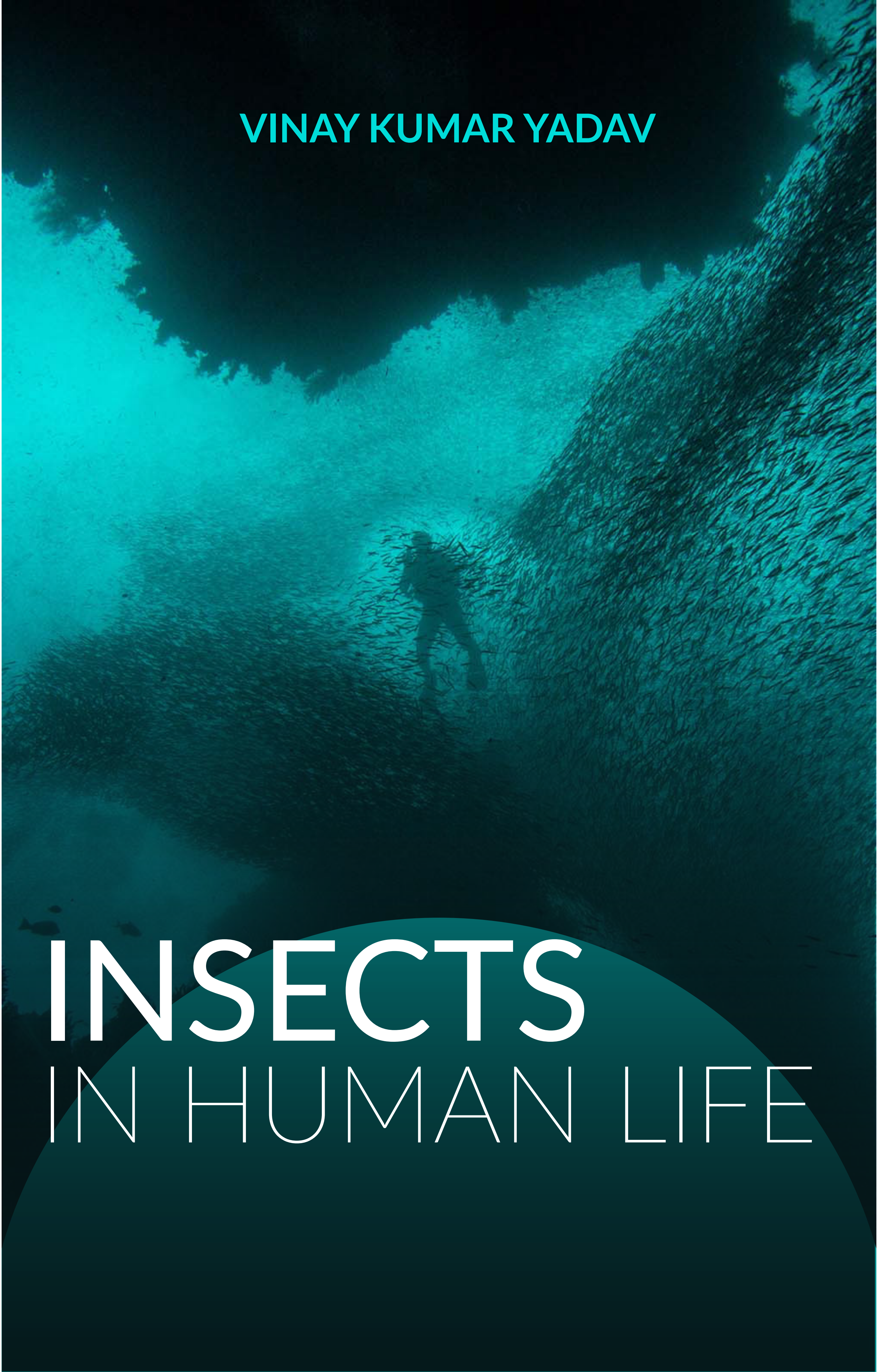

VINAY KUMAR YADAV

INSECTS
IN HUMAN LIFE

INSECTS IN HUMAN LIFE

By VINAY KUMAR YADAV

Insects in Human Life book is composed and reordered by me, Vinay Kumar Yadav. I composed this book while I was a P.G. student. This topic was in my course and when I tried to buy a book which have all these topics, I got that there were many books which were very costly too. But the main problem with those books was, that none of them covered all the topics,which were in my course.
So, I started collecting the matter and composed a book .

I think ,this can be best book for the people who want a general understanding about the importance of insects in Human Life.

-Vinay Kumar Yadav


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Insect

Insects or **Insecta** (from Latin *insectum*) are hexapod invertebrates and the largest group within the arthropod phylum. Definitions and circumscriptions vary; usually, insects comprise a class within the Arthropoda. As used here, the term Insecta is synonymous with **Ectognatha**. Insects have a chitinous exoskeleton, a three-part body (head, thorax and abdomen), three pairs of jointed legs, compound eyes and one pair of antennae. Insects are the most diverse group of animals; they include more than a million described species and represent more than half of all known living organisms.[2][3] The total number of extant species is estimated at between six and ten million;[2][4][5] potentially over 90% of the animal life forms on Earth are insects.[5][6] Insects may be found in nearly all environments, although only a small number of species reside in the oceans, which are dominated by another arthropod group, crustaceans.

Nearly all insects hatch from eggs. Insect growth is constrained by the inelastic exoskeleton and development involves a series of molts. The immature stages often differ from the adults in structure, habit and habitat, and can include a passive pupal stage in those groups that undergo four-stage metamorphosis. Insects that undergo three-stage metamorphosis lack a pupal stage and adults develop through a series of nymphal stages.[7] The higher level relationship of the insects is unclear. Fossilized insects of enormous size have been found from the Paleozoic Era, including giant dragonflies with wingspans of 55 to 70 cm (22 to 28 in). The most diverse insect groups appear to have coevolved with flowering plants.

Adult insects typically move about by walking, flying, or sometimes swimming. As it allows for rapid yet stable movement, many insects adopt a tripedal gait in which they walk with their legs touching the ground in alternating triangles, composed of the front & rear on one side with the middle on the other side. Insects are the only invertebrates to have evolved flight, and all flying insects derive from one common ancestor. Many insects spend at least part of their lives under water, with larval adaptations that include gills, and some adult insects are aquatic and have adaptations for swimming. Some species, such as water striders, are capable of walking on the surface of water. Insects are mostly solitary, but some, such as certain bees, ants and termites, are social and live in large, well-organized colonies. Some insects, such as earwigs, show maternal care, guarding their eggs and young. Insects can communicate with each other in a variety of ways. Male moths can sense the pheromones of female moths over great distances. Other species communicate with sounds: crickets stridulate, or rub their wings together, to attract a mate and repel other males. Lampyrid beetles communicate with light.

Insect

Temporal range: 396–0 Ma

PreЄ Є O S D C P T J K PgN

Early Devonian[1] (but see text) – Present

Clockwise from top left: dance fly (*Empis livida*), long-nosed weevil (*Rhinotia hemistictus*), mole cricket (*Gryllotalpa brachyptera*), German wasp (*Vespula germanica*), emperor gum moth (*Opodiphthera eucalypti*), assassin bug (Harpactorinae)

0:00 / 0:00

A chorus of several *Magicicada* species

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Clade:	Pancrustacea
Subphylum:	Hexapoda
Class:	Insecta Linnaeus, 1758

Subgroups

See text.

Synonyms
▪ Ectognatha ▪ Entomida

Humans regard certain insects as pests, and attempt to control them using insecticides, and a host of other techniques. Some insects damage crops by feeding on sap, leaves, fruits, or wood. Some species are parasitic, and may vector diseases. Some insects perform complex ecological roles; blow-flies, for example, help consume carrion but also spread diseases. Insect pollinators are essential to the life cycle of many flowering plant species on which most organisms, including humans, are at least partly dependent; without them, the terrestrial portion of the biosphere would be devastated.[8] Many insects are considered ecologically beneficial as predators and a few provide direct economic benefit. Silkworms produce silk and honey bees produce honey and both have been domesticated by humans. Insects are consumed as food in 80% of the world's nations, by people in roughly 3000 ethnic groups.[9][10] Human activities also have effects on insect biodiversity.

Contents

Etymology

The word "insect" comes from the Latin word *insectum*, meaning "with a notched or divided body", or literally "cut into", from the neuter singular perfect passive participle of *insectare*, "to cut into, to cut up", from *in-* "into" and *secare* "to cut";[11] because insects appear "cut into" three sections. A calque of Greek ἔντομον [*éntomon*], "cut into sections", Pliny the Elder introduced the Latin designation as a loan-translation of the Greek word ἔντομος (*éntomos*) or "insect" (as in entomology), which was Aristotle's term for this class of life, also in reference to their "notched" bodies. "Insect" first appears documented in English in 1601 in Holland's translation of Pliny. Translations of Aristotle's term also form the usual word for "insect" in Welsh (*trychfil*, from *trychu* "to cut" and *mil*, "animal"), Serbo-Croatian (*zareznik*, from *rezati*, "to cut"), Russian (насекомое *nasekomoje*, from *seč'/-sekat'*, "to cut"), etc.[11][12]

Definitions

The precise definition of the taxon Insecta and the equivalent English name "insect" varies; three alternative definitions are shown in the table.

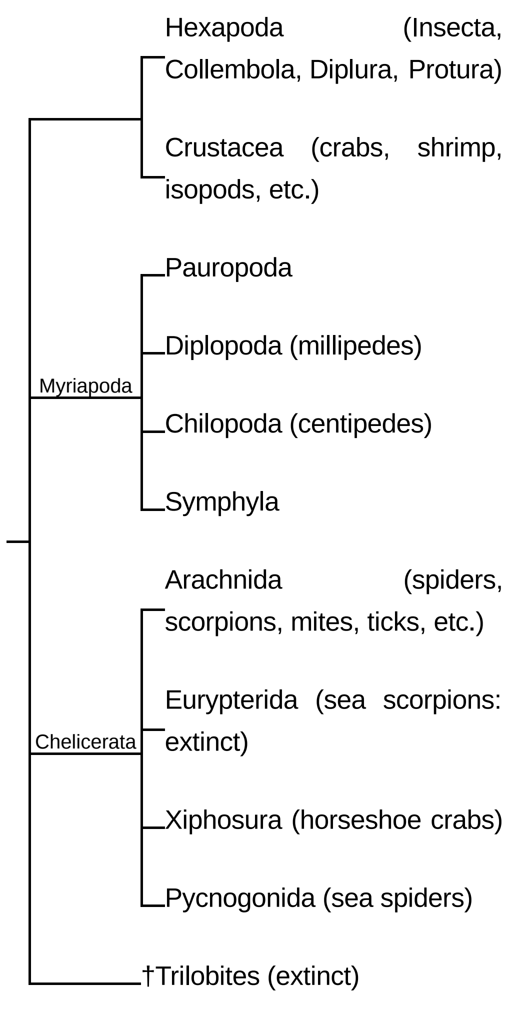
Definition of Insecta

<table>
<tr><th>Group</th><th colspan="3">Alternative definitions</th></tr>
<tr><td>Collembola (springtails)</td><td rowspan="6">Insecta sensu lato
=Hexapoda</td><td rowspan="3">Entognatha
(paraphyletic)</td><td rowspan="5">Apterygota
(wingless hexapods)
(paraphyletic)</td></tr>
<tr><td>Protura (coneheads)</td></tr>
<tr><td>Diplura (two-pronged bristletails)</td></tr>
<tr><td>Archaeognatha (jumping bristletails)</td><td rowspan="3">Insecta sensu stricto
=Ectognatha</td></tr>
<tr><td>Zygentoma (silverfish)</td></tr>
<tr><td>Pterygota (winged insects)</td><td>Insecta sensu strictissimo</td></tr>
</table>

In the broadest circumscription, Insecta *sensu lato* consists of all hexapods.[13][14] Traditionally, insects defined in this way were divided into "Apterygota" (the first five groups in the table)—the wingless insects—and Pterygota—the winged insects.[15] However, modern phylogenetic studies have shown that "Apterygota" is not monophyletic,[16] and so does not form a good taxon. A narrower circumscription restricts insects to those hexapods with external mouthparts, and comprises only the last three groups in the table. In this sense, Insecta *sensu stricto* is equivalent to Ectognatha.[13][16] In the narrowest circumscription, insects are restricted to hexapods that are either winged or descended from winged ancestors. Insecta *sensu strictissimo* is then equivalent to Pterygota.[17] For the purposes of this article, the middle definition is used; insects consist of two wingless taxa, Archaeognatha (jumping bristletails) and Zygentoma (silverfish), plus the winged or secondarily wingless Pterygota.

