yellow and black mud dauber wasp, *Sceliphron servillei*, that builds series of mud cells on stones and walls and provisions them with spiders. (From Essig, Insects of Western North America, by permission of The Macmillan Co.)

Superfamily Apoidea, the bees. This group, fig. 259, includes all the native and domestic bees, comprising the six families keyed on p. 297. They are very similar morphologically to the Sphecidae, possessing the same characteristic round lobe at the corner of the pronotum. The bees differ in having branched body hairs, fig. 260, which give them a fuzzy or velvety appearance, and in having the hind basitarsus widened and provided with fairly long hairs; in the males of some genera and in both sexes of a few inquiline genera this tarsal enlargement is slight. Most of our 3000 species are solitary in habit, making cells in burrows or cavities as do many solitary wasps. The bees provision the nest cells with honey and pollen, which constitutes the food of the larvae. Certain genera of bees are "parasitic," laying their eggs in the cells or nests of other bees. The intruder larva matures faster than the host larva and eats up the stored food. These "parasitic" bees could be called "cowbird bees."

Of our native fauna only the bumblebees (the genus *Bombus*, family Apidae) have developed social living. In this group fertilized females overwinter in log cavities or ground cover. They emerge in spring, find a protected site in a hole in the ground or in a deserted mouse nest, and begin a colony. A brood of eggs and young is raised, the mother, or queen, feeding the larvae on honey. This brood is composed of sterile females or workers that take over the task of gathering food for succeeding larvae. Toward fall no more workers are produced, but instead a swarm of males and functional females. The males die soon after mating, and the workers also die at the approach of winter. The new brood of fertilized queens disperses for hibernation, and the entire colony is disbanded.

The habits of the domestic honey bee *Apis mellifera* are much more specialized than those of the bumblebee. In the first place the colonies



Fig. 259. The honey bee. a, worker; b, queen; c, drone. (From U.S.D.A., E.R.B.)



do not die out during the winter; their members live during this period on honey stored up throughout the summer. Individual queens have lost the ability to forage for themselves; hence they cannot start a new colony alone but must be accompanied by some workers from the parent colony. The phenomenon of "swarming" is the colonization flight in which the old queens set out to form a new nest.

The honey bee is of considerable importance in that it affords a large cash return from the sale of honey. But the greatest role of the bees, including both our native species and the honey bee, is the pollination of a great variety of wild and domestic plants, including most of our commercial fruits and legume crops.

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### Order COLEOPTERA: Beetles and Weevils

The adults usually have two pairs of wings: The first pair is veinless, hard, and shell-like, and folds together over the back to make a stout wing cover; the second pair, used for flight, is membranous, usually veined, and in repose folds up under the wing covers or elytra, fig. 261.

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Fig. 261. A stag beetle Copris minutus. (From Illinois Nat. Hist. Survey)

The body is normally hard and compact. The mouthparts are of the chewing type; the antennae are well developed, usually 10- to 14-segmented; the compound eyes are usually conspicuous; and the legs are heavily sclerotized. The larvae, fig. 268, normally have distinct head capsules, chewing mouthparts, antennae, and thoracic legs, but no abdominal legs. The pupae, fig. 275, have the adult appendages folded against but not fused with the body.

The Coleoptera comprise the largest order of the Insecta. There are about twenty-five thousand species in North America, representing about one hundred and fifty families. The adults vary in size from less than a millimeter long to several inches (up to 100 mm.). The shape and coloring varies just as much, but the most brilliantly colored, weirdshaped, and gigantic species occur in the tropical regions of the world.

Most of the beetles are either plant feeders or are predaceous on other insects. Usually both adults and larvae of the same species have similar food habits; that is, both forms will be phytophagous, or both will be predaceous, although the larva may not feed on either the same species of plant or the same part of the plant. Thus the June beetles which are phytophagous utilize different parts of plants for food during their development. The adults feed on the foliage of forest trees, but the larvae, known as white grubs, feed on the roots of trees, shrubs, herbs, or grasses. The predaceous beetles are active hunters, stalking their prey. Certain groups have more specialized food habits. Some are endoparasites of other insects or feed on insect egg masses.

The order as a whole is terrestrial. Certain families, however, are aquatic, both larvae and adults living in water. The larvae usually leave the water to pupate, making an earthen cell in near-by soil. As is the case with the land forms, the aquatic group includes both herbivorous and predaceous species, the latter predominating.

The great majority of beetles have a single generation per year and a simple life cycle similar to the following. The oval or round eggs are

laid in spring or early summer and hatch in 1 or 2 weeks. The larvae are voracious feeders, usually attaining full growth during the summer and pupating in the soil. The adults emerge in a few weeks, feeding and maturing throughout the remainder of the summer and autumn. With the advent of cold weather they hibernate. The following spring these adults emerge and lay eggs, and the cycle begins again. The old adults usually die soon after egg laying is completed.

There are many deviations from this biological pattern. For example, some ladybird beetles have continuous and overlapping generations throughout the warmer seasons. In other groups, notably many species whose larvae live in soil or rotten wood, the winter is passed in the larval stage, and the adults occur for only a limited span during spring or summer.

#### SYNOPSIS OF PRINCIPAL SUBORDERS

- 2. First sclerotized sternite of abdomen completely divided by posterior coxae into two or three separated parts, two lateral sclerites, and sometimes a small mesal sclerite between the bases of the metacoxae, fig. 262 (1)

#### Adephaga

First sclerotized sternite of abdomen forming a complete band from one side to the other; the posterior coxae may extend over and above this band, but the sclerite itself is intact underneath them, fig. 262 (2)......Polyphaga

#### Key to Common Families

1. Front of head produced into a definite beak, fig. 286, that may be long or short, the antennae arising from side of beak; palpi vestigial

#### Curculionidae, p. 341



Fig. 262. (1) Ventral view of a ground beetle Harpalus sp., Carabidae. Left legs are removed. (2) Ventral view of a May beetle Phyllophaga sp., Scarabaeidae. Right legs are removed. (3) Ventral view of part of thorax and abdomen of a soldier beetle Chauliognathus pennylvanicus, Cantharidae. Acx, antecoxal piece; Ant, antenna;  $Cx_{1-3}$ , 1st, 2d, and 3d coxae;  $Cxc_{1-3}$ , 1st, 2d, and 3d coxal cavities; E, eye; El, elytron; Ep, epipleuron; Epm<sub>1-3</sub>, epimera of the pro-, meso-, and metathorax;  $Eps_{1-3}$ , episterna of pro-, meso-, and metathorax; F, femur; G, gula; GS, gular suture; Lb, labium; LbPlp, labial palpus; Lm, labrum; Mb, membrane; Md, mandible; MxPlp, maxillary palpus; PN, pronotum; S<sub>1</sub>, S<sub>2</sub>, S<sub>3</sub> pro-, meso-, and metasterna; Sc, suture separating pronotum from episternum; Sp, spiracle; 1 Tar to 5 Tar, the five tarsal segments; Tb, tibia; Tr, trochanter; TS, transverse suture; 1 to 6, abdominal sternites; viiiT, 8th tergite. (After Matheson, Entomology for introductory courses, by permission of Comstock Publishing Co.)



Fig. 263. Diagnostic characters of Coleoptera. A, antenna of Nicrophorus, Silphidae, insets showing concave end segments and an end view of one; B, antenna of Scolytus, Scolytidae; C, antenna of Thyce, Scarabeidae; D, tibia and tarsus of Heterocerus, Heteroceridae; E, antenna of Silpha, Silphidae; F, antenna of Attagenus, Dermestidae; G, antenna of Languria, Languriidae; H, antenna of Stegobium, Anobiidae; I, antenna of Anthrenus, Dermestidae;  $\mathcal{J}$ , antenna of Melanotus, Elateridae; K, head of Dineutes, Gyrinidae; L, legs of Dineutes, Gyrinidae; M, profile of Mordellistena, Mordellidae; N and O, head and prothorax of Dendroctonus, Scolytidae; P, head of a short-snouted weevil, Curculionidae; Q, head of Tropisternus, Hydrophilidae. a, antenna; c, coxal plate; f, femur; p, maxillary palpus; ta, tarsus, ti, tibia.

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	this fashion; eye seldom divided, and then only by a continuation of a head flange or by an antennal base, fig. $265K$
3.	Maxillary palpi longer than antennae and slender, resembling antennae, fig. 263Q; chiefly aquatic
	Maxillary palpi shorter than antennae, and not antenna-like; antennae
4.	various
	right angle to long axis of antenna
~ <b>5</b> .	Elytra short and squarely truncate, exposing three full tergites of abdomen, there tarrites heavily selection and hard for $266R$ Silphidae
	Elytra longer usually rounded at apex usually covering entire dorsum of
	abdomen buť in a few species exposing one or two tergites, fig. 279
	Searabeidae, p. 337
6.	Elytra short, exposing five or more sclerotized abdominal tergites, fig. 268A7
	Elytra covering all or most of abdomen, never more than two or three sclero-
	tized tergites visible from above; occasionally the abdomen of a female of ,
. •	this group may be extremely distended with eggs, and a third or fourth seg-
۰,	soft and semimembranous
7.	Elytra truncate, parallel-sided, and abutting evenly down the meson, fig. 268:
2 ° °	abdomen hard and regular in outline
	Elytra ovate, overlapping considerably at base; abdomen flabby and shrinking
	irregularly when the specimen dries
8.	Hind tarsus 4-segmented, front and usually middle tarsi 5-segmented9
	Either hind tarsus having 3 or 5 segments, or all tarsi having the same number of segments
9.	Body narrow and deep, bilaterally compressed, and with the hind coxa form-
.`	ing a large plate that appears as a major sclerite in the side of the thorax,
÷ -	fig. 263M; small beetles often found abundantly in flowers Mordellidae
•	Body wider than deep, often flattened, hind coxae no larger than in fig. 262,2
10.	Each front coxal cavity closed posteriorly by a projection of the pleuron which meets the apex of the sternum, fig. 265D; lateral edge of pronotum forming a sharp flange or delineated by a ridge or carina (compare fig. 265H) <b>Tenebrionidae.</b> p. 336
	Front coxal cavities open posteriorly, the posteromesal corner of propleuron
	not extending mesad of outer portion of coxa, fig. $265C$ ; lateral edge of
	pronotum rounding inconspicuously into pleural regionMeloidae, p. 333
11.	Head not retracted within prothorax
	265H
12.	Ventral portion of head having a large convex gular region with a single gular

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2-	suture down the middle; and the palpi very short or indistinct, fig. 263N; antennae always elbowed, with a long first segment, and sometimes ending
24	in a flat club, fig. 263B
13.	elbowed or the first segment shorter in proportion to the remainder 14 Antenna long, fig. 263 <i>P</i> , usually ending in a small cylindrical, elliptic club; side of head having a deep groove for reception of antenna furculionidae p. 341
	Antenna short, fig. 263 <i>N</i> , <i>O</i> , ending in a large flat club or comb, fig. 263 <i>B</i> ; side of head without antennal groove
14.	Hind and middle tarsi either 3- or 4-segmented, or fourth segment very small in comparison with the third, fig. 264b, c
· 15.	third, fig. 264a
×	channeled dorsally; the fourth segment extremely small, either sunken into the cleft of the third or arising from dorsum of the base of the third, fig.
Ϋ́κ	be seen, or it appears as a minute subdivision of the base of the fifth seg-
•	Either tarsi only 3-segmented, or third segment not enlarged, channeled, or bilobed.
16.	Antennae about as long as or longer than the body, fig. 284 Many Cerambycidae p. 339
	Many Clambyeluae, p. 555
	Antennae distinctly shorter than body 17
17.	Antennae distinctly shorter than body
17 <i>.</i> 18.	Antennae distinctly shorter than body
17 <i>.</i> 18.	Antennae distinctly shorter than body
17. 18. 19.	Antennae distinctly shorter than body
17. 18. 19.	Antennae distinctly shorter than body. 17   Last tergite (pygidium) exposed, almost completely visible beyond or below end of elytra, fig. 265 <i>E</i> , <i>F</i> . 18   Last tergite almost entirely or completely covered by elytra. 21   Hind tibia little, if any, longer than basitarsus, and having a pair of long apical spurs, fig. 265 <i>P</i> . <b>Bruchidae</b> , p. 340   Hind tibia much longer than basitarsus, frequently with only short spurs or none. 19   Elytra short, each only about twice as long as wide; stocky short species, the pygidium oblique, and at a definite angle to dorsal contour of the body, fig. 265 <i>F</i> . 20   Elytra long, each four times or more as long as wide; elongate species, the pygidium nearly horizontal, following dorsal contour of the body, fig. 265 <i>E</i> . 339
17. 18. 19.	Antennae distinctly shorter than body. 17   Last tergite (pygidium) exposed, almost completely visible beyond or below end of elytra, fig. 265 <i>E</i> , <i>F</i> . 18   Last tergite almost entirely or completely covered by elytra. 21   Hind tibia little, if any, longer than basitarsus, and having a pair of long apical spurs, fig. 265 <i>P</i> . <b>Bruchidae</b> , p. 340   Hind tibia much longer than basitarsus, frequently with only short spurs or none. 19   Elytra short, each only about twice as long as wide; stocky short species, the pygidium oblique, and at a definite angle to dorsal contour of the body, fig. 265 <i>F</i> . 20   Elytra long, each four times or more as long as wide; elongate species, the pygidium nearly horizontal, following dorsal contour of the body, fig. 265 <i>E</i> . 339   Anterior part of prothorax forming a cylinder against which the flat head fits like a lid; eyes oval, fitting against margin of prothorax, fig. 265 <i>H</i> some <b>Chrysomelidae</b> , p. 338
17. 18. 19.	Antennae distinctly shorter than body. 17   Last tergite (pygidium) exposed, almost completely visible beyond or below end of elytra, fig. 265 <i>E</i> , <i>F</i> . 18   Last tergite almost entirely or completely covered by elytra. 21   Hind tibia little, if any, longer than basitarsus, and having a pair of long apical spurs, fig. 265 <i>P</i> . <b>Bruchidae</b> , p. 340   Hind tibia much longer than basitarsus, frequently with only short spurs or none. 19   Elytra short, each only about twice as long as wide; stocky short species, the pygidium oblique, and at a definite angle to dorsal contour of the body, fig. 265 <i>F</i> . 20   Elytra long, each four times or more as long as wide; elongate species, the pygidium nearly horizontal, following dorsal contour of the body, fig. 265 <i>E</i> . 339   Anterior part of prothorax forming a cylinder against which the flat head fits like a lid; eyes oval, fitting against margin of prothorax, fig. 265 <i>H</i> some <b>Chrysomelidae</b> , p. 338   Anterior part of prothorax narrow, head projecting freely beyond it; eyes incised and V-shaped, head constricted behind them, fig. 265 <i>I</i>
17. 18. 19. 20.	Antennae distinctly shorter than body. 17   Last tergite (pygidium) exposed, almost completely visible beyond or below end of elytra, fig. 265 <i>E</i> , <i>F</i> . 18   Last tergite almost entirely or completely covered by elytra. 21   Hind tibia little, if any, longer than basitarsus, and having a pair of long apical spurs, fig. 265 <i>P</i> . <b>Bruchidae</b> , p. 340   Hind tibia much longer than basitarsus, frequently with only short spurs or none. 19   Elytra short, each only about twice as long as wide; stocky short species, the pygidium oblique, and at a definite angle to dorsal contour of the body, fig. 265 <i>F</i> . 20   Elytra long, each four times or more as long as wide; elongate species, the pygidium nearly horizontal, following dorsal contour of the body, fig. 265 <i>E</i> . 339   Anterior part of prothorax forming a cylinder against which the flat head fits like a lid; eyes oval, fitting against margin of prothorax, fig. 265 <i>H</i> some <b>Chrysomelidae</b> , p. 338   Anterior part of prothorax narrow, head projecting freely beyond it; eyes incised and V-shaped, head constricted behind them, fig. 265 <i>I</i> most <b>Bruchidae</b> , p. 340   Last 3 to 5 antennal segments enlarged to form a large loose club, fig. 263 <i>G</i> ;
17. 18. 19. 20.	Antennae distinctly shorter than body. 17   Last tergite (pygidium) exposed, almost completely visible beyond or below end of elytra, fig. 265 <i>E</i> , <i>F</i> . 18   Last tergite almost entirely or completely covered by elytra. 21   Hind tibia little, if any, longer than basitarsus, and having a pair of long apical spurs, fig. 265 <i>P</i> . <b>Bruchidae</b> , p. 340   Hind tibia much longer than basitarsus, frequently with only short spurs or none. 19   Elytra short, each only about twice as long as wide; stocky short species, the pygidium oblique, and at a definite angle to dorsal contour of the body, fig. 265 <i>F</i> . 20   Elytra long, each four times or more as long as wide; elongate species, the pygidium nearly horizontal, following dorsal contour of the body, fig. 265 <i>E</i> . 339   Anterior part of prothorax forming a cylinder against which the flat head fits like a lid; eyes oval, fitting against margin of prothorax, fig. 265 <i>H</i> some <b>Chrysomelidae</b> , p. 338   Anterior part of prothorax narrow, head projecting freely beyond it; eyes incised and V-shaped, head constricted behind them, fig. 265 <i>I</i> most <b>Bruchidae</b> , p. 340   Last 3 to 5 antennal segments enlarged to form a large loose club, fig. 263 <i>G</i> ;

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	elongate, smooth, and highly polished speciesLanguriidae
	Antenna of uniform thickness throughout, or widening gradually to form a
	club, or forming a round compact club; form various
22,	Hind femur greatly enlarged, short, and oval in outline, fig. 283; flea beetles
	and their relatives
	Hind femur elongate or more parallel-sided, or constricted at base and en-
	larged only at apex, fig. 265L
23.	First abdominal sternite very long, its mesal length nearly equal to that of the
	following four sternites, combined, fig. 265G; several genera of varied form
	(e.g., Donacia, Crioceris) Chrysomelidae, p. 338
	First abdominal sternite considerably shorter in proportion to following seg-
	ments
24.	Either antenna as long as or longer than body, or hind femur having basal
	portion slender and apical portion enlarged and clavate, fig. $265L$
	Cerambycidae, p. 339
	Antenna shorter than body, and hind femur without a basal stalklike por-
	tion
25.	Tibia having a pair of well-developed tibial spurs at apex
	Cerambycidae, p. 339
	Tibia having either no tibial spurs or very minute ones
26.	Mesal margin of eye deeply incised, with the antenna situated in the incision,
	fig. 265 $K$ , or the eye completely divided, the antenna situated between the
	two parts Cerambycidae, p. 339



Fig. 264. Tarsi of Coleoptera. *a, Harpalus,* Carabidae; *b, Leptinotarsa*, Chrysomelidae; *c, Chelpmorpha*, Chrysomelidae; *d, Epilachna*, Coccinellidae; *e*, toothed tarsal claws. (From Matheson, Entomology for introductory courses, by permission of the Comstock Publishing Co.)

	Either eye not incised, or antenna not at all in incision of eye
07	<b>Chrysomelidae</b> , p. 338
27.	Find coxa having a wide long ventral plate which covers coxa, trochanter,
	and most of the femur, fig. 203A; small to medium-sized stout aquatic
	Hind cove at most being only a small outer plate, which does not cover
,	trochanter or femur
28	Apices of hind coxae forming a double-knobbed process: base of each coxa
20.	extremely large and platelike appearing as a dominant sclerite of the
	sternum fig. 265 <i>B</i> : hind legs fringed for swimming
•••	Hind coxa neither with such a knobbed apex nor with such a platelike base.
	fig. 262,1,2
29.	First abdominal sternite completely divided by the hind coxal cavities, the
	sternite appearing as a pair of triangular sclerites, one on each side of the
	coxae; first three abdominal sternites immovably united, the separating
	sutures appearing partly as extremely fine lines, fig. 262,1
	Either first abdominal sternite not completely or not at all cut into by the
	coxal cavities, or the first three sternites with separating sutures extremely
	well developed across the entire width of the segment, as are those between
00	the more apical segments, fig. 262,2
30.	Clypeus fairly narrow, the antennal sockets wider apart than the width of the
	Clympus much widen for 265 M the enternal sockets situated alosen together
	than the width of the clypeus
31	Abdomen having 6 or more exposed sternites 32
51,	Abdomen having not more than 5 exposed sternites, fig. 262.2 35
32.	Last 3 to 5 antennal segments enlarged to form a club, fig. 263ESilphidae
	Antenna the same width throughout, often beadlike or serrate
33.	Tarsus slender and smooth, segments 1 to 4 very short and ringlike, segment
	5 long, about equal in length to first 4 combined, fig. $265Q$ aquatic forms
v	Psephenidae
	Tarsus stout and densely setose, segment 5 no longer than segment 1, some of
	the basal segments elongate, as in fig. 264a
<b>3</b> 4.	Prothorax with broad anterior and lateral margins forming a hood that covers
•	most or all the head from above, fig. 269; head partially retracted, viewed
	trom side
	down or projecting forward freely
<b>3</b> 5	Antenna elbowed and capitate the club appearing as one round segment
35.	sometimes having faint cross sutures: very hard shining black beetles having
	short stout legs the tibiae expanded and spurred for digging, much as in
	fig. 262.2. Kisteridae
	Antenna not elbowed, and either not thickened toward tip, or the enlarged
	portion composed of 2 or 3 well-separated segments or a single elongate
3	segment; legs or body shape different to above
<b>3</b> 6.	Antennae elongate and serrate throughout, fig. 2637
	Antennae short, filiform, or clavate

, . 37. Pronotum having a sharp projection at each posterolateral corner, fig. 270 Elateridae, p. 329

Pronotum having posterolateral corners rounded and not pointed, fig. 271 Buprestidae, p. 329



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Fig. 265. Diagnostic characters of Coleoptera. A, venter of Haliplus, Haliplidae; B, venter of Dytiscus, Dytiscidae; C, prosternum showing open coxal cavities, diagrammatic; D, prosternum showing closed coxal cavities, diagrammatic; E, abdomen of Leptura, Cerambycidae; F, abdomen of Bruchus, Bruchidae; G, venter of Criocerus, Chrysomelidae; H, head and prothorax of Cryptocephalus, Chrysomelidae; I, head and prothorax of Acanthoscelides, Bruchidae; J, head and prothorax of Helichus, Dryopidae; K, head of Saperda, Cerambycidae; L, hind femur of Neoclytus, Cerambycidae; M, head of Cicindela, Cicindelidae; N, head of a Carabidae; O, hind leg of Amphicerus, Bostrichidae; P, hind leg of Amblycerus, Bruchidae; Q, hind tarsus of Psephenus, Psephenidae. a, abdomen; c, coxa; cl, clypeus; cp, coxal process; f, femur; fr, frons; l, labrum; m, mandible; s, sternum; l, trochanter.

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Fig. 267. Larva of whirligig beetle. (Redrawn from Böving and Craighead)

a pair of long tracheal gills, and at the end of the abdomen are a pair of hooks. Both adults and larvae are predaceous, the adults feeding chiefly on small organisms falling or alighting on the water surface, the larvae on small organisms they find in sheltered places on the bottom of the pond or stream.

#### SUBORDER POLYPHAGA

This includes the great bulk of the beetles, containing over one hundred and thirty families, and embracing forms diverse in appearance and life history. Some families, such as the Chrysomelidae and Coccinellidae, are abundant and include species of considerable economic importance. Many families, however, are rare or seldom seen except as a result of specialized collecting and have no known economic importance. There are certain groups of families which form fairly definite units of closely related forms, and families from a selection of these are discussed in the following paragraphs.

**Staphylinidae, rove beetles.** Slender elongate beetles, fig. 268*A*, with short truncate elytra beneath which the pair of flying wings are folded. The antennae are fairly long, either filiform or slightly enlarged at the tip. The larvae are also elongate and look much like small carabid larvae. Both adults and larvae are scavengers or predators, with the exception of a few species that have parasitic larvae. The adult rove beetles are found on flowers, in ground cover, under bark, in rotting organic material, in ant and termite nests, and in many other situations. The larvae are more secretive and occur chiefly in humid places. The



Fig. 268. Rove beetles. A, Stenus adult; B, first-instar larva of Aleochara curtula, left, before feeding; right, after feeding. (A, after Sanderson; B, modified from Kemner)

species that are predaceous feed on mites, small insects, insect and mite eggs, and especially on small dipterous larvae. Certain species are valuable factors in the natural control of pests. An interesting example is the genus *Baryodma*, whose larva is a parasite of the cabbage-maggot pupa. The larva of *Baryodma* is unusual in that during the first instar it is a slender free-running form with relatively large tergal plates. It searches in the soil for a fly puparium and enters it by boring an opening. In the puparium the beetle larva feeds on the fly pupa and grows amazingly, becoming greatly distended and grublike before molting. Later instars are always grublike. The same phenomenon occurs in some species of *Aleochara*, fig. 268*B*.

Lampyridae, fireflies. These are moderate-sized soft-bodied beetles, having serrate antennae and having the margins of the pronotum projecting like a flange or shelf, which partially covers the head. The elytra are relatively soft. A common eastern species is *Photurus pennsyl*vanicus, fig. 269. The adults occur in summer and fly actively on warm nights, almost invariably following a dipping up-and-down course only a few feet above the ground. As they start their "upstroke," each individual flashes a bright light, a mating signal. When swarms of adults are on the wing, the entire countryside is lighted up with these tiny dots of light. From this comes the name firefly. In certain genera the females are wingless and grublike; these and the larvae are also lumi-

nous and are called glowworms. Both larvae and adults are predaceous, although some adults may feed partly on plant material or not at all.

Elateridae, click beetles or wireworms. The adults are trim and hard bodied, fig. 270, having five-segmented tarsi, a large pronotum with sharp posterior corners, serrate antennae, and a long stout sharp process projecting backwards from the prosternum. If placed on their backs, these beetles can spring several inches into the air, at the same time making a loud click, usually alighting right side up. This leap is engineered by using the ventral process of the prosternum as a sort of spring release when the body is tensed. The adults are frequently encountered during spring and summer. These beetles and their acrobatics are well known to youngsters in rural districts.

The larvae, called wireworms, fig. 270, are wormlike and hard-bodied and live in soil or rotten wood. The soil-inhabiting larvae feed on roots of grasses and related plants and are extremely destructive to many of the grain crops. Especially injurious are species of the genera *Melanotus*, *Agriotes*, and *Monocrepidius*. Several hundred species occur in North America. Of unusual interest to the collector of immature insects are the odd wormlike larvae of the group to which *Horistonotus* belongs, fig. 270D.

**Buprestidae, metallic or flatheaded wood borers.** These beetles, fig. 271, resemble the click beetles in that the adults have serrate anten-



Fig. 269. A firefly *Photurus pennsylvanicus*. A, adult male; B, mature larva; C, left mandible of larva to show mandibular canal. AO, opening of canal; PO, opening of canal to mouth; c, condyle; T, tooth on mandible; D, beginning of pupal chamber; E, completed pupal chamber; F, pupa in chamber. (From Matheson, after Hess)



Fig. 270. Elateridae. A, B, the dry-land wireworm Ludius inflatus, adult and larva; C, D, the sand wireworm Horistonolus uhlerii, adult and larva. (From U.S.D.A., E.R.B.)

nae, five-segmented tarsi, and hard bodies, but they differ in having the first two sternites of the abdomen fused and in the coppery or bright metallic coloring of the body and elytra. They are usually more robust and have a shorter pronotum. The larvae of the larger species, fig. 271, bore in wood, attacking live trees or newly felled or killed trees, and feeding either beneath the bark or into the solid wood. These larvae are legless and elongate, having the thorax expanded and flattened. They attack a wide variety of trees, including deciduous and coniferous species. The flatheaded apple tree borer *Chrysobothris femorata* is often an orchard pest of importance. A few genera of small buprestids have leaf-mining larvae, which are more cylindrical than the wood borers and have minute legs.

**Dryopidae and their allies, the dryopid beetles.** In this group of aquatic beetles both the adults and larvae live in the water. Both are sluggish, crawling over stones or submerged wood, and feeding on surface encrustments. The adult is clothed with fine hair which holds a film of air when under water. The insect uses this film as a means of gas exchange with the surrounding water. The larvae respire by means

of tracheal gills situated on various parts of the body, many retractile within ventral pouches. As with other aquatic Coleoptera, the mature larvae leave the water and pupate in damp soil. Most of the dryopids live in cold rapid streams and are frequently found in large numbers in siftings from gravel bars. The adults leave the water periodically for mating or dispersal flights.

**Dermestidae, carpet beetles.** Convex oval beetles, figs. 272, 273, having short clubbed antennae, five-segmented tarsi, and abdomens with only five sclerotized sternites. The larvae are elongate or oval, clothed distinctively with large tufts or bands of long barbed hair. They feed on dried animal products, including fur, skins, and dried meat. The last is attacked readily by species of the genus *Dermestes*, especially *D. lardarius* the larder beetle. Some of the smaller species, particularly the carpet beetle *Anthrenus scrophulariae*, fig. 273, and the black carpet beetle *Attagenus piceus*, fig. 272, attack furs, carpets, and upholstery, in fact, anything made from animal hair. These pests are so widespread that they are a constant menace to household goods and many stored materials. In nature the species feed on dead insects or animal carcasses. The adults feed on the same material as the larvae, but during dispersal flights they feed on pollen and at this time are often found on garden flowers.

**Coccinellidae, ladybird beetles.** Moderately small round convex shining beetles, fig. 274, sometimes prettily patterned with red, yellow, black, or blue markings. The antennae are short and clavate. The tarsi are four-segmented but appear to be three-segmented; the third segment is extremely minute, situated between the padlike second segment and the large end segment bearing the claws. The larvae either



Fig. 271. Buprestidae. Left, the flatheaded apple tree borer, Chrysobothris femorata; center, the Pacific flatheaded borer, C. mali; and, right, larva in burrow. (From U.S.D.A., E.R.B.)



Fig. 272. The black carpet beetle Attagenus piceus. A, adult; B, larva. (From Connecticut Agricultural Experiment Station)





Fig. 273. The carpet beetle Anthrenus scrophulariae. A, larva; B, adult. (From Connecticut Agricultural Experiment Station)



Fig. 274. A ladybird beetle *Hippodamia convergens. a*, adult; *b*, pupa; *c*, larva. (From U.S.D.A., E.R.B.)

are warty creatures or are covered with a waxy secretion and have extremely short antennae but long legs. Two categories of ladybird beetles are of economic importance. Species of the first feed on aphids and scale insects and function as effective means of natural control against some of these pests. The best known of these predators is the vedalia *Rodolia cardinalis*, a native of Australia, which was introduced into California for the control of the cottony-cushion scale. The vedalia has been very effective in this capacity. A common and widespread native species is *Hippodamia convergens*, fig. 274. The second important category of ladybird beetles includes plant-feeding species. In North America the Mexican bean beetle, *Epilachna varivestis*, fig. 275, is one of the most destructive defoliators of beans in many central and southern areas. Both adults and larvae feed on the foliage.