Phylogeny and evolution

The evolutionary relationship of insects to other animal groups remains unclear.



A phylogenetic tree of the arthropods and related groups[18]

Although traditionally grouped with millipedes and centipedes—possibly on the basis of convergent adaptations to terrestrialisation[19]—evidence has emerged favoring closer evolutionary ties with crustaceans. In the Pancrustacea theory, insects, together with Entognatha, Remipedia, and Cephalocarida, make up a natural clade labeled Miracrustacea.[20]

Insects form a single clade, closely related to crustaceans and myriapods.[21]

Other terrestrial arthropods, such as centipedes, millipedes, scorpions, and spiders, are sometimes confused with insects since their body plans can appear similar, sharing (as do all arthropods) a jointed exoskeleton. However, upon closer examination, their features differ significantly; most noticeably, they do not have the six-legged characteristic of adult insects.[22]

The higher-level phylogeny of the arthropods continues to be a matter of debate and research. In 2008, researchers at Tufts University uncovered what they believe is the world's oldest known full-body impression of a primitive flying insect, a 300-million-year-old specimen from the Carboniferous period.[23] The oldest definitive insect fossil is the Devonian *Rhyniognatha hirsti*, from the 396-million-year-old Rhynie chert. It may have superficially resembled a modern-day silverfish insect. This species already possessed dicondylic mandibles (two articulations in the mandible), a feature associated with winged insects, suggesting that wings may already have evolved at this time. Thus, the first insects probably appeared earlier, in the Silurian period.[1][24]

Four super radiations of insects have occurred: beetles (evolved about 300 million years ago), flies (evolved about 250 million years ago), and moths and wasps (evolved about 150 million years ago).[25] These four groups account for the majority of described species. The flies and moths along with the fleas evolved from the Mecoptera.

The origins of insect flight remain obscure, since the earliest winged insects currently known appear to have been capable fliers. Some extinct insects had an additional pair of winglets attaching to the first segment of the thorax, for a total of three pairs. As of 2009, no evidence suggests the insects were a particularly successful group of animals before they evolved to have wings.[26]

Late Carboniferous and Early Permian insect orders include both extant groups, their stem groups,[27] and a number of Paleozoic groups, now extinct. During this era, some giant dragonfly-like forms reached wingspans of 55 to 70 cm (22 to 28 in), making them far larger than any living insect. This gigantism may have been due to higher atmospheric oxygen levels that allowed increased respiratory efficiency relative to today. The lack of flying vertebrates could have been another factor. Most extinct orders of insects developed during the Permian period that began around 270 million years ago. Many of the early groups became extinct during the Permian-Triassic extinction event, the largest mass extinction in the history of the Earth, around 252 million years ago.[28]


Evolution has produced enormous variety in insects. Pictured are some possible shapes of antennae.

The remarkably successful Hymenoptera appeared as long as 146 million years ago in the Cretaceous period, but achieved their wide diversity more recently in the Cenozoic era, which began 66 million years ago. A number of highly successful insect groups evolved in conjunction with flowering plants, a powerful illustration of coevolution.[29]

Many modern insect genera developed during the Cenozoic. Insects from this period on are often found preserved in amber, often in perfect condition. The body plan, or morphology, of such specimens is thus easily compared with modern species. The study of fossilized insects is called paleoentomology.

Evolutionary relationships

Insects are prey for a variety of organisms, including terrestrial vertebrates. The earliest vertebrates on land existed 400 million years ago and were large amphibious piscivores. Through gradual evolutionary change, insectivory was the next diet type to evolve.[30]

Insects were among the earliest terrestrial herbivores and acted as major selection agents on plants.[29] Plants evolved chemical defenses against this herbivory and the insects, in turn, evolved mechanisms to deal with plant toxins. Many insects make use of these toxins to protect themselves from their predators. Such insects often advertise their toxicity using warning colors.[31] This successful evolutionary pattern has also been used by mimics. Over time, this has led to complex groups of coevolved species. Conversely, some interactions between plants and insects, like pollination, are beneficial to both organisms. Coevolution has led to the development of very specific mutualisms in such systems.

Taxonomy

Traditional morphology-based or appearance-based systematics have usually given the Hexapoda the rank of superclass,[33]:180 and identified four groups within it: insects (Ectognatha), springtails (Collembola), Protura, and Diplura, the latter three being grouped together as the Entognatha on the basis of internalized mouth parts. Supraordinal relationships have undergone numerous changes with the advent of methods based on evolutionary history and genetic data. A recent theory is that the Hexapoda are polyphyletic (where the last common ancestor was not a member of the group), with the entognath classes having separate evolutionary histories from the Insecta.[34] Many of the traditional appearance-based taxa have been shown to be paraphyletic, so rather than using ranks like subclass, superorder, and infraorder, it has proved better to use monophyletic groupings (in which the last common ancestor is a member of the group). The following represents the best-supported monophyletic groupings for the Insecta.

Insects can be divided into two groups historically treated as subclasses: wingless insects, known as Apterygota, and winged insects, known as Pterygota. The Apterygota consist of the primitively wingless order of the silverfish (Zygentoma). Archaeognatha make up the Monocondylia based on the shape of their mandibles, while Zygentoma and Pterygota are grouped together as Dicondylia. The Zygentoma themselves possibly are not monophyletic, with the family Lepidotrichidae being a sister group to the Dicondylia (Pterygota and the remaining Zygentoma).[35][36]

Paleoptera and Neoptera are the winged orders of insects differentiated by the presence of hardened body parts called sclerites, and in the Neoptera, muscles that allow their wings to fold flatly over the abdomen. Neoptera can further be divided into incomplete metamorphosis-based (Polyneoptera and Paraneoptera) and complete metamorphosis-based groups. It has proved difficult to clarify the relationships between the orders in Polyneoptera because of constant new findings calling for revision of the taxa. For example, the Paraneoptera have turned out to be more closely related to the Endopterygota than to the rest of the Exopterygota. The recent molecular finding that the traditional louse orders Mallophaga and Anoplura are derived from within Psocoptera has led to the new taxon Psocodea.[37] Phasmatodea and Embiidina have been suggested to form the Eukinolabia.[38] Mantodea, Blattodea, and Isoptera are thought to form a monophyletic group termed Dictyoptera.[39]

The Exopterygota likely are paraphyletic in regard to the Endopterygota. Matters that have incurred controversy include Strepsiptera and Diptera grouped together as Halteria based on a reduction of one of the wing pairs—a position not well-supported in the entomological community.[40] The Neuropterida are often lumped or split on the whims of the taxonomist. Fleas are now thought to be closely related to boreid mecopterans.[41] Many questions remain in the basal relationships among endopterygote orders, particularly the Hymenoptera.

The study of the classification or taxonomy of any insect is called systematic entomology. If one works with a more specific order or even a family, the term may also be made specific to that order or family, for example systematic dipterology.

Classification

Insecta

Monocondylia

-Archaeognatha - 470

Dicondylia

Apterygota

-Zygentoma<200
-Monura

Pterygota

Paleoptera

-Ephemeroptera- 2,500–<3,000
-Odonata- 6,500

Neoptera

-Blattodea – 3,684–4,000
-Coleoptera – 360,000–400,000
-Dermaptera – 1,816
-Diptera – 152,956
-Embioptera – 200–300
-Hemiptera – 50,000–80,000
-Hymenoptera – 115,000
-Lepidoptera – 174,250
-Mantodea – 2,200
-Mecoptera – 481
-Megaloptera – 250–300
-Neuroptera – 5,000
-Notoptera – 30
-Orthoptera – 24,380
-Phasmatodea – 2,500–3,300
-Phthiraptera – 3,000–3,200
-Plecoptera – 2,274
-Psocoptera – 5,500
-Raphidioptera – 210
-Siphonaptera – 2,525
-Strepsiptera – 596
-Thysanoptera – 5,000
-Trichoptera –

Diversity

Estimates on the total number of insect species, or those within specific orders, often vary considerably. Globally, averages of these estimates suggest there are around 1.5 million beetle species and 5.5 million insect species, with about 1 million insect species currently found and described.[42]

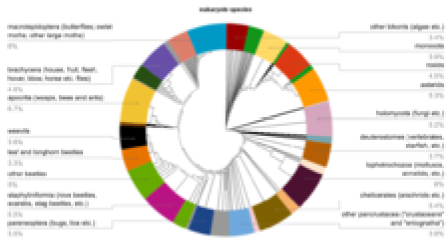
Between 950,000–1,000,000 of all described species are insects, so over 50% of all described eukaryotes (1.8 million) are insects (see illustration). With only 950,000 known non-insects, if the actual number of insects is 5.5 million, they may represent over 80% of the total. As only about 20,000 new species of all organisms are described each year, most insect species may remain undescribed, unless the rate of species descriptions greatly increases. Of the 24

12,627
-Zoraptera – 28

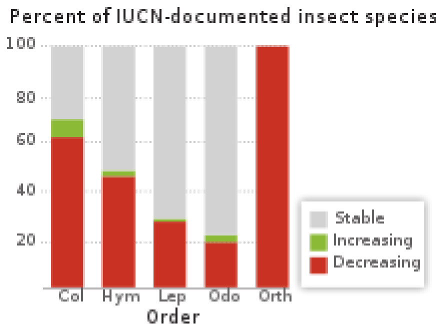
Cladogram of living insect groups,[32] with numbers of species in each group.[5] The Apterygota, Palaeoptera, and Exopterygota are possibly paraphyletic groups.

orders of insects, four dominate in terms of numbers of described species; at least 670,000 identified species belong to Coleoptera, Diptera, Hymenoptera or Lepidoptera.