**Meloidae, blister beetles.** The adults, fig. 276, are moderately large beetles with relatively soft bodies and elytra, long simple antennae, and a prominent round or oval head that is well set off from the thorax. The tarsi of the front and middle legs are five-segmented, but the tarsi



Fig. 275. The Mexican bean beetle *Epilachna varivestis*. *a*, larva; *b*, adult; *c*, pupa; *d*, eggs. (From U.S.D.A., E.R.B.)

of the hind legs are four-segmented. This characteristic marks off a group of some twenty beetle families sometimes referred to as the *Heteromera*. The blister beetles contain an oil, cantharidin, which is a powerful skin irritant and causes the formation of large water blisters on human skin. A sufficient amount of cantharidin to cause irritation is picked up by just handling the live adults.

In most subfamilies the larvae feed on bee larvae or as inquilines on provisions of bee nests. In one subfamily, containing the common and widespread genera *Epicauta* and *Henous*, the larvae feed on grasshopper egg pods. In all of them the life history is complex. The eggs are laid in masses of 50 to 300 about an inch deep in the soil. The first instar is an active, slender, well-sclerotized form called a *triungulin*. In the bee inquiline groups the triungulins crawl into flowers, attach to bees, and are thus carried to bee nests, where the triungulins dismount and begin feeding. In the grasshopper egg predators the triungulins simply search out the grasshopper egg pods.

The development of the larvae is peculiar in many ways. This is well illustrated by that found in *Epicauta pennsylvanica*, fig. 277. The triungulin seeks out a grasshopper egg mass, digs down to it, punctures an egg, and starts feeding on its contents. In a few days, when the triungulin is swollen and fully fed, the first molt occurs. The grublike thin-skinned second instar is relatively inactive and continues feeding on the grasshopper egg mass.

The third, fourth, and fifth instars follow in rapid succession and are similar to the second. The fifth instar, when full grown, leaves the food mass, burrows a few inches farther into the soil, and makes an earthen cell in which it molts to form the sixth-instar larva. This sixth instar, called the coarctate form, is unique among beetles. It is nonfeeding, heavily sclerotized, oval in shape, and rigid. Only humplike legs are



Fig. 276. A blister beetle, Epicauta vittata. (Original by C. O. Mohr)



Fig. 277. Immature stages of the black blister beetle *Epicauta pennsylvanica*. A, unfed first instar; B, fully fed first instar; C, D, E, second, third, and fourth instars; F, newly molted fifth instar; G, gorged fifth instar; H, sixth instar; I, seventh instar;  $\mathcal{J}$ , pupa. A-E,  $\times 17$ ; F, G,  $\times 9$ ;  $H-\mathcal{J}$ ,  $\times 5$ . (After Horsfall)

present. Usually the winter is passed in this stage. The next summer the coarctate larva molts to form a seventh instar much like the fifth; this larva gives rise to the pupa, which transforms in a few weeks to the adult. The coarctate larva is extremely resistant to desiccation, and it provides a margin of safety to the species in drought years. For, if conditions are too dry during the summer after hibernation, the coarctate larva will not molt, but will "lay over" an additional year or even 2 years, if necessary, when less arid conditions prevail and the normal life cycle can be resumed.

Meloid adults are leaf feeders and cause appreciable damage to potatoes, tomatoes, squash, certain legumes, and other crops. The threestriped blister beetle *Epicauta vittata*, fig. 276, is a colorful representative often injurious to these plants. One of the species frequently feeding on potatoes, *Meloe angusticollis*, is unusual among beetles in that the elytra overlap at the base. Another short-winged meloid is the squash blister beetle *Henous confertus*.

**Tenebrionidae, the darkling beetles.** Hard-shelled beetles, normally dark in color, and oval or parallel-sided in outline, fig. 278; tarsi of the front and middle pairs of legs are five-segmented, those of the posterior legs four-segmented; antennac moderately long, usually filiform or clavate. The larvae feed chiefly on dead plant material and fungi, especially bracket types, or mycelium in rotten wood; a few are predaceous, and a few attack stored grain. The larvae are elongate and cylindrical, with stout legs. Those of the western genus *Eleodes* feed on plant roots and are called false wireworms because of their resemblance to true wireworms (Elateridae larvae). Another western false wireworm is *Embaphion muricatum*, whose larva is destructive to wheat. Some of the species attacking stored grains and prepared foods are wide-



Fig. 278. The rust-red flour beetle Tribolium castaneum, and the confused flour beetle Tribolium confusum. Below, larva of T. castaneum. (From U.S.D.A., E.R.B.)

spread and cause large commercial loss. Among this group are the mealworms *Tenebrio* sp., which are relatively large, the adults reaching a length of 15 mm. and the larvae 25 or 30 mm.; and the confused flour beetle *Tribolium confusum*, and several related species of *Tribolium*, which are very small, the adults being only 3 or 4 mm. in length.

Scarabeidae, the lamellicorn beetles, or scarabs. This is one of the largest families of beetles, characterized most conspicuously by the lamellicorn antennae, in which the apical segments are leaflike and appressed in repose. The scarabs vary greatly in size and shape; most of them are stout and very hard shelled; the larvae are sluggish, stout, usually white, and with a characteristic curved outline, fig. 279; a number of groups of scarabs are scavengers, and feed on dung, rotting hides, or fungi. Of unusual interest are *Canthon* and certain other genera; the adult fashions a ball of dung, rolls it away, and buries it. Eggs are laid on this ball, and the developing larvae utilize it as food. The remainder of the scarabs are phytophagous, many species of great economic importance. The most publicized member of the family is the Japanese beetle Popillia japonica, fig. 279: the larvae feed on grass roots and are especially destructive to lawns and golf courses, and the adults defoliate fruit and shade trees. Another group of destructive species are the June beetles, fig. 148. members of the genus *Phyllophaga*; the adults defoliate deciduous trees, and the larvac, known as white grubs, eat the roots of various grass crops, including corn, small grains, and pasture plants.

In the tropics there are many species of large scarabs, often brilliantly colored or ornamented with spines or projections on the head or pronotum. In the United States the largest species is *Dynastes tityus* the rhinoceros beetle, which is larger than a shrew, fig. 280. The larva lives in rotten wood.



Fig. 279. The Japanese beetle Popillia japonica. (From Connecticut Agricultural Experiment Station)

**Chrysomelidae, the leaf beetles.** These comprise a large family, the species small to moderate in size, usually oval, stout, or wide bodied, and having filiform fairly long antennae, fig. 281. The most outstanding characteristics are found in the tarsi, fig. 264b, c. These appear four-segmented; the third segment is enlarged to form a large kidney-shaped pad; the last segment, really the fifth, is long and slender and appears to be attached within the median incision of the third; actually the fourth segment is an extremely reduced ring at the base of the fifth, but it is so small that it is seldom seen without one's first making a special preparation of the leg. The larvae of the leaf beetles are varied, but most of them are stout grubs with short legs and antennae; a number bear spines and processes; and some of the leaf-mining species are long and flat. The eggs are laid in soil or under bark or deposited on stems or leaves.

With few exceptions adult Chrysomelidae feed on plant foliage, and their larvae on roots or leaves. Many attack commercial crops, and the family includes a large number of important economic species. The Colorado potato beetle *Leptinotarsa decemlineata*, fig. 281, is one of the most destructive insects attacking potato; both larvae and adults feed on the foliage. The asparagus beetle *Crioceris asparagi* is a common showy species wherever asparagus is grown; both larvae and adults feed on the foliage; the eggs are black and stuck by one end into the heads of the plants. The larvae of many species, such as *Acalymma vittata*, fig. 282, are known as rootworms. The adults of many small species jump like fleas and for this reason are called flea beetles. Of these, the genera *Phyllotreta* and *Epitrix* contain several species whose adults eat holes in leaves, and the elongate larvae eat roots of cabbage, turnips, potatoes,



Fig. 280. Dynastes tityus, Illinois' largest beetle, and a shrew Sorex longirostris, Illinois' smallest mammal. (Drawing loaned by C. O. Mohr)



Fig. 281. The Colorado potato beetle Leptinotarsa decemlineata. a, adult; b, larva; c, pupa. (From U.S.D.A., E.R.B.)

cucumbers, and other plants. An important species is the tobacco flea beetle *Epitrix hirtipennis*, fig. 283. Not all flea beetles have root-feeding larvae; those of the genus *Haltica*, for instance, are leaf feeders like the adults.

**Cerambycidae, longhorn beetles.** Elongate beetles, many of them attractively colored, having long legs and unusually long antennae, fig. 284. In other characters the longhorns are almost identical with the Chrysomelidae, including the curious tarsi with the enlarged third segment and the reduced fourth. The larvae of the longhorns are cylindrical and elongate, with a round head, and either no legs or minute ones; they are known as roundheaded borers. Most of them bore either in the cambium layer or through the heartwood of trees; a few bore in the roots and lower stems of succulent herbs such as milkweeds and ragweeds, or in the stems of shrubs such as willow and raspberries. Certain species are of considerable economic importance.



Fig. 282. The striped cucumber beetle Acalymma vittata. a, adult; b, larva. (From U.S.D.A., E.R.B.)

Fig. 283. The tobacco flea beetle Epitrix hirtipennis. a, adult; b, larva; c, head of larva; d, posterior leg of same; e, anal segment, dorsal view; f, pupa. (From U.S.D.A., E.R.B.)



The roundheaded apple tree borer *Saperda candida*, fig. 284, is a brown and white striped species that is locally a serious pest of apple, the larvae boring through the trunk and making extensive tunnels. The locust borer *Cyllene robiniae* has a handsome adult with a geometric yellow pattern on black; its larvae bore in young black locust trees and weaken them so that wind breaks them easily; many black locust plantings, established for soil-erosion purposes, have been entirely destroyed in this manner.

Most of the longhorn species are pests of forest trees, attacking both deciduous and coniferous species. Under improper or careless lumbering conditions or unusual weather, various longhorn species may become abundant enough to cause considerable loss to commercial stands of trees.

**Bruchidae, bean and pea weevils.** This is a most interesting family closely related to the Chrysomelidae. The adults are short and stout, the larvae are grublike and almost legless, living inside legume seeds Several species are pests of considerable importance in various kinds or stored peas and beans; a common example is the pea weevil *Bruchu: pisorum,* fig. 285.

**Curculionidae, typical weevils.** Head with a definite beak, some times elongate and curved, fig. 286; antennae usually elbowed anc clubbed; body, elytra, and legs very hard, forming a solid well-armorec exterior. The <u>larvae are legless</u> grubs, usually having dark head cap sules and white bodies.



Fig. 284. The roundheaded apple tree borer Saperda candida; larvae, adults, and exit holes, natural size. (After Rumsey and Brooks)

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The Curculionidae is a large family, containing over two thousand nearctic species and many extremely important economic species. The larvae feed on plant material in a variety of ways; they include root feeders, stem borers, leaf feeders, and those which feed in fruits such as hazelnuts, acorns, cherries, and plums; in rotten wood; or in stored grain. The adults usually feed on the leaves or fruiting bodies of the plant species which serves as host for the larvae.

The boll weevil Anthonomus grandis, fig. 286, is one of the most serious cotton pests in the United States and is high on the list of insects causing excessive commercial damage. The adults attack the plants first in the season, feeding on the leaves and in the flowers and young bolls. The females deposit their eggs in feeding holes in the bolls, one egg to each hole. The larvae feed inside the boll, thus making a cell in which they pupate. Adults emerge in a few weeks, cause additional damage by their feeding, and then go into hibernation at the onset of winter. The boll weevil is a native of tropical America and entered Texas from Mexico about 1890. Since that time it has spread gradually throughout most of the cotton-growing region of the United States.

The plum curculio *Conotrachelus nenuphar* attacks plums, cherries, and related fruits; the larvae feed in the body of the fruit. This species is frequently a serious pest.

Of especial importance to stored grains are the granary weevil *Sitophilus granarius* and the rice weevil *Sitophilus oryza*; the larvae of both species live and feed inside grain kernels, and the adults feed either in the old larval burrows or promiscuously on the grain.

Scolytidae, the bark beetles. The species of this family feed chiefly in trees, either alive or dead. The beetles have only an indistinct snout and are almost cylindrical in body shape, fig. 287. The larvae are legless grubs with typical weevil characteristics. Both adults and larvae feed in galleries, fig. 288. In some species these galleries are in the cambium layer of the tree and if sufficiently numerous result in girdling the tree. Many species of this family attack commercial timber, especially pine, and sometimes cause the premature death of large stands of it.

Fig. 285. The pea weevil Bruchus pisorum. a, adult; b, larva; c, pupa. (From U.S.D.A., E.R.B.)



Fig. 286. The boll weevil Anthonomus grandis. On the right a cotton plant attacked by the boll weevil, showing at a, a hanging dry infested square; at b, a flared square with weevil punctures; at c, a cotton boll sectioned to show attacking weevil and larva in its cell; g, adult female with wings spread as in flight; d, adult from the side; h, pupa ventral view and e, larva. (From Metcalf and Flint, Destructive and useful insects, by permission of McGraw-Hill Book Co.)



Fig. 287. The peach bark beetle Phloeotribus liminaris. (From U.S.D.A., E.R.B.)

sheddy





Fig. 288. Brood chambers and larval galleries of peach tree bark beetle. At right is shown a brood chamber with egg pockets and early larval galleries. (From U.S.D.A., E.R.B.)

**Other Polyphaga.** The families mentioned are only a few of the many beetle families in the suborder Polyphaga. Concerning families not discussed here, students will find a great deal of information on life history and identification in the books listed at the end of the section on Coleoptera.

## SUBORDER STREPSIPTERA

This suborder, fig. 289, comprising the stylopids or twisted wing flies, is truly the most remarkable group of the Coleoptera, combining extreme specialization in parasitic habits with equal specialization in structure. It contains two families, the Stylopidae and Mengeidae, both seen only rarely by the collector.





Fig. 289. Strepsiptera, important characteristics and life cycle. (From Essig, College entomology, by permission of The Macmillan Co.)

**Stylopidae.** The male is winged and free flying, more like a fly than a beetle, its elytra reduced to twisted finger-like organs, the hind wings large and fan-shaped, and the metathorax greatly enlarged. The antennae are short and have at least some leaflike segments; the eyes are berry-shaped, with each ommatidium protruding and distinct. The female is extremely degenerate, being only a sac enveloped by the last larval skin; it remains embedded in the host, with only an anterior portion, called a cephalothorax, projecting on the outside of the host integument.

The female is viviparous; the first-instar larvae develop inside her body and escape to the outside by crawling through a slit in the exposed cephalothorax. These larvae, called triungulinids because of their similarity to meloid triungulins, are curious active creatures, having three pairs of legs, well-developed sclerites, reduced mouthparts and ocelli, several well-developed eve facets, and one or two pairs of long terminal filaments. The larvae can run and jump with great agility. Each attaches and burrows into an individual host and soon molts into a legless grub. The grub lies quiescent in the host body and absorbs its food by diffusion from the host blood stream. Thus there is no actual destruction of tissues like that caused by the usual type of insect parasitic larva which macerates and ingests its food by mouth. When full grown, the stylopid larva pushes its anterior end between the abdominal sclerites of the host so that the head and thoracic region is exposed, forming a round or flattened structure. If the larva is a male, it transforms within the larval skin to a typical beetle pupa; when mature, the adult breaks through the exposed larval skin and escapes to the outside. If the larva is a female, it has no definite pupal stage, molting directly into the saclike adult female which remains within the larval skin. The eggs develop and hatch within the body of the mother, until she is merely a sac of eggs or young. The number of progeny of one of these females is enormous; counts of young range from twenty-five hundred to seven thousand per female.

The North American species of stylopids attack chiefly various groups of bees and wasps. In other parts of the world different groups of stylopids attack Hemiptera (Pentatomidae, Cicadellidae, Fulgoridae, and certain allied families) and Cursoria (Mantidae).

The closely allied family Mengeidae is similar in most respects to the Stylopidae, but has a free-living larviform female. The host of the only nearctic genus is unknown, but European species parasitize silverfish.

The Stylopidae and their close allies are regarded by some authors as comprising a separate order, the Strepsiptera. Most workers agree, however, that this group originated with the beetle complex. The

and grammas

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triungulinid larva, reduced wing venation, and parasitic habit suggest a relationship near the Meloidae.

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# VOrder MECOPTERA: Scorpionflies

The adults, ranging in size from small to medium, either have two pairs of large net-veined wings, fig. 290, or have the wings short or aborted. The antennae are long; eyes large; and legs slender, in some families long and spindly. The mouthparts are of a chewing type, and are situated at the end of a snoutlike elongation of the head. The larvae are grublike or caterpillar-like, always with thoracic legs and in some groups having abdominal larvapods also, fig. 291.

The adults are omnivorous, feeding chiefly on small insects, but supplementing their diet with nectar, pollen, petals, fruits, and mosses. The winged forms are active fliers. The males of the Panorpidae, fig.



Fig. 290. A male scorpionfly Panorpa chelata. (From Illinois Nat. Hist. Survey)



Fig. 291. Larva of Apterobittacus apterus. (Redrawn from Applegarth)

290, have a large bulbous genital capsule which resembles to some extent the abdomen of a scorpion, and from this the order derives its name "scorpionflies."

The eggs are ovoid and are laid in or on the ground, either singly or in clusters of one hundred or more. The larvae live in moss, rotten wood, or the rich mud and humus around scepage areas in densely wooded situations. Their food consists of various types of organic matter. Pupation occurs in the soil. There is only one generation per year.

In the small species found in the genus *Boreus* the adults have small short wings and, since they mature in winter or early spring, are often found running about on the snow. These larvae live in moss and rotten wood.

#### Key to Families

1.	Ocelli lacking; wings always well developed, oval, less than 3 times as long as
	wide, with very dense venation. Contains only the rare eastern Merope tuber
· •	Meropeidae
	Ocelli present; if well-developed wings more than 3 times as long as wide, with
	only moderately dense venation
2.	Tarsus raptorial, with a single claw Bittacidae
	Tarsus with 2 claws
3.	Wings, whether well developed or short, with a well-defined and complete set
	of veins Panorpidae
	Wings reduced to small oval pads or short, hard, tapered structures, devoid of
4	venation. Sole genus, Boreus Boreidae

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#### Order TRICHOPTERA: Caddisflies

Mothlike insects, having aquatic larvae and pupae. The adults, fig. 292, vary in length from 1.5 to 40 mm. They have chewing-type mouth-

parts, with all parts greatly reduced or subatrophied except for the two pairs of palpi; long multisegmented antennae; large compound eyes; and long legs. Except for the wingless or brachypterous females of a few species, the adults have two pairs of large membranous wings, with a fairly complete set of longitudinal veins, but a reduced number of crossveins. In most species the body and wings have hair but no scales; in a few species the antennae, palpi, legs, and wings may have patches of scales or a scattering of scales among the longer hair. The larvae, figs. 293 and 294, are diverse in general appearance and habits. The eyes are each represented by a single facet, the antennae are small and one-segmented, the mouthparts are of the chewing type and well developed. The thorax has three pairs of strong legs, the abdomen a pair of strong anal legs bearing hooks and frequently a set of finger-like gills.



Fig. 292. Caddisflies. At left, Rhyacophila fenestra; at right, Eubasilissa pardalis. (From Illinois Nat. Hist. Survey)





Fig. 293. Larva and pupa of a casemaking caddisfly *Limnephilus submonilifer*. (From Illinois Nat. Hist. Survey)

Most of the adults are somber in color or tawny, but a few have wings which are marked with yellow or orange, or have silvery streaks.

Caddisfly larvae live in both lakes and streams, showing a definite preference for colder and unpolluted water. As a group they have a wide ecological tolerance but a more restricted one than midge larvae (Chironomidae) in relation to pollution.

Casemaking has been developed to a high degree by the larvae of most families of these insects. The cases, which are portable "houses" built by the larvae, have fascinated observers of fresh-water insect life. Cases, figs. 295, 296, are of varied shapes, ranging from a straight tube to the coiled case of *Helicopsyche*, which resembles a snail shell, fig. 297. Many types of materials are used in the construction of these cases. Small stones, sand grains, bits of leaves, sticks, conifer needles, and frequently small snail shells may be utilized. In most instances a given genus or species constructs a case of characteristic shape, but genera in different families often make very similar cases.

Caddisfly females lay from three hundred to one thousand eggs each. In some species the eggs are discharged in strings, fig. 298*B*; the female enters the water and lays the eggs on stones or other objects, grouping



Fig. 294. Free-living caddisfly larva Rhyacophila finestra. (From Illinois Nat. Hist. Survey)



Fig. 295. Purselike caddisfly case and larva, Ochrotrichia unio. (From Illinois Nat. Hist. Survey)



Fig. 296. Caddisfly larva in cylindrical case, *Limnephilus rhombicus*. (From Illinois Nat. Hist. Survey)
Fig. 297. The snail-like case of *Helicopsyche*. (From Illinois Nat. Hist. Survey)

the strings into irregular masses containing up to eight hundred eggs. Females of other groups extrude the eggs and form them into a large mass at the tip of the abdomen before depositing them, fig. 298*A*. The eggs are incased in a gelatinous matrix which swells on absorbing moisture. These masses are attached to sticks or stones which are submerged in, adjacent to, or overhanging water.

Females of the family Limnephilidae frequently deposit egg masses on branches overhanging water. On numerous occasions observers have reported that these egg masses swell and liquefy, and the eggs hatch during rain. The gelatinous drops formed by this process run down the twigs and drop into the water, carrying the larvae along.

The larvae are all active, most of them feeding chiefly on small aquatic animals or microorganisms which encrust decayed organic matter in the water. A few genera, notably *Rhyacophila* and *Oecetis*, are predominantly predaceous, feeding on small insect larvae. Larvae of the genus *Rhyacophila*, fig. 294, are free living, constructing no larval case. Three families, the Philopotamidae, Psychomyiidae, and Hydropsychidae, have larvae that weave a fixed net and shelter, the net presumably being used to trap small aquatic organisms which constitute their food. In all other families the larvae construct portable cases of various types. The larva uses these to protect the greater part of the body, which has



Fig. 298. Caddisfly eggs. A, Triaenodes tarda; B, Cyrnellus marginalis. (From Illinois Nat. Hist. Survey)

and sea

thin integument. Only the heavily sclerotized head, legs, and anterior portion of the thorax are extruded from the case when the larva is actively moving about, figs. 295, 296.

Prior to pupation, the larvae of all caddisflies spin a cocoon. The casemakers form this very simply by spinning a silken lining inside the case and closing the ends of the case with a barred or slit membrane. The free-living and net-making species spin an ovoid cocoon of silk and sand, stones, or bits of debris, which is firmly attached to a stone, log, or other rigid support. The pupae develop in the cocoon until the adult structures (except wings) are completely formed and fully sclerotized. The pupae, fig. 293, are unusual in possessing strong mandibles. With these, the mature pupa cuts its way out of the cocoon. It then swims to the surface, crawls on a log or stone, and transforms into an adult.

Usually the complete life cycle requires a year, most of it spent in the larval stage. The egg stage lasts only a short time; the pupal stage requires 2 to 3 weeks; and the adults live about a month.

Of interest among caddisflies are the larval habits of "micro" caddisflies, or Hydroptilidae. This family contains only small individuals, ranging from 1.5 to 6 mm. in length. The first instars are minute freeliving forms, with small abdomens; the last instar builds a portable case and develops a swollen abdomen. Information is available only on two North American genera, *Mayatrichia* and *Ochrotrichia*. In the latter there are differences in the structure of the claws between the free-living and casemaking instars. This dimorphism is similar in many respects to typical examples of hypermetamorphosis.

The caddisfly fauna of the nearctic region contains over eight hundred species grouped in seventeen families.

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#### Order LEPIDOPTERA: Moths and Butterflies

Insects with two pairs of wings, fig. 299, except for a few species which have apterous females. The body, wings, and other appendages are covered with scales which are often brilliant in color and arranged in showy patterns. Adult mouthparts are greatly reduced; in most forms only the maxillae are well developed. These are fused and elongated



Fig. 299. A typical moth, showing scales on wings and body, and sucking tube which is coiled under head when not in use. (From Illinois Nat. Hist. Survey)

to form a coiled tube for sucking up liquid food. The large compound eyes, the long antennae, and the legs are all well developed. The species have complete metamorphosis. The larvae, fig. 310, are cylindrical (the familiar caterpillars); most of them have a definite head, thoracic legs, and five pairs of larvapods (including the end pair). The pupae are usually hard and brown, and the appendages appear cemented onto the body.

The order is a large one, embracing about ten thousand North American species. The adults of these vary greatly in size from minute forms a millimeter or two long to large species with a wing span of 6 inches or more. The wings are distinctively patterned, and the order as a whole presents an attractive array of color and beauty.

The larvae of the Lepidoptera are plant feeders except for a scattering of species which are predaceous, scavengers, or feed on stored products. The great bulk of the species feed externally on foliage; a large number of the minute species mine inside leaves or leaf petioles; and another large group, including both large and small species, bore inside stems, trunks, or roots. A great number of these species attack cultivated plants and cause a high annual loss of crops and stored products. The order is therefore one of great economic importance.

In addition to its destructive species, the order Lepidoptera contains one of great commercial value—the silkworm *Bombyx mori*. This insect is the sole source of natural silk. The propagation of the species and the harvesting of the silk, known as sericulture, is an important industry

in many parts of the world, with an annual harvest in oriental countries of many million dollars' worth of silk. At the turn of the century a sericulture industry was established in California. This failed because of high labor costs. In 1945 a new venture was started in Texas in which a large part of the work was done mechanically.

#### Key to Common Families

1	Wings reduced to small pads or entirely lacking, fig. 313b
1.	Wings well developed at least nearly as long as abdomen, fig. 299
2	Legs lacking or reduced to short stubs: usually associated with a baglike case.
۷.	fig 305 <b>Psychidae</b> , p 359
	T any law of malin appearance for 313h
	Legs elongate and normal in appearance, ng. 5155
3.	Abdomen having closely set scales or spines, or bristling dark-gray hair; usually
	not found near coco <sup>on</sup>
	Abdomen smoothly clothed with fine light woolly hair; moth usually found
	clinging to cocoon
4.	Front wing having a jugum, a lobe at the base of the posterior margin for use
	in wing coupling, fig. 300A; front and hind wings similar in venation and
	shape (Jugatae)
	Front wing without a jugum; either anterior margin of hind wing having an
	enlarged lobe at base, fig. 302D, H, I, or with a long basal spine, or frenulum,
	fig. 300E, both used for wing coupling; or front and hind wings markedly
	different in shape and venation



Fig. 300. Wings of Lepidoptera. A and B, front and hind wings of Mnemonica, Eriocraniidae; C, front wing of Achroia, Pyralidae; D and E, front and hind wings of Archips, Tortricidae. f, frenulum; j, jugum. (C loaned by Dr. Kathryn M. Sommerman)



Fig. 301. Diagnostic parts of Lepidoptera. A, front wing of Pamphila, Hesperiidae; B, front wing of Pieris, Pieridae; C, front wing of Papilio, Papilionidae; D, front (small) and middle legs of Brenthis, Nymphalidae; E, tip of antenna of same; F, tip of antenna of Thanaos, Hesperiidae.

5. Hind wing without a frenulum, and antenna clubbed or hooked at apex, fig.
301 <i>E</i> , <i>F</i> ( <b>Rhopalocera</b> )
Either hind wing having a frenulum, or antenna not clubbed or hooked; in-
stead either threadlike, or serrate, or pectinate (Frenatae) 10
6. Front wing having each of the 5 branches of radius and 3 of media arising
from the discal cell, fig. $301A$ ; antennae usually hooked at apex, fig. $301F$
Hesperiidae, p. 370
Front wing having some of these fused at base, branching beyond discal cell,
fig. 301 <i>B</i> , <i>C</i>
7. Front wing having $Cu_1$ appearing 4-branched, fig. 301C, because both $M_2$ and
$M_3$ are more closely associated with it than with $R_5$ Papilionidae, p. 371
Front wing having $Cu_1$ appearing 3-branched, fig. 301B, because $M_2$ is more
closely associated with $R_5$
8. Front legs reduced, and much shorter than the other legs, fig. $301D$
Nymphalidae
Front legs larger in proportion to the others

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Fig. 302. Wings of Lepidoptera. A, B, front and hind, Acidalia, Geometridae; C, D, front and hind, Malacosoma, Lasiocampidae; E, hind, Halisidota, Arctiidae; F, front, Protoparce, Sphingidae; G, hind, Hyperaeschra, Notodontidae; H, hind, Citheronia, Citheroniidae; I, hind, Samia, Saturniidae.

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9. Front wing having  $M_1$  fused for a considerable distance with posterior branch of radius, fig. 301B; colors white, yellow, or orange, plus black marks Pieridae, p. 371 Front wing having  $M_{1}$ , either not fused with R, or only slightly so, thus arising from discal cell or very near it; colors coppery, blue, or brown. Lycaenidae 10. Hind wing having a posterior fringe as long as wing is wide, figs, 303, 307; wing usually lanceolate. A large number of families of small moths difficult to identify, including Yponomeutidae, Gelechiidae, and Tineidae Not keyed further here Hind wing markedly wider than its fringe, figs, 308, 309, ..... 11 11. Front wing narrow, more than four times as long as wide; hind wing and sometimes front wing having transparent areas devoid of scales, fig. 308 Aegeriidae, p. 361 Front wing wider, hind wings usually entirely covered with scales ...... 12 13. Front wing with  $Cu_2$  fairly well developed, at least towards apex, fig. 300D Tortricidae, p. 362 Front wing with Cu<sub>2</sub> atrophied, fig. 300C.....Pyralidae, p. 363 14. Front wing with 1A evenly bowed anteriorly, the vein coming close to central portion of  $Cu_1$  or apex of  $Cu_{1b}$ , fig. 302F.....Sphingidae, p. 365 15. Front wing having both  $M_2$  and  $M_3$  associated closely with  $Cu_1$ , which therefore appears 4-branched, fig. 302C..... 16 Front wing having  $M_2$  either midway between  $M_3$  and  $R_5$ , or closer to  $R_5$ , so 16. Hind wing without a frenulum, the base of the front margin greatly expanded, fig. 302D......Lasiocampidae, p. 364 Hind wing with a frenulum ..... 17 17. Hind wing having  $Sc + R_1$  and  $R_s$  fused for about half length of discal cell, then the two veins separating, fig. 302E..... Arctiidae, p. 369 Hind wing having  $Sc + R_1$  fused with  $R_s$  for only a short distance, or the veins 19. Hind wing having  $Sc + R_1$  arcuate, curving forward from its base and well separated from  $R_s$  for its entire distance, fig. 302H, I; frenulum obsolete... 20 # Hind wing having  $Sc + R_1$  either fused for a distance with  $R_s$ , fig. 302B, or run-20. Hind wing having two anal veins, fig. 302H..... Citheroniidae, p. 367 21. Hind wing with Sc making a short sharp angulation at the base of the wing, fig. 302B.....Geometridae, p. 365 Hind wing with Sc not angulate at base, fig. 302G..... Notodontidae 

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Fig. 303. The tapestry moth *Trichophaga taprtzella*, one of the Microlepidoptera. (From U.S.D.A., E.R.B.)