As of 2017, at least 66 insect species extinctions had been recorded in the previous 500 years, which generally occurred on oceanic islands.[44] Declines in insect abundance have been attributed to artificial lighting,[45] land use changes such as urbanization or agricultural use,[46][47] pesticide use,[48] and invasive species.[49] Studies summarized in a 2019 review suggested a large proportion of insect species are threatened with extinction in the 21st century.[50] Though ecologist Manu Sanders notes the 2019 review was biased by mostly excluding data showing increases or stability in insect population, with the studies limited to specific geographic areas and specific groups of species.[51] Claims of pending mass insect extinctions or "insect apocalypse" based on a subset of these studies have been popularized in news reports, but often extrapolate beyond the study data or hyperbolize study findings.[52] For some insect groups such as some butterflies, bees, and beetles, declines in abundance and diversity have been documented in European studies. Other areas have shown increases in some insect species, although trends in most regions are currently unknown. It is difficult to assess long-term trends in insect abundance or diversity because historical measurements are generally not known for many species. Robust data to assess at-risk areas or species is especially lacking for arctic and tropical regions and a majority of the southern hemisphere.[52]



A pie chart of described eukaryote species, showing just over half of these to be insects



Insects with population trends documented by the International Union for Conservation of Nature, for orders *Collembola, Hymenoptera, Lepidoptera, Odonata,* and *Orthoptera.* Of 203 insect species that had such documented population trends in 2013, 33% were in decline.[43]

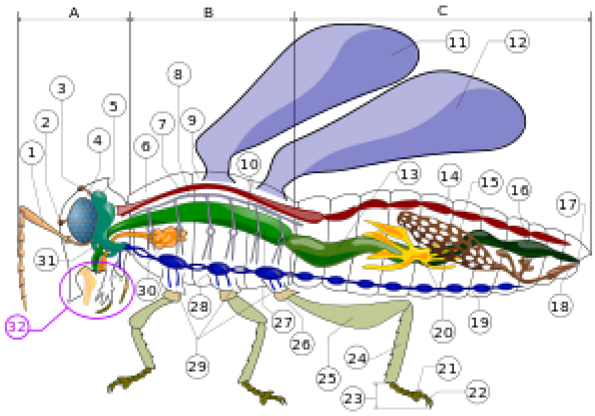
Estimates of total extant insect species[42]

Order	Estimated total species
Archaeognatha	513
Zygentoma	560
Ephemeroptera	3,240
Odonata	5,899
Orthoptera	23,855
Neuroptera	5,868
Phasmida	3,014
Embioptera	463
Grylloblattodea	34
Mantophasmatodea	20
Plecoptera	3,743
Dermaptera	1,978
Zoraptera	37
Mantodea	2,400
Blattodea	7,314
Psocoptera	5,720
Phthiraptera	5,102
Thysanoptera	5,864
Hemiptera	103,590
Hymenoptera	116,861
Strepsiptera	609
Coleoptera	386,500
Megaloptera	354
Raphidioptera	254
Trichoptera	14,391
Lepidoptera	157,338
Diptera	155,477
Siphonaptera	2,075
Mecoptera	757

Morphology and physiology

External

Insects have segmented bodies supported by exoskeletons, the hard outer covering made mostly of chitin. The segments of the body are organized into three distinctive but interconnected units, or tagmata: a head, a thorax and an abdomen.[53] The head supports a pair of sensory antennae, a pair of compound eyes, zero to three simple eyes (or ocelli) and three sets of variously modified appendages that form the mouthparts. The thorax is made up of three segments: the prothorax, mesothorax and the metathorax. Each thoracic segment supports one pair of legs. The meso- and metathoracic segments may each have a pair of wings, depending on the insect. The abdomen consists of eleven segments, though in a few species of insects, these segments may be fused together or reduced in size. The abdomen also contains most of the digestive, respiratory, excretory and reproductive internal structures.[33]:22–48 Considerable variation and many adaptations in the body parts of insects occur, especially wings, legs, antenna and mouthparts.



Insect morphology

A- Head **B**- Thorax **C**- Abdomen

1. antenna
2. ocelli (lower)
3. ocelli (upper)
4. compound eye
5. brain (cerebral ganglia)
6. prothorax
7. dorsal blood vessel
8. tracheal tubes (trunk with spiracle)
9. mesothorax
10. metathorax
11. forewing
12. hindwing
13. mid-gut (stomach)
14. dorsal tube (Heart)
15. ovary
16. hind-gut (intestine, rectum & anus)
17. anus
18. oviduct
19. nerve chord (abdominal ganglia)
20. Malpighian tubes
21. tarsal pads
22. claws
23. tarsus
24. tibia
25. femur
26. trochanter
27. fore-gut (crop, gizzard)
28. thoracic ganglion
29. coxa
30. salivary gland
31. subesophageal ganglion
32. mouthparts

Segmentation

The head is enclosed in a hard, heavily sclerotized, unsegmented, exoskeletal head capsule, or epicranium, which contains most of the sensing organs, including the antennae, ocellus or eyes, and the mouthparts. Of all the insect orders, Orthoptera displays the most features found in other insects, including the sutures and sclerites.[54] Here, the vertex, or the apex (dorsal region), is situated between the compound eyes for insects with a hypognathous and opisthognathous head. In prognathous insects, the vertex is not found between the compound eyes, but rather, where the ocelli are normally. This is because the primary axis of the head is rotated 90° to become parallel to the primary axis of the body. In some species, this region is modified and assumes a different name.[54]:13

The thorax is a tagma composed of three sections, the prothorax, mesothorax and the metathorax. The anterior segment, closest to the head, is the prothorax, with the major features being the first pair of legs and the pronotum. The middle segment is the mesothorax, with the major features being the second pair of legs and the anterior wings. The third and most posterior segment, abutting the abdomen, is the metathorax, which features the third pair of legs and the posterior wings. Each segment is dilineated by an intersegmental suture. Each segment has four basic regions. The dorsal surface is called the tergum (or *notum*) to distinguish it from the abdominal terga.[33] The two lateral regions are called the pleura (singular: pleuron) and the ventral aspect is called the sternum. In turn, the notum of the prothorax is called the pronotum, the notum for the mesothorax is called the mesonotum and the notum for the metathorax is called the metanotum. Continuing with this logic, the mesopleura and metapleura, as well as the mesosternum and metasternum, are used.[54]

The abdomen is the largest tagma of the insect, which typically consists of 11–12 segments and is less strongly sclerotized than the head or thorax. Each segment of the abdomen is represented by a sclerotized tergum and sternum. Terga are separated from each other and from the adjacent sterna or pleura by membranes. Spiracles are located in the pleural area. Variation of this ground plan includes the fusion of terga or terga and sterna to form continuous dorsal or ventral shields or a conical tube. Some insects bear a sclerite in the pleural area called a laterotergite. Ventral sclerites are sometimes called laterosternites. During the embryonic stage of many insects and the postembryonic stage of primitive insects, 11 abdominal segments are present. In modern insects there is a tendency toward reduction in the number of the abdominal segments, but the primitive number of 11 is maintained during embryogenesis. Variation in abdominal segment number is considerable. If the Apterygota are considered to be indicative of the ground plan for pterygotes, confusion reigns: adult Protura have 12 segments, Collembola have 6. The orthopteran family Acrididae has 11 segments, and a fossil specimen of Zoraptera has a 10-segmented abdomen.[54]

Exoskeleton

The insect outer skeleton, the cuticle, is made up of two layers: the epicuticle, which is a thin and waxy water resistant outer layer and contains no chitin, and a lower layer called the procuticle. The procuticle is chitinous and much thicker than the epicuticle and has two layers: an outer layer known as the exocuticle and an inner layer known as the endocuticle. The tough and flexible endocuticle is built from numerous layers of fibrous chitin and proteins, criss-crossing each other in a sandwich pattern, while the exocuticle is rigid and hardened.[33]:22–24 The exocuticle is greatly reduced in many insects during their larval stages, e.g., caterpillars. It is also reduced in soft-bodied adult insects.

Insects are the only invertebrates to have developed active flight capability, and this has played an important role in their success.[33]:186 Their flight muscles are able to contract multiple times for each single nerve impulse, allowing the wings to beat faster than would ordinarily be possible.

Having their muscles attached to their exoskeletons is efficient and allows more muscle connections.

Internal

Nervous system

The nervous system of an insect can be divided into a brain and a ventral nerve cord. The head capsule is made up of six fused segments, each with either a pair of ganglia, or a cluster of nerve cells outside of the brain. The first three pairs of ganglia are fused into the brain, while the three following pairs are fused into a structure of three pairs of ganglia under the insect's esophagus, called the subesophageal ganglion.[33]:57

The thoracic segments have one ganglion on each side, which are connected into a pair, one pair per segment. This arrangement is also seen in the abdomen but only in the first eight segments. Many species of insects have reduced numbers of ganglia due to fusion or reduction.[55] Some cockroaches have just six ganglia in the abdomen, whereas the wasp *Vespa crabro* has only two in the thorax and three in the abdomen. Some insects, like the house fly *Musca domestica*, have all the body ganglia fused into a single large thoracic ganglion.

At least a few insects have nociceptors, cells that detect and transmit signals responsible for the sensation of pain.[56] This was discovered in 2003 by studying the variation in reactions of larvae of the common fruitfly Drosophila to the touch of a heated probe and an unheated one. The larvae reacted to the touch of the heated probe with a stereotypical rolling behavior that was not exhibited when the larvae were touched by the unheated probe.[57] Although nociception has been demonstrated in insects, there is no consensus that insects feel pain consciously[58]

Insects are capable of learning.[59]

Digestive system

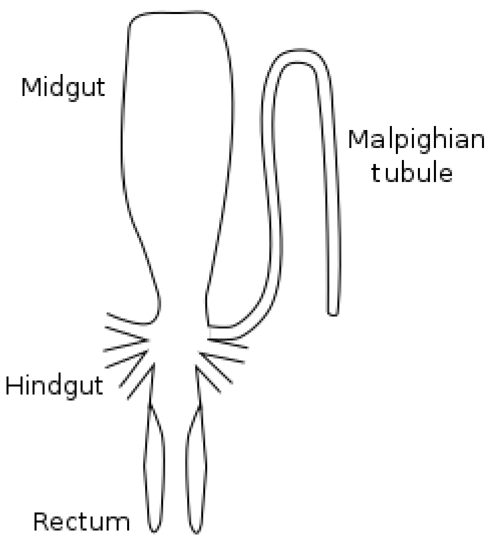
An insect uses its digestive system to extract nutrients and other substances from the food it consumes.[60] Most of this food is ingested in the form of macromolecules and other complex substances like proteins, polysaccharides, fats and nucleic acids. These macromolecules must be broken down by catabolic reactions into smaller molecules like amino acids and simple sugars before being used by cells of the body for energy, growth, or reproduction. This break-down process is known as digestion.

It should be emphasized that there is extensive variation among different orders, life stages, and even castes in the digestive system of insects.[61] This is the result of extreme adaptations to various lifestyles. The present description focus on a generalized composition of the digestive system of an adult orthopteroid insect, which is considered basal to interpreting particularities of other groups.

The main structure of an insect's digestive system is a long enclosed tube called the alimentary canal, which runs lengthwise through the body. The alimentary canal directs food unidirectionally from the mouth to the anus. It has three sections, each of which performs a different process of digestion. In addition to the alimentary canal, insects also have paired salivary glands and salivary reservoirs. These structures usually reside in the thorax, adjacent to the foregut.[33]:70–77 The salivary glands (element 30 in numbered diagram) in an insect's mouth produce saliva. The salivary ducts lead from the glands to the reservoirs and then forward through the head to an opening called the salivarium, located behind the hypopharynx. By moving its mouthparts (element 32 in numbered diagram) the insect can mix its food with saliva. The mixture of saliva and food then travels through the salivary tubes into the mouth, where it begins to break down.[62][63] Some insects, like flies, have extra-oral digestion. Insects using extra-oral digestion expel digestive enzymes onto their food to break it down. This strategy allows insects to extract a significant proportion of the available nutrients from the food source.[64]:31 The gut is where almost all of insects' digestion takes place. It can be divided into the foregut, midgut and hindgut.

Foregut

The first section of the alimentary canal is the foregut (element 27 in numbered diagram), or stomodaeum. The foregut is lined with a cuticular lining made of chitin and proteins as protection from tough food. The foregut includes the buccal cavity (mouth), pharynx, esophagus and crop and proventriculus (any part may be highly modified), which both store food and signify when to continue passing onward to the midgut.[33]:70



Stylized diagram of insect digestive tract showing malpighian tubule, from an insect of the order Orthoptera

Digestion starts in buccal cavity (mouth) as partially chewed food is broken down by saliva from the salivary glands. As the salivary glands produce fluid and carbohydrate-digesting enzymes (mostly amylases), strong muscles in the pharynx pump fluid into the buccal cavity, lubricating the food like the salivarium does, and helping blood feeders, and xylem and phloem feeders.

From there, the pharynx passes food to the esophagus, which could be just a simple tube passing it on to the crop and proventriculus, and then onward to the midgut, as in most insects. Alternately, the foregut may expand into a very enlarged crop and proventriculus, or the crop could just be a diverticulum, or fluid-filled structure, as in some Diptera species.[64]:30–31

Midgut

Once food leaves the crop, it passes to the midgut (element 13 in numbered diagram), also known as the mesenteron, where the majority of digestion takes place. Microscopic projections from the midgut wall, called microvilli, increase the surface area of the wall and allow more nutrients to be absorbed; they tend to be close to the origin of the midgut. In some insects, the role of the microvilli and where they are located may vary. For example, specialized microvilli producing digestive enzymes may more likely be near the end of the midgut, and absorption near the origin or beginning of the midgut.[64]:32

Hindgut

Bumblebee defecating. Note the contraction of the abdomen to provide internal pressure

In the hindgut (element 16 in numbered diagram), or proctodaeum, undigested food particles are joined by uric acid to form fecal pellets. The rectum absorbs 90% of the water in these fecal pellets, and the dry pellet is then eliminated through the anus (element 17), completing the process of digestion. Envaginations at the anterior end of the hindgut form the Malpighian tubules, which form the main excretory system of insects.