#### SUBORDER JUGATAE

The Jugatae are the most primitive present-day Lepidoptera. In addition to possessing a jugum, adults of this suborder have front and hind wings of very similar shape and venation. In one group the pupae have long stout mandibles used for cutting an exit from the cocoon; the adult mouthparts include well-developed mandibles and lobelike maxillae and labium, which are not elongated and appressed to form the usual sucking tube. These characters are of great interest, because they are also found in the Trichoptera, and they demonstrate the close relationship between primitive members of the Trichoptera and of the Lepidoptera.

The Jugatae are represented in North America by only a few species. The family Micropterygidae has mandibulate adults of small size; its larvae feed on moss. The Eriocraniidae also includes small species but these have vestigial mandibles and a sucking tube; the larvae are leaf miners. The Hepialidae includes a few larger species (with a wing expanse up to 2 inches) called swifts because of their rapid flight; their larvae are wood borers or root feeders.

## Suborder Frenatae

Here belong the greater number of the Lepidoptera, representing a great variety of shapes, sizes, and habits. The adult, in addition to lacking a jugum, has hind wings which differ in shape from the front ones, and which also have the radial sector usually reduced to a single vein; in the front wings the radial sector usually has three or four branches. The pupa is obtect; that is, the appendages appear embedded in the body of the pupa and are incapable of movement.

In North America we have fifty families represented, many of them containing species of great economic importance. The diagnosis and identification of these families are difficult and require making special

preparations of the wings after their scales have been removed, a process known as denuding.

The "MICROS." Many families of the Frenatae comprise small slender moths having the hind wings either with vein 1A present, or bearing a long posterior fringe, or extremely narrow and pointed in outline. These are frequently termed the Microlepidoptera. Most of them belong to the group called the Microfrenatae. A few members of the Microfrenatae are quite large, so that size is only an average characteristic for the group. Although it is impractical to give defining characters for them here, a few families are mentioned which contain common species of importance.

**Tineidae.** The larvae feed chiefly on fungi or fabrics, or as scavengers. Included in the Tineidae are our common clothes moths, fig. 304. The webbing clothes moth *Tineola bisselliella* has a larva which makes an indefinite web; in addition to fabrics, it has a marked liking for old feathers. The larva of the casemaking clothes moth *Tinea pellionella* makes a portable case of silk and fabric fragments. Both species are common pests of fabrics of animal origin, such as wool, furs, and feathers.

Psychidae, the bagworms. This family has relatively large species,



Fig. 304. The casemaking clothes moth *Tinea pellionella*. A, cocoon cut open showing fully formed pupa within; B, empty pupal skin projecting from door of cocoon after the moth has emerged; C, adult moth; D, the larva which does the damage to clothes. (After Snodgrass)

some attaining a wing spread of 30 mm. The larvae construct a case or bag of silken fabric and bits of leaf or bark, fig. 305. Only the heavily sclerotized head and thorax project from the case. These bags are a familiar sight hanging from the twigs or leaves of many species of coniferous and deciduous trees. The common bagworm in the eastern states is Thyridopteryx ephemeraeformis, fig. 306. The males have fuzzy dark bodies, pectinate antennae, and usually clear wings. The females are larviform and have almost lost the power of locomotion. The life history has some peculiarities. By late summer the larva is full grown, whereupon it fastens its bag to a twig and pupates inside the bag. When mature, the male pupa emerges partially out of the bag, and the adult male emerges from it in this position. The female pupa stays within the bag; the female adult works itself partway out of the pupal skin and awaits fertilization. The males fly about looking for bags containing mature females and mate with them by means of an elongate extensile copulatory apparatus that can be extended deep into the bag containing the female. Soon after fertilization the female lays eggs, simply allowing them to fall into her old pupal skin, which becomes half filled with them. This completed, the spent female crawls out of the bag, falls to the ground, and dies. The eggs lie dormant over winter and hatch the next spring. The newly hatched larvae crawl out of the old bag, disperse, and begin feeding.

Gelechiidae. The larvae of this family exhibit a wide diversity of food and hosts. Several eastern species of *Gnorimoschema* make large stem galls on goldenrod and related Compositae; the larva feeds within the galls and when full grown pupates there. The pink bollworm



Fig. 305. Stages in the life cycle of the bagworm *Thyridopteryz ephemeraeformis. a*, full-grown larva; *b*, head of same; *c*, male pupa; *d*, female pupa; *i*, adult female; *f*, adult male. (From U.S.D.A., E.R.B.)



Fig. 306. Bagworms at successive stages (a, b, c). c, male bag; d, female bag. (From U.S.D.A., E.R.B.)

Pectinophora gossypiella tunnels through the developing cotton boll and feeds on the seeds. It is a native of Asia that has spread to all the cottongrowing regions of the world and is one of the worst pests of this crop. Also included in the family are species which mine the needles of pine and other conifers and attack potatoes, fig. 307, and tomatoes, and some which bore in twigs and fruits of certain trees. One species is a worldwide pest of stored grain, the Angoumois grain moth Sitotroga cerealella.

Aegeriidae, the Clear-Wings. These are moderate-sized narrow-



Fig. 307. Left, the potato tuberworm *Gnorimoschema operculella*; right, the eggplant leaf miner *C. glochinella*. (From U.S.D.A., E.R.B.)



Fig. 308. The peach tree borer Sanninoidea exitiosa. A, male; B, female. (From U.S.D.A., E.R.B.)

winged forms in which the front and hind wings are coupled by a series of interlocking spines situated near the middle of the wing margins. In most species the wings have definite window-like areas free from scales; hence the name "clear-wing" moths. The adults are diurnal and extremely rapid in flight, and in many the body and wings are banded with purple, red, and yellow, apparently mimicking some of the common wasps. The larvae are stem borers, attacking herbs, shrubs, andtrees. Two of notable economic importance are the peach tree borer Sanninoidea exitiosa, fig. 308, and the squash vine borer Melittia cucurbitae.

**Tortricidae.** A very large family of small to medium-sized moths, having wide wings, the front pair with the apical margin truncate or even concave or excised. The larvae feed on nuts, fruits, and leaves, and in stems. In many species the larvae make nests by rolling and tying leaves, from which they get their common name, leaf rollers. The group includes the red-banded leaf roller *Argyrotaenia velutinana*, fig. 309, which feeds on many wild and cultivated trees and shrubs. Some other



Fig. 309. The red-banded leaf roller Argyrotaenia relutinana. a, b, moth; c, larva; d, pupa; e, tip of pupal abdomen. (From U.S.D.A., E.R.B.)

economic species in the family are the oriental fruit moth *Grapholitha* molesta, which feeds in the twigs and fruits of peaches, plums, and related fruit trees; the pine shoot moths, several species of *Rhyacionia*, which destroy the terminal buds of pine; and the grape berry moth *Polychrosis viteana*, which feeds on the leaves and in the fruits of grapes.

**Pyralidae.** This is a large family, economically one of the most important in the order. In taxonomic position the pyralids are intermediate in many characters between the "micros" and the "macros." The moths vary greatly in size and shape, but are usually delicate, trim, and have a rather detailed and soft coloration pattern. The larvae exhibit a wide range of food habits: feeding on leaves, fruits, and flowers; boring in stems or stalks; some being saprophagous and a few predaceous. Many spin an extensive web over their food and surroundings and are called webworms, such as the garden webworm *Loxostege similalis*, fig. 310. The family includes some of the most troublesome pests of agricultural crops. The European corn borer *Pyrausta nubilalis* and the southwestern corn borer *Diatraea grandiosella* are serious pests of corn; the greenhouse leaf tier *Udea rubigalis* is a pest of chrysanthemums and other greenhouse crops; the greater wax moth *Galleria mellonella* is often a serious pest of beehives. Several species, including the Indian-meal



Fig. 310. The garden webworm Loxostege similalis, adult and larva. (From U.S.D.A., E.R.B.)

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moth *Plodia interpunctella*, attack stored grain and prepared foods, and *Ephestia elutella* feeds on stored tobacco and other dried vegetable products. Many other species attack a wide assortment of crops.

THE "MACROS." In the Frenatae, most of the moth families containing the larger species, such as the miller moths, the various native "silkworm" moths, and the hawk moths, are usually referred to as the Macrofrenatae, or "macros." In these the hind wing usually is broad, has only a short fringe, and lacks vein 1*A*. As is the case with the "micros," the "macros" contain many families which are difficult for the nonspecialist to identify.

Lasiocampidae. To this small family belong a few species of moderate size that have hairy larvae and velvety large-bodied adults. Tent caterpillars of the genus *Malacosoma*, fig. 311, are the best known of these. The larvae feed on a variety of deciduous trees, including fruit trees, and periodically occur in outbreak numbers, the hordes of caterpillars defoliating thousands of acres of trees.

In the genus *Malacosoma*, winter is passed in the egg stage. The eggs hatch in late spring, and the young caterpillars of an egg mass spin a colonial webbed nest, usually around the fork of a branch. The caterpillars leave this to feed on foliage, each individual returning via a silken thread left in its wake. The larvae leave the nest and pupate singly in a protected spot under bark or debris where the cocoons are constructed. Adults emerge in late summer, and, after mating, females deposit eggs in bands around small twigs. Each egg mass contains several hundred



Fig. 311. Stages of the eastern tent caterpillar Malacosoma americanum. a, egg mass; b, larva; c, pupa; d, cocoon;  $\mathfrak{P}$ , female moth;  $\mathfrak{F}$ , male moth. (From U.S.D.A., E.R.B.)

eggs, the whole incased in a secretion which hardens and becomes impervious to the elements.

During an outbreak year the adults may be attracted in huge numbers to the lights of towns. On a summer night in 1925 I witnessed a tremendous flight in Edmonton, Alberta. Throughout the entire business section the moths were about 6 inches deep, their greasy bodies completely stopping streetcar and automobile traffic, and making it difficult to walk. Under each street light and show window the moths formed piles reaching an apex from 2 to 3 feet high. The great majority died from suffocation by their fellows. Their rotting bodies gave a distinctive odor to the city streets for some time.

Sphingidae, hawk or sphinx moths. These moths are all large, most of them having a wing spread of over 65 mm.  $(2\frac{1}{2} \text{ inches})$ . The body is stout and spindle-shaped, frequently tapering to a sharp point at the posterior end. When spread, the posterior margins of the hind wings are seldom back as far as the middle of the abdomen; the front wings are long and proportionately narrow. The antennae are long and simple, frequently slightly thickened towards the tip. The moths are extremely rapid fliers and feed on nectar. The larvae are leaf feeders; most forms have a sharp horn on the eighth abdominal segment and are commonly called hornworms. In the main our species feed on a wide variety of herbs, vines, and trees. A few are of economic importance, particularly the tomato hornworm *Protoparce quinquemaculata* and the tobacco hornworm *Protoparce sexta*, fig. 312.

Geometridae, measuring worms, geometers. These are fragile moths, with slender or pectinate antennae, large delicate wings, and slender bodies, fig. 313. The larvae are well known for their peculiar walking habit, consisting of a series of looping movements. They have long slender bodies but only two or three pairs of large abdominal legs, located near the end of the body. When they are walking, the abdomen is raised in a high loop, and the hind legs are brought forward to grasp a supporting position close to the thoracic legs; these latter are then released, the body stretched forward, and a new grip taken by the thoracic legs at the end of the reach. The hind legs then let go, the body arches, and the operation is repeated. Geometers make up a large family; their host list includes many plant families and genera. Certain species are common defoliators of deciduous and coniferous trees. Some species, known as cankerworms, fig. 313, are locally very destructive to shade and fruit trees; these species have normal winged males but completely apterous females.

Saturniidae, giant silkworm moths. Here belong the largest North American moths and caterpillars. The adults are velvety or woolly, with



Fig. 312. A hornworm infesting tomato and tobacco, *Protoparce sexta. a*, adult; *b*, larva; *c*, pupa. (From U.S.D.A., E.R.B.)



Fig. 313. The spring cankerworm *Paleacrita vernata*. *a*. male; *b*, female; *c*, eggs; *d*, larva; *c*, pupa. (From Wellhouse, How insects live, by permission of The Macmillan Co.)

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The Orders of Insects



Fig. 314. The promethea moth *Callosamia promethea*. (From Comstock, Introduction to entomology, by permission of the Comstock Publishing Co.)

broad wings having a showy pattern. The hind wings have no trace of a frenulum; instead the basal portion of the anterior margin is enlarged and projects under the front wing in the flight position, thus synchronizing the two pairs. The antennae are feathery in the males and frequently in the females also. The caterpillars are leaf feeders; the larger ones have a voracious appetite and will consume an entire large leaf with astonishing speed. The larvae are stout bodied, bear spiny tubercles or tufts of stiff hairs, and may attain a length of 100 mm. (nearly 4 inches). The full-grown larvae spin large brown cocoons on branches or twigs near the ground, pupate, and pass the winter in this stage. A common eastern species is the promethea moth *Callosamia promethea*, fig. 314, which has a reddish or brown adult; the larva is green with yellow, red, and blue spiny tubercles.

The related family Citheroniidae contains the green-striped mapleworm *Anisota rubicunda*, fig. 315, a widespread species east of the Rocky Mountains.

Liparidae. This also is a small family containing species of only moderate size. The caterpillars are hairy, the adults frequently fuzzy. In several genera the females cannot fly, having only small padlike wings. To this family belong a few species of extreme economic importance, including the gypsy moth *Porthetria dispar* and the brown-tail moth *Nygmia phaeorrhoea*, fig. 316. Both these gained entrance to the United States from Europe and are destructive enemies of shade trees in northeastern United States. Another species of Liparidae attacking a wide variety of deciduous trees is the white-marked tussock moth *Hemerocampa* 



Fig. 315. The green-striped mapleworm Anisota rubicurda. a, female moth and antenna of male; b, egg showing embryo within; c, egg mass; d, c, larva; f, pupa. (From U.S., D.A., E.R.B.)

*leucostigma*, fig. 317. The tussock moth larvae has tufts of long nettling hairs at each end of the body, and "pencils" of white hairs on some of the central segments. It makes a cocoon on the bark of trees. The female is grublike; she lays a large group of eggs encased in a foamy white secretion that forms a protective covering for them.

**Phalaenidae** (*Noctuidae*), owlet or miller moths. This is by far the largest family of the Lepidoptera. The adults vary greatly in size, shape, and color; the structural characters are also diverse, so that the family can be distinguished from its relatives only on the basis of a combination of several critical differences. The larvae are usually leaf feeders or stem or root borers and for the most part are unadorned with horns or conspicuous processes. From the standpoint of agriculture the family is an important one. It includes many species whose larvae, called cutworms, attack a wide variety of grain, truck, and field crops. Other economic species are the armyworm *Pseudaletia unipuncta* and the

fall armyworm Laphygma frugiperda, fig. 318, which attack pasture grasses, corn, and small grains; the corn earworm or cotton bollworm *Heliothis zea*, which attacks cotton, corn, tomatoes, and other crops; and the cabbage looper *Trichoplusia ni* which feeds on cruciferous crops and "loops" like a geometrid larva, but has only two middle pairs of abdominal legs. In all these the larvae do the damage.

Arctiidae, the arctiid moths. This family is a close relative of the Phalaenidae, differing from it mainly in that the adults are usually white or yellow or have intricate bright or yellow patterns. The larvae have thick tufts of hairs, and hence many of them are called woolly bears. These larvae are a common sight in late summer, hurrying along the ground looking for a sheltered place to make a cocoon and pupate.

Other Moths. There are many other moths, some of striking appearance, others similar in general characteristics to the few just mentioned. To identify these the student is referred to the works listed at the end of the section on Lepidoptera.

#### Suborder Rhopalocera

Butterflies and Skippers. In this suborder the hind wings have no frenulum, and in both front and hind wings the stem of media has been lost, resulting in a large central discal cell. Most of the species are brightly patterned. The adults are diurnal in habit and lovers of sunshine, in marked contrast to the crepuscular or nocturnal habit of most



Fig. 316. The brown-tail moth Nygmia phaeorrhoea; female above, male below, larva in center, enlarged larva to right. (From U.S.D.A., E.R.B.)



Fig. 317. The white-marked tussock moth *Hemerocampa leucostigma*. a, larva; b, female pupa; c, male pupa; d, e, male moth; f, female moth; g, same ovipositing; h, egg mass; i, male cocoons; k, female cocoons, with moths laying eggs. (From U.S.D.A., E.R.B.)

of the moths. When at rest, the Rhopalocera hold their wings upright over the body instead of folding them flat on the body as do the moths. The suborder is divided into two well-marked groups: the skippers and the butterflies.

**Skippers.** These are very rapid on the wing, able to fly in a straight line like a wasp or hawk moth. Most of our species belong to the Hesperiidae; they are dull colored, with yellow and brown predominating, and are less than 30 mm. from wing tip to wing tip. Except for a few species, the larva has a large head accentuated by a small neck-like prothorax. Most of the species live in a nest made by sewing together a few leaves of the host plant. A common eastern species is the silver-spotted skipper *Epargyreus tityrus*, which feeds on several legumes; *Wisteria* is a favorite.

**Butterflies.** The inversion "flutterbys" is descriptive of the flight of most members of this group. They have a very slow rate of wing stroke and hence fly in a series of up-and-down movements producing an erratic course. The butterfly group is represented in North America by seven families, most of which have members well known to the naturalist.

**Papilionidae, the swallowtailed butterflies.** In this small family, fig. 319, the margin of the hind wing is usually notched, and the vein  $M_3$  ends in a finger-like projection or tail. These are large butterflies, many of them gaudily spotted or striped with many colors, yellow predominating in several species. The larvae are leaf feeders and may be as conspicuously marked as the adults. They are unique in having a forked eversible stink gland, or *osmeterium*, fig. 319b, on the dorsum of the pronotum. This is shot out when the larva is alarmed; it is usually bright orange and emits a pronounced odor.

**Pieridae, the whites and sulphurs.** These are predominantly white, yellow, or orange butterflies, some with extensive black markings. The larvae have an abundant supply of stiff hairs and look bristly. The imported cabbageworm *Pieris rapae*, fig. 320, whose adult is white marked with black dots, occurs commonly in the central and northern states. The larvae are green and are pests of cabbage and related plants. This is an introduced species from Europe. A native species of the same genus, *P. protodice* the southern cabbageworm, is a pest of cruciferous



Fig. 318. The fall armyworm Laphygma frugiperda. A, egg mass; B, eggs; C, adult; D, larva; E, pupa. (From U.S.D.A., E.R.B.)



Fig. 319. The celery swallowtail *Papilio polyxenes.* a, larva from side; b, larva showing head with odoriferous appendages; c, male butterfly; d, outline of egg; e, young larva; f, chrysalis. (From U.S.D.A., E.R.B.)



Fig. 320. The imported cabbageworm *Pieris rapae.* a, female butterfly; b, egg (above as seen from above, below as seen from side); c, larva, or worm, in natural position on cabbage leaf; d, suspended chrysalis. (From U.S.D.A., E.R.B.)

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crops in the southern states. Another pierid that is often a pest locally is *Colias philodice eurytheme* the alfalfa caterpillar or orange sulphur. It is a highly variable species in color and occurs over most of the continent. The larva feeds on alfalfa, clover, and certain other legumes.

Other Butterflies. In North America there are many species of butterflies in addition to the few just listed. Every locality on the continent has a selection from strikingly colored to somber forms, many of them abundant locally. For more information regarding their identification characters, hosts, and range, the student is referred to Dr. Holland's "Butterfly Book" and Dr. Klots' "Field Guide."

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# Order DIPTERA: Flies

Typical adults, fig. 321, have a single (front) pair of membranous wings, rarely scaled. The wings have few crossveins and a moderate number of veins. The hind wings are represented only by a pair of slender knobbed balancing organs, called *halteres*. Mouthparts are of various types; in some groups they are modified for piercing and sucking, in other groups for rasping and lapping. The body form is diverse. In a few groups the adults are completely apterous. The eyes



Fig. 321. Typical flies. A, Meromyza americana; B, Euarosta solidaginis; h, haltere. (From Illinois Nat. Hist. Survey)

Nematocera

are usually large; the antennae vary from 3- to 40-segmented. These are holometabolous insects with legless larvae, usually either with a distinct mandibulate head, fig. 329, or with an internal sclerotized skeleton attached to a pair of hooklike mandibles. The pupa is either free or formed within the skin of the third-instar larva.

The order Diptera is a large one, including over fifteen thousand North American species. The food and habitat of the adults are usually very different from those of the larvae.

Adults of many families feed chiefly on nectar and plant sap or on free liquids associated with rotting organic matter. Certain groups, such as mosquitoes and horse flies, feed on animal blood; these have mouthparts highly modified for piercing and sucking. In a few groups, for example, the bot flies, the mouthparts are so vestigial that it is doubtful if the adults take any nourishment.

As a group, fly larvae are moisture-loving, the great majority living in water, in rotting flesh, inside the bodies of other animals, in decaying fruit or other moist organic material, or inside living plant tissue. A few live in relatively dry soil or move about exposed to the air, but these are the exceptions rather than the rule.

For the most part, fly eggs are simple, ovoid or elongate, and are normally laid singly, in, on, or near the larval food. Some, such as those of *Drosophila*, have lateral or polar floats which prevent them from sinking into semiliquid food and drowning. Eggs of certain mosquitoes are sufficiently well protected against the elements to withstand months of alternate drying, wetting, and freezing. In some groups, such as the flesh flies and some parasitic flies, the eggs may hatch just before leaving the body of the female and are deposited as minute larvae. This habit is carried to extreme development in the sheep-tick groups (Pupipara) where the larvae hatch and grow to their full size in the body of the female. Of unusual interest in the order is the paedogenesis exhibited by some species of midges (see p. 189).

The Diptera comprise three well-marked groups or suborders, the Nematocera, Brachycera, and Cyclorrapha.

#### Synopsis of Suborders

1. Larval mandibles working in a horizontal (from side to side) plane, and usually having teeth or brushes used in gathering or grasping food. Adult antennae composed of at least 7 segments which are not fused into a solid structure

2. Either pupa free, not enclosed in last larval skin, or the adult escaping from



Fig. 322. Wings of Diptera. A, Psychoda, Psychodidae; B, Aedes, Culicidae; C, Chironomus, Chironomidae; D, Simulium, Simuliidae; E, Bibio, Bibionidae; F, Rhagio, Rhagionidae; G, Stratiomys, Stratiomyiidae; H, Tabanus, Tabanidae; I, Thereva, Therevidae; J, Asilus, Asilidae; K, Anthrax, Bombyliidae; L, Scaeva, Syrphidae; sv, spurious vein.

	Key to Common Families
1.	Abdomen only indistinctly segmented; the coxae of the 2 legs of each segment far apart. Adults living as parasites on birds, mammals, or bees 2 Abdomen having distinct segments; the 2 legs of each segment held fairly closely together, sometimes the coxae almost contiguous. Not living as ectoparasites in the adult stage
2.	Mesonotum short, resembling the abdominal segments; minute (1.5 mm. long), wingless, parasitic on honeybees. Includes only <i>Braula caeca</i>
3.	Braulidae, p. 399 Mesonotum different in appearance from abdominal segments, fig. 345 3 Palpi long and slender, forming a sheath for the mouthparts. Living on birds and mammals with the exception of bats
4.	Antenna having more than 3 segments, fig. $325F-H$ not counting a style or
	arista, borne by the third
	Antenna having 3 segments or less; usually the third bears a style, fig. 325 <i>I</i> , or arista, fig. 325 <i>J</i>
5.	Small mothlike flies, never longer than 5 mm., having body and wings densely clothed with hair or scales; wings having about 10 longitudinal veins, and having crossveins only at extreme base, fig. 322 <i>A</i> ; aquatic or semiaquatic moth flies
6.	Appearance not mothlike, or venation of a different type
	Mesonotum with praescutal suture transverse, indistinct, or atrophied, fig. 325B, C
7.	Antenna having 6 or more well-marked ringlike or beadlike segments, fig. 325F
	Antenna having only 4 or 5 segments, fig. 325G, or the terminal segments sometimes indistinctly subdivided, fig. 325H 16
8.	Wing having cell $Cu_{1b}$ either open at apex, fig. $322F$ , or lost due to atrophy of veins
0	Wing having cell $Cu_{1b}$ entirely closed at apex by fusion of veins $Cu_{1b}$ and $1A$ , fig. $322H$
9.	Wing having both $R_{2+3}$ and $M_{1+2}$ branched, and the venation fairly parallel, fig. 322B; mouthparts often forming a long slender beak, fig. 55; wings more or less clothed with scales
N N	Wing having either $R_{2+3}$ or $M_{1+2}$ unbranched, the venation frequently markedly divergent, fig. 322E; mouthparts never forming a long beak; wings without scales
10.	Ocelli present
11	Ocelli absent
11.	Anterior margin of wing only slightly more heavily scierotized than apical and posterior margins
	Anterior margin of wing having a sclerotized thickening that stops abruptly

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	at or just beyond juncture with $R_{4+5}$
12	Antennae inserted below level of eyes, fig. 325L; front femur often enlarged;
	the March fliesBibionidae
•	Antennae inserted on a level with middle of eyes; coxae often greatly elon-
	gated; the fungus gnats
13	3. Wing having 2 or 3 strong parallel veins near anterior margin and a group of
	6 or 8 oblique very weak veins running from anterior region to or near ,
	posterior margin of wing, fig. 322D; antennae short, 12-segmented, the last
•	10 annular and closely knit, fig. 330 Simuliidae, p. 386
	Wing having a different venation, either more veins equally sclerotized, or
	most of them longitudinal in general course rather than oblique, fig. 322C;
	antennae usually elongate, with well-separated segments
14	Anterior margin of wing only slightly more heavily sclerotized than apical
	and posterior margins
	Anterior margin of wing having a sclerotized thickening that stops abruptly
÷.,	at or just beyond juncture with $R_{4+5}$ , fig. $322C$
15	b. Postnotum very large, projecting some distance posterior to scutellum, fig.
	325 <i>C</i> ; slender elongate flies Chironomidae, p. 383
	Postnotum smaller, scarcely projecting at all from beneath the scutellum, fig.
	325B; small stouter flies, the punkies or "no-see-ums" Ceratopogonidae
10	5. Tarsus having 3 whitish pulvillar pads, fig. $325D$ ; the middle one (the empo-
	dium) is sometimes dorsad of the lateral pulvilli, which are sometimes
	small
	arsus at most having 2 pulvillar pads, the empodium reduced to a seta, fig.
1	325E; the 2 pulvilli may be reduced, in which case the tarsus lacks pads. 18
1	7. Wing with branches of $R_s$ close to front margin, forming a group of narrow
	cens along it, lig. 5226, tibla without apical spurs, soldier lifes
	Wing with branches of $R$ not crowded to front margin $R$ and $R$ diverging
•	to form a triangular cell embracing apex of wing fig. $322H$
	Tabanidae. p. 389
1	<b>8</b> Antenna having third segment elongate fourth clavate without arista or style
•	fig 325G very large species Mydaidae n 391
	Antenna having apical segment not clavate 19
ł	Top of head support to form a deep excavation between eves for $325M$ :
*	wing with $M$ present and $M$ having its base almost or entirely free from
	$C_{\mu}$ the latter 2 yeins sometimes fused for a short distance at base and/or
	apex fig 3227 Asilidae. p 391
	Top of head without a deep excavation: wing having $M_0$ atrophied, and $M_{0,1}$
	fused near base for a considerable distance with $Cu_{a}$ fig. 322K; hover
	fliesBombyliidae
2	<b>b.</b> Wing at most having Sc and stem of R sclerotized, remaining venation con-
	sisting of 3 or 4 weak veins arranged as in fig. 323A; antenna composed of
	1 segment and its arista Phoridae, p. 392
	Wing having a more extensive venation, figs. $323B-D$ ; antenna may have 1 to
	3 segments
	i

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Fig. 323. Diagnostic parts of Diptera. A, wing of Megaselia, Phoridae; B, wing of Hylemya, Anthomyiidae; C, wing of Empis, Empididae; D, wing of Sarcophaga, Sarcophagidae; E, costal region of Rhagoletis, Tephritidae; F, scutellum of Zenillia, Tachinidae; G, squamae of Anthomyia, Anthomyiidae; H, squamae of Musca, Muscidae; I, thorax, diagrammatic, of higher Diptera. ls, lower squama; us, upper squama; x, secondary convexity on scutellum.

24. Top of head sunken to form a deep excavation between eyes, fig. 325M
Asilidae, p. 391
Top of head flat or convex, confluent in outline with top of eyes
25. Wing having $M_{3+4}$ not fused at base with $Cu_{1a}$ but frequently fusing with $Cu_{1a}$
near margin; $M_2$ present, fig. 3221. Moderate-sized species similar to
Asilidae in habits
Wing having $M_2$ atrophied and $M_{3+4}$ fused at base with $Cu_{1a}$ , fig. $322K$ 26
26. Wing having $Cu_{1b}$ reaching wing margin or fusing with 1A near wing margin,
fig. 322KBombyliidae
Wing having $Cu_{1b}$ fused with 1A considerably before wing margin, as in fig.
322 <i>H</i> <b>Empididae</b>
27. Wing with $Cu_{1b}$ straight and long, angled only slightly from stem of $Cu$ , fig.
322L
Wing with $Cu_{1b}$ markedly angled from its parent vein, appearing like a cross-
vein, fig. 323B-D; spurious vein never developed
28. Wing with $M_1$ sinuate; a linear, veinlike thickening (the spurious vein) usually
present between $R_s$ and $M$ , fig. $322L$ Syrphidae, p. 392
Wing with $M_1$ short and straight, appearing to be a crossvein; no spurious
vein present
29. Lower squama large and platelike, the portion projecting beyond the upper
squama as long as the upper squama, fig. 323H, 324E
-ls



Fig. 324. Parts of Diptera. A, squamae of Scopeuma, Scopeumatidae; B, of Pegomyia, Anthomyiidae; C, D, of Fannia, Fanniidae; E, of Musca, Muscidae; F, head of Agromyza, Agromyzidae; G, diagram of upper part of head showing ocelli and associated bristles; H, head of Euthycera, Sciomyzidae; I, of Nemopoda, Sepsidae. a, arista; ls, lower squama; o, ocellar bristle; ot, ocellar triangle; po, postocellar bristles; us, upper squama; v, vertical bristle. In A to E the upper squama is shown in broken outline. (H, I, after Curran)



Fig. 325. Diagnostic parts of Diptera. A, mesonotum of Helobia, Tipulidae; B, mesonotum of Palpomyia, Ceratopogonidae; C, mesonotum of Chironomus, Chironomidae; D, tarsal claws and pads of Tabanus, Tabanidae; E, tarsal claws and pads of Zenillia, Tachinidae; F, antenna of Bibio, Bibionidae; G, antenna of Mydas, Mydaidae; H, antenna of Tabanus, Tabanidae; I, antenna of Geosargus, Stratiomyiidae; J, antenna of Pollenia, Calliphoridae; K and L, face of Bibio, Bibionidae, male and female; M, face of Asilus, Asilidae; N, head of Hylemya, Anthomyiidae; O, face of Dolichopus, Dolichopodidae; P, face of Gasterophilus, Gasterophilidae; Q, Tephrita, Tephritidae. a, arista; fr, frontal ridge or suture; mo, mouth opening; ov, oral vibrissa; p, pulvillar pads; pr, proboscis.