Excretory system

Insects may have one to hundreds of Malpighian tubules (element 20). These tubules remove nitrogenous wastes from the hemolymph of the insect and regulate osmotic balance. Wastes and solutes are emptied directly into the alimentary canal, at the junction between the midgut and hindgut.[33]:71–72, 78–80

Reproductive system

The reproductive system of female insects consist of a pair of ovaries, accessory glands, one or more spermathecae, and ducts connecting these parts. The ovaries are made up of a number of egg tubes, called ovarioles, which vary in size and number by species. The number of eggs that the insect is able to make vary by the number of ovarioles with the rate that eggs can develop being also influenced by ovariole design. Female insects are able make eggs, receive and store sperm, manipulate sperm from different males, and lay eggs. Accessory glands or glandular parts of the oviducts produce a variety of substances for sperm maintenance, transport and fertilization, as well as for protection of eggs. They can produce glue and protective substances for coating eggs or tough coverings for a batch of eggs called oothecae. Spermathecae are tubes or sacs in which sperm can be stored between the time of mating and the time an egg is fertilized.[54]:880

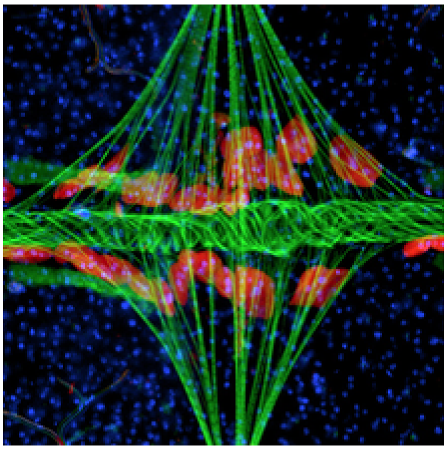
For males, the reproductive system is the testis, suspended in the body cavity by tracheae and the fat body. Most male insects have a pair of testes, inside of which are sperm tubes or follicles that are enclosed within a membranous sac. The follicles connect to the vas deferens by the vas efferens, and the two tubular vasa deferentia connect to a median ejaculatory duct that leads to the outside. A portion of the vas deferens is often enlarged to form the seminal vesicle, which stores the sperm before they are discharged into the female. The seminal vesicles have glandular linings that secrete nutrients for nourishment and maintenance of the sperm. The ejaculatory duct is derived from an invagination of the epidermal cells during development and, as a result, has a cuticular lining. The terminal portion of the ejaculatory duct may be sclerotized to form the intromittent organ, the aedeagus. The remainder of the male reproductive system is derived from embryonic mesoderm, except for the germ cells, or spermatogonia, which descend from the primordial pole cells very early during embryogenesis.[54]:885

Respiratory system

Insect respiration is accomplished without lungs. Instead, the insect respiratory system uses a system of internal tubes and sacs through which gases either diffuse or are actively pumped, delivering oxygen directly to tissues that need it via their trachea (element 8 in numbered diagram). In most insects, air is taken in through openings on the sides of the abdomen and thorax called spiracles.

The respiratory system is an important factor that limits the size of insects. As insects get larger, this type of oxygen transport is less efficient and thus the heaviest insect currently weighs less than 100 g. However, with increased atmospheric oxygen levels, as were present in the late Paleozoic, larger insects were possible, such as dragonflies with wingspans of more than two feet.[65]

There are many different patterns of gas exchange demonstrated by different groups of insects. Gas exchange patterns in insects can range from continuous and diffusive ventilation, to discontinuous gas exchange.[33]:65–68 During continuous gas exchange, oxygen is taken in and carbon dioxide is released in a continuous cycle. In discontinuous gas exchange, however, the insect takes in oxygen while it is active and small amounts of carbon dioxide are released when the insect is at rest.[66] Diffusive ventilation is simply a form of continuous gas exchange that occurs by diffusion rather than physically taking in the oxygen. Some species of insect that are submerged also have adaptations to aid in respiration. As larvae, many insects have gills that can extract oxygen dissolved in water, while others need to rise to the water surface to replenish air supplies, which may be held or trapped in special structures.[67][68]



The tube-like heart (green) of the mosquito *Anopheles gambiae* extends horizontally across the body, interlinked with the diamond-shaped wing muscles (also green) and surrounded by pericardial cells (red). Blue depicts cell nuclei.

Circulatory system

Because oxygen is delivered directly to tissues via tracheoles, the circulatory system is not used to carry oxygen, and is therefore greatly reduced. The insect circulatory system is open; it has no veins or arteries, and instead consists of little more than a single, perforated dorsal tube that pulses peristaltically. This dorsal blood vessel (element 14) is divided into two sections: the heart and aorta. The dorsal blood vessel circulates the hemolymph, arthropods' fluid analog of blood, from the rear of the body cavity forward.[33]:61–65[69] Hemolymph is composed of plasma in which hemocytes are suspended. Nutrients, hormones, wastes, and other substances are transported throughout the insect body in the hemolymph. Hemocytes include many types of cells that are important for immune responses, wound healing, and other functions. Hemolymph pressure may be increased by muscle contractions or by swallowing air into the digestive system to aid in moulting.[70] Hemolymph is also a major part of the open circulatory system of other arthropods, such as spiders and crustaceans.[71][72]

Reproduction and development

The majority of insects hatch from eggs. The fertilization and development takes place inside the egg, enclosed by a shell (chorion) that consists of maternal tissue. In contrast to eggs of other arthropods, most insect eggs are drought resistant. This is because inside the chorion two additional membranes develop from embryonic tissue, the amnion and the serosa. This serosa secretes a cuticle rich in chitin that protects the embryo against desiccation. In Schizophora however the serosa does not develop, but these flies lay their eggs in damp places, such as rotting matter.[73] Some species of insects, like the cockroach *Blaptica dubia*, as well as juvenile aphids and tsetse flies, are ovoviviparous. The eggs of ovoviviparous animals develop entirely inside the female, and then hatch immediately upon being laid.[7] Some other species, such as those in the genus of cockroaches known as *Diploptera*, are viviparous, and thus gestate inside the mother and are born alive.[33]:129, 131, 134–135 Some insects, like parasitic wasps, show polyembryony, where a single fertilized egg divides into many and in some cases thousands of separate embryos.[33]:136–137 Insects may be *univoltine*, *bivoltine* or *multivoltine*, i.e. they may have one, two or many broods (generations) in a year.[74]

Other developmental and reproductive variations include haplodiploidy, polymorphism, paedomorphosis or peramorphosis, sexual dimorphism, parthenogenesis and more rarely hermaphroditism.[33]:143 In haplodiploidy, which is a type of sex-determination system, the offspring's sex is determined by the number of sets of chromosomes an individual receives. This system is typical in bees and wasps.[75] Polymorphism is where a species may have different *morphs* or *forms*, as in the oblong winged katydid, which has four different varieties: green, pink and yellow or tan. Some insects may retain phenotypes that are normally only seen in juveniles; this is called paedomorphosis. In peramorphosis, an opposite sort of phenomenon, insects take on previously unseen traits after they have matured into adults. Many insects display sexual dimorphism, in which males and

A pair of *Simosyrphus grandicornis* hoverflies mating in flight.

A pair of grasshoppers mating.

females have notably different appearances, such as the moth *Orgyia recens* as an exemplar of sexual dimorphism in insects.

The different forms of the male (top) and female (bottom) tussock moth *Orgyia recens* is an example of sexual dimorphism in insects.

Some insects use parthenogenesis, a process in which the female can reproduce and give birth without having the eggs fertilized by a male. Many aphids undergo a form of parthenogenesis, called cyclical parthenogenesis, in which they alternate between one or many generations of asexual and sexual reproduction.[76][77] In summer, aphids are generally female and parthenogenetic; in the autumn, males may be produced for sexual reproduction. Other insects produced by parthenogenesis are bees, wasps and ants, in which they spawn males. However, overall, most individuals are female, which are produced by fertilization. The males are haploid and the females are diploid.[7] More rarely, some insects display hermaphroditism, in which a given individual has both male and female reproductive organs.

Insect life-histories show adaptations to withstand cold and dry conditions. Some temperate region insects are capable of activity during winter, while some others migrate to a warmer climate or go into a state of torpor.[78] Still other insects have evolved mechanisms of diapause that allow eggs or pupae to survive these conditions.[79]

Metamorphosis

Metamorphosis in insects is the biological process of development all insects must undergo. There are two forms of metamorphosis: incomplete metamorphosis and complete metamorphosis.

Incomplete metamorphosis

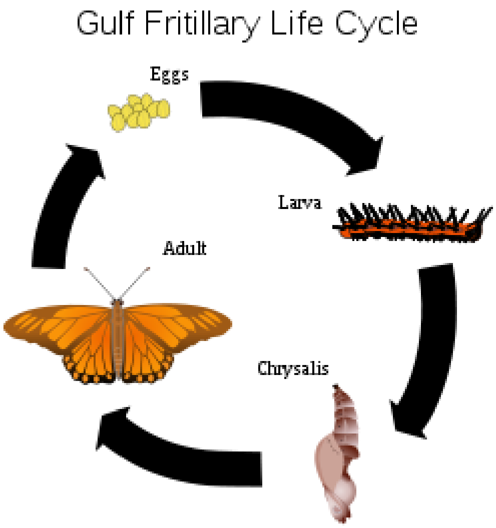
Hemimetabolous insects, those with incomplete metamorphosis, change gradually by undergoing a series of molts. An insect molts when it outgrows its exoskeleton, which does not stretch and would otherwise restrict the insect's growth. The molting process begins as the insect's epidermis secretes a new epicuticle inside the old one. After this new epicuticle is secreted, the epidermis releases a mixture of enzymes that digests the endocuticle and thus detaches the old cuticle. When this stage is complete, the insect makes its body swell by taking in a large quantity of water or air, which makes the old cuticle split along predefined weaknesses where the old exocuticle was thinnest.[33]:142[80]

Immature insects that go through incomplete metamorphosis are called nymphs or in the case of dragonflies and damselflies, also naiads. Nymphs are similar in form to the adult except for the presence of wings, which are not developed until adulthood. With each molt, nymphs grow larger and become more similar in appearance to adult insects.

This southern hawker dragonfly molts its exoskeleton several times during its life as a nymph; shown is the final molt to become a winged adult (eclosion).

Complete metamorphosis

Holometabolism, or complete metamorphosis, is where the insect changes in four stages, an egg or embryo, a larva, a pupa and the adult or imago. In these species, an egg hatches to produce a larva, which is generally worm-like in form. This worm-like form can be one of several varieties: eruciform (caterpillar-like), scarabaeiform (grub-like), campodeiform (elongated, flattened and active), elateriform (wireworm-like) or vermiform (maggot-like). The larva grows and eventually becomes a pupa, a stage marked by reduced movement and often sealed within a cocoon. There are three types of pupae: obtect, exarate or coarctate. Obtect pupae are compact, with the legs and other appendages enclosed. Exarate pupae have their legs and other appendages free and extended. Coarctate pupae develop inside the larval skin.[33]:151 Insects undergo considerable change in form during the pupal stage, and emerge as adults. Butterflies are a well-known example of insects that undergo complete metamorphosis, although most insects use this life cycle. Some insects have evolved this system to hypermetamorphosis.



Gulf fritillary life cycle, an example of holometabolism.