30.	Lower squama at most slightly longer than upper squama, fig. 324 <i>C</i> , <i>D</i> , fre- quently appearing as only a cordlike band, fig. 324 <i>A</i> , <i>B</i>
31	Oral opening large, fig. 325Q; body usually not fuzzy but often spiny in appearance
32	Hypopleura with a row of bristles, fig. 323 <i>I</i>
54.	Tachinidae. p. 397
	Mesopostnotum having no well-developed extra bump, at most a gentle con-
	vexity below scutellum; the flesh flies
33.	Arista of antenna with feathering not extending much beyond middle; body
	dull black or striped with gray and blackSarcophagidae
	Arista feathered to tip, fig. 3257, or body entirely metallic blue or green
94	Calliphoridae
34. •	Oral opening round and minute, mouthparts vestigial, cheeks inflated, ng.
	Oral opening large mouthparts well developed 35
35	Front of head lacking subures or ridges running ventrolaterad from base of
00.	antennae, fig. 3250.
	Front of head having a pair of frontal sutures or ridges, fr, each running from
	near the antenna toward the oral excavation, fig. 325Q
36.	Crossvein $r-m$ situated at the base of the wing, and inconspicuous, sometimes
	difficult to find; free end of $M_{3+4}$ lacking; predaceous species in moist
	habitatsDolichopodidae
	Either crossvein $r-m$ situated at least one-third distance from base to apex of
97	wing, or $M_3$ present, fig. 323C Empididae
57.	does, fig. $323B$ , D (this character best seen from anterodorsal view of
	wing)
	Sc either partially atrophied, or fused at tip with $R_1$ , or abruptly angled, fig.
20	323E
50.	antennal sogment small fig 3241
	Either head not spherical, or every situated a considerable distance from ventral
	margin or second antennal segment massive, fig. 324H
39.	Dorsum of head and mesonotum flat, all but the lateral areas clothed only
	with abundant, short, stiff setae; seashore species
	Dorsum of mesonotum convex and arched, often with long bristles scattered
	over much of its area
40.	Oral vibrissae present (compare fig. 325N) 41
	Oral vibrissae absent
41.	Lower squama differentiated as a flap of the axillary cord, fig. $324B-D$ $42$
	Lower squama not differentiated, being simply a thin, fuzzy edge of the
42	Analyzin reaching wing margin although the end of the yein may be faint
<i>π</i> ∠.	mai veni reaching wing margin, arthough the end of the veni may be failt,

¢

	fig. 323 <i>B</i>
43.	Postocellar bristles long and convergent, fig. 324 <i>G</i> ; body never hoary
	Helomyzidae, p. 393
	Postocellar bristles either short, absent, or divergent; body often hoary with
	long, thick hair
44.	Some or all of the tibiae with a preapical dorsal bristle
	Tibiae without preapical bristlesOtitidae, p. 393
45.	Postocellar bristles convergent; second antennal segment always small; small
	flies, rarely over 6 mm. long Lauxaniidae, p. 393
	Postocellar bristles parallel, divergent, or absent; second antennal segment
	often massive, as large as third, fig. $324H$ ; moderate-sized flies
	Sciomyzidae, p. 393
<b>4</b> 6.	Wing having costal cell wide and having <i>Sc</i> ending abruptly or angled abruptly
	much before apex of cell, either Sc beyond this point weak or atrophied, or
	C with a distinct break, at which point there are several stout bristles, fig.
	323 <i>E</i>
	Wing either having costal cell narrow, or $Sc$ gradually fading out towards its
17	apex, or fusing with $R_1$ , or absent
41/.	Posterior basitarsus short and emarged <b>Dorbornale</b> , p. 595
	rosterior basitaisus ittle ir at an tilleker than succeeding segments and usually
4.9	Wing with 14 and Cy. almost entirely atrophiad cell Cy. therefore open or
<b>T</b> U,	absent
	Wing with 1A and $Cu_{1b}$ present and enclosing cell $Cu_{1b}$
<b>4</b> 9.	Dorsum of head with a large, triangular, sclerotized area (the ocellar triangle, fig. 324F, ot) flanked by wide membranous areas; wing having vein $Cu_{1a}$
	slightly sinuate
	Dorsum of head with sclerotized areas either very small, or quadrangular, or
	occupying all of dorsal aspect; wing with vein $Cu_{1a}$ not sinuate
	Ephydridae, p. 393
50.	Postocellar bristles convergent, as in fig. 324G Drosophilidae, p. 394
	Postocellar bristles parallel or divergent Agromyzidae, p. 393

## Suborder Nematocera

The North American fauna contains representatives of about twenty families of Nematocera. Midges, crane flies, mosquitoes, and black flies are examples of the more abundant and conspicuous families. The larvae of most families have a well-defined sclerotized head, fig. 328, retracted into the thorax only in the Tipulidae.

**Tipulidae, crane flies.** The adults are long-legged slender-winged flies, fig. 326; the antennae are threadlike, with many distinct segments, and the mesonotum has a V-shaped transverse furrow or suture. The adults are extremely abundant in moist woods and sheltered ravines, and along wooded stream banks. The larvae are elongate and worm-



Fig. 326. A cranefly *Epiphragma* fascipennis, adult female.

Fig. 327. *Epiphragma.* a, larva; b, end of larva from above; c, pupa. (After Needham)

like, fig. 327; many are aquatic, living especially in submerged clusters of rotting leaves; many feed in leaf mold; and a few feed on living plant roots or mine in leaves. They vary greatly in size and appearance but have in common a stout head which is partly retracted within the thorax (in certain species it is further retractile and may be completely hidden in the thorax when the insect is disturbed) and strong toothed mandibles which work from side to side.

**Chironomidae (Tendipedidae), midges.** These are frail insects, fig. 328, frequently mistaken for mosquitoes, but they do not bite and have several structural differences which set them off. The male antennae are plumose with whorls of long silky hair. The larvae are all aquatic, some free living, others spinning a loose web of bottom particles and silk and in certain genera making a definite case. They are slender and wormlike, with a small but distinct sclerotized head, and a 12-segmented body. In some groups the prothorax, or the last body segment, or both, may have a pair of nonjointed leglike protuberances or pseudopods. The larvae feed on organic matter on the bottom of bodies

of water and are found in rivers, lakes, ditches, and stagnant ponds. The pupae are also aquatic, some of them free living, but most of them staying in the web or case made by the larva. In many bodies of water these midge larvae are tremendously abundant and form one of the principal items of fish food. When the adults emerge, they appear in clouds and at night blanket near-by lights in a humming mass. The eggs are laid in water and hatch in a few days.

**Culicidae, mosquitoes.** Long-legged slender insects, fig. 329, having beadlike antennae (in the males they are plumose as in the Chironomidae) and many-veined wings. One small subfamily, the Chaoborinae (non-biting mosquitoes), have mouthparts that resemble pads. All the true mosquitoes belong to the subfamily Culicinae. In these the mouthparts form a beak, composed of a highly modified assemblage of piercing-sucking parts (see fig. 55, p. 70).



Fig. 328. Life history stages of Chironomidae. A, larva of Chironomus tentans; B, pupa of Cricotopus trifasciatus; C, adult male of Chironomus ferrugineovittatus. (From Illinois Nat. Hist. Survey)



Fig. 329. The yellow fever mosquito Aedes aegypti. Adult above; larva at left; pupa at right (From U.S.D.A., E.R.B.)

In certain genera eggs are laid on water, either singly or glued together to form rafts; they hatch in a few days. In other genera eggs are laid in humus or just above the water line on the sides of containers; these eggs hatch at some later time when the water rises and inundates them. The larvae are aquatic, most of them living in still water, but a few species live in slowly moving water. In other parts of the world there are species which breed in rapid streams, quite in contrast with the habits of nearctic species. The larvae are called wrigglers; they have large heads with fairly long antennae, a large swollen thorax, and a cylindrical abdomen. In all the true mosquitoes and certain of the others the abdomen bears a dorsal breathing tube or plate on the eighth segment. In the main, mosquito larvae feed on microorganisms and organic matter in or on the water. A few groups are predaceous and feed solely on other mosquito larvae. The pupae, which are called tumblers, are also aquatic, free living, and active. Their breathing tubes are situated on the thorax. Adult females of a few species and males of all mosquito species feed only on nectar or water. But unfortunately in most species the females seek a blood meal, which under natural conditions is necessary for reproduction.

Economically, mosquitoes are of tremendous importance to man. Some species, principally those of the genera *Anopheles* and *Aedes*, transmit an imposing list of human diseases, including malaria, dengue, yellow fever, and filariasis. For this reason mosquitoes are of utmost importance in a consideration of medical entomology. As a direct nuisance mosquitoes have an economic influence. The severity of their attacks decreases property values, especially in resort areas, and has undoubtedly had an influence in the settlement of extreme northern areas where mosquitoes are unusually abundant.

Simuliidae, black flies. This family, often referred to as buffalo gnats, has aquatic larvae and pupae and bloodsucking adults, like the Culicidae. The black flies are short, stubby, and humpbacked, with short legs and compact, usually 11-segmented antennae, fig. 330. Unlike the mosquitoes, both sexes bite. Horses, cattle, ducks, and many wild animals are attacked. Certain species attack man also, gathering



Fig. 330. Adult black fly Simulium vittatum. (After Knowlton and Rowe)
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Fig. 333. The hessian fly *Phytophaga destructor. a*, female fly; *b*, eggs, one at hatching; *c*, larva; *d*, head and breastbone of same; *c*, pupa; *f*, puparium; *g*, infested wheat stem showing emergence of pupae and adults; *h*, antennae, male and female. (From U.S.D.A., E.R.B.)

h = 1 and deer flies. The adults, fig. 334, are B

around the ears, eyes, and exposed areas of the face, hands, and ankles. They draw a great amount of blood and produce burning welts on the victim's skin. These welts may itch and burn for a week or more.

The eggs are laid in clusters near the water edge or in the water. The larvae are sedentary, elongate, and slightly vasiform, fig. 331, and occur only in running water; the posterior end is anchored by a hooked sucker-disc to some support such as a rock, log, or trailing leaves; the head has a pair of feathery branched rakes which are supposedly used as strainers to obtain food from the running water, primarily microorganisms and organic material. The pupae are also aquatic, formed in a boot-shaped cocoon, fig. 331. On the prothorax of the pupa are a pair of long respiratory processes, usually branching into many slender filaments.

Cecidomyiidae (*Itonididae*), the gall gnats. The adults, fig. 332, are inconspicuous fragile flies, having greatly reduced wing venation, and elongate beadlike antennae. The adults feed only on aqueous material such as sap; the larval period of the life cycle is the part in which

have large heads with fairly long antennae, a large swollen thorax, and a cylindrical abdomen. In all the true mosquitoes and certain of the others the abdomen bears a dorsal breathing tube or plate on the eighth segment. In the main, mosquito larvae feed on microorganisms and organic matter in or on the water. A few groups are predaceous and feed solely on other mosquito larvae. The pupae, which are called tumblers, are also aquatic, free living, and active. Their breathing tubes are situated on the thorax. Adult females of a few species and males of all mosquito species feed only on nectar or water. But unfortunately in most species the females seek a blood meal, which under natural conditions is necessary for reproduction.

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**Simuliidae, black flies.** This family, often referred to as buffalo gnats, has aquatic larvae and pupae and bloodsucking adults. likmost of the Tood is consumed. Many genera of the family are gall makers, and it is by these galls, especially on willows, deciduous trees, and many herbs, that the family is known to most observers. The family exhibits a wide range of other habits. Some larvae are predaceous, feeding on mites and small insects, fig. 332; others feed on developing plant seeds; some feed on decomposing organic matter; and still others feed in or on the tissues of leaves or stems of plants. To the latter category belongs the most notable economic species of the family, the hessian fly *Phytophaga destructor*, fig. 333; the larvae feed in the lower stems of grasses and are especially injurious to wheat and barley.

#### SUBORDER BRACHYCERA

The adults of this suborder average larger and stouter bodied than the Nematocera and are stronger on the wing. The larvae have hooked or blade-shaped mandibles which work up and down, rather than sideways; the head is frequently much retracted within the thorax, fig. 335, and may have stout internal supports extending far into the body. About fifteen families are represented in North America; some of them are abundant, and in one, the Tabanidae or horse flies, the adults are voracious bloodsuckers.



Fig. 333. The bessian fly *Phytophaga destructor*. *a*, female fly; *b*, eggs, one at hatching; *c*, larva; *d*, bead and breastbone of same; *e*, pupa; *f*, puparium; *g*, infested wheat stem showing emergence of pupae and adults; *h*, antennae, male and female. (From U.S.D.A., E.R.B.)

Tabanidae, horse flies, and deer flies. The adults, fig. 334, are large-headed stout-bodied insects, often attaining a length of 25 to 30 mm., having strong wings with fairly complete venation and frequently a striking color pattern. The venation features a wide V-shaped cell  $R_4$ , which embraces the apex of the wing. The females are blood-



Fig. 334. A horse fly *Tabanus lineolus*. (From U.S.D.A., E.R.B.)

suckers; their mouthparts are developed for cutting skin and sucking the blood which oozes from the wound. The males feed on nectar. Eggs are laid in masses on stems or other objects growing over water; the newly hatched young crawl or drop into their breeding place. The larvae live in swamps or sluggish streams, staying in the bottom mire, and are rarely seen swimming in the clear water. They are predaceous, feeding on snails, insects, and other aquatic organisms. The larval body is tough and leathery, usually white or banded; the head is completely retractile within the thorax. The pupae are cylindrical and brown, normally formed in a mass of peat or dead vegetation which is damp but above the free-water level.

Farm livestock, especially cattle and horses, are often bothered by adult horse flies. Locally these pests may assume major importance in



Fig. 335. A robber fly *Promachus vertebratus*. A, adult; B, legless larva attacking white grub. (From Illinois Nat. Hist. Survey)

# The Orders of Insects

reducing condition of stock. Many species of horse flies and deer flies abound in marshy areas of the northern and humid montane areas of the continent and discourage vacationers and settlers.

Asilidae, robber flies. These are also large flies, fig. 335, usually with a humped thorax and elongate abdomen, but in some genera the body is stout, hairy, and brightly colored, resembling a bumble bee. In many genera also the lower part of the face has a beardlike brush of hair called a mystax. These flies are predators on other insects, capturing and eating bumble bees and dragonflies in addition to smaller forms. The adults are not easily frightened and are both conspicuous and easily taken in a sweep net. The larvae are found chiefly in soil and rotten wood and are predaceous on insects found there. Some of them are important natural enemies of white grubs and other soilinhabiting species attacking cultivated crops, fig. 335.

**Mydaidae, mydas flies.** This is a small family, but it contains some of our largest and showiest species. The antennae are clubbed, and the wings have a modified venation, the ends of many veins bending forward towards the anterior margin of the wing. The common eastern species *Mydas clavatus*, is black with an orange band and has a wing spread of 155 mm. The larvae, resembling large asilid larvae, are predaceous and found in rotten logs.

Other families of the Brachycera contain species of great diversity as regards structural peculiarities and habits. Most of them, for example, the family Dolichopodidae, are predaceous on other insects in both adult and larval stages and have free pupae; larvae of most species live in rotten logs or in soil and pupate there.

#### SUBORDER CYCLORRHAPHA

This is by far the largest of the three suborders of Diptera. It contains over forty families, many of them composed of a large number of species. For the most part the adults are relatively short and stout bodied, having broad wings in which vein  $R_{4+5}$  is undivided,  $M_2$  has atrophied, and  $Cu_{1b}$  is only a short recurved stub. The antennae are usually three-segmented, the third segment bearing a style or arista. The larvae have practically no external sclerites of the head capsule remaining, so that the head appears to be only a conical membranous anterior segment of the body. The two mouth hooks (mandibles) are connected with a complex internal pharyngeal skeleton, which provides the attachment basis for muscles controlling feeding. The fourth larval instar and the pupa are formed within the larval skin of the third instar, which hardens to become a puparium. The Cyclorrhapha may be divided into four series of families illustrating the stage or branching that they represent in the evolution within the suborder. These series are the Aschiza, Acalyptrata, Calyptrata, and Pupipara.

Series Aschiza. Here belong a few primitive families which are transitional between the Brachycera and Cyclorrhapha, such as the Phoridae (small flies, larvae living in rotting organic matter or as parasites in insects) and the Syrphidae. In these flies the emerging adult does not push off the cap of the puparium; at the time of eclosion the puparium simply splits down the dorsum as do those of the Brachycera which have puparia. The venation of the adults and well-developed internal pharyngeal skeleton of the larvae are typical of the Cyclorrhapha.

Syrphidae, flower flies, syrphid flies. Small to large flics, fig. 336, characterized by the upturned ends of some of the wing veins, and the presence of a veinlike thickening or *spurious vein* in front of media. These flies feed almost exclusively on flowers and have a remarkable ability for hovering apparently motionless in the air. Many are brilliantly striped or marked with yellow, red, white, and black; among the family are found mimics of various wasps, bumble bees, and other bees.



Fig. 336. A flower fly *Didea fasciata*. Right, adult; left, larva: center, puparium; *a*, anterior spiracle; *b*, caudal spiracles. (After Metcalf)



Fig. 339. Vinegar gnats *Drosophila melanogaster. a*, adult; *b*, antenna of same; *c*, base of tibia and first tarsal joint of same; *d*, puparium, side view; *e*, puparium from above; *f*, full-grown larva; *g*, anal spiracles of same. (From U.S.D.A., E.R.B.)

omyiidae, and Fanniidae (also scavengers). This series has evolved into some of the largest and most important families of the Diptera.

Gasterophilidae, bot flies. These are moderate-sized flies about the size of a honeybee, somewhat hairy in appearance, and are banded with black, yellow, or red, fig. 340. The larvae are internal parasites of horses, mules, man, and some of the larger wild mammals. In North America we have only the single genus *Gasterophilus*, represented by four species which infest horses. The horse bot fly *G. intestinalis* lays its eggs on the hairs of the horse's legs and forequarters. When the horse licks these eggs, they hatch, and the young larvae work their way through the mouth and throat tissues into the horse's stomach. Here the young bots attach to the lining and feed, growing into stout spiny grubs 15 mm. or more in length. They pass the summer and winter in the horse; in spring they loosen their hold, are passed by the horse, and pupate in the ground. The adults emerge in a few weeks.

**Muscidae, the house fly and its allies.** This family contains probably the world's commonest and most ubiquitous insect, the house fly *Musca domestica*, fig. 341. House fly larvae are white maggots which breed in many types of decaying organic matter. The adult flies transmit several dangerous and widespread diseases, including typhoid fever, several kinds of dysentery, cholera, and trachoma. Another widespread member of this family is the stable fly *Stomoxys calcitrans*, the adult of which inflicts a painful bite and attacks man and domestic animals. Its larvae breed in decaying organic matter; rotting piles of new grass and lawn clippings and manure are high on the list of favorites.

Anthomyiidae. Members of this family are similar in general



A



Fig. 340. Bot flies. A, Gasterophilus intestinalis; B, G. haemorrhoidalis. (From Canadian Department of Agriculture)

appearance to the house fly. Economic species in the family include the onion maggot *Hylemya antiqua*, fig. 342, and the cabbage maggot *Hylemya brassicae*, which feed on the roots of their respective hosts.

Oestridae, or warble flies. These, fig. 343, comprise a small group of fast-flying fuzzy bumble bee-like flies, parasites of mammals; some of



Fig. 341. Stages of the house fly *Musca domestica*. Puparium at left; adult next; larva and enlarged parts at right. (From U.S.D.A., E.R.B.)

them have a life cycle as specialized as that of the Gasterophilidae. Many species have a simple life cycle. For example, the sheep bot fly Oestrus ovis deposits young larvae in the nostrils of sheep; the larvae migrate into the sinuses and horns, where they mature. The mature larvae escape to the ground through the sheep's nostrils and pupate. Much more complex is the life cycle of the northern cattle grub Hypoderma bovis, which attacks cattle. The fly lays eggs on the hairs of the hind legs or flank of the animal. The larvae soon hatch, crawl down the hair, and burrow beneath the skin, making their way slowly through connective tissue to the oesophagus; this journey takes about 4 months. After 3 months' development in the oesophagus the maggots (still fairly small) journey through connective tissue again and come to rest beneath the skin in the lumbar region. Here the larvae attain most of their growth, each causing a swelling called a warble, provided with a small hole through the skin. Through this the larva first obtains air while maturing and then escapes to the ground for pupation.

**Tachinidae** (*Larvaevoridae*). tachina flies. This, fig. 344, is one leas prey on birds and occasionally are a pest of domestic fowl.

#### Key to Common Families

- 2. Abdominal tergites with only a single row of setae, fig. 346, Pulex; when telescoped, abdomen therefore appears to have a series of similar rows of setae Pulicidae



A



Fig. 340. Bot flies. A. Gasterophilus intestinalis: B, G. hacmorrhoidalis. (From Canadian Department of Agriculture)

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**Tachinidae** (*Larvaevoridae*). tachina flies. This, fig. 344, is one neas prey on birds and occasionally are a pest of domestic --

#### KEY TO COMMON FAMILIES

1.	Thorax extremely short, all three segments combined shorter than the first
	abdominal tergite, fig. 348 Tungidae (Hectopsyllidae)
	Thorax considerably longer than first abdominal tergite, fig. 346 2

2. Abdominal tergites with only a single row of setae, fig. 346, *Pulex;* when telescoped, abdomen therefore appears to have a series of similar rows of setae **Pulicidae** 



Fig. 343. A warble fly, the adult of the common cattle grub Hypoderma lineatum. (From Canadian Department of Agriculture)



Fig. 340. Bot flies. A. Gusterophilus intestinalis; B. G. haemorrhoidalis. (From Canadian Department of Agriculture)

appearance to the house fly. Economic species in the family include the onion maggot *Hylemya antiqua*, fig. 342, and the cabbage maggot *Hylemya brassicae*, which feed on the roots of their respective hosts.

**Oestridae, or warble flies.** These, fig. 343, comprise a small group of fast-flying fuzzy bumble bee-like flies, parasites of mammals; some of

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# The Orders of Insects

living as ectoparasites on the bodies of birds, mammals, or bees. So far as known, most members of the Pupipara have the feature, very unusual among insects, of uterine development of the young. The larvae are retained in the body of the female in a special uterine pouch and nourished on glandular secretions. When mature, the larvae are "born" and glued to the hair of the host, in which position they pupate immediately. The best-known species in North America is the sheeptick Melophagus ovinus, fig. 345. This is a wingless ticklike insect common locally on sheep. It belongs to the family Hippoboscidae. Also famous is the minute parasite of the honey bee, Braula caeca, the sole member of the Braulidae. This species lays eggs.

The origin of this series is obscure, but it probably arose from a primitive branch of the Acalyptrata. Px 9

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Fig. 345. The sheeptick *Melophagus or inus*. (From Kentucky Agricultural Experiment Station)

# ✓Order SIPHONAPTERA: Fleas

All adults are wingless, fig. 346, and have long stout spiny legs and short clubbed antennae which in repose fit into a depression along the side of the head. The mouthparts are fitted for piercing skin and sucking blood and consist of a beak, a pair of palps, and a pair of short blade-like maxillae. These insects are small, most of them 2 to 4 mm., but a few species attain a length of 6 to 8 mm. The larvae are slender and wormlike, fig. 347. They have round heads, no legs, and long hairs on each body segment. The segments of thorax and abdomen are similar in appearance. The mouthparts are minute and inconspicuous, of the chewing type. The pupae are formed in a cakelike cocoon made of earth or grass.

Fleas feed on the blood of mammals or birds and are found on the body of the host or in the nest or runways of the host. The eggs are

#### The Orders of Insects

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the host or in the nest. The eggs have no adhesive, so that, if laid on the host animal, they slip through the hair and fall into the litter of the nest or retreat, where they soon hatch. The larvae live in the soil or debris in the nest and feed on debris or grass. When full grown, the larvae spin an irregular cocoon in the nest of the host and pupate. The eggs, larvae, and pupae are seldom seen except by diligent search.

The adult fleas of most species are extremely active. They slip through hair or feathers with great ease; and in many species the body has combs of spines which further aid this progress. In some species the adults stay on the body of the host almost all the time; in others the adults stay in the nest and get on the host only for feeding periods. For this reason it is necessary to collect both from the bodies and in the nests of the hosts to be sure of finding all the species connected with it.

The order Siphonaptera is not a large one. The North American fauna includes about sixty genera and over two hundred species. The



Fig. 347. Larva of a flea. (From Illinois Nat. Hist. Survey)

great percentage of these occur with native mammals, especially various kinds of mice, shrews, ground and tree squirrels, gophers, and rabbits. Bears, beavers, coyotes, and many others support a flea fauna. A few fleas prey on birds and occasionally are a pest of domestic fowl.

#### Key to Common Families

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**Pulicidae.** Many species of this family are of especial importance to nan. The dog and cat fleas, *Clenocephalides canis* and *C. felis* and the numan flea *Pulex irritans* attack man and invade dwellings, causing great discomfort and inconvenience. The bites inflicted by the fleas are painful, usually cause hard itching swellings, and may be the source of secondary infections through scratching. Most important of the fleas are certain rat species, particularly *Xenopsylla cheopis* (and *Nosopsyllus fasciatus* of the Ceratophyllidae) which transmit the dread bubonic plague from rats to man. In their role as disseminators of this disease, which many times has spread like wildfire through crowded cities in many parts of the world, fleas have been responsible for millions of human deaths. At present, public-health organizations all over the globe keep close watch on the rat-flea-plague focal points, in an effort to break up new incipient outbreaks of the disease, through control of the rats and fleas.

Two species of Tungidae, the sticktight and chigoe fleas, have unusual habits in contrast with other fleas. The females of both species are minute and attach themselves firmly to the host, feeding more or less continuously. The sticktight flea *Echidnophaga gallinacea*, fig. 348, attacks domestic fowl, attaching to the face and wattles. The chigoe *Tunga* 



Fig. 348. The sticktight flea Echidnophaga gallinacea. Left, infested head of rooster (dark patches are clusters of fleas); right, adult female. (From U.S.D.A., E.R.B.)

# The Orders of Insects

*penetrans* attacks man, especially on the feet. It burrows beneath the skin and forms a painful swelling out of which protrudes only the end of the flea's abdomen. Both species drop eggs to the ground and have typical flea metamorphosis.

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CHAPTER

HE existing insect fauna that we see about us is the result of eons of change and evolution and a struggle for existence among the insects. When they first arose as a group, insects were undoubtedly few in numbers of both individuals and species; furthermore, they had only a limited range of ecological conditions under which to live. As the entire organic world developed, there evolved in the insect group members having biological and physiological characteristics enabling them to take advantage of new ecological niches. If we look over the existing insect fauna as a whole, it is apparent that certain orders, such as the Lepidoptera and Hymenoptera, are large and flourishing, exhibiting a great diversity of structure and habits, but they are relatively young orders in geologic time. We have other orders, for instance, the Mecoptera and Ephemeroptera, that are represented now by relatively few remnants; yet their geological records indicate a beginning of great antiquity. These remnants, like the horsetails and ginkgoes of the plant world, are lonely survivors of what may have been once great orders. Some an-



Fig. 349. Family tree of the insect orders plotted against geological time scale. Solid lines, branch of order after earliest known fossil; broken lines, portion of dating suggested by various methods of deduction. (1) This point refers to *Rhyniella praecursor;* (2) this branch also contains the Protohemiptera, Megasecoptera, and possibly other extinct orders; (3) this branch also contains the Protoelytroptera (Protocoleoptera), Caloneurodea, Protoperlaria, and possibly other extinct orders. (See also fig. 163, p. 204.)

cient orders, such as the Palaeodictyoptera, were dominant insect groups in the geologic past, but apparently were unable to change with climate or compete with new forms and are long since extinct.

The principal avenue of discovery for knowledge of this past history is through fossil remains from strata, or layers of rock, representing the various periods of geologic time. Insect fossils are not found in so many places as are fossils of some other groups because of special conditions needed to insure adequate preservation. Because of their small size, the delicacy of their parts, and the minute nature of identification criteria, insect remains must be preserved in a medium of extremely fine texture providing a grainless matrix. Satisfactory materials are mud and volcanic ash, resulting in shales; concretions; fine humus, such as coal; and resin of coniferous trees, giving amber. Fossil-bearing deposits have been found in scattered localities all over the world. Some in North America are productive of valuable additions to the record. Along Mazon Creek, near Morris, Ill., are found iron nodules, or concretions, containing Pennsylvanian (Paleozoic) insects. In Kansas and Oklahoma deposits have been explored containing large numbers of Permian insects. In several localities in the western states occur deposits containing abundant fossils of Cenozoic insects, and other deposits containing a few Mesozoic forms. In northern Manitoba there have been located deposits of amber containing many insect remains thought to be Cretaceous in origin.

Eras	Remarks
Cenozoic—Modern life Glacial—Pleistocene Pliocene Miocene	Age of man, extending to present
Tertiary { Oligocene Eocene Paleocene }	Bloom of modern insect genera
Mesozoic—Medieval life Cretaceous Jurassic Triassic	Age of reptiles. Rise of specialized orders and modern insect families, including some modern genera. Rise of primitive mammals and of flowering plants
Paleozoic—Ancient life	Rise of modern orders of insects
Pennsylvanian Carboniferous	Rise of primitive reptiles and insects
Devonian }	Age of sharks. First extensive land floras, first amphibians
Silurian Ordovician Cambrian	Age of invertebrates. Rise of land plants
Proterozoic—Age of primitive invertebrates	Few primitive invertebrates
Archeozoic-Age of unicellular life	Primitive organisms

TABLE 5. CONDENSED GEOLOGIC TIMETABLE REPRESENTED BY THE FOSSIL RECORD

In the main, wings are the principal insect structures clearly preserved in fossils. In amber insects other structures are frequently seen with 7



Fig. 350. A fossil from an iron nodule, Mazon Creek, Ill.; hind wing of an ancestral mayfly *Lithoneura mirifica*. A, photograph of fossil impression; B, reconstruction of venation. (After Carpenter)

great clarity, resembling a balsam preparation on a microscope slide, fig. 351. In shale and concretion specimens, however, it is only occasionally that the structure of body and appendages can be determined.

Although there are tremendous gaps in the known insect fossil record, enough has been discovered to gain a fair idea of the general trend. In the brief account that follows, the main emphasis has been placed on the biological and ecological implications of the evidence. This is given in relation to the geological timetable in general use, Table 5, with which the student should become familiar.





Fig. 351. Cryptoserphus succinalis, a hymenopteron described from Baltic amber. A, drawing made from specimen in the amber block shown in B. (After Brues)

Table 5 represents the period of evolution of all known life on the earth. This time is established by various geologists and physicists at from 1000 to 2000 million years. If we take the thickest known deposits laid down in all these periods and add them together, it would result in deposits 80 miles deep. Such a mass of material means the wearing

away to sea level, one after another, of more than 20 ranges of mountains like the present European Alps or American Rockies. Visualize the amount of time it would take erosion to do this, and then add the much longer quiescent periods when the low-lying lands furnished little sediment, and we have some idea of this length of time.

## EARLY GEOLOGIC ERAS

Several long eras passed in the geological record before insects appeared. The first forms of life were unicellular organisms which probably began before the Archeozoic. From these evolved the many kinds of multicellular plants and animals. Through the Archeozoic and Proterozoic for which no good fossils are known, life was presumably marine. The same was true through the Cambrian and Ordovician periods of the early Paleozoic, when the seas were shallow, extensive, and warm. At this time the Arthropods were well developed, represented by Trilobita, complex Crustacea, and Eurypterida. All the animal phyla as we know them today are represented in the fossils of these periods, including the first vertebrate fossils, primitive fish. It is interesting to speculate on the appearance of the world at this time. The land was barren, at most with encrustations of lower plants, and away from the seas probably had not even these signs of living matter.

In the Silurian came the first feeble beginnings of a land biota, with the appearance in the fossil record of a few land plants and the first known air-breathing animals, scorpions, and myriapods. It seems almost certain that primeval wingless insects also must have evolved in this era. All these animals were probably littoral, occurring along the beaches in the warm moist Silurian climate.

The Devonian and Mississippian periods are termed the "Age of Sharks" by geologists. Although these animals attained great evolutionary development, the event of most interest from an entomological viewpoint was the rise of land biotas. Forests developed along stream edges and in low-lying swamps. This development, providing shelter, humid conditions, and food, was essential for the extension of animal. life beyond the limited areas of the beaches. The fossil record of the land fauna is fragmentary but demonstrates the presence of amphibians, diplopods, and a few specimens (*Rhyniella praecursor* from the Devonian of Scotland) which bear a striking resemblance to modern Collembola, fig. 353. Judging from the sudden appearance of several diverse winged groups in the Pennsylvanian, fig. 354, it is practically certain that winged insects evolved in the Devonian, at least by the Mississippian, even though no fossil evidence is yet known to substantiate this deduction.



Fig. 352. Restoration of two Silurian scorpions, among the earliest known air-breathing animals. The similarity between these and recent forms is remarkable. *A*, dorsal view of *Palaeophonus nuncius; B*, ventral view of *P. hunteri*. (From Pirsson after Pocock)

We may infer from the scarcity of terrestrial animal fossils in this period that, even after the forests had become stabilized, their successful invasion by land animals was a slow process.

## LATE PALEOZOIC ERA

#### Pennsylvanian

In this second period of the coal measures, often called the Upper Carboniferous, luxuriant, tropical swamps were more extensive than at any other time in the earth's history, supporting a varied flora and fauna of



Fig. 353. Rhyniella praecursor, a Devonian fossil bearing a striking resemblance to Collembola. (After Aubert)

ancient types, fig. 355. In this setting occurred the oldest extensive insect fauna of which we have record. Specimens from even the earliest Pennsylvanian beds are all of winged insects fully as well developed regarding general structure as are some existing today. The 1500 species of fossil insects known from this period show further that already two large groups of orders had developed, the ancient flying insects or Pale-





Fig. 354. Pennsylvanian insects and a spider. *A*, the largest known insect of all time, *Meganeuron monyi*, from the coal measures of Belgium. A reconstruction by R. J. Tillyard. About one-seventh natural size. *B*, left, a cockroach *Aphthoroblattina johnsoni*; center, a paleodictyopteran *Stenodictya lobata*; right, a spider *Eophtynus prestwichii*. (After Schuchert and Dunbar, A textbook of geology, Pt. II, Historical geology)

optera and the folding-wing insects or Neoptera. The Paleoptera were represented by the Ephemeroptera and by several orders now extinct, including the Paleodictyoptera, fig. 354B, and Protodonata (ancestral to the true Odonata). The ancestral Ephemeroptera, fig. 350, were primitive forms having the front and hind wings the same size, whereas modern forms have greatly reduced hind wings. The Neoptera were



Fig. 355. Pennsylvanian flora and amphibia, as restored by J. Smit. In the background are *Sigillaria*, with tree ferns and conifers in the middle distance. In the foreground are *Calamites* and seed-bearing fernlike plants. Amphibia are represented by a small four-limbed microsaurian (*Keraterpeton*), a large-headed form (*Loxomma*), and a snakelike gill-bearing stegocephalian (*Dolichosoma*) from Linton, Ohio. (From Schuchert after Knipe, A textbook of geology, Pt. II, Historical geology)

represented by the Cursoria (cockroaches) and by a group of orders now extinct but considered close relatives of the orthopteroid orders, including the Protorthoptera, Caloneurodea, and Protelytroptera (includes the Protocoleoptera which are not related to the beetles). So abundant are cockroach fossils in these strata that the Pennsylvanian is called the "Age of Cockroaches."

It is thought that the nymphs of several of these insect orders were aquatic or semiaquatic and lived in the swamp pools which were extensive in many areas of the earth's surface. Here also insects attained their greatest size, including Protodonata (primitive dragonflies) with a wing span of 29 inches.

Insects and amphibians dominated the swamps. The competition between these two groups must have been ferocious for, whereas the adult amphibians undoubtedly fed on insects, many of the large predaceous insect nymphs surely fed on the vulnerable larval amphibians. This competition, together with competition among the insects themselves, may have exerted a strong evolutionary pressure toward the development of large size in certain insect groups. The climate would not discourage this tendency but rather encourage it by providing uniform growing conditions throughout the year. In spite of the glamor surrounding these giant insects, they were nevertheless a minority in their class. The great bulk of the insects from the Pennsylvanian were smaller than their closest living relatives.

#### Permian

During this period many new types of both animals and plants evolved, including forms thought to have been better adapted than any of the Pennsylvanian forms to cooler and drier climates. This increased diversity of biota was associated with climatic changes in many areas, following extensive mountain making in late Mississippian and culminating in the Permian.

Thousands of Permian insect fossils have been collected in Kansas and Oklahoma. Evidence from these and other sources indicates that all the common Pennsylvanian insect orders continued into the Permian, and many new ones appeared. These include the Plecoptera and three hemipteroid orders, the Corrodentia, Thysanoptera, and Hemiptera. Here also appear five neuropteroid orders, the Coleoptera, Rhaphidiodea, Megaloptera, Neuroptera, and Mecoptera. Some members of the Megaloptera and Neuroptera were remarkably similar in basic features to families existing today. It is plain, therefore, that complete metamorphosis had evolved before the end of the Pennsylvanian, and that

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Fig. 356. Photograph of a fossil of a primitive insect *Dunbaria fascilipennis*, from the Early Permian period (Late Paleozoic). (From Mavor, General biology, by permission of The Macmillan Co.)

the basic ancestors of our modern fauna evolved before or during the Permian.

Few of the older orders prospered beyond the Permian. The Ephemeroptera, Protodonata, and Cursoria continued, but, judging from the fossil record, all the other abundant coal measure orders became extinct at the end of the Permian. Some investigators believe that widespread arid or cold conditions caused this extinction of primitive forms, whereas others believe that competition with new forms caused the change in biota. More likely a combination of many factors brought about these results.

## MESOZOIC ERA

Relatively few early Mesozoic fossil insect deposits have been discovered; hence we have a very imperfect picture of insect evolution in this cra. In addition, apparently a long period elapsed between known deposits of late Paleozoic and early Mesozoic, with the result that there is a marked advance in many Mesozoic insects in comparison with their relatives of the Paleozoic.

## Triassic

In this period great areas were desert or semidesert, caused in North America by the extensive emergence of the continent. Forests were re-

stricted to low-lying areas in river basins and coastal plains. These medieval floras were strange in their varied types of rushes, ferns, cycads, and conifers. This plant world was populated in the main by dinosaurs, a group of reptiles which became dominant and for which the Mesozoic is called the "Age of Reptiles." These were the most extraordinary animals the world had ever seen, as diversified in form and size as are living mammals. Among them were huge swift carnivorous forms; also sluggish duck-billed types feeding on swamp vegetation; other vegetarians had great snakelike necks for browsing on tall trees. In addition to the dinosaurs there were many small reptiles of varied habit and a few very primitive mammals. The varied dinosaur types were the ecological equivalents in the Mesozoic of the herbivorous, carnivorous, and insectivorous mammals of today.

In this period fossils of the true bugs, the suborder Heteroptera, are first found, but these forms are so well developed that the group undoubtedly occurred in the Permian. By this time most of the ancient orders such as the Paleodictyoptera had apparently died out completely, and the general character of the fauna was more like that of today. Many groups had developed specialized habits of feeding familiar to us in present-day insects. A striking example of this is the preservation in petrified Triassic trees of feeding tunnels typical of modern Buprestidae and Scolytidae, fig. 357. The Orthoptera and Trichoptera apparently evolved at this time.

#### Jurassic

In the early part of this period conditions were somewhat as in the Triassic. At this time arose the curious assemblage of flying reptiles called Pterodactyls. Some of these were huge, soaring like buzzards. Many frequented ocean shores and probably fed on fish, but small types flitted about over the ground and probably were insect feeders.

The insects were smaller than their present-day relatives. Two orders appear for the first time—Dermaptera and Hymenoptera, most of their representatives belonging to modern families. In middle Jurassic the climate moderated over the entire world, and insects increased in size and numbers. It is probable that the plant-feeding habit became better established on the varied floras which developed at this time. As far as is known, plant flowers were inconspicuous, and it is unlikely that many insects visited them.

Toward the close of Jurassic time, extensive mountain uplifts increased the areas of the world having varied climatic zones and definite winters. These conditions probably helped to establish the ascendency of those plant and animal land groups which possessed provision or adaptations for overwintering.



Fig. 357. Feeding tunnels of A, a buprestid beetle, and B, a scolytid beetle in perified Triassic trees, Petrified Forest National Monument, Ariz. (After Walker)

## Cretaceous

Much of the modern plant and insect life was established in this period. The Angiosperm flowering plants had begun their ascendancy over the spore-bearing floras and the archaic gymnosperms (the cycads and their allies), so that by the end of the period 90 per cent of the plant genera were of the woody kinds known today, including elms, oaks, figs, magnolia, beech, birch, and maple. Sedges and grasses appeared. Although most of these were wind-pollinated groups, some of those mentioned and many other genera known from this horizon were undoubtedly insect-pollinated as they are today. The evolution of insectpollinated plants and pollen- and nectar-feeding insects were complementary developments. This association, which probably started in the Jurassic, was the beginning of a partnership which has proved highly successful for both. Today over 65 per cent of the flowering plants are insect-pollinated, and 20 per cent of the insects, at least in some stage of their development, depend on flowers for food.

The relatively few Cretaceous insect fossils are varied in taxonomic composition and include stoneflies, dragonflies, cockroaches, springtails, midges, aphids, caddisflies, and a large number of parasitic Hymenoptera. Many of these are close relatives, or actually members, of existing



Fig. 358. Suggested geography of Upper Cretaceous. Stippled areas are principal epeiric seas. P. I. indicates Peninsular India, the possible area of isolation of many tropical genera. (Compiled from various sources)

genera; some others represent genera of a primitive nature. A few are of exceptional interest because they represent families intermediate between existing families; an example is the collembolan family Protentomobryidae described from the Cretaceous amber of Manitoba, a family having distinctive characteristics yet intermediate in antennal structure and body segmentation between the Recent families Entomobryidae and Poduridae.

The rise in the Cretaceous of many favorable host plants must have encouraged great evolutionary development among phytophagous insects. The appearance of numerous parasitic Hymenoptera indicates that populations of their insect host species were at least fairly large and that the present-day interrelations of the groups had already been established. It is interesting to note that reptiles, which had dominated the land life and much of the aquatic up to this time in the Mesozoic, were rapidly being supplanted by the primitive land mammals. A circumstance in the Cretaceous of great importance in determining later composition of the world faunas was the widespread dispersal of many genera.

Throughout geologic history the shape of the continents as well as their topography has changed. For instance, North America has sometimes been reduced to half its present size and also has been increased far beyond the present margins and has had various connections with Northern Eurasia. North and South America have been connected broadly at some times, widely separated at others. One has only to allow a little freedom of imagination to visualize what this has done to the migration and isolation of floras and faunas.

On the basis of both geologic and biogeographic data it seems that during the latter part of the Cretaceous mountain chains and many land bridges, fig. 358, provided avenues for both temperate and tropical forms to disperse between Australia, Eurasia, North America, and South America. Changes in land bridge conditions caused populations of various widespread forms to become isolated in different areas. Each isolate gave rise to a new evolving line. Some of these isolated lines have remained fundamentally little changed to the present; others have evolved at a more rapid rate and are now quite different from their Cretaceous progenitors.

# CENOZOIC ERA

The Cenozoic prior to the glacial age consists of five distinct periods, the Paleocene, Eocene, Oligocene, Miocene, and Pliocene, collectively called the Tertiary. The last period of the Cenozoic is the Pleistocene

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or glacial age. Of great significance in the present distribution of insects were the continental and climatic conditions of the Cenozoic.

Through the Tertiary as a whole there occurred a vast development of plant species and diverse kinds of modern birds and mammals. Certain insects had unquestionably become associated with them back in the Mesozoic and continued to evolve along with their hosts. For example, bugs of the family Polyctenidae (ectoparasites of bats) have been associated with bats so long that the parasite bug genera essentially parallel the host bat genera as regards phylogeny and distribution.

#### Paleocene

This was a time of accelerated mountain uplift, when the Laramide orogeny reached its peak. Temperate areas were cooler than in the Cretaceous. It is probable that warm-adapted groups were restricted to small equatorial areas, but that cool-adapted forms spread freely between Eurasia and North America.

#### Eocene

In this period conditions were apparently reversed. General temperatures reached a higher point than at any other time in the Cenozoic. It is estimated, for example, that isotherms in North America were nearly 30° north of their present location. As a result, cool-adapted forms were probably restricted to the higher altitudes in mountainous areas, and warm-adapted groups probably dispersed between the continents more freely than at any other time. It is likely that the greatest number of our tropicopolitan genera became world-wide in distribution at this time. For the world as a whole, practically every large genus or tribe of insects had evolved by the end of this period.

#### Oligocene

More moderate temperatures appear to have followed the Eocene, together with land connections between Asia and North America. Of especial importance at this time was the formation of a broad belt of temperate deciduous forest, composed of oaks, linden, sycamore, and other trees, which extended from the Atlantic coast of North America, across the continent and completely across Eurasia. This temperate belt was apparently north of its present range in America, and possibly covered much of the northern half of the continent. South of the deciduous forest belt the continent was warm temperate to subtropical. What

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Fig. 359. An osmylid lacewing (Neuroptera) Lithosmylus columbianus, from the Oligocene shales of Florissant, Colo. (Photograph loaned by F. M. Carpenter)

is now the Great Plains area was arid or semiarid scrub, possibly as far north as Nebraska, much like that now covering much of northeastern Mexico and western Texas. The stream banks and marshes of this area supported luxuriant forests, which were probably more extensive towards the southeastern part of the continent. This plains area was much lower in elevation than at present, much of it only a thousand feet in elevation where it is now five or six thousand. The older ranges of the Rocky Mountains flanked the semiarid area westward, but it is likely that the more northern ranges were low or not yet formed. Such a situation would account for the continuous transcontinental belt of temperate deciduous forest.

At Florissant, Colo., large numbers of insect fossils have been found, preserved in fine sediments of volcanic ash which settled in the ponds and backwaters at the foot of the old Rocky Mountains along the edge of the generally semiarid area. The genera represented by this Oligocene fauna indicate that the fossilized insects came from an extremely varied assortment of habitats, ranging from tropical to cool temperate, and show that the Oligocene insect fauna contained fully as many genera as does that of the present day.

Some of the insect genera found in the Oligocene beds at Florissant no longer occur in North America but are known from other regions.

Species of the genus *Glossina* (the tsetse flies, carriers of trypanosomiasis) were fossilized in these beds, but at present the genus occurs only in equatorial Africa. Fossils of the curious lacewing family Osmylidae occur in the Florissant Oligocene, fig. 345; living species are restricted to tropical areas of the world.

#### Miocene

It is thought that little change from Oligocene conditions occurred in the earliest part of this period. Soon, however, majestic orogenic movements took place in many parts of the world. In Asia the highest ranges of the Himalayas arose, and in western North America many ranges were re-elevated and others pushed up. The subsequent arid conditions to leeward of the new mountains disrupted the northern trans-Holarctic forests and brought about many features of the landscape that exist today.

The Great Plains area became increasingly elevated and winter temperatures dropped, probably over the whole continent. The temperate deciduous forest became restricted to the eastern part of the continent and has never been reconnected with any of the Old World remnants. In this isolated condition the insect fauna of our eastern deciduous forest has evolved many distinctive genera or species groups, many of them still moderately or completely restricted to this forest. The Great Plains area gradually became grassland, which replaced the temperate deciduous forest to the north, and much of the semiarid scrub flora to the south. It is believed that the grasslands of the Great Plains had reached their present extent by the end of the Miocene.

#### Pliocene

The mountain making of the Miocene continued through this period, as did the southward movement of tropical and temperate boundaries. There is evidence of some faunal interchange of cool-adapted insect groups between northwestern North America and northeastern Asia, but apparently very little if any other faunal interchange involving insects of other ecological characteristics. Very likely the tropical elements in North America had shrunk to about their present areas by the end of the Pliocene.

#### Pleistocene, the Great Ice Age

After the extensive mountain elevation of the Pliocene, there was a temperature reduction over the entire world. Glaciers were formed in MACGINITIE, H. D., 1953. Fossil plants of the Florissant beds, Colorado. Carnegie Institution Washington, Publ. 599. 198 pp.

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CHAPTER

HEN we look at life in natural surroundings, we see that the landscape is broken up into different types of interlocking areas, such as prairies, forests, deserts, lakes, and streams. The type of vegetation, that is, whether it is desert, prairie, or forest, is determined by climatic factors of temperature, rainfall, and evaporation. In the main, forests occur in regions with a high rainfall, prairies in regions having lower rainfall, and deserts where rain is scant and evaporation high. Types of aquatic habitat depend on slope, rainfall, and a large variety of local factors including acidity and leaching qualities of the soil, drainage, seepage, and temperature. The vegetation type of the landscape is therefore a reflection of the climate, and widely separated areas having similar climate have the same kind of landscape aspects. Each of these is divided into smaller units. A forest, for instance, has an edge area and may have small open areas or glades scattered through it; in one place the forest may be well drained and high, with a preponderance of oaks and hickories, in another place it may be low and swampy, having elms, gums, and other trees different from those in the better-drained areas.

Each of these fairly uniform areas is considered by the ecologists as the biological unit of natural areas and is called a community. Each community has a definite set of animal species living in it, a set that persists year after year with only minor change. The animal species living in similar communities are practically the same. Thus oak-hickory communities in Wisconsin, Indiana, Missouri, and Oklahoma are each populated by very nearly the same species of animals.

Although an elm or gum forest community contains a fair proportion of the species found in an oak-hickory community, it lacks many species found there but possesses in addition species distinctive to itself. If we go further afield, a prairie community has a species make-up differing greatly from that of a forest community, and both have almost nothing in common with aquatic communities.

Examining communities more closely, we see that the animal species in each are stratified in various ways. In terrestrial communities some of the animals live in the soil, some on the herbs, and some in the trees, if the habitat is a forest. There is a vital relationship between various organisms in the community, as between herbivorous animals and the plants they eat, or between predatory animals and their prey. Altogether these coordinated relations make a network of dependency that binds all the diverse individuals of a community into a biological whole.

There are two ways of looking at these phenomena. One is from the standpoint of the community as a whole, studying its development. population, the interrelationships of its component species, and the distribution of the kinds of communities over the face of the earth. Study from this viewpoint is synecology. The other way is from the standpoint of individual species involved, to find out in what communities they are distributed, what niches they occupy, and why. This study is autecology. Synecology and autecology together are the broader field of ecology. which may be defined as the study of the relations between living organisms and their environment. A treatment of ecology as a whole is beyond the aim of this book. There is, however, a great deal of important information about insects in relation to their environment that car best be organized according to ecological factors. This material having a direct bearing on insects is dealt with in this chapter. Ecological considerations are becoming of increasing importance in insect studies and are giving valuable aid to taxonomy, zoogeography, and insect control

## AUTECOLOGY

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Each insect species is specially adapted to live in a particular "niche' in the community. In a sense, the species is a prisoner in its abode, be-

cause there are various environmental factors such as weather and food that restrict the species to its type and habitat. The limits of these factors within which the species can exist are spoken of as its ecological tolerance, which varies for different species in regard to the several factors involved. Correlated with its ecological tolerance, the individuals of a species have instinctive reactions which tend to insure that the individuals will always move to the place in the community which affords optimum conditions for their success. Both ecological tolerance and behavior are distinctive for each species; hence it is highly important to obtain the accurate identification of species which are subjects of ecological study.

Most ecological studies concerning insect species fall into one or more of three important categories: (1) environmental factors that determine where the species may live; (2) instinctive reactions or tropisms that enable the insects to find suitable living conditions; and (3) the effect of the sum of all these on the distribution and abundance of the species. This third category is termed *population dynamics*.

#### **Environmental Factors**

The most important environmental factors concerning the distribution and abundance of insects are climate, physical and chemical conditions of the medium, food, enemies, and competition.

#### WEATHER

The weather forms a blanket over the entire community and directly or indirectly affects conditions and organisms in practically all parts of the community. Weather is a composite condition of which light, temperature, relative humidity, precipitation, and wind are the most important ecological components. It is not the annual averages of these components (climate) which affect the species populations, but conditions from day to day. A single night's frost, for instance, may decimate a population of a subtropical insect, although the average temperatures for that year may be high. Similarly local conditions differ notoriously, and may result in great population differences in a short distance. In hilly country the single night's frost would be most severe in the valleys and might not affect the portion of our insect population on the hill crests.

LIGHT. Little definite information is available concerning the ecological effect of wavelengths making up the greater part of sunlight (ultraviolet to red). In most experimental work on the subject there is considerable doubt if light is the only variant factor involved. A great number of insects normally diurnal in habit have been reared success-

fully for many generations either in artificial light deficient in many wavelengths or in total darkness. It would appear, therefore, that the effect of light on most insects is indirect and expressed through quality of food caused by plant reactions to light. Light, however, is an extremely important factor in insect behavior and is considered in this relation in the section on tropisms.

TEMPERATURE. In the lives of insects temperature is one of the most critical factors. Insects are cold-blooded, so that within narrow limits their body temperatures are the same as that of the surrounding medium. Except for a few unusual instances, insects are unable to control the temperature of their medium; instead they have physiological adjustments that enable each species to survive temperature extremes normally occurring in its ecological niche (see p. 139).

The honeybee is the best-studied example of an insect that regulates the temperature of its surrounding medium, in this case, the air within the hive. In summer the hive is maintained at about 95°F. If the temperature rises above this point, bees at the hive entrance set up ventilating currents by fanning their wings, and other bees may bring water and put it on the comb to obtain the cooling effect of its evaporation. In winter the bees keep the hive up to a safe temperature by heat obtained through oxidation of foods in the insects' bodies. Other social bees and ants exercise a certain amount of control over nest temperatures.

Effects of temperature are shown in two ways, the effect on rate of development, and the effect on mortality.

EFFECT ON DEVELOPMENT. Because they are cold-blooded and their body temperature reflects that of their medium, the temperature of insects is not constant. The chemical reactions of metabolism therefore automatically speed up with an increase in temperature. As a result we find that temperature has a marked effect on insect development and activities. Now all chemical reactions do not respond at the same rate to temperature increase, and certain physical factors, such as the solubility of gases in liquids, tend to produce unfavorable metabolic conditions as temperature increases. As a result, insect development is not equally responsive to changes over the entire temperature scale. There is a definite low point at which development stops, called the threshold temperature; this point may be 10° to 50° above the actual point of death from low temperature. There is also a definite high point for each species at which development stops; this point is usually very close to that of lethal high temperature.

Between these two points, rate of development responds to temperature changes. But the response is not uniform throughout the insect world. Each species has its own individual rate of development. Figure 361 illustrates differences in rate of development for four species of

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Fig. 361. Rates of development of four species of grasshoppers at constant temperatures from 22° to 37°C. (= 71° to 98°F.). (After Chapman, Animal ecology, by permission of McGraw-Hill Book Co.)

grasshoppers. Within a species each developmental stage may have a different rate of development. This is well illustrated by the various stages of the Japanese beetle as graphed in fig. 362. The eggs and pupae have a much higher rate than do the larval stages, at identical temperatures.

An interesting example of dissimilar developmental rate is shown by eggs and nymphs of the red-legged grasshopper. The rates of development for eggs and nymphs are extremely different from each other. For the nymphs the developmental rate increases steadily with increase



Fig. 362. Comparison of the rates of development of each stage of the Japanese beetle. Temperature scale in centigrade,  $10^{\circ}$  to  $40^{\circ}$ C. (=  $12^{\circ}$  to  $104^{\circ}$ F.). Numbers 1, 2, and 3 refer to the three larval instars. (After Ludwig)

in temperature to a point close to the lethal high temperature. The rate for the eggs increases with the lower range of increased temperature and then decreases with additional temperature increase. With the eggs this point of decreased development is reached far below the lethal temperature.

These cases show the necessity of studying separately the various stages of the life history in order to obtain accurate information on the developmental phase of the species.

SEASONAL COORDINATION. The different rates of growth of species feeding on plants or cold-blooded animals are correlated extremely closely with the growth rate of their hosts. The result achieved is that, when the host has reached a point favorable for a certain insect to attack it, that insect has reached the proper stage to make the attack. Let us examine this relation in two species of Hymenoptera, a sawfly (Tenthredinidae) and its ichneumonid wasp parasite (Ichneumonidae). The sawfly adults emerge first early in spring at a time when the host plants have young leaves suitable for oviposition. The eggs hatch 1 or 2 weeks later when the plant is in the midst of vigorous growth and is providing a bountiful supply of food for the larvae. The ichneumon wasp has either a slower development or one that starts at a higher temperature, so that the adult ichneumonid emerges about 3 or 4 weeks after the adult sawfly. At this time the sawfly larva is nearly full grown and at the right stage for the ichneumon adult to lay eggs on it.

Another example is a group of aphids or plant lice (Aphididae) feeding in the spring on apple. The developmental rate of the overwintering eggs is such that the young aphids hatch at almost the exact time the apple buds first begin to open in spring. The aphids feed immediately on the minute leaves of the opening buds.

So constant is this coincidence of certain insect events with definite plant events that the plant phenomena (which are easy to see) are used as guides in many control programs. There are "bud sprays" for early aphid control, "petal-fall sprays," "calyx sprays," and so on, in which plant development is taken as a griterion for insect development.

EFFECT ON MORTALITY. If the temperature range that insects can withstand varies tremendously with the species. The most heat-resistant insects known die at temperatures of 118° to 125°F. Probably the great majority have a high lethal point from 100° to 110°F. Species that live in cool places have correspondingly lower heat tolerances, such as the mountain genus *Grylloblatta*. The optimum for this group is about 38°F, and normal activity occurs between the approximate range 30 to 60°F; heat prostration occurs at about 82°F.

<sup>5</sup> Temperatures low enough to cause death vary as much as lethal high temperatures. Insects of tropical origin usually succumb as the tem-

perature drops near freezing, fig. 363. The confused flour beetle, for example, will die in a few weeks at 44°F. Many insects die at temperatures only a few degrees below 32°F. (0°C.). Hibernating stages of most northern insects are remarkably resistant to cold. The hibernating pupa of the promethea moth, for example, can survive continued exposure to -31°F., and some other insects are known to survive -58°F.

Insects occurring in regions having freezing winters almost invariably exhibit a different temperature tolerance in each stage of their life cycles. At least one stage is resistant to low temperatures, and in this stage the species is able to withstand the winter temperatures (see p. 139). Parasites of warm-blooded animals are exceptions. The resistant form may be the egg, nymph, larva, pupa, or adult. In most cases only a single stage is cold-resistant; when winter arrives, the resistant form lives, and individuals in any other condition die. Thus in chinch bugs only the adults are cold-resistant; when extremely low winter temperatures occur, the adults live, and any nymphs still remaining in the field die.

In their natural environment insects are well adjusted to prevailing



Fig. 363. Days of exposure required for assuring complete mortality of eggs, larvae, pupae, and adults of the cigarette beetle at various temperatures ranging from  $15^{\circ}$  to  $40^{\circ}$ F. (After Swingle)

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usual temperatures. Temperature operates as a restricting factor in unusual or unseasonable periods of hot or cold weather. Generally unusual temperatures modify or control the range of a species along some frontier. The southern house mosquito *Culex quinquefasciatus* may migrate northward and extend its range during years with mild winters, but is cut back southward during severe winters.

Unseasonable temperatures, such as early or late frosts, may be as effective as temperature extremes in this action, because unfavorable conditions may occur before a species has entered the stage at which it is immune to them, or after it has passed to a susceptible stage. For instance, in the north-central states hibernating chinch bugs cannot withstand many alternate periods of freezing and thawing. A winter that has a number of unusual warm thawing periods, each followed by a zero or subzero period, produces this alternation of freezing and thawing and is extremely destructive to chinch-bug populations. Unseasonable temperatures would affect any one species more frequently at some periphery of its range, and thus contribute to restricting its distribution. Such temperatures would also occur hit-and-miss anywhere over the range of the species and affect abundance in local areas throughout the main body of the range.

PRECIPITATION. Insects are ordinarily not affected directly by normal precipitation, but indirectly through the effect of precipitation on humidity, soil moisture, and plant food supply. Snow has an unusually important effect on soil temperatures. Bare soil is responsive to temperature changes to a depth of 2 feet; when covered with snow, even surface soil is remarkably insulated from changes in air temperature, fig. 364. Thus a snow cover has a marked effect on both the extremes of temperature and average temperature to which insects in the soil are subjected.