Complete metamorphosis is a trait of the most diverse insect group, the Endopterygota.[33]:143 Endopterygota includes 11 Orders, the largest being Diptera (flies), Lepidoptera (butterflies and moths), and Hymenoptera (bees, wasps, and ants), and Coleoptera (beetles). This form of development is exclusive to insects and not seen in any other arthropods.

Senses and communication

Many insects possess very sensitive and specialized organs of perception. Some insects such as bees can perceive ultraviolet wavelengths, or detect polarized light, while the antennae of male moths can detect the pheromones of female moths over distances of many kilometers.[81] The yellow paper wasp (*Polistes versicolor*) is known for its wagging movements as a form of communication within the colony; it can waggle with a frequency of 10.6±2.1 Hz (n=190). These wagging movements can signal the arrival of new material into the nest and aggression between workers can be used to stimulate others to increase foraging expeditions.[82] There is a pronounced tendency for there to be a trade-off between visual acuity and chemical or tactile acuity, such that most insects with well-developed eyes have reduced or simple antennae, and vice versa. There are a variety of different mechanisms by which insects perceive sound; while the patterns are not universal, insects can generally hear sound if they can produce it. Different insect species can have varying hearing, though most insects can hear only a narrow range of frequencies related to the frequency of the sounds they can produce. Mosquitoes have been found to hear up to 2 kHz, and some grasshoppers can hear up to 50 kHz.[83] Certain predatory and parasitic insects can detect the characteristic sounds made by their prey or hosts, respectively. For instance, some nocturnal moths can perceive the ultrasonic emissions of bats, which helps them avoid predation.[33]:87–94 Insects that feed on blood have special sensory structures that can detect infrared emissions, and use them to home in on their hosts.

Some insects display a rudimentary sense of numbers,[84] such as the solitary wasps that prey upon a single species. The mother wasp lays her eggs in individual cells and provides each egg with a number of live caterpillars on which the young feed when hatched. Some species of wasp always provide five, others twelve, and others as high as twenty-four caterpillars per cell. The number of caterpillars is different among species, but always the same for each sex of larva. The male solitary wasp in the genus *Eumenes* is smaller than the female, so the mother of one species supplies him with only five caterpillars; the larger female receives ten caterpillars in her cell.

Light production and vision

A few insects, such as members of the families Poduridae and Onychiuridae (Collembola), Mycetophilidae (Diptera) and the beetle families Lampyridae, Phengodidae, Elateridae and Staphylinidae are bioluminescent. The most familiar group are the fireflies, beetles of the family Lampyridae. Some species are able to control this light generation to produce flashes. The function varies with some species using them to attract mates, while others use them to lure prey. Cave dwelling larvae of *Arachnocampa* (Mycetophilidae, fungus gnats) glow to lure small flying insects into sticky strands of silk.[85] Some fireflies of the genus *Photuris* mimic the flashing of female *Photinus* species to attract males of that species, which are then captured and devoured.[86] The colors of emitted light vary from dull blue (*Orfelia fultoni*, Mycetophilidae) to the familiar greens and the rare reds (*Phrixothrix tiemanni*, Phengodidae).[87]


Most insects have compound eyes and two antennae.

Most insects, except some species of cave crickets, are able to perceive light and dark. Many species have acute vision capable of detecting minute movements. The eyes may include simple eyes or ocelli as well as compound eyes of varying sizes. Many species are able to detect light in the infrared, ultraviolet and the visible light wavelengths. Color vision has been demonstrated in many species and phylogenetic analysis suggests that UV-green-blue trichromacy existed from at least the Devonian period between 416 and 359 million years ago.[88]

Sound production and hearing

Insects were the earliest organisms to produce and sense sounds. Insects make sounds mostly by mechanical action of appendages. In grasshoppers and crickets, this is achieved by stridulation. Cicadas make the loudest sounds among the insects by producing and amplifying sounds with special modifications to their body to form tymbals and associated musculature. The African cicada *Brevisana brevis* has been measured at 106.7 decibels at a distance of 50 cm (20 in).[89] Some insects, such as the *Helicoverpa zea* moths, hawk moths and Hedylid butterflies, can hear ultrasound and take evasive action when they sense that they have been detected by bats.[90][91] Some moths produce ultrasonic clicks that were once thought to have a role in jamming bat echolocation. The ultrasonic clicks were subsequently found to be produced mostly by unpalatable moths to warn bats, just as warning colorations are used against predators that hunt by sight.[92] Some otherwise palatable moths have evolved to mimic these calls.[93] More recently, the claim that some moths can jam bat sonar has been revisited. Ultrasonic recording and high-speed infrared videography of bat-moth interactions suggest the palatable tiger moth really does defend against attacking big brown bats using ultrasonic clicks that jam bat sonar.[94]

Very low sounds are also produced in various species of Coleoptera, Hymenoptera, Lepidoptera, Mantodea and Neuroptera. These low sounds are simply the sounds made by the insect's movement. Through microscopic stridulatory structures located on the insect's muscles and joints, the normal sounds of the insect moving are amplified and can be used to warn or communicate with other insects. Most sound-making insects also have tympanal organs that can perceive airborne sounds. Some species in Hemiptera, such as the corixids (water boatmen), are known to communicate via underwater sounds.[95] Most insects are also able to sense vibrations transmitted through surfaces.

Communication using surface-borne vibrational signals is more widespread among insects because of size constraints in producing air-borne sounds.[96] Insects cannot effectively produce low-frequency sounds, and high-frequency sounds tend to disperse more in a dense environment (such as foliage), so insects living in such environments communicate primarily using substrate-borne vibrations.[97] The mechanisms of production of vibrational signals are just as diverse as those for producing sound in insects.

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Cricket in garage with familiar call.

Some species use vibrations for communicating within members of the same species, such as to attract mates as in the songs of the shield bug *Nezara viridula*.[98] Vibrations can also be used to communicate between entirely different species; lycaenid (gossamer-winged butterfly) caterpillars, which are myrmecophilous (living in a mutualistic association with ants) communicate with ants in this way.[99] The Madagascar hissing cockroach has the ability to press air through its spiracles to make a hissing noise as a sign of aggression;[100] the death's-head hawkmoth makes a squeaking noise by forcing air out of their pharynx when agitated, which may also reduce aggressive worker honey bee behavior when the two are in close proximity.[101]

Chemical communication

Chemical communications in animals rely on a variety of aspects including taste and smell. Chemoreception is the physiological response of a sense organ (i.e. taste or smell) to a chemical stimulus where the chemicals act as signals to regulate the state or activity of a cell. A semiochemical is a message-carrying chemical that is meant to attract, repel, and convey information. Types of semiochemicals include pheromones and kairomones. One example is the butterfly *Phengaris arion* which uses chemical signals as a form of mimicry to aid in predation.[102]

In addition to the use of sound for communication, a wide range of insects have evolved chemical means for communication. These chemicals, termed semiochemicals, are often derived from plant metabolites include those meant to attract, repel and provide other kinds of information. Pheromones, a type of semiochemical, are used for attracting mates of the opposite sex, for aggregating conspecific individuals of both sexes, for deterring other individuals from approaching, to mark a trail, and to trigger aggression in nearby individuals. Allomones benefit their producer by the effect they have upon the receiver. Kairomones benefit their receiver instead of their producer. Synomones benefit the producer and the receiver. While some chemicals are targeted at individuals of the same species, others are used for communication across species. The use of scents is especially well known to have developed in social insects.[33]:96–105

Social behavior

Social insects, such as termites, ants and many bees and wasps, are the most familiar species of eusocial animals.[103] They live together in large well-organized colonies that may be so tightly integrated and genetically similar that the colonies of some species are sometimes considered superorganisms. It is sometimes argued that the various species of honey bee are the only invertebrates (and indeed one of the few non-human groups) to have evolved a system of abstract symbolic communication where a behavior is used to *represent* and convey specific information about something in the environment. In this communication system, called dance language, the angle at which a bee dances represents a direction relative to the sun, and the length of the dance represents the distance to be flown.[33]:309–311 Though perhaps not as advanced as honey bees, bumblebees also potentially have some social communication behaviors. *Bombus terrestris*, for example, exhibit a faster learning curve for visiting unfamiliar, yet rewarding flowers, when they can see a conspecific foraging on the same species.[104]

A cathedral mound created by termites (Isoptera).

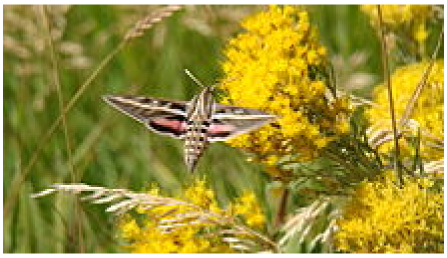
Only insects that live in nests or colonies demonstrate any true capacity for fine-scale spatial orientation or homing. This can allow an insect to return unerringly to a single hole a few millimeters in diameter among thousands of apparently identical holes clustered together, after a trip of up to several kilometers' distance. In a phenomenon known as philopatry, insects that hibernate have shown the ability to recall a specific location up to a year after last viewing the area of interest.[105] A few insects seasonally migrate large distances between different geographic regions (e.g., the overwintering areas of the monarch butterfly).[33]:14

Care of young

The eusocial insects build nests, guard eggs, and provide food for offspring full-time (see Eusociality). Most insects, however, lead short lives as adults, and rarely interact with one another except to mate or compete for mates. A small number exhibit some form of parental care, where they will at least guard their eggs, and sometimes continue guarding their offspring until adulthood, and possibly even feeding them. Another simple form of parental care is to construct a nest (a burrow or an actual construction, either of which may be simple or complex), store provisions in it, and lay an egg upon those provisions. The adult does not contact the growing offspring, but it nonetheless does provide food. This sort of care is typical for most species of bees and various types of wasps.[106]

Locomotion

Flight

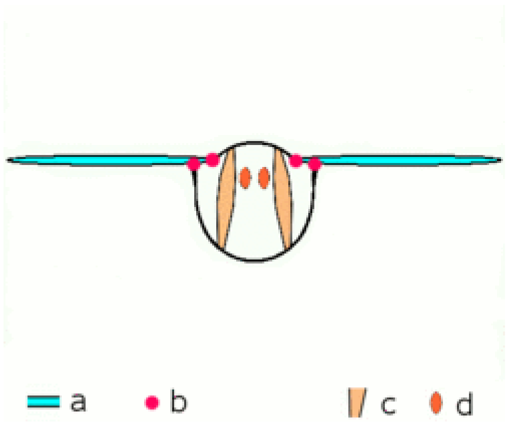


White-lined sphinx moth feeding in flight

Insects are the only group of invertebrates to have developed flight. The evolution of insect wings has been a subject of debate. Some entomologists suggest that the wings are from paranotal lobes, or extensions from the insect's exoskeleton called the nota, called the *paranotal theory*. Other theories are based on a pleural origin. These theories include suggestions that wings originated from modified gills, spiracular flaps or as from an appendage of the epicoxa. The *epicoxal theory* suggests the insect wings are modified epicoxal exites, a modified appendage at the base of the legs or coxa.[107] In the Carboniferous age, some of the *Meganeura* dragonflies had as much as a 50 cm (20 in) wide wingspan. The appearance of gigantic insects has been found to be consistent with high atmospheric oxygen. The respiratory system of insects constrains their size, however the high oxygen in the atmosphere allowed larger sizes.[108] The largest flying insects today are much smaller and include several moth species such as the Atlas moth and the white witch (*Thysania agrippina*).

Insect flight has been a topic of great interest in aerodynamics due partly to the inability of steady-state theories to explain the lift generated by the tiny wings of insects. But insect wings are in motion, with flapping and vibrations, resulting in churning and eddies, and the misconception that physics says "bumblebees can't fly" persisted throughout most of the twentieth century.