Certain expressions of precipitation, however, have a direct effect on insects. Excessive precipitation may inflict severe physical damage to insects. An inch of rain coming as a gentle sustained rain in one area may cause no harm, but coming as a sudden pelting downpour in another area may beat into the ground and kill most of the aphids or early stage chinch bug nymphs. Hail inflicts the same type of physical damage. HUMIDITY AND EVAPORATION. It is difficult to separate the factors of humidity and evaporation in their effect on insects, either experimentally or zoogeographically. Humidity pertains to the amount of moisture in the air, and evaporation to the actual water loss of a surface. In experimental work, if insects are subjected to low humidities, the evaporation from their bodies increases. Because of their small size, increased evaporation quickly depletes the water content of insects' bodies. In prolonged experiments, to test the effect of humidity it is therefore necessary



Fig. 364. Air temperatures and soil temperatures at different depths in bare (A) and snow-covered (B) ground for December in Montana. (After Mail)

to allow the insects to replenish their water supply by feeding. Unless this precaution is taken, effects due to desiccation may be attributed to humidity conditions of the medium. The graph in fig. 365 delineates the relation between evaporation and humidity for a common grasshopper under conditions of starvation.

There is little conclusive evidence available for making generalizations regarding the effect of humidity on insects. Much more work is needed before this can be done. Available data indicate that, in general, humidity is not so critical a factor as is temperature, but that each species has  $\overline{an}$  optimum, which may be different for various stages of the life cycle. In the bean weevil the larvae develop faster at high humidities, but the eggs and pupae develop more rapidly at low humidities. In many cases, however, the rate of growth has been found to be practically constant over a wide range of humidity conditions.

Humidity also affects mortality rate. Low humidity has been found to increase mortality of *Drosophila*, and high humidities are recorded as interfering with hatching and molting in some species of aphids. In certain cases it has been found that high humidities apparently reduce



Fig. 365. Rate of loss of weight in *Chortophaga viridifasciata* at different relative humidities indicated at the end of each curve. Vertical figures represent weight as percentage of original weight, horizontal figures indicate time in hours. (From Wigglesworth, after Ludwig)

the resistance of a species to fungus attack and act unfavorably to the insect in this manner.

There seems little doubt that humidity and evaporation constitute the barrier that restricts the geographic range of many species of insects along some periphery. There are many species occurring in eastern North America whose range extends westward to about the Mississippi River. The less humid conditions to the west appear to be the factor that prevents further extensive spread of these species in that direction. Conversely, there are other species occurring in the Great Plains area which do not extend much further eastward, probably because their optimum humidity requirements are lower than those of eastern species. The assumption that humidity is the limiting factor in these cases is based on the fact that, in general, lines of equal rainfall go from north to south in the area east of the Rocky Mountains, the heavy rainfall bands occurring to the east, and the scant rainfall bands to the west, fig. 366.

TEMPERATURE AND HUMIDITY. Together these two have a marked effect on both general development and distribution of insect species. Their action is frequently critical on different phases of a species and at different times of the year. Critical cold temperatures, for instance, might operate in winter against the hibernating mature larvae, whereas adverse humidities might operate during the summer against eggs or actively feeding larvae.

DAILY RHYTHM. During the 24-hour cycle of day and night there is a daily rhythm of temperature and humidity characteristic of each area. Except during diapause activities of most insects are correlated very definitely with this rhythm. The most conspicuous example of this is found in areas having hot days. During the heat of a summer day, when the humidity is depressed, many insects will be relatively inactive, frequenting cooler and moister niches. Toward dusk there is a drop in temperature and a sudden increase in humidity. During this period a great number of insects emerge from daytime hiding and swarm over the ground and foliage, and in the air.

AIR MOVEMENT. As it concerns physiological effects, air movement has little direct action on insects. It acts indirectly by influencing evaporation and humidity; by causing evaporation it is an aid in reducing body temperature. As drafts or wind it plays a remarkable role in insect dissemination. The upward drafts caused by dawn and dusk air-convection currents carry an astonishing diversity of insects hundreds of feet in the air. Insects caught up by these currents include not only a large array of winged insects but also small wingless forms such as springtails (Collembola). It is principally on this group of air-borne insects that the swifts and nighthawks feed.

Many cases are on record of strong-winged insects such as the *Erebus* moth being blown by storms a thousand miles or more north from their tropical homes. Occasional specimens of the *Erebus* moth have been



Fig. 366. Climatic moisture bands in the United States. (Adapted from U.S.D.A.)

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found, still alive, in Canada, the end of a journey started in Mexico, the West Indies, or southward. Shorter wind dispersals of large numbers of butterflies and moths are fairly common.

PERIODIC DISPERSAL. Several widespread species of insects which become abundant each year in northern states either die out during the winter or become greatly reduced in the northern part of their range. Overwintering populations persist in the extreme southern states, and the species move back into the northern states each spring. The army worm *Pseudaletia unipuncta*, the six-spot leafhopper *Macrosteles fascifrons*, the potato leafhopper *Empoasca fabae*, and the potato psyllid *Paratrioza cockerelli*, fig. 367, are examples of species which behave in this manner. Evidence to date indicates that the spring northern dispersal is windborne. The manner in which depleted overwintering populations are built up in the South is still a mystery. It is possible that this wind-borne type of dispersal occurs in many more species than the few for which it is known.

#### Physical and Chemical Conditions of the Medium

The medium in which insects live may either temper or accentuate weather conditions and, in addition, impose definite conditions peculiar to itself on the organisms living within it. From a practical standpoint, three media are of paramount importance: terrestrial, subterranean, and aquatic.

TERRESTRIAL MEDIUM. For the purposes of this discussion, the terrestrial medium is considered as the surface of the earth and everything above it. This includes the aerial and arboreal regions, but it is difficult to draw a satisfactory line between these, because so many insects move frequently and rapidly from one to another.

In the case of free-living insects, conditions of the terrestrial medium are essentially those of the atmosphere. Differences from it depend on cover. In exposed areas such as treetops, the upper foliage of desert and grassland plants, and bare unshaded soil or rock, sun temperatures rather than shade temperatures (which are official weather temperatures) tend to prevail. Insects under leaves or other cover enjoy a moderation of temperature extremes, as do insects living within and under the tree canopy of a forest. The diurnal and seasonal rhythm of temperature and humidity is greatest in the more exposed areas and progressively less in the more shaded or protected areas.

Microhabitats of various types have peculiar conditions. Rotting organic matter produces heat of fermentation that adds to the temper-



Fig. 367. Distribution of the potato psyllid *Paratrioza cockerelli* in the United States. The crosshatching indicates the area of greatest injury, the diagonal shading the approximate overwintering areas, and the heavy lines the eastern and western limits of summer occurrence. (After Wallis)

/ ature. Insects in fungi, plant galls, leaf mines, and tunnels in living trees enjoy a high humidity that approaches an aquatic environment. Insects in rotten logs find a moderation of extreme temperatures due to insulation, and their medium approaches the subterranean in character.

SUBTERRANEAN MEDIUM. No insects live in rock, so that we may consider as the subterranean medium for insects only that part of the substratum that classifies as soil and sand. This medium reflects the general climate but tempers its extremes and at the same time possesses several important characteristics of its own.

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TEMPERING OF CLIMATE. Depending on circumstances, soil acts as a sponge, an insulator, and a radiator. It stores rain, giving it up slowly, so that its humidity, or moisture content, fluctuates over a much narrower range than does that of the air. Its surface layers soak up heat and insulate the part beneath; the absorbed heat is also given up slowly, so that diurnal rhythm and temperature extremes are greatly moderated in comparison to those of the terrestrial medium.

SOIL PROPERTIES. Many properties of soil are characteristics of the soil itself and are not superimposed by the immediate climate. Important among these are texture, moisture, drainage, chemical composition, and physiography.

These characteristics are almost entirely a direct result of the geological history of an area and reflect the type of strata exposed, glacial action, wind-carried material, or volcanic activity. To these factors are added the accumulated effects of the vegetation over a long period of recent time. Prairie plants, for instance, have built up thick black soils in many areas; forests tend to build thinner and lighter soils.

Man's activities have disturbed natural soil conditions more than any other element of the ecological pattern. Not only does cultivation change the original condition of the soil, but also ploughing and tilling keep changing it at various intervals, drainage or irrigation decreases or increases moisture content, and methods of farming can increase or decrease chemical constituents and organic content, the latter sometimes influencing texture profoundly. These changes have been detrimental to many insect species but have allowed others to increase and become major crop pests.

TEXTURE. Soil texture varies from hard-packed clays to loose sands. Few insects occur on the harder-packed types, since they are unable to push or dig their way through them. The loams are probably the favorite soils for insect use. These allow digging and burrowing operations and are usually favorable in other characteristics, such as moisture content, drainage, and organic content.

The critical effect of soil texture on species abundance was demonstrated by the pale western cutworm *Porosagrotis orthogonia*. A species of the northern prairies, it was a collectors' rarity in the early days of collecting in central North America. After extensive breaking of the prairie sod and cultivation of the land in northern United States and Canada, this cutworm increased sharply in numbers, and the larvae became extremely destructive to grain crops. Investigation of the cause of increase revealed this situation. The larvae live only in soil of fairly light texture, in which they move around freely in response to daily or seasonal temperature and moisture changes. In the primeval northern

prairie they occurred only in local sandy areas having loose soil, but not in the unbroken prairie sod. Cultivation transformed the sod into soil of optimum texture for the cutworm larvae, and opened to them thousands of square miles of new habitat.

DRAINAGE AND MOISTURE. The moisture content of the soil is affected greatly by drainage. Impervious layers of substrata, such as clay or rock, may retard natural drainage, resulting in permanent or temporary semimarsh conditions or wet soils. In such situations occur only those insects that are at least partially modified for aquatic existence, such as many larvae of Diptera. In other cases impervious substrata may cause the water to percolate a considerable distance underground and, as seepage water, affect moisture conditions in other areas.

More open types of subsoil, such as sand, gravel, or shale, allow free drainage, contributing to the maintenance of better-aerated soils and more rapid restoration of normal moisture content after rains. Wellaerated soil is a prerequisite of all soil insects that have no modifications for aquatic or semiaquatic existence.

An interesting demonstration of the effect of soil moisture on an insect species is the case of the Colorado corn rootworm *Diabrotica virgifera*. Collecting records indicate that until recent years this species was a fairly rare one occurring in the arid regions of New Mexico, Colorado, and Nebraska. The larvae feed on corn roots and, if present in large numbers, may destroy the root system of the plant and cause great reduction in yield. Since about 1890 the species has been a constant pest in south-central Nebraska but practically disappeared during the drought years. In the last decade, however, the species has become of major importance in the irrigated portion of the Platte River valley, owing to the increase in soil moisture resulting from more widespread irrigation.

Wireworms in the Pacific Northwest afford another striking example of changes in species composition and abundance due to changes in soil moisture. In that region four species of wireworms, *Limonius californicus, infuscatus, canus,* and *subauratus,* are wet-land pests, normally restricted to swamp and river-bottom areas. When arid land was irrigated and used for farming, these wet-land wireworms became important pests of potatoes, corn, lettuce, onions, and many other crops grown in irrigated fields. The high soil moisture maintained by irrigation apparently allows the wireworms to increase in great numbers, fig. 368.

Drainage and texture together exert considerable influence on the distribution of insects that live part of their life in the soil. The range of the destructive Texas leaf-cutting ant *Atta texana* extends into Louisiana, and there the species nests only in fine sandy loams having light subsoils and excellent drainage.



Fig. 368. Distribution of wet-land wireworms in the Pacific Northwest. Black areas represent irrigation projects on which one or more species of wireworms cause serious injury to crops annually. Circles represent localities where wireworms are known to occur naturally, without benefit of irrigation, and to cause occasional injury. (From U.S.D.A., E.R.B.)

CHEMICAL COMPOSITION. Chemicals naturally present in the soil affect both the abundance and distribution of phytophagous insects. Deficiencies of mineral elements, resulting in similar plant deficiencies, inhibit the growth of some insects but seemingly not others. Nitrogen deficiency lowers the productivity of some species of insects, but seems to contribute to outbreak numbers of others. In some cases the results are caused by changes in plant morphology, such as leaf toughness, which might make it difficult for the insect to eat or pierce. Many studies on this subject have shown little correlation between soil chemistry and insect growth, but few studies have been made in sufficient detail to be considered conclusive.

Soil chemistry also determines the species of plants that grow naturally in an area. This determines the hosts available for phytophagous insects, and in this fashion the distribution of many host-specific plant feeders.

PHYSIOGRAPHY. In itself, physiography has few direct effects, but it has a marked influence on several soil factors. Flat country has slow rain runoff and must have adequate subsurface drainage to maintain good soil aeration. Hilly or mountainous country has rapid water run-

off insuring good general soil aeration. In addition south, east, and west exposures have a higher soil temperature, greater evaporation, and, as a result, differences in the biota.

AQUATIC MEDIUM. Conditions in water are obviously different from those on land or in soil. There does not exist the question of moisture and evaporation, the most critical single problem in the terrestrial medium. Instead, oxygen and respiration are the critical complementary problems of aquatic insects, and many characteristics of the aquatic medium are important because they have a direct bearing on these. In other words, for insects living in air, water is the chief problem; for those living in water, air is the problem.

AERATION. Of great importance from the standpoint of many aquatic insects are the diffusion of excess carbon dioxide out of the water and the diffusion or solution of oxygen into it. In most cases the latter is the more important. The oxygen comes from the air, and any stirring movement that brings more water into direct contact with the air increases the oxygen supply. In lakes and ponds wind action is the chief agent. Waterfalls, rapids, or movement of current are stirring agents in streams, in order of greatest efficiency.

Temperature has a direct bearing on aeration, because the colder the water, the greater is the amount of gases (including oxygen) that will dissolve in a given volume of water. High temperatures greatly decrease the solubility of gases in water.

An important distinction must be made regarding aeration among aquatic insects. Many groups, such as mosquito larvae, horsefly larvae, and certain aquatic bugs have extensile respiratory tubes that reach the surface, or the individuals periodically come to the surface to breathe; others, such as the water boatmen or adult diving beetles, take a bubble or film of air into the water with them, coming to the surface to replenish it from time to time (see p. 132). These groups are almost independent of the aeration factor in water, and many live in water almost devoid of oxygen.

Aquatic insects without modifications for obtaining direct contact with air are dependent for respiration on oxygen in the water. As with other ecological factors, various insects have different aeration requirements and are limited in distribution by it. Certain dragonfly nymphs and midge larvae are examples of forms able to tolerate very poor aeration and are often found in stagnant ponds. Larvae of the midge family Blepharoceratidae have extremely high oxygen requirements and occur only in rapid mountain cascades.

TEMPERATURE. Aquatic temperatures do not have the same range as air temperatures, but in most bodies of water there is a definite temperature response to air conditions. Insect species usually show a definite restriction to water of a certain temperature range. In many cases this is undoubtedly correlated directly with aeration, but in some cases temperature is probably the factor. Certain mosquito larvae, for instance, live and transform normally in water at  $65^{\circ}$ F. but die during molting in water at  $80^{\circ}$ F. Since mosquitoes are not dependent on water for oxygen, it appears that in this case temperature is a factor.

A few aquatic insects have been found in hot springs with temperatures ranging from  $110^{\circ}$ F. to  $120^{\circ}$ F. These are chiefly aquatic beetles and fly larvae that obtain oxygen directly from the air.

Temperature plays the same part in relation to growth and activity in aquatic insects as in other insects, as discussed on page 140. Through adjustment to temperature, various aquatic species appear at various times throughout the year. For the most part development and activity increase as water temperatures rise, resulting in the production of great swarms of adults through late spring and summer.

In the stonefly genus *Allocapnia* the reverse is true. The nymphs live in streams throughout the north-central and eastern states. During summer, nymphal growth seems to be retarded but increases with the advent of cool autumn weather. As a result the adults emerge during the winter months, beginning during late November and continuing until February or March, fig. 369.

DEPTH. In lakes and ponds depth has a marked influence on oxygen, temperature, and light; in running water the effect of depth is less marked owing to the stirring action of the current.

Water absorbs heat and light passing through it, converting the latter to heat. Heat rays and the red end of the light spectrum are absorbed first; at greater depths the other wavelengths are gradually absorbed



Fig. 369. Seasonal succession of adult emergence for 15 stonefly species at Oakwood, Ill. The widest part of the spindle indicates the time of maximum abundance of adults for each species. (From Illinois Natural History Survey)

until, even in very clear lake water, almost all light is absorbed at about a hundred feet. This has a profound effect on plant life. Practically none exists below the 60-foot level, and most of it is concentrated in the first 6 or 10 feet of water where there is a good supply of light for photosynthesis. This produces a zonation of food supply that in turn limits the distribution of many insects.

Depth in deep lakes (100 feet or more deep) is accompanied by another phenomenon of great biological interest, the thermocline. In summer the surface waters of a large lake are appreciably warmer than the water at the bottom, which remains near its point of greatest density,  $38-40^{\circ}$ F. (=  $4-5^{\circ}$ C.), fig. 370. This bottom layer being the heaviest, the upper warmer waters "float" on it, rather than mixing with it. Between the two is a relatively narrow dividing area, the *thermocline*, intermediate in general conditions between the fairly uniform upper and lower strata. The upper stratum, the *epilimnion*, is churned and agitated by wind action so that it is almost uniform in temperature and well aerated. The bottom stratum, the *hypolimnion*, is stagnant, and its oxygen is gradually used up by organic oxidation. Almost all the life in a deep lake occurs in the epilimnion; the hypolimnion is practically a biological desert.

TURBIDITY. Minute particles of earth or "blooms" of algae and other organisms usually cloud water to some extent. The clouding or turbidity has an indirect effect on insects, because it reduces light penetration and therefore plant production on the bottom. Under conditions of continuous high turbidity, there is persistent settling of suspended material on the bottom, thus modifying its character and its fauna.

BOTTOM. The great proportion of aquatic insects live on or in the bottom, and most species will live only where the bottom is of a particular type. The most useful categories for purposes of classifying the bottom types are based on size of particle: namely, muddy, sandy, and rocky. Mud bottoms are highest in organic material that serves as food; sandy bottoms and rocky bottoms have the least. Mud bottoms in streams, however, are usually associated with slow current, lower oxygen content of the water, and higher temperatures. Sandy bottoms are relatively unstable and usually have a small fauna. Rocky bottoms afford the most stable footing and are the favorite habitat for a large number of groups.

VEGETATION. To some insects aquatic vegetation is primarily food; to others it is a haven. Vegetation beneath the water provides shelter and footing, especially valuable to species that are the prey of other animals or that have no special adaptation for swimming. Aquatic vegetation is especially abundant in lakes, and it is there that it is most

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Fig. 370. Diagrams illustrating a thermocline. The circulation of the water (A) in a lake of equal temperature, (B) in a lake of unequal temperature. W, represents the direction of the wind; T, thermocline; H, hypolimnion. (From Ward and Whipple, after Birge)

useful. Relatively few lake-inhabiting insects frequent open water; they stay on the bottom and in the weed beds most of the time. Those that move about freely in the open water usually do so only at dusk or night, hiding on the bottom during the daytime.

#### Food

Food is one of the most important factors influencing the distribution and abundance of insects. For many insect species it is a factor that has been changed radically by man's agriculture, travel, and transportation.

As a Factor IN DISTRIBUTION. Often the range of the host plant for a given species of insects extends much beyond that of the insect, demonstrating that some other factor such as temperature or soil condition is the actual factor limiting the insect's success and distribution. In other cases it is obvious that the insect is usually present wherever a suitable food is present and is prevented from extending its range because of the food factor. This is graphically shown in the case of many plant lice that have become successfully established on agricultural crops far beyond the range of the native hosts of the insects.

GENERAL FEEDERS. Many insects have a wide assortment of acceptable hosts or prey or feed on material such as decayed or dead organic matter that is widely distributed through most biotic communities. In these food is only infrequently a limiting factor of distribution. Areas in which such species are absent usually have food material, but other factors such as temperature or moisture may be intolerable for the species.

SPECIFIC FEEDERS. A great number of insect species, including chiefly plant feeders and parasites, feed on only a small number of diverse host species, or are restricted to a group of closely related host species, or may be restricted to a single host species. All intermediate conditions of host specificity or tolerance occur between these extremes. The species that have the most limited host tolerance are the ones that are most likely to have their distribution limited by food. The over-all range of the Hepatica sawfly *Pseudodineura parvula* appears to cover all the north-central and northeastern states; yet in the north-central states the sawfly occurs only in the scattered localities in which its host, *Hepatica*, is found. The black-locust sawfly *Nematus tibialis* is normally confined by the rather restricted eastern range of its host, *Robinia pseudoacacia*. Whenever the host has been planted in other localities, the sawfly has ultimately been found, even in England, indicating that the sawfly has a much wider ecological tolerance than that indicated by the natural range of its host.

HOST CROSSOVER. In the case of insects feeding on a definite species of plant host, this latter may become defoliated, and it is necessary for the species to adopt a new host or to have its numbers reduced to the carrying capacity of the original host. Experimental investigations' of this crossover of an insect from one host to another have brought out some exceedingly interesting information:

1. Some species, such as the forest tent caterpillar, make the change to closely related hosts with ease and without evident ill effects. Chinch bugs, for instance, will feed on oats or wheat until nearly full grown and can transfer to corn readily and without noticeable mortality due to food reactions.

2. Other species will make a change from one host to a close relative with the greatest difficulty, either after compulsion of a period of starvation (in the case of immature stages) or under circumstances of extreme necessity (in the case of ovipositing females). In most cases of this kind the transfer cannot be made by advanced larvae. They will eat the new food but develop symptoms of intestinal disturbance, such as diarrhea, and die. If first-instar larvae are put on the new host, they will eat but suffer an extremely high mortality. During succeeding instars the mortality rate decreases until the pupal stage is reached, and here the mortality is again high. But out of thousands of first-instar larvae a few adults will finally be obtained. These will prefer to oviposit on the new host, and the resulting larvae will feed on it readily and without ill effects.

An interesting case of this type was supplied by the satin moth *Stilp*notia salicis. A European pest of Lombardy poplar, it was introduced on the Pacific Coast about 1922 and in a few years became very abundant, completely defoliating Lombardy and other introduced poplars

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in each locality to which it spread. In British Columbia by the late 1920's it had spread up the valley of the Lower Fraser River. There it built up a large population and practically exterminated the Lombardy poplars in that region. When Lombardy poplars were no longer available, the satin moths began laying eggs on the native cottonwood *Populus trichocarpa hastata*, an abundant tree in this region. At first only sporadic colonies became established on this new host which is also a member of the poplar genus, but in a few years the satin moth was the most serious insect enemy of cottonwood in this area. Laboratory rearings demonstrated that in making this host crossover the satin moth went through the initial high mortality process just described.

An example of a species that does not follow this behavior is the gypsy moth *Porthetria dispar*. The gypsy moth larvae are plant feeders and will feed on over four hundred and fifty species of plants. Of these forty-two are favored hosts, including willows, birches, and oaks; later instars of the larvae may switch to one of the other four hundred and fifty host species, one of the favorites being white pine. They suffer no ill effects and develop to maturity. For normal development, however, it is necessary for the first two larval instars to feed on one of the forty-two favored species.

The complete host relationships of only a relatively small number of insect species have been studied comprehensively. Undoubtedly much interesting material will continue to be discovered on this subject.

3. A third group of species appear to be tied irrevocably to a single species of host. If put on even a closely related species, they will die before they will feed, or all die if they do feed.

These phenomena of host crossover have a great effect on the distribution and abundance of the insects involved and represent an important type of ecological tolerance so far as food is concerned. They may be of economic importance if crossover cases involve agricultural species. There is always the possibility of this happening when new plants are brought into the national agricultural economy, as, for instance, the soy bean. When the soy bean was introduced into the central states it was virtually unattacked by any of the native insect species. Gradually some of these began using it as a host, and now the soy bean in this country has several serious insect enemies, including grasshoppers, root maggots, and white grubs.

As a FACTOR IN ABUNDANCE. Amount of available food is an important factor affecting the population of a species in a given community. It is not uncommon for a species to utilize its entire available food supply with a resulting sharp reduction in population due to starvation.

Although there may be considerable variation in size between differ-

ent individuals of the same species, there seems to be a definite minimum amount of food required for the normal development of an individual. Housefly maggots, for instance, die during pupation if the larvae are removed prematurely from their food supply. Most sawfly larvae will die without further development if removed from their food only two or three feedings prior to completing their full food intake. If, therefore, an excessive number of individuals are feeding on an insufficient amount of food, those with a head start complete their normal food intake and mature, and many of the remainder run out of food and fail to develop.

The most notable exceptions to this are found in certain parasitic species having a wide range of hosts. In these, the size of the individual parasite is determined by the size of the respective host species. An excellent example of this is the mutillid wasp *Dasymutilla bioculata;* larvae feeding on small prey species develop into small individuals, those feeding on large prey species develop into large individuals, fig. 371.

Agriculture has changed the insect food factor in several ways: (1) by providing suitable food when or where it would not be present under



Fig. 371. Correlation in size between *Dasymutilla bioculata* and its hosts *Microbembix monodonta* (left) and *Bembix pruinosa* (right). Each vertical row has *Dasymutilla* male and female above, host wasp at bottom. (Material, courtesy of C. E. Mickel, photo by W. E. Clark)

natural conditions, (2) by providing better food, and (3) by simply providing a greater food supply.

EXTENSION OF FOOD SUPPLY. A striking example of this factor came to light in the extensive sampling of grain in granaries in the late 1930's and early '40's. It was discovered that in many states, especially in the corn belt, a tenebrionid beetle *Cynaeus angustus* had become extremely abundant and widespread and had developed into a major pest of stored grain. This beetle was first described in 1852 from California and prior to 1938 remained a collector's rarity. It was known to occur at the base of yucca plants. In 1938 the beetle was encountered as a stored-grain pest in Washington, Kansas, and Iowa. By 1941 it was known to be widely distributed through the corn belt. The species reached population peaks in the man-made conditions of grain storage which are in astonishing contrast to the scarcity of the species in its natural habitat.

BETTER FOOD. It has been shown in some cases that certain introduced agricultural crops increased the fecundity and thereby the abundance of native insect species. The two grasshoppers, *Melanoplus differentialis* and *M. bwittatus*, showed marked increases in fecundity on a diet of soy beans and alfalfa, respectively. This is correlated with field observations of the increase in population of the two species following the planting of large acreages of the two crops mentioned.

ADDITIONAL HOST MATERIAL. Practically every crop favors at least a few insects in supplying more food. The Colorado potato beetle, the corn aphids, and other pests on potatoes and corn certainly have flourished on the thousands of acres of host crops that man has planted and have built up huge populations that dwarf the scattered colonies that existed before agriculture, when their hosts were relatively sparse and the individual plants not so luxuriant as those of improved agriculural varieties.

#### Enemies

A wide array of organisms prey on or parasitize insects. Some of the \parasites, such as the malarial organisms *Plasmodium* sp., seem to do the insect no harm, but the majority have a harmful effect on the insect host. These enemies constitute an environmental factor having a definite effect on the abundance, and sometimes the distribution, of the host species. Each stage of the host species may be subject to attack by a different set of enemies, or several stages may be attacked by the same one. As a rule, predaceous enemies and plant enemies such as fungi are more general in their attack on various stages, and internal parasites are restricted regarding the stage they attack.

INTERNAL PARASITES. Insects are attacked by several groups of internal parasites, of which the most important are certain groups of insects, parasitic worms, bacteria, and fungi. Other groups also parasitize insects.

INSECTS. The larvae of many families of Hymenoptera (Ichneumonidae, Chalcididae, Scelionidae, and many others) and a few families of Diptera (Pyrgotidae, Tachinidae) are entirely endoparasitic on insects or closely allied arthropods. A few Lepidoptera have endoparasitic larvae, and several Coleoptera, including the entire small suborder Strepsiptera, or stylopids. On the basis of rough estimates there are about eleven thousand species of parasitic insects known at present in North America. Most of these are fairly specific at least as to what group they attack. Some, for instance, will attack a wide variety of lepidopterous caterpillars; others will attack only certain primary parasites in these caterpillars (see p. 305).

OTHER ANIMALS. Some species of Protozoa and invertebrate metazoan parasites pass one stage of their life cycles in insects. Examples of such protozoan parasites are the malarial organisms *Plasmodium* sp. and sleeping-sickness organisms *Trypanosoma* sp. Among the parasitic worms that spend part of their life cycle in insects are trematodes, nematodes (for example, *Filaria*), and Acanthocephala (for example, *Macracanthorhynchus hirudinaceus* the thorny-headed worm of swine). In each case only one of the early stages of development is passed in the insect, which is an intermediate host for the parasite. This group of parasites does not appear to have a deleterious effect on the insect, at least not the fatal effect of the insectan parasites. It is probable, therefore, that this class of noninsectan parasites is a negligible factor in relation to insect populations.

FUNGI AND BACTERIA. Many species of these groups attack insects in various stages and at times are destructive to their hosts. Anyone who has carried on rearing experiments with insects can well attest this, for cultures are very susceptible to attack by fungous and bacterial organisms. The reason for this is that the best development of both types of these parasitic organisms is attained under conditions of relatively high humidity and temperature which are frequently increased to an unnatural degree in caged experiments.

Among common fungus diseases of insects is *Empusa muscae* the house fly fungus, fig. 372. Other members of the same genus attack a large variety of insects, including grasshoppers, aphids, and chinch bugs. A famous fungus disease is *Beauveria globulifera*, often referred to as *Sporotrichum globulifera*, the white fungus of the chinch bug. During warm and humid seasons this fungus kills large numbers of chinch bugs and other insects in late spring and early summer and at times has controlled the bugs to the point of local extermination. Entomophagous fungi of



Fig. 372. Empusa muscae the common fly fungus. A, house fly (Musca domestica), surrounded by fungus spores (conidia); B, group of conidia in several stages of development; C, basidium (b) bearing conidium (c) before discharge. (From Folsom and Wardle, Entomology, by permission of P. Blakiston's Son & Co.)

the genus *Isaria* are the chief species attacking insects under artificial conditions.

Of unusual interest is the fungus family Laboulbenaceae. Most of the species are entomophagous and produce elongate or ornate fruiting structures outside the body of the host insect. A species occasionally encountered in the eastern states is *Cordyceps ravenelii*, a parasite of white grubs, fig. 373.

Bacterial diseases are less numerous than fungi in species but at times are strikingly devastating. Flacherie, an infectious and highly fatal disease of silkworms, is caused by a bacterium. Grasshoppers and chinch bugs are attacked by similar bacteria, but attempts to control these insect pests by propagating and disseminating the disease have failed. Greater success has been achieved with *Bacillus popilliae*, the organism causing a disease of Japanese-beetle larvae called milky disease. The bacterial spores are mixed with an inert dust and the mixture applied on top of the soil in grub-infested areas. Rain washes the spores into the ground and into contact with the grubs. This control method has proved sufficiently satisfactory to be used on extensive areas.

Virus diseases are extremely toxic to susceptible insect species. Polyhedrosis viruses in particular have proved sufficiently virulent against certain sawfly and lepidopterous larvae to be employed successfully as control agents.

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## Ecological Considerations

EXTERNAL PARASITES. Insects have few ectoparasites of the type of the lice or fleas, in which the adult stage or both immature and adult stage use the body of the host as a home. A few mites infest various insects, but only scant information is known regarding the ecological significance of the groups. An unusual ectoparasite is the bee louse *Braula caeca*, a curious minute fly that is ectoparasitic in the adult stage on honeybees.

In the Hymenoptera, some families whose larvae are mostly endoparasites, such as the Braconidae, contain genera whose larvae are attached externally to their host larvae. These parasites have the same host relation as their endoparasitic allies, in that normally only one parasite individual lives on one host individual, the latter almost always dying when or before the parasite is mature.

PREDATORS. As in the case of internal parasites, so in this category too insects are their own worst enemies. Carabidae and Staphylinidae are two very large beetle families that feed in both adult and larval stages almost exclusively as predators on other insects. Many families of wasps are predaceous, as are larvae of Tabanidae, Dolichopodidae, and some other large families of Diptera. Odonata (damselflies and dragonflies)



Fig. 373. Fruiting structures of a fungus Cordyceps ravenelii, arising from the body of a white grub Phyllophaga. (After Riley)

are predaceous as both nymphs and adults. The same is true of certain families of Hemiptera such as Pentatomidae (stink bugs), Reduviidae (assassin bugs), and Phymatidae (ambush bugs); in some other families of Hemiptera, such as the Miridae (plant bugs), most genera are phytophagous, but some are predaceous. There are many other small groups of predaceous forms.

Noninsectan predators of insects include members of several large groups. Spiders are primarily insectivorous; there are about three thousand species of spiders in North America, and each spider population takes its toll of insects. Centipedes feed on insects to a large extent also.

Vertebrates contain many groups that are insectivorous. Among the fish, perch, sunfish, crappies, bass, and sheepshead use insects for a large share of their diet. Reptiles and amphibians are largely insectivorous, as are bats and moles; other mammals such as mice, skunks, shrews, and raccoons eat large numbers of insects.

Birds are the outstanding vertebrate insect eaters. Swifts, nighthawks, and flycatchers feed entirely on insects caught on the wing. Robins, wrens, chickadees, cuckoos, quail, and prairie chickens live almost entirely on insects when the latter are abundant. During insect outbreaks many birds of omnivorous food habits switch temporarily to an insect diet. Crows, blackbirds, gulls, owls, and small hawks are in this group and have been noted especially feeding on grasshoppers during periods of abundance.

All these animals are abundant and, being comparatively large individuals, eat proportionately large numbers of insects. In doing so they exert a steady ecological force against insect populations.

PREDACEOUS PLANTS. A list of insect predators would not be complete without mention of those curious plants that trap animal prey and digest them. Bladderworts (*Utricularia*) are aquatic plants that trap small organisms in bladder-like pouches; sundews (*Drosera*) are bog plants having sticky tentacle hairs on their leaves that encompass prey; and pitcher plants (*Sarracenia*) have leaves in the shape of pitchers, partially filled with water, with stiff hairs pointing to the water; the hairs allow insects to get to the bottom of the pitcher but prevent their escape. None of these plants is sufficiently abundant to be of importance ecologically by reducing insect numbers.

#### PROTECTION AGAINST ENEMIES

Insects appear to have little or no protection against several groups of their enemies, notably fungi and bacteria. Against insect parasites and predators their only protection seems to be evasion; many insect

stages are extremely limited in locomotion and obtain no protection by this means.

The principal group of enemies against which insects have achieved some measure of protection is the land-vertebrate group. Against this group such devices as protective resemblance, the building of protective structures, poison hairs, bites, stings, noxious secretions, and the mimicking of species possessing some of the foregoing offer protection to some extent.

PROTECTIVE RESEMBLANCE. We have all been surprised at one time or another to discover a "stick' come to life in the net, or, in examining a tree trunk, to see what appeared to be a section of bark take wings and fly away. This protective resemblance is common in several insect groups. The walkingstick insects (Phasmidae), fig. 374, resemble sticks; in spring they are green; then when mature in autumn many become brown, resembling the color of the foliage or twigs on which they feed and rest. Many moths at rest resemble bark. Some of the larger forms are the



Fig. 374. Protective mimicry and coloration. At left, a walkingstick insect on a twig; at right, an underwing (*Catocala*) with wings spread (A) and at rest on bark (B). (From Folsom and Wardle, Entomology, by permission of P. Blakiston's Son & Co.)

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underwing or Catocala moths, perfect bark mimics with wings folded, but often conspicuous in flight owing to brightly colored underwings, fig. 374. Grasshoppers resemble lichens, various types of soil, dried leaves, or grass, depending on the species and its food. Psocids have similar protective color patterns, especially those that feed on algae or lichens on bark or rock bluffs. A few larvae at rest curl up and resemble a fresh bird dropping, notably the sawfly *Megaxyela avingrata*. In general most of the leaf-feeding larvae are green or are mottled so that they blend into the foliage on which they feed.

BUILDING PROTECTIVE STRUCTURES. Certain larvae build cases, houses, or canopies that give the occupant some physical protection and in addition may resemble the host or surroundings and result in protective resemblance. Bagworms (Lepidoptera), fig. 306, are a common example, and also caddisfly larvae of many kinds, fig. 296. Cases of the latter may be very difficult to see unless the insect is in motion. The larvae of several leaf-feeding beetles construct an urnlike case that is difficult to see in its natural surroundings.

POISONS, BITES, AND STINGS. Certain insects gain protection by inflicting pain on their assailants. Several caterpillars have sharp hairs, containing a poisonous fluid that causes a rash and extreme pain. So delicate are these hairs that one has only to brush against them lightly to feel the excruciating nettling sensation that they produce. Tussock moth larvae and eucleid moth or saddleback larvae, fig. 375, are protected by these. Other insects bite the aggressor, as, for instance, ants. Still others, such as bees and wasps, are provided with painful stings; bees use these only for protection; some wasps use these both for protection and for paralyzing prey.

NOXIOUS SECRETIONS. A large number of insects have mechanisms for producing and ejecting noxious smelly substances. Swallowtail butterfly larvae have an eversible pair of horns, the osmeterium, on the pronotum, that give off an odor thought to be repellent to some animals. Stink bugs and many Heteroptera have stink glands on the dorsum of the abdomen. Other insects, without such definite glands, apparently have a disagreeable taste, because birds especially refuse them as food. Swallowtail butterfly and milkweed butterfly adults, and both larvae and adults of many brightly colored leaf-feeding beetles are in this category.

It is pertinent to note here that a large number of species possessing protective devices discussed in the two preceding paragraphs are strikingly marked or gaudily colored, fig. 376. This striking ornamentation may be a display of warning colors, to aid the memory of an assailant



Fig. 375. Caterpillars having nettling hairs annoying to man. Left, the saddleback Sibine stimulea; right, Automerus io. (From U.S.D.A., E.R.B.)

who has attacked a protected species and become aware of its defense. It is certain that birds and other vertebrates have no instincts to avoid protected species, so that each individual must learn for itself.

PROTECTIVE MIMICRY. Among insects having no known protective mechanism, there are some that share the protection of those that do by looking almost exactly like them. Thus there are harmless plant bugs that look like ants, harmless flies that resemble bees or wasps, fig. 377, and edible butterflies that have the appearance of distasteful species. Among our fauna the best example of the latter type, fig. 378, is the viceroy Basil-



Fig. 376. A brightly colored mal-tasting butterfly *Papilio ajox*. (From Folsom and Wardle, Entomology, by permission of P. Blakiston's Son & Co.)



Fig. 377. Mimicry in bees and wasps. A, drone bee Apis melliferd; B, dronefly Eristalis lenax. (From Folsom and Wardle, Entomology, by permission of P. Blakiston's Son & Co.)



Fig. 378. The viceroy, below, and the milkweed butterfly, above. (From Folsom and Wardle, Entomology, by permission of P. Blakiston's Son & Co.)

archia archippus, an edible species that resembles in pattern and general color the distasteful milkweed butterfly Anosia plexippus. In tropical faunas similar cases are common.

The advantage gained by a species through these types of protection is average, for none of these methods are absolute. Insects inedible to birds may be delectable to other animals, or if refused by one kind of bird may be eaten readily by another. But if even a small advantage is gained by a species, that species has a tremendous advantage over a long period of time.

#### Competition

If we suppose an individual of a species in a situation having suitable climate and conditions of medium and food, and, further, that its enemies are not a critical factor, that individual may discover that another individual having similar wants is there also. If there is only sufficient food for one, then the two individuals are in vital competition from which only one can emerge as the survivor.

Among insects, competition is chiefly for food. This competition may be between either individuals of the same species or individuals of different species.

Frequently there is no reaction to critical competition, and all individuals may starve. If, for instance, sawfly larvae overpopulate a host, they feed quietly until the entire host is stripped; then all of them wander until exhaustion and death if additional food is not found. In the case of critical competition involving two or more insect species, their different requirements may mitigate in favor of one of them. An interesting example is cited by Willard and Mason (1937) regarding two hymenopterous genera Opius and Tetrastichus, that parasitize the Mediterranean fruit fly larvae in Hawaii. Within a single fruit fly larva there can develop to maturity only a single larva of a species of the braconid Opius, but as many as ten to thirty individuals of the minute chalcid Tetrastichus, fig. 379. If both oviposit in the same fruit fly larva, the Opius larva kills most of the Tetrastichus larvae, but a few of the latter escape destruction. These develop more rapidly than the Opius larva and reach maturity, but leave too little food for the larger braconid larva, so that the Opius larva invariably dies.

Competition for food is frequently active and aggressive. Pemberton and Willard (1918) give an account of such an example occurring in wasps of the genus *Opius* previously referred to. In Hawaii three species, *tryoni, fullawayi*, and *humilis*, parasitize fruit fly larvae. The female wasps lay their eggs in the fly larvae, and several individual wasps of

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Fig. 379. Parasitic wasps Tetrastichus giffardianus, in puparium of fruit fly. (After Pemberton and Willard)



Fig. 380. First-instar larva of Opius humilis. Note the sharp heavily sclerotized mandibles m. (Redrawn from Pemberton and Willard)

all three species may oviposit in the same larva. Only one survives, and this one is the result of a battle among the newly hatched larvae. The first instar of each *Opius* larva has a relatively large hard head bearing a pair of long sharp mandibles that can be opened and shut with great force and speed, fig. 380. These larvae are cannibalistic and attack any other parasite larva within the fly larva, using these sharp mandibles to pierce and lacerate their antagonist's body. Whether the struggle is between individuals of the same species or of different species, only one *Opius* larva remains after the struggle is over. It was discovered that *O. tryoni* was almost invariably the victor over the other two species, owing to its greater agility, reaction time, force in use of mandibles, and other combative advantages.

Cannibalistic tendencies occur in many insect groups, and are invariably accentuated by crowding. The confused flour beetle lives and feeds on a variety of stored-grain products; generations are continuous, and adults, eggs, and all stages of larvae occur together in the food. Large larvae and adults may feed on eggs and small larvae of their own species but apparently make no effort to hunt them out. When the infestation of these beetles is small in relation to the volume of their food medium, the older individuals encounter the younger stages less frequently. As the infestation increases per unit volume of food medium, these encounters are more frequent, and cannibalism increases accordingly. By this mechanism a population point is reached where the

losses due to cannibalism are equal to the reproductivity of the adults, and overcrowding beyond this point is prevented.

It is pertinent to note in connection with these phenomena, that there exists no conscious sense of competition by the insect itself. The competing individuals react instinctively throughout, and these instincts under certain conditions of crowding produce the elimination of excess numbers.

#### Tropisms

Instinctive behavior plays an important role in the distribution of members of an insect population. The reaction of each individual to stimuli or to a pattern of stimuli causes the individual to remain in an environment compatible with its needs. If the individual is removed from such an environment, the reactions to the stimuli will enable it to return or find a new environment with the maximum compatible components.

The basis of instinctive behavior is in automatic responses to definite stimuli, and each such response is called a tropism. Each insect species exhibits a wide range of tropisms, a great number relating to sexual behavior and mating, fig. 381, and others relating to ecological factors



Fig. 381. A response to sound associated with sexual behavior. Area in front of tuning fork in cage of male mosquitoes. Left, before sounding fork; right, after sounding fork. (Courtesy of L. J. Roth)

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of the environment. It is this latter group of tropisms that we shall consider here.

PHOTOTROPISM, REACTION TO LIGHT. Most insects have an extremely well-developed response to light, moving toward the light source or away from it. Cockroaches move away from the light and are termed negatively phototropic; bees and wasps move toward it, and are thus positively phototropic. But the reaction often is different in various stages of an insect's life cycle. Housefly maggots are negatively phototropic and move away from light; adult houseflies are positively phototropic and move toward light.

Some aquatic insects, such as mayfly nymphs, maintain their dorsoventral position, that is, stay right side up, by orientation to light from above. This response is most pronounced when the insect is swimming, and is inhibited if the insect is at rest.

There is a definite response by some insects not merely to light in general but also to certain wavelengths of light. In most cases this is an aid to finding food or, in the case of ovipositing females, placing their eggs on the correct type of foliage. Thus, butterflies in search of food are guided by their perception of color in distinguishing yellow, red, and blue from green and approach the flowers of the former colors in preference to the green foliage. But some of these same butterflies will lay their eggs only on a green surface, which under natural conditions would be a healthy leaf suitable for larval food.

GEOTROPISM, REACTION TO GRAVITY. Many insects if placed in a vertical tube will go steadily to the top or bottom, rather than wandering haphazardly around the tube. Leafhoppers always go up; if the tube is inverted so that the insects are again at the bottom, they will start their upward climb again. This is a negative response to gravity, or negative geotropism. Other insects have a positive geotropism, normally going down or toward the earth. Many soil-inhabiting larvae such as wireworms have this reaction; thus, if they hatch from eggs laid on or near the soil surface, they burrow down into the soil.

THIGMOTROPISM, RESPONSE TO CONTACT. Many insects that normally live under bark, in soil, or in curled leaves have a well-developed touch or tactile reaction that causes them to remain in contact with some object, fig. 382. This is known as positive thigmotropism. Observation of the behavior involved indicates that the touch sensation acts as a sort of hypnosis, temporarily immobilizing the insect.

In all insects of active habits, the sense of touch serves as a detector of enemies. Frequently some area or structure at the apex of the abdomen, such as the cerci, has tactile hairs of extreme sensitivity to aid in these "escape" reactions.
#### Ecological Considerations

CHEMOTROPISM, RESPONSE TO ODORS. The number of responses that insects make to various odors is legion. In relation to the environment these are mostly correlated with food, as in the case of an individual locating food for its immediate use, or of a female finding a suitable place for laying eggs in relation to the food of the resultant immature stages, fig. 383. In general, each insect is responsive to only the particular food odors that immediately concern the species. For instance, butterfly females of the genus *Macroglossa* will oviposit only on a surface having the odor of the plant *Galium*, on which the larvae feed; other odors cause no oviposition response.

Most insects follow odor-laden air currents, orienting their line of approach either by direction of air current or by increase or decrease in odor intensity. There are some insects, however, that follow the trail of scent left by their prey as a dog follows a rabbit. The braconid wasp *Microbracon* follows the scent trail of its host, the larva of the mealworm



Fig. 382. An example of positive thigmotropism. Position taken by the earwig *Forficula* in a circular glass container. (From Wigglesworth, after Weyrauch)

Fig. 383. An illustration of chemotropism. Tracks followed by *Drosophila* flies (deprived of wings) when exposed to (A) an odorless stream of air, and (B) air carrying odor of pears. (From Wigglesworth after Flügge)

*Ephestia*, the hunting wasp running along with its antennae held close to the ground. Ants use this method to follow trails to and from the nest, locating it by the routes marked with formic acid secreted and dropped by the ants.

THERMOTROPISM AND HYGROTROPISM. Insects respond to various degrees of heat and humidity, moving towards the condition closer to their optimum. Insects that feed on warm-blooded animals use temperature as a guide to their hosts. Thus, mosquitoes and bedbugs are positively thermotropic to temperatures near 98°F., that is, near mammal blood heat.

COORDINATED TROPISMS. Many activities of insects are dependent on responses involving two or more tropisms at the same time. It has been demonstrated, for instance, that ovipositing *Macroglossa* butterflies require both a green color and the odor of *Galium* to induce egg laying. Certain newly hatched caterpillars that feed in trees have both a negative geotropism and a positive phototropism, insuring that the larvae travel upwards to the natural food. In many other activities there is a fixed chain of responses, following each other in definite order. With the stable fly *Stomoxys*, different reactions to smell, taste, warmth, and moisture control the fly's approach to its animal host, the extension of its proboscis, probing of the host tissues, and, finally, feeding.

#### **Population Dynamics**

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The distribution and abundance of an insect species are measures of its success under the effect of the sum total of its environmental conditions. In usual years a number of conditions will be favorable and others unfavorable to the increase of the species. Futhermore the combination will be different in various parts of the species range. The two sets of factors, favorable and unfavorable, tend to offset each other and "balance out." As a result the abundance of a species in the wild varies from year to year but normally within moderately narrow limits. Occasionally, however, the favorable factors predominate and the insects multiply to unusual or outbreak numbers. Frequently, but not always by any means, these favorable factors are the result of man's changing of the environment.

Outbreaks may expand from a local start and follow an amoeboid type of distribution, such as the tent caterpillar outbreak in Minnesota in 1949–1954, fig. 384. Other outbreaks, especially of grasshoppers and locusts, may result in migratory swarms which leave their point of origin and travel from area to area. The most persistent, destructive, and



Fig. 384. History of an outbreak of the forest tent caterpillar *Malacosoma disstria* in **Min**nesota during 1949-1954. (After Butcher)

well-known example is the Old World desert locust Schistocerca gregaria, which periodically migrates through and devastates large areas in Africa and southwestern Asia, fig. 385. In North America two of the most persistent migratory species are the Mormon cricket Anabrus simplex and the Rocky Mountain locust Melanoplus mexicanus. The latter is common over much of the continent every year in a nonmigratory stage but on occasion builds up huge local populations which become migratory swarms. The last spectacular swarming occurred in the summers of 1938 and 1939, fig. 386. The following flights in 1940 were fewer and shorter, and the swarming phenomenon disappeared in 1941.

Many outbreaks are not spectacular but nevertheless inflict large monetary losses if they affect something valuable to man. The causes of outbreaks are therefore a matter of great interest. Detailed studies have been made on many species, and complex statistical methods are frequently employed in attempting to verify correlations between insect abundance and different factors of the environment. The ultimate aims of these studies are better prediction of outbreaks and better methods of control.

COMPLEXITY OF HABITAT. Some investigators believe that the chances of insect outbreaks are inversely proportional to the complexity of the ecological community to which the insect belongs. According to this view, the abundance of a species is the result of a balance between all the fact tors in the community, both climatic and biotic. In a complex ecological

community such as a mixed forest there are a vast number of species of different organisms, hence a very large total number of factors (some favorable, some unfavorable) governing the population of any one species. Should only one factor change favorably for a species, it would have a relatively small influence on the abundance of the species. On the other hand, in a simple ecological community such as a wheat field there are few species in the total biota, and hence few factors balancing the population of any one species. In this situation a single factor changing in favor of a particular species would theoretically have a much greater influence toward increasing the population of that species.

This viewpoint agrees with the observation that insect outbreaks are much more frequent in forests composed of extensive pure stands of single tree species as compared with mixed forests, and more frequent in single-crop areas as compared with areas of highly diversified farming.

OUTBREAKS AND DAMAGE. It should be pointed out that insects affecting man and his commodities need not occur in outbreak numbers to be of economic importance. A relatively small population (ecologically speaking) of a disease vector might be sufficient to cause tremendous losses to animals and plants because of the disease involved. In the case of fruit, a small infestation of certain insects results in lowering the mar-



Fig. 385. Outbreak areas of the desert locust *Schistocerca gregaria*. Maximum invasion area shaded; known and suspected outbreak areas of 1950, black. (After Uvarov)



Fig. 386. Main migration routes and areas of heaviest egg laying by the migratory grasshopper *Melanoplus mexicanus* in 1938 and 1939. (After Parker, Newton, and Shotwell)

ket grade of the product, with greatly reduced cash profit to the grower. At the same time there are other species which do little noticeable damage at low levels of abundance, such as aphids on grain crops, but which cause tremendous losses when occurring in outbreak proportions.

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## CHAPTER 10

# Control Considerations

HE over-all picture of insect control in the United States and Canada has been changing steadily. In the first place, data show that insects do more damage to all types of food and fiber than was formerly thought. For many years 10 per cent was used widely as the estimated insect damage to food and fiber. Better surveys and better controls have demonstrated that this loss is at least 20 per cent, and in the case of crops such as clover seed there may be a perennial potential of 50 to 75 per cent. The monetary values of both the marketed crop and the cost of production have increased. These facts together mean that it is now necessary for operators of many types (individual, corporate, and governmental) to follow practices giving insurance against excessive losses from insects.

Another control factor has changed which is of especial importance to the crop entomologist. Not many decades ago wormy apples and caterpillars in the flour were no novelty and were tolerated in this country. Now the consumer demands insect-free products, and this is reflected in higher legal and market standards which must be met by



Fig. 387. Potatoes showing virtually complete destruction by the potato leafhopper; insert is a stand of healthy, sprayed potatoes taken on the same day to show contrast and condition. (From Illinois Natural History Survey)

the producer. Whenever this challenge has been met with more thorough chemical control efforts, there have arisen questions concerning residual insecticides on possible human food. This has led to the necessity of determining the permissible residual tolerances of insecticides and their breakdown chemicals. In practice, therefore, the entomologist is faced with the problem of achieving a more nearly perfect control of insects attacking edibles, but at the same time having fewer chemicals left on the marketed product.

#### HOW INSECTS CAUSE DAMAGE

Insects cause injury or damage to man and domestic animals, to a wide variety of crops, to stored products, and to buildings and many of their contents. Each item may be attacked by several or by many insect species, each causing a different type of damage. Sometimes the damage is direct, in that it is the result of the insect's own activities, such as feeding or oviposition. In other cases the principal damage is caused by a disease organism introduced into a plant or animal by the insect.

#### **Direct Damage**

FEEDING-CHEWING TYPE. Insects with chewing mouthparts, such as grasshoppers and caterpillars, as a rule cause the most conspicuous damage, because they remove a noticeable portion of the host.

Most readily noticed on plants is the work of forms feeding externally above the ground, since these attack leaves, fruits, buds, or twigs. Familiar examples are caterpillars on cabbage, fig. 388; grasshoppers feeding on corn, wheat, soy beans, and other crops; and adult Japanese beetles feeding on foliage and fruits of many trees. Another group includes a variety of small beetles, flies, and moths, whose larvae feed within the leaf tissues, and are called leaf miners. The spinach leaf miner *Pegonyia hyoscyanii* makes an irregular blotch in the leaf; the aquilegia leaf miner, a minute fly, makes a winding serpentine mine, fig. 389.

Roots and underground tubers and bulbs are eaten by larvae of many beetles, flies, and a few moths. Root feeders may be inconspicuous, but, if they destroy sufficient root material, the plants either fall over or



Fig. 388. Two heads of cabbage from adjoining plats. A, sprayed for protection from insects; B, not sprayed and badly injured by chewing insects. (From Metcalf and Flint, after Wilson and Gentner)



Fig. 389. Mine of the aquilegia leaf miner. (After Frost)

suffer from lack of moisture and nourishment. Excessive feeding by rootworms (larvae) of *Diabrotica* and related beetle genera causes serious lodging or stunting and death to corn stands, fig. 390. White grubs, Japanese beetle larvae, and wireworms are other larvae that feed on roots. A variety of dipterous larvae, or maggots, attack roots; these include species feeding on onions, cabbage, corn, and soy beans. The maggots tend to feed on and in the larger roots and, when numerous, inflict serious damage or death to the plants. Larvae of a few species of the fly family Syrphidae attack underground bulbs of tulips and other bulb crops, and a wide variety of beetle larvae attack tubers of Irish potatoes, and sweet potatoes, and root crops.

Boring insects are seldom seen, but there are many such species, and they cause considerable damage. Those attacking plants may bore into leaf petioles, branches, trunks, crown, fruits, or roots. Trunk and stem borers of living plants include larvae of clear-wing moths (Aegeriidae),

longhorn beetles (Cerambycidae), bark beetles (Scolytidae), and many miller moths. Twig borers and borers in herbaceous plants may remove so much tissue that the plant dies or is greatly weakened, becoming a prey to wind. Borers in trees may girdle the cambium layer, as do bark beetles, fig. 288, causing the death of the host. Others may tunnel through the heartwood and cause injury to the living host, and their tunnels may greatly reduce the value of the wood for lumber, fig. 391. All stages of powder post beetles (Lyctidae) and termites (Isoptera) bore into and eat dead wood. Borers in fruits include some of our worst agricultural pests such as codling moth larvae in apples; plum curculio larvae in plums, peaches, and cherries; and oriental fruit moth larvae in both twigs and fruits of peach and related fruits.

Man and other animals are also attacked by chewing insects. The entire order Mallophaga, the chewing lice, live externally on vertebrates, where they feed on skin, feathers, and surface debris. Several fly families have species whose maggots live in dead animal carcasses and a few which attack living animals. The screw-worm fly larva *Callitroga hominivorax* gains entrance into the body of mammals by way of a wound and continues to eat through live tissue under the skin. Maggots of the fly families, Oestridae and Gasterophilidae, live internally in the bodies



Fig. 390. Serious root damage to corn caused by rootworms of the genus *Diabrolica*. Normal roots at left, damaged ones at right. (After Tate and Barc)



Fig. 391. Injury by the locust borer. (From the Connecticut Agricultural Experiment Station)

of animals in the stomach, nasal passages, or under the skin. There is some question as to how these maggots feed, but at least in the fullgrown stages they simply suck in gastric contents or secretions produced by the host animal, without any cutting or chewing by the larval mouthparts.

FEEDING-SUCKING TYPE. Insects having piercing-sucking type of mouthparts leave no gaping wounds but sap the vitality of the host. As these insects feed, they pump saliva into the feeding puncture or wound, and frequently the physiological reaction of the host to this saliva is worse than the effect of the withdrawal of blood or sap. For instance, horses may be killed by the bites of blackflies, death resulting from a pathologic reaction to the blackfly saliva rather than from loss of blood.

On living plant leaves sucking insects empty the plant cells, removing the green color and causing a whitening or etiolation followed by production of scar tissue. Each feeding puncture results in a tiny white spot, and, when they are extremely numerous, the entire leaf may appear blanched, fig. 392. Frequently curling of the leaf follows heavy feeding,



Fig. 392. Hollyhock leaves showing effect of feeding by plant bugs. At left, little feeding; at right, excessive feeding that has caused complete etiolation. (From Illinois Natural History Survey)

as in fig. 393. On fruits the feeding punctures cause the formation of scar tissue called catfacing, fig. 394. Sucking insects attacking roots or stems rarely produce feeding symptoms other than the reduced vitality or wilting of the host.

Vertebrates suffer from many more species of sucking insects than from chewing insects. Sucking lice, mosquitoes, horseflies, and fleas are examples of large groups that attack vertebrates almost exclusively. Feeding punctures, or "bites," of these insects usually cause a local irritation accompanied by swelling. Individuals react differently, however, so that no general diagnosis of the effect of bites can be given. The actual damage inflicted by these insects is twofold: (1) irritation. loss of blood,



Fig. 393. Leaf curl on snowball caused by aphids. Normal foliage at left, infested foliage at right. (From Illinois Natural History Survey)



Fig. 394. Catfacing of peaches caused by feeding of plant bugs. (From Illinois Natural History Survey)

pathologic reaction, and loss of condition of the victim, and (2) the possible transmission of certain diseases by some of the insect species. This latter is discussed in a later section of this chapter.

TOXINS. When feeding, certain phytophagous sucking insects apparently inject a material which is poisonous to its host. These materials, called toxins, usually produce many of the same symptoms as do virus infections and are extremely destructive. Two well-known North American examples, both occurring on potatoes, are the potato or bean leafhopper *Empoasca fabae*, fig. 387, and the potato psyllid *Paratrioza cockerelli*. In this latter species only the nymphs produce the toxin, and a small number of nymphs can destroy a healthy potato plant.

INJURY BY OVIPOSITION. A few groups of insects damage plants by laying eggs in them, fig. 395. Tree crickets of the genus *Oecanthus* drill rows of egg cavities in raspberry and blackberry canes and in twigs of fruit trees, causing a later splitting or decay of the injured stems. Cicadas (Cicadidae) and treehoppers (Membracidae) cause the same type of injury to many kinds of fruit and shade trees. The feeding of these insects causes little damage, or it may occur entirely on noneconomic herbaceous plants in which the insects do not oviposit. Fruits may be injured and buds stunted by egg punctures.

SPOILAGE. The damage some insects cause is due to spoiling a product rather than feeding on it. The hop aphid *Phorodon humuli* usually causes little injury to the development of the hops; aphids feeding in the hop cones, however, produce honeydew (feces) which provides a growth medium for molds. This discolors the hops and greatly reduces their

market value. Cockroaches in houses and stores drop feces on various merchandise, causing discoloration and sometimes an offensive odor, which reduce the value of the merchandise. On greenhouse and truck crops, insect webbing, aphid honeydew, or frass will often result in drastic reductions in sale value of the crop.

STINGS AND OTHER IRRITANTS. There are some protective devices of insects that cause injury or extreme irritation, such as bee and wasp stings, ant bites, and nettling or poison hairs of certain caterpillars. Although very unpleasant and painful, these are only a negligible part of insect injury as a whole.

#### **Transmission of Plant Diseases**

Insects affect certain plants seriously by disseminating plant diseases. In many instances the diseases are much more destructive than the insect injury by feeding. Under these circumstances control of the



Fig. 395. Injury to plants caused by egg laying. A, twig split by periodical cicada; B, holes in raspberry cane made by tree cricket; C, slits in bark of apple twig made by treehopper; D, twig of pecan nearly cut in two by twig girdler; E, cherry showing two egg punctures of plum curculio. (After Metcalf and Flint, Destructive and useful insects, by permission of McGraw-Hill Book Co.)

disease may resolve itself into a problem of very thorough control of the insect, because even a few insects would be able to inflict, indirectly, staggering losses.

A number of plant diseases, not actually carried by insects, gain entrance to the plant through insect feeding or oviposition punctures. Brown rot of peach commonly enters through feeding punctures of plum curculio adults, and bacterial rot of cotton through feeding and oviposition punctures of various insects.