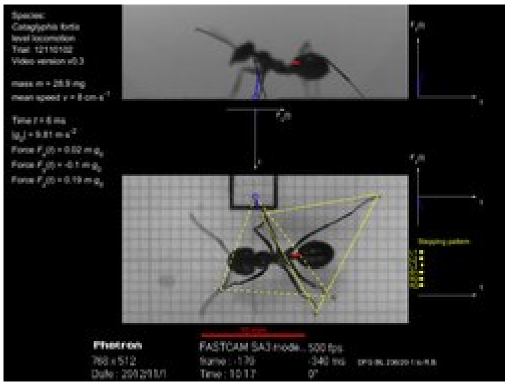
Unlike birds, many small insects are swept along by the prevailing winds[109] although many of the larger insects are known to make migrations. Aphids are known to be transported long distances by low-level jet streams.[110] As such, fine line patterns associated with converging winds within weather radar imagery, like the WSR-88D radar network, often represent large groups of insects.[111]



Basic motion of the insect wing in insect with an indirect flight mechanism scheme of dorsoventral cut through a thorax segment with
a wings
b joints
c dorsoventral muscles
d longitudinal muscles.

Walking

Many adult insects use six legs for walking and have adopted a tripedal gait. The tripedal gait allows for rapid walking while always having a stable stance and has been studied extensively in cockroaches and ants. The legs are used in alternate triangles touching the ground. For the first step, the middle right leg and the front and rear left legs are in contact with the ground and move the insect forward, while the front and rear right leg and the middle left leg are lifted and moved forward to a new position. When they touch the ground to form a new stable triangle the other legs can be lifted and brought forward in turn and so on.[112] The purest form of the tripedal gait is seen in insects moving at high speeds. However, this type of locomotion is not rigid and insects can adapt a variety of gaits. For example, when moving slowly, turning, avoiding obstacles, climbing or slippery surfaces, four (tetrapod) or more feet (wave-gait[113]) may be touching the ground. Insects can also adapt their gait to cope with the loss of one or more limbs.


Play media
Spatial and temporal stepping pattern of walking desert ants performing an alternating tripod gait. Recording rate: 500 fps, Playback rate: 10 fps.

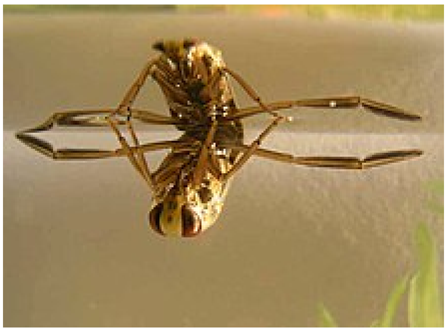
Cockroaches are among the fastest insect runners and, at full speed, adopt a bipedal run to reach a high velocity in proportion to their body size. As cockroaches move very quickly, they need to be video recorded at several hundred frames per second to reveal their gait. More sedate locomotion is seen in the stick insects or walking sticks (Phasmatodea). A few insects have evolved to walk on the surface of the water, especially members of the Gerridae family, commonly known as water striders. A few species of ocean-skaters in the genus *Halobates* even live on the surface of open oceans, a habitat that has few insect species.[114]

Use in robotics

Insect walking is of particular interest as an alternative form of locomotion in robots. The study of insects and bipeds has a significant impact on possible robotic methods of transport. This may allow new robots to be designed that can traverse terrain that robots with wheels may be unable to handle.[112]

Swimming

A large number of insects live either part or the whole of their lives underwater. In many of the more primitive orders of insect, the immature stages are spent in an aquatic environment. Some groups of insects, like certain water beetles, have aquatic adults as well.[67]



The backswimmer *Notonecta glauca* underwater, showing its paddle-like hindleg adaptation

Many of these species have adaptations to help in under-water locomotion. Water beetles and water bugs have legs adapted into paddle-like structures. Dragonfly naiads use jet propulsion, forcibly expelling water out of their rectal chamber.[115] Some species like the water striders are capable of walking on the surface of water. They can do this because their claws are not at the tips of the legs as in most insects, but recessed in a special groove further up the leg; this prevents the claws from piercing the water's surface film.[67] Other insects such as the Rove beetle *Stenus* are known to emit pygidial gland secretions that reduce surface tension making it possible for them to move on the surface of water by Marangoni propulsion (also known by the German term *Entspannungsschwimmen*).[116][117]

Ecology

Insect ecology is the scientific study of how insects, individually or as a community, interact with the surrounding environment or ecosystem.[118]:3 Insects play one of the most important roles in their ecosystems, which includes many roles, such as soil turning and aeration, dung burial, pest control, pollination and wildlife nutrition. An example is the beetles, which are scavengers that feed on dead animals and fallen trees and thereby recycle biological materials into forms found useful by other organisms.[119] These insects, and others, are responsible for much of the process by which topsoil is created.[33]:3, 218–228

Defense and predation

Insects are mostly soft bodied, fragile and almost defenseless compared to other, larger lifeforms. The immature stages are small, move slowly or are immobile, and so all stages are exposed to predation and parasitism. Insects then have a variety of defense strategies to avoid being attacked by predators or parasitoids. These include camouflage, mimicry, toxicity and active defense.[121]

Perhaps one of the most well-known examples of mimicry, the viceroy butterfly (top) appears very similar to the monarch butterfly (bottom).[120]

Camouflage is an important defense strategy, which involves the use of coloration or shape to blend into the surrounding environment.[122] This sort of protective coloration is common and widespread among beetle families, especially those that feed on wood or vegetation, such as many of the leaf beetles (family Chrysomelidae) or weevils. In some of these species, sculpturing or various colored scales or hairs cause the beetle to resemble bird dung or other inedible objects. Many of those that live in sandy environments blend in with the coloration of the substrate.[121] Most phasmids are known for effectively replicating the forms of sticks and leaves, and the bodies of some species (such as *O. macklotti* and *Palophus centaurus*) are covered in mossy or lichenous outgrowths that supplement their disguise. Very rarely, a species may have the ability to change color as their surroundings shift (*Bostra scabrinota*). In a further behavioral adaptation to supplement crypsis, a number of species have been noted to perform a rocking motion where the body is swayed from side to side that is thought to reflect the movement of leaves or twigs swaying in the breeze. Another method by which stick insects avoid predation and resemble twigs is by feigning death (catalepsy), where the insect enters a motionless state that can be maintained for a long period. The nocturnal feeding habits of adults also aids Phasmatodea in remaining concealed from predators.[123]

Another defense that often uses color or shape to deceive potential enemies is mimicry. A number of longhorn beetles (family Cerambycidae) bear a striking resemblance to wasps, which helps them avoid predation even though the beetles are in fact harmless.[121] Batesian and Müllerian mimicry complexes are commonly found in Lepidoptera. Genetic polymorphism and natural selection give rise to otherwise edible species (the mimic) gaining a survival advantage by resembling inedible species (the model). Such a mimicry complex is referred to as *Batesian*. One of the most famous examples, where the viceroy butterfly was long believed to be a Batesian mimic of the inedible monarch, was later disproven, as the viceroy is more toxic than the monarch, and this resemblance is now considered to be a case of Müllerian mimicry.[120] In Müllerian mimicry, inedible species, usually within a taxonomic order, find it advantageous to resemble each other so as to reduce the sampling rate by predators who need to learn about the insects' inedibility. Taxa from the toxic genus *Heliconius* form one of the most well known Müllerian complexes.[124]

Chemical defense is another important defense found among species of Coleoptera and Lepidoptera, usually being advertised by bright colors, such as the monarch butterfly. They obtain their toxicity by sequestering the chemicals from the plants they eat into their own tissues. Some Lepidoptera manufacture their own toxins. Predators that eat poisonous butterflies and moths may become sick and vomit violently, learning not to eat those types of species; this is actually the basis of Müllerian mimicry. A predator who has previously eaten a poisonous lepidopteran may avoid other species with similar markings in the future, thus saving many other species as well.[125] Some ground beetles of the family Carabidae can spray chemicals from their abdomen with great accuracy, to repel predators.[121]

Pollination

Pollination is the process by which pollen is transferred in the reproduction of plants, thereby enabling fertilisation and sexual reproduction. Most flowering plants require an animal to do the transportation. While other animals are included as pollinators, the majority of pollination is done by insects.[126] Because insects usually receive benefit for the pollination in the form of energy rich nectar it is a grand example of mutualism. The various flower traits (and combinations thereof) that differentially attract one type of pollinator or another are known as pollination syndromes. These arose through complex plant-animal adaptations. Pollinators find flowers through bright colorations, including ultraviolet, and attractant pheromones. The study of pollination by insects is known as *anthecology*.

European honey bee carrying pollen in a pollen basket back to the hive

Parasitism

Many insects are parasites of other insects such as the parasitoid wasps. These insects are known as entomophagous parasites. They can be beneficial due to their devastation of pests that can destroy crops and other resources. Many insects have a parasitic relationship with humans such as the mosquito. These insects are known to spread diseases such as malaria and yellow fever and because of such, mosquitoes indirectly cause more deaths of humans than any other animal.

Relationship to humans

As pests

Many insects are considered pests by humans. Insects commonly regarded as pests include those that are parasitic (*e.g.* lice, bed bugs), transmit diseases (mosquitoes, flies), damage structures (termites), or destroy agricultural goods (locusts, weevils). Many entomologists are involved in various forms of pest control, as in research for companies to produce insecticides, but increasingly rely on methods of biological pest control, or biocontrol. Biocontrol uses one organism to reduce the population density of another organism—the pest—and is considered a key element of integrated pest management.[127][128]

Aedes aegypti, a parasite, is the vector of dengue fever and yellow fever

Despite the large amount of effort focused at controlling insects, human attempts to kill pests with insecticides can backfire. If used carelessly, the poison can kill all kinds of organisms in the area, including insects' natural predators, such as birds, mice and other insectivores. The effects of DDT's use exemplifies how some insecticides can threaten wildlife beyond intended populations of pest insects.[129][130]

In beneficial roles

Because they help flowering plants to cross-pollinate, some insects are critical to agriculture. This European honey bee is gathering nectar while pollen collects on its body.

A robberfly with its prey, a hoverfly. Insectivorous relationships such as these help control insect populations.

Although pest insects attract the most attention, many insects are beneficial to the environment and to humans. Some insects, like wasps, bees, butterflies and ants, pollinate flowering plants. Pollination is a mutualistic relationship between plants and insects. As insects gather nectar from different plants of the same species, they also spread pollen from plants on which they have previously fed. This greatly increases plants' ability to cross-pollinate, which maintains and possibly even improves their evolutionary fitness. This ultimately affects humans since ensuring healthy crops is critical to agriculture. As well as pollination ants help with seed distribution of plants. This helps to spread the plants, which increases plant diversity. This leads to an overall better environment.[131] A serious environmental problem is the decline of populations of pollinator insects, and a number of species of insects are now cultured primarily for pollination management in order to have sufficient pollinators in the field, orchard or greenhouse at bloom time.[132]:240–243 Another solution, as shown in Delaware, has been to raise native plants to help support native pollinators like *L. vierecki*.[133] Insects also produce useful substances such as honey, wax, lacquer and silk. Honey bees have been cultured by humans for thousands of years for honey, although contracting for crop pollination is becoming more significant for beekeepers. The silkworm has greatly affected human history, as silk-driven trade established relationships between China and the rest of the world.

Insectivorous insects, or insects that feed on other insects, are beneficial to humans if they eat insects that could cause damage to agriculture and human structures. For example, aphids feed on crops and cause problems for farmers, but ladybugs feed on aphids, and can be used as a means to significantly reduce pest aphid populations. While birds are perhaps more visible predators of insects, insects themselves account for the vast majority of insect consumption. Ants also help control animal populations by consuming small vertebrates.[134] Without predators to keep them in check, insects can undergo almost unstoppable population explosions.[33]:328–348[33]:400[135][136]

Insects are also used in medicine, for example fly larvae (maggots) were formerly used to treat wounds to prevent or stop gangrene, as they would only consume dead flesh. This treatment is finding modern usage in some hospitals. Recently insects have also gained attention as potential sources of drugs and other medicinal substances.[137] Adult insects, such as crickets and insect larvae of various kinds, are also commonly used as fishing bait.[138]

In research

The common fruitfly *Drosophila melanogaster* is one of the most widely used organisms in biological research.