Insects assist in the dissemination of some plant diseases by transporting them on the body or in the digestive tract. Fire blight is carried on the legs and body of bees, beetles, and some other insects, as well as by birds and other animals. Spores of certain fungus diseases, such as apple canker, are eaten by insects and pass through the digestive tract in healthy condition. In these cases insects are only one of many ways by which the disease is spread.

More important are cases in which insects are the principal or sole transmitters or vectors of a disease from one plant to another. The insects become infected with the disease, usually either bacterial or virus, by feeding on an infected plant; some of the disease organisms are injected either mechanically or with the saliva into the tissues of the next plant on which the insects feed. Various species of leafhopper transmit aster yellows, and the beet leafhopper transmits curly top of sugar beets, both virus diseases. Many other virus diseases are transmitted by other insects. Bacterial diseases such as cucurbit wilt disease are carried by insects. In cucurbit wilt the bacteria pass the winter in the digestive tract of the hibernating vectors, the cucumber beetles, which start the next year's infections. Many of these virus and bacterial diseases are exceedingly destructive.

#### **Transmission of Animal Diseases**

Some of the most important diseases of man and other vertebrates are transmitted by insects. As with plant diseases, in some cases insect transmission is only one of the several ways by which the disease is spread, and in other cases the insect vector is the only known agent by which the disease is disseminated from one host individual to another.

In the first category are typhoid fever, summer diarrhea, and some kinds of dysentery, all caused by species of the bacterial genus *Bacillus*. Houseflies get the disease organisms on feet or mouthparts through contact with sewage, saliva, or other infected material and then contaminate food or other items on which they alight later. These diseases are transmitted in a variety of mechanical ways, but under some particular

conditions flies may be the principal effective method of dispersal of the diseases.

Bubonic plague (the black death), caused by *Bacillus pestis*, is another contagious disease belonging in this first category. Rats and small mammals serve as the reservoir of the disease, and rat fleas carry it from rat to rat or from rat to human.

Insects are the sole vectors of several important human diseases. Malaria is caused by species of the protozoan genus *Plasmodium*, transmitted from one person to another by some species of mosquitoes belonging to the genus *Anopheles;* yellow fever and dengue (breakbone fever), caused by virus organisms, are carried by several species of mosquitoes of which *Aedes aegypti* is the chief vector in North America; African sleeping sickness is caused by protozoans of the genus *Trypanosoma*, which are carried by flies of the genus *Glossina;* elephantiasis (filariasis), caused by nematode worms of the genus *Filaria*, is transmitted by several species of mosquitoes. In all these instances the mosquito or fly, when feeding on a diseased person, draws up into its buccal cavity or digestive system some of the disease organisms; some of these are discharged during feeding at a later date into the tissues of another person. In this manner healthy persons are inoculated with the disease.

Typhus is caused by an almost ultramicroscopic organism called *Rickettsia*, which is carried by body lice or cooties. These take up disease organisms when feeding and then later expel them in the feces. Scratching on the part of the bitten person works the disease organism into the skin and effects inoculation.

Ticks and mites are the only known vectors of several important diseases, of which three are of especial interest. Texas fever, lethal disease of cattle, is caused by a species of Sporozoa, *Babesia bigemina*. The disease organisms are transmitted by the cattle tick *Margaropus annulatus*. Rocky Mountain spotted fever is a highly fatal human disease of increasing incidence, caused by a *Rickettsia* organism. This disease is maintained in some of the small wild rodents, and a few species of ticks of the genus *Dermacentor* effect the transfer of the disease by feeding on infected rodents during nymphal development and afterwards, when adult, biting man. A third disease is scrub typhus, an oriental disease caused by another *Rickettsia* organism. This is transmitted from wild rodents to man by chiggers (early instars of the mite family Trombidiidae) and was a serious hazard to humans in both the Burma and Pacific theaters during World War II.

Under most circumstances the practical control of these diseases is obtained by control of the vectors. This has been particularly effective in the case of Texas fever; control of the cattle tick has virtually elim-

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inated the disease from the United States. Extremely satisfactory results have been obtained also in reducing outbreaks of typhus by controlling body lice. Mosquitoes, flies, and *Dermacentor* ticks are more difficult to control, and the species involved have a wide dispersal range so that measures aimed at control of these vectors have not always produced such remarkable results as those obtained with Texas fever and typhus.

#### A SURVEY OF PEST INSECTS AND ARACHNOIDS

In North America some ten thousand different species of insects are of economic importance in varying degrees. Of these about one thousand species are the persistent pests that cause the greater proportion of our insect damage. It is not proposed to give here a detailed discussion of these, but instead to present a brief survey of the most destructive species in relation to the crops or commodities they attack, or the damage they do.

#### **Agricultural Crop Pests**

By far the greatest number of important insect pests attack **farm** crops and animals. Injury is of many types, and insect species of widely different habits are involved.

FIELD-CROP INSECTS. All the major field crops with the possible exception of soy beans suffer high losses from insect attack. Serious enemies of cotton are the boll weevil, which feeds inside the boll, destroying the developing cotton fiber; the cotton leafworm, whose larvae eat the foliage; and the cotton aphid, which sucks juices from the leaves and stems. Corn may be almost completely destroyed by grasshoppers feeding on the foliage or by chinch bugs sucking the plant juices. The corn yield is annually reduced by several species of borers in cobs and stalks, including both the European corn borer and the western corn borer. Wheat and other small grains are injured extensively by various species of cutworms, wireworms, aphids, and grasshoppers, depending on climatic conditions and region. Larvae of the hessian fly attack the stems and crowns of grains; and this species is the most destructive single pest attacking wheat. Field enemies of tobacco, a high cash-value crop, are chiefly leaf feeders, such as hornworms and flea beetle adults; cutworms and tobacco budworms also cause serious damage. The potato beetle feeds on potato foliage, and various leafhoppers suck the plant juices. Potato tubers are injured by soil-inhabiting larvae such as wireworms and flea beetle larvae.

Other field crops are attacked by insects of general feeding habits, such as grasshoppers. Each crop has in addition certain pests more specific in their host preference. The most notable exception was the soy bean crop which for many years had no serious insect enemies in North America. About 1954, however, it was apparent that certain species of grasshoppers, root maggots, and white grubs were becoming pests of importance on this crop.

TRUCK CROP AND GARDEN INSECTS. Each plant species grown in truck farm or garden is subject to ravages from one or more insects specific in their food preference. These include such insects as cabbage loopers, cabbage butterflies, and cabbage aphids, that feed on cabbage, cauliflower, and other cruciferous crops; the carrot rust fly, specific on carrots; melonworms, asparagus beetles, and the Mexican bean beetle. In addition to pests specific to each crop, there are many general feeding insects that may attack almost any of these crops. Garden webworms, grasshoppers, blister beetle adults, cutworms, and fall armyworms are among the group most likely to occur occasionally in destructive numbers.

GREENHOUSE INSECTS. In the greenhouse, warm humid conditions are maintained throughout the winter months. As a result we find in them many insect species that are normally tropical and subtropical in distribution. Most troublesome of these are several species of thrips, mealybugs, and scale insects. In addition, several species that are outdoor in habit during the summer invade greenhouses and continue active all winter, instead of becoming dormant. The melon aphid, green peach aphid, and the greenhouse leaf tier are examples of this type.

The different kinds of plants grown under glass are legion, and few are not attacked either by general feeding insects like larvae of leaf tiers or by specific pests such as the chrysanthemum midge, whose larvae make galls on leaves and stems, fig. 396. Normally forty to fifty species of potentially destructive insect species are found during the winter season in greenhouses. When one considers the variety of hosts involved and the fact that these may all occur in a range of glass of only a few thousand square feet, it poses a serious control problem and demands constant alertness on the part of the operator.

FRUIT INSECTS. All classes of fruit—citrus, deciduous, and small—suffer heavily from insect damage, and in each group the major pests are different.

Citrus-fruit trees are injured mostly by scale insects, mealybugs, whiteflies, thrips, and mites. The purple scale, California red scale, and black scale are especially important, damaging fruit and trees or producing honeydew on which grows a black sooty fungus that discolors

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Fig. 396. Injury caused by the chrysanthemum midge *Diarthronomyia hypogaea*. About natural size. (From Metcalf and Flint, Destructive and useful insects, by permission of McGraw-Hill Book Co.)

the fruit. Many of the scales on citrus have a wide host range, but, being subtropical in distribution, they are pests of other fruits only in the citrus belt, in Florida, southern Texas, and southern California.

Deciduous fruits, including apple, pear, cherry, peach, plum, and their allies, have many destructive pests. Apple fruit is attacked chiefly by larvae of the codling moth. This insect is the most important species on the apple control calendar. Peaches, cherries, and other soft fruits are entered by larvae of the plum curculio, which also attacks apples. The branches and foliage of the entire group suffer from San Jose scale, oriental fruit moth, aphids, red spiders, a host of leaf-feeding species, and many that bore in the tree or deform the fruit.

Small fruits are a group of wide taxonomic composition and have more specific insect pests. Grapes are attacked by the grape berry moth, many aphids and leafhoppers, and leaf-eating beetles that eat roots and leaves. Currants, raspberries, and strawberries are attacked by a variety of aphids, leaf-feeding larvae, and stem or crown borers.

#### **Insects Affecting Man and Domestic Animals**

Both man and domestic animals suffer annoyance and exposure to disease from the activities of insects. Certain of these insects, such as the Anoplura, confine their attacks to one or two closely related species

of animals. Others, such as mosquitoes, are general feeders on a wide variety of warm-blooded vertebrates.

Domestic fowl are attacked chiefly by Mallophaga (chewing lice) and mites, several of which live on hens, ducks, turkeys, and geese. On young fowl infestations of lice often cause death; on older birds the lice cause lack of condition and lower egg production. Mites sometimes become very injurious by reducing the general health of the flock. Blackflies transmit at least one duck disease similar in many respects to malaria. Hens suffer also from attacks of specific fleas, of which the southern sticktight flea is the most persistent.

Domestic animals and man have a variety of specific parasites, including Anoplura (sucking lice), fleas, bedbugs, a few Mallophaga, and several kinds of mites. These latter include such annoying forms as itch mites, chiggers, and ticks. Sheep have in addition "sheepticks"; these are odd wingless flies of the family Hippoboscidae. Attacks by ectoparasites result in irritation and loss of condition, but seldom in death unless disease transmission is involved.

Several vertebrates are attacked internally by larvae of bot flies and warble flies. In the horse the larvae attach to various regions of the digestive tract and cause severe loss of weight and condition. Certain warble flies develop in the sinuses of sheep, and other species along the back of cattle where they form a pocket just beneath the hide. Larvae of the screw-worm fly enter wounds, feed beneath the skin, and annually cause large losses to all kinds of livestock.

In addition to these and other specific pests, all warm-blooded vertebrates are attacked by a great number of bloodsucking flies—mosquitoes, horseflies, blackflies, *Symphoromyia* flies, stable flies, and horn flies. Some of the fleas, ticks, mites, and bedbugs are also general feeders. The annoyance these cause is often severe. Blackflies especially may be destructive and occasionally cause the death of large numbers of horses and mules in local areas. Mosquitoes, blackflies, and horseflies are at times abundant enough to cause an exodus of tourists from an area, to reduce land values near suburban centers, or to retard settling of large tracts, as in the extreme northern part of Canada and in Alaska. The effect of these attacks on livestock in general may result in a loss of condition equal to or greater than that caused by specific parasites.

The greatest potential injury to man and animals by insects is through insect-borne diseases. As previously mentioned, insects transmit some of the most destructive diseases of vertebrates. During war the danger from insect-borne diseases is greatly increased, because men are concentrated under conditions in which sanitation and insect control may be difficult, and the crowding offers good opportunities for the rapid spread of disease.

#### Stored-Food-Products Pests

Grain and meat, flour, grain meals, and other highly nutritious foodstuffs are eaten by many insects. When in storage, these commodities suffer a heavy loss from insect ravages and necessitate constant preventive and remedial measures to keep them to a minimum.

In North America the chief pests of stored grains and grain products are the adults and larvae of the sawtooth grain beetle, the confused flour beetle, cadelle, mealworms, and the granary and rice weevils; and the larvae of the Indian meal moth and the Mediterranean flour moth. Peas and beans in storage are eaten by various pea weevils (Bruchidae). Meats and cheeses are eaten by larder beetles and maggots of the cheese skipper.

Large quantities of stored foods are attacked first by the group of insects just listed. After a certain amount of damage is done molds enter, followed rapidly by a host of other insect species, and soon the entire mass of food may be reduced to a small percentage of the original.

#### Pests of Human Habitations

Some insect species have become almost "domesticated," especially north of the frost line, in that they are found almost entirely in human habitations. In the case of ectoparasitic species the relationship antedates civilization and is due to the parasites staying with the warm-blooded host. With other species, however, the relationship is more recent and is due to the relatively high temperatures at which houses and buildings are maintained even through severe winters. Thus some species, originally semitropical, are now found much farther north and are able to maintain themselves in human habitations.

Ectoparasites and pests of stored foods are of prime importance in human habitations. In addition, larvae of clothes moths and carpet beetles eat anything containing animal fibers, such as woolen garments, upholstery, and carpets. Silverfish and cockroaches are general feeders that eat starchy foods such as bookbindings and are an unsightly nuisance. Cockroaches drop excrement promiscuously and spot and taint food and quarters; when very abundant, they will give a house, store, or restaurant a disagreeable and penetrating odor. Ants frequently invade buildings and may become a serious nuisance in the kitchen and foodstorage rooms.

Termites are the most destructive pests of buildings. They eat the wood in foundations, flooring, and walls, necessitating extensive repairs. Other insects live in wood in dwellings, such as Lyctidae beetles, and carpenter ants may eat out extensive galleries in wood of buildings to

use for nests. But of all insects that attack the actual building, termites are by far the most formidable.

#### **Shade Tree and Forest Insects**

Trees in general support thousands of insect species, which may defoliate, girdle, or bore into the tree, or suck its juices. Many of these species have only a slight effect on the host tree, but some damage the tree severely or may even kill it. As a result there is a high annual loss in both shade and forest trees.

Shade trees in the northeastern states are attacked especially by the gypsy and brown-tail moths. Elms suffer most from the elm leaf beetle and from Dutch elm disease, carried from tree to tree by the small European elm bark beetle. Direct injury by bark beetles and wood borers weakens and kills trees of many species.

Forest trees are visited periodically with insect outbreaks that kill huge tracts of timber. This is a loss of natural resources that in past years was given little attention, but, now that our forests are dwindling, increased efforts are being made to find means of checking losses. Larvae of forest tent caterpillars, gypsy and brown-tail moths, hemlock loopers, budworms, and tip moths are perennial defoliators of various deciduous and evergreen trees. Bark beetles are the greatest single enemy of conifers, especially in the West. Sawflies feeding on conifers occasionally appear in outbreak numbers and may cause tremendous damage. The most recent large sawfly outbreak was of the introduced European spruce sawfly, which in 1938 defoliated about twelve thousand square miles of spruce timber, chiefly in the eastern provinces of Canada, fig. 397.

#### NATURAL vs. ARTIFICIAL CONTROL

From time to time insect pests of many kinds are reduced to insignificant numbers by inimical factors of the environment, such as drought, parasites, or disease, as discussed in Chapter 8. The European spruce sawfly, for instance, has been virtually exterminated in large areas by a virus disease. In 1935 the chinch bug was reduced to the status of a rarity in many corn-belt states by adverse winter conditions plus a fungus disease. But these phases of natural control are unpredictable and may be nonoperative for long periods. Furthermore some of our worst pests, such as the codling moth, apparently have at most only partial or insignificant natural checks and so are a menace every year. In order to protect his interests, it has therefore been necessary for man to devise means of combating insects by his own efforts. This type of



Fig. 397. Distribution of the European spruce sawfly in North America during the epidemic of 1938. (Modified after Balch)

control is called *artificial control*, in contrast to the natural control effected by the unaided environment.

#### CONTROL METHODS

In artificial control a great many different methods have been found to reduce the numbers of individual pests. These methods fall into a few general categories and are treated briefly in the following paragraphs.

#### Quarantine

The most obvious way to avoid damage by an insect is to prevent its becoming established in a country if it is not already there. There are hundreds of insects in other parts of the world, especially in temperate areas of Europe and Asia, which we believe might become pests of great economic importance if established in North America. To prevent their entrance, the United States Federal Government maintains an inspection of imports into the country, especially living plants or animals or packing material that is likely to harbor pests and serve as a carrier for them. Most or all of this material is fumigated before being allowed into the country. In addition, states may have restrictive regulations regarding the movement of critical materials within the state or into the state. The Canadian Government maintains a similar service.

It is admittedly impossible to prevent indefinitely the entrance of all potential new pests into the country, but quarantine records show that hundreds and sometimes thousands of new importations are prevented every year. It is impossible also to estimate how much we gain by this. Experience with such destructive importations as the cotton boll weevil, fig. 398, the European corn borer, and the Japanese beetle, however, emphasizes that we cannot afford to take the chance of allowing free entry to every insect species.

#### **Biological Control**

Present types of biological control fall into three categories—use of insect parasites or predators, use of pathogenic organisms, and fertility control.

INSECT PARASITES AND PREDATORS. The possibility of propagating and distributing natural enemies for the control of destructive insects has kindled the imagination of the entomologist for many decades. It has been found, however, that with destructive insects endemic to the United States we can do little to improve on existing natural control. Representing the evolutionary product of great geologic time, natural control has usually reached a peak that cannot be raised profitably by artificial means.

With introduced pests the situation is entirely different. The particular species may have an abundance of parasites or predators holding its numbers in check in its native land. When it is accidentally introduced into another country, usually only the pest without its parasites is transported. Freed from enemies, the pest in the new land is able to flourish at an unimpeded rate.

The ideal control for such an introduced pest would be to establish efficient enemies of it so that they would reduce the numbers of the pest to insignificant proportions. This might result in a permanent control that would obviate the necessity for an annual program of more expensive measures.

This ideal has been achieved only rarely. The most outstanding example has been the control of introduced cottony-cushion scale by the importation and establishment of the Australian vedalia ladybird beetle. So effective are the beetle and its larvae in controlling the scale in California that only occasionally and locally does the scale become important as a pest. Many parasites, especially of introduced pests such as the Japanese beetle, gypsy moth, and European corn borer, are imported by the U. S. Bureau of Entomology and Plant Quarantine, and released in the United States. Many imported parasites fail to



maintain themselves in the United States under natural conditions, owing undoubtedly to their lack of adjustment to climate or the lack of availability of suitable hosts at the right time. Some species have become successfully established and aid in controlling the pest species. It is hoped that eventually sufficient parasite populations will be built up so that the populations of many pest species will drop well below their present destructive level. In some areas this result has already been achieved for the satin moth by introduced hymenopterous parasites, especially in Washington State and British Columbia. Propagation and dispersal of bacterial diseases of Japanese beetles have also given promise of being effective. Considerable success has been achieved in islands such as Hawaii by using a variety of parasites against insects attacking many crops.

Sufficient work has been done in biological control to show that a number of factors influence its success or failure. A few of these factors are the ecological requirements of the parasites, their effect on each other (see under COMPETITION, p. 457), their host specificity, their rate of increase, and the character of their dispersal. To be tried effectively, well-trained personnel and a great amount of specialized equipment are necessary, together with an organization for gathering parasite material in foreign countries and getting it into the United States alive and healthy.

Because of these conditions, the work on biological control in the United States is done chiefly by the Federal Government; a notable exception is much intensive work done by the state of California. The final distribution and liberation of parasites are often performed cooperatively by scientists of the Federal Government and interested state agencies. The Canadian Government is also extremely active in biological-control efforts.

PATHOGENIC ORGANISMS. Spectacular natural outbreaks of fungus or bacterial diseases of chinch bugs and various other insects early led entomologists to hope for insect control through dissemination of pathogenic organisms. Early efforts failed, because years which did not naturally favor spread of the known diseases were ecologically unsuited also for their artificial propagation. Since about 1930 several organisms have been found that are more successful for artificial control. The milky disease of the Japanese beetle has proved useful in some parts of the American range of the beetle. Several kinds of polyhedrosis viruses are proving excellent controls for certain sawflies destructive to conifers. In California both a polyhedrosis virus and the Thuringian bacterium have proved effective as a field control for the alfalfa caterpillar. These successes point to a profitable field of investigation in insect control. FERTILITY CONTROL. An entirely different kind of biological control has been invented and is currently being tested by Dr. E. F. Knipling and his associates in the Entomological Research Branch of the U.S. Department of Agriculture. The test subject is the screw-worm Callitroga hominivorax, destructive to livestock and game animals. In this species the females mate only once in their life. It was further discovered that males could be sterilized by gamma radiation without interfering with their mating behavior. Sterilized males, in numbers calculated to be twice the initial natural population of fertile males, were released in the population at successive intervals. These sterile males outcompeted the indigenous males in mating with the females, with the result that more and more of the latter laid infertile eggs. In a large test of this method on the isolated island of Curacao. Netherlands West Indies, the screw-worm fly was exterminated in several months. This approach to the biological control of insects may prove extremely important in the future against many kinds of insects.

#### Cultural and Management Control

Some insect pests of agricultural or forest crops may be kept below the damage level by various cultural or management practices.

An important general approach is keeping crops healthy, by proper fertilizing, drainage, irrigation, and cultivation, and by planting crops that are well adjusted physiologically to the climate and soil.

Against certain pests specific cultural methods are of value, such as clean cultivation, crop rotation, certain times of harvesting or planting, and the use of insect-resistant or tolerant varieties.

Clean cultivation eliminates weeds that may serve as host to insects that attack the crop. The buffalo treehopper breeds on many herbaceous weeds; the adult hoppers fly into adjacent fruit trees, cut slits in the twigs, and in them lay their eggs. Clean cultivation of an orchard prevents this injury by eliminating the primary host. Weeds and soil debris also serve as hibernating or pupating quarters for a wide variety of harmful insects, and clean cultivation tends to discourage a build-up of population in that area.

Crop rotation has been found especially effective against some insects whose larvae live in soil and feed on roots. *Diabrotica* rootworms can be controlled by crop rotation. These beetle larvae feed primarily on corn roots. If corn is grown continuously on the same ground for over three years in localities favoring these insects, they build up large populations and cause severe damage to corn. If, however, corn is eliminated and wheat or legumes substituted for a year, the rootworms starve.

For this reason a rotation of corn with wheat or other crops arranged so that corn follows corn for no more than 2 or 3 years eliminates rootworm damage almost completely.

Choice of time of planting crops is useful as a control measure for certain insects. The hessian fly, a serious wheat pest whose larva feed in the leaf sheath of wheat, can be successfully controlled by regulating the time of planting winter wheat. The entire fall generation of adult midges normally emerges within a short period, following late summer rains. The adults live only 3 or 4 days, laying their eggs in grooves of wheat leaves. If winter wheat is planted after this generation is past, the plants will have no eggs laid on them and consequently will be entirely free from attack until spring. To take advantage of these conditions entomologists in wheat-growing areas annually establish dates for sowing winter wheat that will (1) allow the plants enough good weather to attain satisfactory growth before winter, and yet (2) be late enough to avoid all but a light infestation of hessian flies, fig. 399. The spring generation of hessian flies attacks only late shoots (tillers) of winter wheat and does little damage.

Early or late planting of corn and other crops is sometimes of assistance in reducing infestation and damage by such pests as rootworms and European corn borers.

In forestry, management practices that tend to keep down the abundance of insect pests are essentially various ways of changing the ecological nature of the forest community. It has been found that some of



Fig. 399. Sample of a chart showing safe dates for sowing wheat in several north central and eastern states to escape injury by the hessian fly. (From U.S.D.A., E.R.B.)

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the most destructive species of bark beetles build up outbreak populations in over-age stands of pine. By cutting the trees for timber before they reach old age, this beetle population increase is prevented, and younger trees in the stand are given a better chance of development. By selective cutting and logging, diversity of the forest can be achieved in regard to both species of trees and age groups represented by these trees. In general, the greater the diversity, the fewer insect outbreaks will occur.

Another important phase of cultural control is the selection of species or varieties of plants that are resistant to or tolerant of insect attack. This is as yet the most successful general method for preventing damage by the European corn borer. It has been found that certain varieties of corn have an unusually strong stalk that will withstand heavy infestations of corn borer larvae without becoming critically weakened. Less tolerant varieties having the same borer infestation break off and lodge, resulting in lower yield and greater difficulties in harvesting the crop.

This same crop-selection principle is used as a remedy for the gypsy moth. We have already mentioned that, for its successful early 'development, one of the species' favored hosts is necessary, but that later instars move over to pines and other nonfavored species, which they may defoliate. To decrease infestation by this pest, the favored host species are kept to a minimum and replanting is done with other species.

#### Mechanical Control

If it is necessary to use more direct methods than those previously mentioned in order to obtain control of an insect, there are several that can be followed. The simplest is mechanical control, which includes removing insects by hand or using mechanical devices to trap or kill them.

Hand picking is practiced on large caterpillars such as tobacco or tomato hornworms. The number of insect individuals is usually only moderate, and the individuals are large in size and easy to see. Nests of larvae can be cut out of trees and destroyed. A number of mechanical devices are used with good effect against a limited number of pests. One of the most common is screening, both screen doors and window screens, to keep insects out of buildings. Various traps of the maze type are used to catch flies. Bands of burlap or paper are fastened around trunks of fruit trees to provide hibernating or pupating quarters for codling moths; periodically these bands are examined and the insect occupants killed. Bands of screen, gauze, or sticky substances are put around trees to prevent ascent of wingless female moths and larvae, fig. 400.

Against migrating wingless insects, such as Mormon crickets or chinch



Fig. 400. Banding traps used to prevent ascent of larvae and wingless female moths. (From U.S.D.A., E.R.B.)

bugs, attacking field crops, various mechanical barriers were formerly used, especially furrows in the soil or wooden or paper barriers.

#### **Physical Control**

We have noted previously that insects can endure only limited extremes of heat, cold, and other physical phenomena. This limited endurance is utilized to kill insect pests. It is difficult to control such physical factors over a large space, so that with a few exceptions their use is restricted to buildings and tight enclosures.

Superheating is employed by many mills and elevators as a control measure. During hot weather in summer, the building heating plant is used to raise the temperature to about 140°F. for several hours, and this kills all the insects in the building.

Cooling is used extensively in storage for insect control. Furs, tapestries, and other valuable articles of animal origin are kept in lockers below 40°F. This does not kill all the insects, but at this temperature they are completely inactive and do no damage.

Electricity is used to some extent to kill insects. Screens and lights can be fitted with electrically charged grills that electrocute insects coming between the elements.

#### **Chemical Control**

Various chemical compounds are toxic or repellent to insects and are used extensively for their control. Because it is usually more expensive, such chemical control is applied when control by other methods is too slow or too ineffective.

TYPES OF CHEMICALS. Insecticides may be divided into six categories: stomach poisons, contact poisons, general purpose, systemics, fumigants, and repellents.

STOMACH POISONS are substances that kill the insect when they are eaten and taken into the digestive tract. The most widely used are the arsenicals, especially Paris green, lead arsenate, and calcium arsenate. Hellebore and fluorine compounds such as sodium fluoride and sodium fluosilicate are also commonly used stomach poisons.

Stomach poisons are used primarily against insects that have chewing mouthparts and bite off and swallow portions of the food. The poison is applied to the surface of the food as a spray, dip, or dust, and the insect is sure to take some of it with its meal. Against some insects such as ants and cockroaches, the poison is mixed with an attractive bait put where the insect can find and eat it. For ants the baits are usually liquid and are set near nests or runways.

CONTACT POISONS kill the insects by contact without being swallowed. Often the lethal agent is a gas that enters the spiracles and causes suffocation, as in the case of nicotine; in other instances the lethal compound may affect the nervous system.

Until about 1940, the principal contact poisons in use against insects were nicotine alkaloid (volatile), extracted from tobacco; pyrethrum, extracted from the dried flower heads of certain species of the aster



Fig. 401. Application of insecticides; the use of airplane equipment has been of great aid in many situations. (From Ohio Agricultural Experiment Station)

genus *Chrysanthemum*; sulphur and several sulphur compounds; and several lubricating oils, miscible oils, and oil emulsions. Since 1940, there have been developed a number of synthetic organic compounds (discussed in general purpose compounds, below) that are far more toxic to many insects than the contact poisons of older vintage.

Contact poisons are of especial use against insects having sucking mouthparts, such as aphids, which do not take up poisons applied to the food surface; insects that cannot be reached when feeding, such as bottom-feeding mosquito larvae which are killed by contact poisons when they come to the surface for oxygen; and insects such as adult mosquitoes that are scattered generally throughout an area. Contact poisons toxic to a variety of insects have the advantage of killing both the sucking and chewing insects at the same time. These poisons are applied as a dip, dust, spray, or colloidal mist (aerosol).

GENERAL PURPOSE COMPOUNDS include an array of substances which act either as a stomach poison or contact poison, depending on the manner in which the insect encounters them. These include chlorinated hydrocarbons and various organic phosphorus and sulphur compounds. Of the very large variety of these substances available the following are probably the most commonly used: DDT, chlordane, heptachlor, aldrin, dieldrin, endrin, methoxychlor, toxaphene, parathion, malathion, and BHC (benzene hexachloride). Each of these has advantages under specific conditions; information is readily available from local entomological centers.

SYSTEMICS are poisons which are absorbed by the host and translocated to various parts of the organism, from which they may be taken up by the feeding insect. This phenomenon was recognized early with regard to selenium. Ornamental plants grown on soil containing selenium absorb the latter, which kills mites and insects feeding on the plants; this selenium method cannot be used on edible crops, however, because of the extreme toxicity of selenium to humans and livestock. Potatoes sprayed with Bordeaux mixture (a copper compound) and bean plants sprayed with derris show this phenomenon. More recently special insecticides have been developed using this principle. Systox and schradan are used on various plants. Insecticides having similar action are being tested on livestock. Many entomologists believe that there may be a great future for this type of control.

FUMIGANTS are toxic gases, usually applied in an inclosure such as a box, building, or tent. Compounds in general use are hydrocyanic acid, nicotine, paradichlorbenzene (PDB), methyl bromide, and chloropicrin. The use of fumigants is aimed at killing all the insects in the inclosure, and fumigants are employed commonly to rid houses, greenhouses, warehouses, stores, mills, and elevators of insects. Box fumigation is used for small quantities of material, such as clothing. In World War II fumigation stations were used extensively to rid clothing of lice and other vermin.

In California gastight tents are used to inclose citrus trees for fumigation with hydrocyanic acid, fig. 402. Prior to fumigation buildings need to be checked for gas leaks and the leaks closed in order to maintain the desired gas concentration as long as needed.



Fig. 402. Tents used for fumigation of citrus trees with hydrocyanic acid gas. Above, preparing the temporary tent; below, the tent in position for fumigation (early illustrations of the method). This method, developed before 1900, is extremely sedentary compared with airplane insecticide application, but is nevertheless one of the most effective methods today for treating insect enemies of citrus trees. (From U.S.D.A., E.R.B.)