Insects play important roles in biological research. For example, because of its small size, short generation time and high fecundity, the common fruit fly *Drosophila melanogaster* is a model organism for studies in the genetics of higher eukaryotes. *D. melanogaster* has been an essential part of studies into principles like genetic linkage, interactions between genes, chromosomal genetics, development, behavior and evolution. Because genetic systems are well conserved among eukaryotes, understanding basic cellular processes like DNA replication or transcription in fruit flies can help to understand those processes in other eukaryotes, including humans.[139] The genome of *D. melanogaster* was sequenced in 2000, reflecting the organism's important role in biological research. It was found that 70% of the fly genome is similar to the human genome, supporting the evolution theory.[140]

As food

In some cultures, insects, especially deep-fried cicadas, are considered to be delicacies, whereas in other places they form part of the normal diet. Insects have a high protein content for their mass, and some authors suggest their potential as a major source of protein in human nutrition.[33]:10–13 In most first-world countries, however, entomophagy (the eating of insects), is taboo.[141] Since it is impossible to entirely eliminate pest insects from the human food chain, insects are inadvertently present in many foods, especially grains. Food safety laws in many countries do not prohibit insect parts in food, but rather limit their quantity. According to cultural materialist anthropologist Marvin Harris, the eating of insects is taboo in cultures that have other protein sources such as fish or livestock.

Due to the abundance of insects and a worldwide concern of food shortages, the Food and Agriculture Organization of the United Nations considers that the world may have to, in the future, regard the prospects of eating insects as a food staple. Insects are noted for their nutrients, having a high content of protein, minerals and fats and are eaten by one-third of the global population.[142]

As pets

Many species of insects are sold and kept as pets.

In culture

Scarab beetles held religious and cultural symbolism in Old Egypt, Greece and some shamanistic Old World cultures. The ancient Chinese regarded cicadas as symbols of rebirth or immortality. In Mesopotamian literature, the epic poem of Gilgamesh has allusions to Odonata that signify the impossibility of immortality. Among the Aborigines of Australia of the Arrernte language groups, honey ants and witchety grubs served as personal clan totems. In the case of the 'San' bush-men of the Kalahari, it is the praying mantis that holds much cultural significance including creation and zen-like patience in waiting.[33]:9

See also

- Chemical ecology
- Defense in insects
- Entomology
- Ethnoentomology
- Flying and gliding animals
- Insect biodiversity
- Insect ecology
- Insect-borne diseases
- Prehistoric insects
- Pain in invertebrates

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Insect physiology

Insect physiology includes the physiology and biochemistry of insect organ systems.[1]

Although diverse, insects are quite similar in overall design, internally and externally. The insect is made up of three main body regions (tagmata), the head, thorax and abdomen. The head comprises six fused segments with compound eyes, ocelli, antennae and mouthparts, which differ according to the insect's particular diet, e.g. grinding, sucking, lapping and chewing. The thorax is made up of three segments: the pro, meso and meta thorax, each supporting a pair of legs which may also differ, depending on function, e.g. jumping, digging, swimming and running. Usually the middle and the last segment of the thorax have paired wings. The abdomen generally comprises eleven segments and contains the digestive and reproductive organs.[2] A general overview of the internal structure and physiology of the insect is presented, including digestive, circulatory, respiratory, muscular, endocrine and nervous systems, as well as sensory organs, temperature control, flight and molting.

Contents

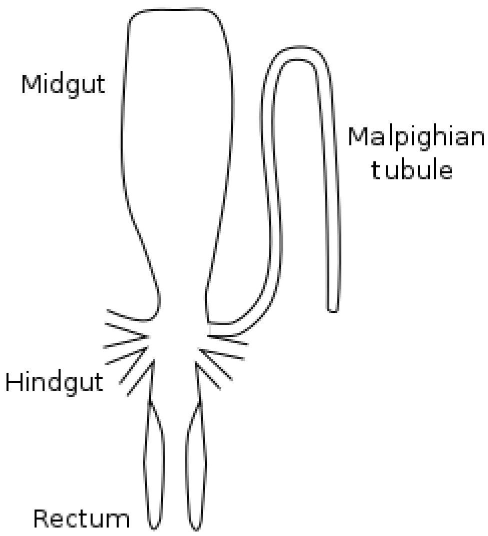
Digestive system

An insect uses its digestive system to extract nutrients and other substances from the food it consumes.[3] Most of this food is ingested in the form of macromolecules and other complex substances (such as proteins, polysaccharides, fats, and nucleic acids) which must be broken down by catabolic reactions into smaller molecules (i.e. amino acids, simple sugars, etc.) before being used by cells of the body for energy, growth, or reproduction. This break-down process is known as digestion.

The insect's digestive system is a closed system, with one long enclosed coiled tube called the alimentary canal which runs lengthwise through the body. The alimentary canal only allows food to enter the mouth, and then gets processed as it travels toward the anus. The alimentary canal has specific sections for grinding and food storage, enzyme production, and nutrient absorption.[2][4] Sphincters control the food and fluid movement between three regions. The three regions include the foregut (stomatodeum)(27,) the midgut (mesenteron)(13), and the hindgut (proctodeum)(16).

In addition to the alimentary canal, insects also have paired salivary glands and salivary reservoirs. These structures usually reside in the thorax (adjacent to the fore-gut). The salivary glands (30) produce saliva; the salivary ducts lead from the glands to the reservoirs and then forward through the head to an opening called the salivarium behind the hypopharynx; which movements of the mouthparts help mix saliva with food in the buccal cavity. Saliva mixes with food, which travels through salivary tubes into the mouth, beginning the process of breaking it down.[3][5]

The stomatedeum and proctodeum are invaginations of the epidermis and are lined with cuticle (intima). The mesenteron is not lined with cuticle but with rapidly dividing and therefore constantly replaced, epithelial cells.[2][4] The cuticle sheds with every moult along with the exoskeleton.[4] Food is moved down the gut by muscular contractions called peristalsis.[6]



Stylised diagram of insect digestive tract showing Malpighian tubule (Orthopteran type)

1. **Stomatodeum** (foregut): This region stores, grinds and transports food to the next region.[7] Included in this are the buccal cavity, the pharynx, the oesophagus, the crop (stores food), and proventriculus or gizzard (grinds food).[4] Salivary secretions from the labial glands dilute the ingested food. In mosquitoes (Diptera), which are blood-feeding insects, anticoagulants and blood thinners are also released here.
2. **Mesenteron** (midgut): Digestive enzymes in this region are produced and secreted into the lumen and here nutrients are absorbed into the insect's body. Food is enveloped by this part of the gut as it arrives from the foregut by the peritrophic membrane which is a mucopolysaccharide layer secreted from the midgut's epithelial cells.[2] It is thought that this membrane prevents food pathogens from contacting the epithelium and attacking the insects' body.[2] It also acts as a filter allowing small molecules through, but preventing large molecules and particles of food from reaching the midgut cells.[7] After the large substances are broken down into smaller ones, digestion and consequent nutrient absorption takes place at the surface of the epithelium.[2] Microscopic projections from the mid-gut wall, called microvilli, increase surface area and allow for maximum absorption of nutrients.
3. **Proctodeum** (hindgut): This is divided into three sections; the anterior is the ileum, the middle portion, the colon, and the wider, posterior section is the rectum.[7] This extends from the pyloric valve which is located between the mid and the hindgut to the anus.[4] Here absorption of water, salts and other beneficial substances take place before excretion.[7] Like other animals, the removal of toxic metabolic waste requires water. However, for very small animals like insects, water conservation is a priority. Because of this, blind-ended ducts called Malpighian tubules come into play.[2] These ducts emerge as evaginations at the anterior end of the hindgut and are the main organs of osmoregulation and excretion.[4][7] These extract the waste products from the haemolymph, in which all the internal organs are bathed).[2] These tubules continually produce the insect's uric acid, which is transported to the hindgut, where important salts and water are re-absorbed by both the hindgut and rectum. Excrement is then voided as insoluble and non-toxic uric acid granules.[2] Excretion and osmoregulation in insects are not orchestrated by the Malpighian tubules alone, but require a joint function of the ileum and/or rectum.[7]

Circulatory system

The main function of insect blood, hemolymph, is that of transport and it bathes the insect's body organs. Making up usually less than 25% of an insect's body weight, it transports hormones, nutrients and wastes and has a role in osmoregulation, temperature control, immunity, storage (water, carbohydrates and fats) and skeletal function. It also plays an essential part in the moulting process.[2][4] An additional role of the hemolymph in some orders, can be that of predatory defence. It can contain unpalatable and malodourous chemicals that will act as a deterrent to predators.[7]

Hemolymph contains molecules, ions and cells.[7] Regulating chemical exchanges between tissues, hemolymph is encased in the insect body cavity or haemocoel.[6][7] It is transported around the body by combined heart (posterior) and aorta (anterior) pulsations which are located dorsally just under the surface of the body.[2][4][7] It differs from vertebrate blood in that it doesn't contain any red blood cells and therefore is without high oxygen carrying capacity, and is more similar to lymph found in vertebrates.[6][7]

Body fluids enter through one way valved ostia which are openings situated along the length of the combined aorta and heart organ. Pumping of the hemolymph occurs by waves of peristaltic contraction, originating at the body's posterior end, pumping forwards into the dorsal vessel, out via the aorta and then into the head where it flows out into the haemocoel.[6][7] The hemolymph is circulated to the appendages unidirectionally with the aid of muscular pumps or accessory pulsatile organs which are usually found at the base of the antennae or wings and sometimes in the legs.[7] Pumping rate accelerates due to periods of increased activity.[4] Movement of hemolymph is particularly important for thermoregulation in orders such as Odonata, Lepidoptera, Hymenoptera and Diptera.[7]

Respiratory system

Insect respiration is accomplished without lungs using a system of internal tubes and sacs through which gases either diffuse or are actively pumped, delivering oxygen directly to tissues that need oxygen and eliminate carbon dioxide via their cells.[7] Since oxygen is delivered directly, the circulatory system is not used to carry oxygen, and is therefore greatly reduced; it has no closed vessels (i.e., no veins or arteries), consisting of little more than a single, perforated dorsal tube which pulses peristaltically, and in doing so helps circulate the hemolymph inside the body cavity.[7]

Air is taken in through spiracles, openings which are positioned laterally in the pleural wall, usually a pair on the anterior margin of the meso and meta thorax, and pairs on each of the eight or less abdominal segments, Numbers of spiracles vary from 1 to 10 pairs.[2][4][6][7] The oxygen passes through the tracheae to the tracheoles, and enters the body by the process of diffusion. Carbon dioxide leaves the body by the same process.[4]

The major tracheae are thickened spirally like a flexible vacuum hose to prevent them from collapsing and often swell into air sacs. Larger insects can augment the flow of air through their tracheal system, with body movement and rhythmic flattening of the tracheal air sacs.[4] Spiracles are closed and opened by means of valves and can remain partly or completely closed for extended periods in some insects, which minimises water loss.[2][4]

There are many different patterns of gas exchange demonstrated by different groups of insects. Gas exchange patterns in insects can range from continuous, diffusive ventilation, to discontinuous gas exchange.[7]

Terrestrial and a large proportion of aquatic insects perform gaseous exchange as previously mentioned under an open system. Other smaller numbers of aquatic insects have a closed tracheal system, for example, Odonata, Trichoptera, Ephemeroptera, which have tracheal gills and no functional spiracles. Endoparasitic larvae are without spiracles and also operate under a closed system. Here the tracheae separate peripherally, covering the general body surface which results in a cutaneous form of gaseous exchange. This peripheral tracheal division may also lie within the tracheal gills where gaseous exchange may also take place.[7]

Muscular system

Many insects are able to lift twenty times their own body weight like Rhinoceros beetle and may jump distances that are many times greater than their own length. This is because their energy output is high in relation to their body mass. [4][6]

The muscular system of insects ranges from a few hundred muscles to a few thousand.[4] Unlike vertebrates that have both smooth and striated muscles, insects have only striated muscles. Muscle cells are amassed into muscle fibers and then into the functional unit, the muscle.[6] Muscles are attached to the body wall, with attachment fibers running through the cuticle and to the epicuticle, where they can move different parts of the body including appendages such as wings.[4][7] The muscle fiber has many cells with a plasma membrane and outer sheath or sarcolemma.[7] The sarcolemma is invaginated and can make contact with the tracheole carrying oxygen to the muscle fiber. Arranged in sheets or cylindrically, contractile myofibrils run the length of the muscle fiber. Myofibrils comprising a fine actin filament enclosed between a thick pair of myosin filaments slide past each other instigated by nerve impulses.[7]

Muscles can be divided into four categories:

1. **Visceral**: these muscles surround the tubes and ducts and produce peristalsis as demonstrated in the digestive system.[6]
2. **Segmental**: causing telescoping of muscle segments required for moulting, increase in body pressure and locomotion in legless larvae.[6]
3. **Appendicular**: originating from either the sternum or the tergum and inserted on the coxae these muscles move appendages as one unit.[6] These are arranged segmentally and usually in antagonistic pairs.[4] Appendage parts of some insects, e.g. the galea and the lacinia of the maxillae, only have flexor muscles. Extension of these structures is by haemolymph pressure and cuticle elasticity.[4]
4. **Flight**: Flight muscles are the most specialised category of muscle and are capable of rapid contractions. Nerve impulses are required to initiate muscle contractions and therefore flight. These muscles are also known as neurogenic or synchronous muscles. This is because there is a one-to-one correspondence between action potentials and muscle contractions. In insects with higher wing stroke frequencies the muscles contract more frequently than at the rate that the nerve impulse reaches them and are known as asynchronous muscles.[2][7]

Flight has allowed the insect to disperse, escape from enemies and environmental harm, and colonise new habitats.[2] One of the insect's key adaptations is flight, the mechanics of which differ from those of other flying animals because their wings are not modified appendages.[2][6] Fully developed and functional wings occur only in adult insects.[7] To fly, gravity and drag (air resistance to movement) have to be overcome.[7] Most insects fly by beating their wings and to power their flight they have either direct flight muscles attached to the wings, or an indirect system where there is no muscle-to-wing connection and instead they are attached to a highly flexible box-like thorax.[7]

Direct flight muscles generate the upward stroke by the contraction of the muscles attached to the base of the wing inside the pivotal point. Outside the pivotal point the downward stroke is generated through contraction of muscles that extend from the sternum to the wing. Indirect flight muscles are attached to the tergum and sternum. Contraction makes the tergum and base of the wing pull down. In turn this movement lever the outer or main part of the wing in strokes upward. Contraction of the second set of muscles, which run from the back to the front of the thorax, powers the downbeat. This deforms the box and lifts the tergum.[7]

Endocrine system

Hormones are the chemical substances that are transported in the insect's body fluids (haemolymph) that carry messages away from their point of synthesis to sites where physiological processes are influenced. These hormones are produced by glandular, neuroglandular and neuronal centres.[7] Insects have several organs that produce hormones, controlling reproduction, metamorphosis and moulting.[4] It has been suggested that a brain hormone is responsible for caste dermination in termites and diapause interruption in some insects.[4]

Four endocrine centers have been identified:

1. **Neurosecretory cells** in the brain can produce one or more hormones that affect growth, reproduction, homeostasis and metamorphosis.[4][7]
2. **Corpora cardiaca** are a pair of neuroglandular bodies that are found behind the brain and on either sides of the aorta. These not only produce their own neurohormones but they store and release other neurohormones including PTTH prothoracicotropic hormone (brain hormone), which stimulates the secretory activity of the prothoracic glands, playing an integral role in moulting.
3. **Prothoracic glands** are diffuse, paired glands located at the back of the head or in the thorax. These glands secrete an ecdysteroid called ecdysone, or the moulting hormone, which initiates the epidermal moulting process.[7] Additionally it plays a role in accessory reproductive glands in the female, differentiation of ovarioles and in the process of egg production.

4. **Corpora allata** are small, paired glandular bodies originating from the epithelium located on either side of the foregut. They secrete the juvenile hormone, which regulate reproduction and metamorphosis.[4][7]

Nervous system

Insects have a complex nervous system which incorporates a variety of internal physiological information as well as external sensory information.[7] As in the case of vertebrates, the basic component is the neuron or nerve cell. This is made up of a dendrite with two projections that receive stimuli and an axon, which transmits information to another neuron or organ, like a muscle. As for vertebrates, chemicals (neurotransmitters such as acetylcholine and dopamine) are released at synapses.[7]

Central nervous system

An insect's sensory, motor and physiological processes are controlled by the central nervous system along with the endocrine system.[7] Being the principal division of the nervous system, it consists of a brain, a ventral nerve cord and a subesophageal ganglion which is connected to the brain by two nerves, extending around each side of the oesophagus.

The brain has three lobes:

- **Protocerebrum**, innervating the compound eyes and the ocelli
- **Deutocerebrum**, innervating the antennae
- **Tritocerebrum**, innervating the foregut and the labrum.[4][7]

The ventral nerve cord extends from the suboesophageal ganglion posteriorly.[4] A layer of connective tissue called the neurolemma covers the brain, ganglia, major peripheral nerves and ventral nerve cords.

The head capsule (made up of six fused segments) has six pairs of ganglia. The first three pairs are fused into the brain, while the three following pairs are fused into the subesophageal ganglion.[7] The thoracic segments have one ganglion on each side, which are connected into a pair, one pair per segment. This arrangement is also seen in the abdomen but only in the first eight segments. Many species of insects have reduced numbers of ganglia due to fusion or reduction.[8] Some cockroaches have just six ganglia in the abdomen, whereas the wasp *Vespa crabro* has only two in the thorax and three in the abdomen. And some, like the house fly *Musca domestica*, have all the body ganglia fused into a single large thoracic ganglion. The ganglia of the central nervous system act as the coordinating centres with their own specific autonomy where each may coordinate impulses in specified regions of the insect's body.[4]

Peripheral nervous system

This consists of motor neuron axons that branch out to the muscles from the ganglia of the central nervous system, parts of the sympathetic nervous system and the sensory neurons of the cuticular sense organs that receive chemical, thermal, mechanical or visual stimuli from the insects environment.[7] The sympathetic nervous system includes nerves and the ganglia that innervate the gut both posteriorly and anteriorly, some endocrine organs, the spiracles of the tracheal system and the reproductive organs.[7]

Sensory organs

Chemical senses include the use of chemoreceptors, related to taste and smell, affecting mating, habitat selection, feeding and parasite-host relationships. Taste is usually located on the mouthparts of the insect but in some insects, such as bees, wasps and ants, taste organs can also be found on the antennae. Taste organs can also be found on the tarsi of moths, butterflies and flies. Olfactory sensilla enable insects to smell and are usually found in the antennae.[2] Chemoreceptor sensitivity related to smell in some substances, is very high and some insects can detect particular odours that are at low concentrations miles from their original source.[4]

Mechanical senses provide the insect with information that may direct orientation, general movement, flight from enemies, reproduction and feeding and are elicited from the sense organs that are sensitive to mechanical stimuli such as pressure, touch and vibration.[4] Hairs (setae) on the cuticle are responsible for this as they are sensitive to vibration touch and sound.[2]

Hearing structures or tympanal organs are located on different body parts such as, wings, abdomen, legs and antennae. These can respond to various frequencies ranging from 100 Hz to 240 kHz depending on insect species.[4] Many of the joints of the insect have tactile setae that register movement. Hair beds and groups of small hair like sensilla, determine proprioreception or information about the position of a limb, and are found on the cuticle at the joints of segments and legs. Pressure on the body wall or strain gauges are detected by the campiniform sensilla and internal stretch receptors sense muscle distension and digestive system stretching.[2][4]

The compound eye and the ocelli supply insect vision. The compound eye consists of individual light receptive units called ommatidia. Some ants may have only one or two, however dragonflies may have over 10,000. The more ommatidia the greater the visual acuity. These units have a clear lens system and light sensitive retina cells. By day, the image flying insects receive is made up of a mosaic of specks of differing light intensity from all the different ommatidia. At night or dusk, visual acuity is sacrificed for light sensitivity.[2] The ocelli are unable to form focused images but are sensitive mainly, to differences in light intensity.[4] Colour vision occurs in all orders of insects. Generally insects see better at the blue end of the spectrum than at the red end. In some orders sensitivity ranges can include ultraviolet.[2]

A number of insects have temperature and humidity sensors[2] and insects being small, cool more quickly than larger animals. Insects are generally considered cold-blooded or ectothermic, their body temperature rising and falling with the environment. However, flying insects raise their body temperature through the action of flight, above environmental temperatures.[4][6]

The body temperature of butterflies and grasshoppers in flight may be 5 °C or 10 °C above environmental temperature, however moths and bumblebees, insulated by scales and hair, during flight, may raise flight muscle temperature 20–30 °C above the environment temperature. Most flying insects have to maintain their flight muscles above a certain temperature to gain power enough to fly. Shivering, or vibrating the wing muscles allow larger insects to actively increase the temperature of their flight muscles, enabling flight.[4]

Until very recently, no one had ever documented the presence of nociceptors (the cells that detect and transmit sensations of pain) in insects,[9] though recent findings of nociception in larval fruit flies challenges this[10] and raises the possibility that some insects may be capable of feeling pain.

Reproductive system

Most insects have a high reproductive rate. With a short generation time, they evolve faster and can adjust to environmental changes more rapidly than other slower breeding animals.[2] Although there are many forms of reproductive organs in insects, there remains a basic design and function for each reproductive part. These individual parts may vary in shape (gonads), position (accessory gland attachment), and number (testicular and ovarian glands), with different insect groups.[7]

Female

The female insect's main reproductive function is to produce eggs, including the egg's protective coating, and to store the male spermatozoa until egg fertilisation is ready. The female reproductive organs include paired ovaries which empty their eggs (oocytes) via the calyces into lateral oviducts, joining to form the common oviduct. The opening (gonopore) of the common oviduct is concealed in a cavity called the genital chamber and this serves as a copulatory pouch (bursa copulatrix) when mating.[7] The external opening to this is the vulva. Often in insects the vulva is narrow and the genital chamber becomes pouch or tube like and is called the vagina. Related to the vagina is a saclike structure, the spermatheca, where spermatozoa are stored ready for egg fertilisation. A secretory gland nourishes the contained spermatozoa in the vagina.[4][4]

Egg development is mostly completed by the insect's adult stage and is controlled by hormones that control the initial stages of oogenesis and yolk deposition.[7] Most insects are oviparous, where the young hatch after the eggs have been laid.[4]

Insect sexual reproduction starts with sperm entry that stimulates oogenesis, meiosis occurs and the egg moves down the genital tract. Accessory glands of the female secrete an adhesive substance to attach eggs to an object and they also supply material that provides the eggs with a protective coating. Oviposition takes place via the female ovipositor.[4][6]

Male

The male's main reproductive function is to produce and store spermatozoa and provide transport to the reproductive tract of the female.[7] Sperm development is usually completed by the time the insect reaches adulthood.[4] The male has two testes, which contain follicles in which the spermatozoa are produced. These open separately into the sperm duct or vas deferens and this stores the sperm.[7] The vas deferentia then unite posteriorally to form a central ejaculatory duct, this opens to the outside on an aedeagus or a penis.[4] Accessory glands secrete fluids that comprise the spermatophore. This becomes a package that surrounds and carries the spermatozoa, forming a sperm-containing capsule.[4][7]

Sexual and asexual reproduction

Most insects reproduce via sexual reproduction, i.e. the egg is produced by the female, fertilised by the male and oviposited by the female. Eggs are usually deposited in a precise microhabitat on or near the required food.[6] However, some adult females can reproduce without male input. This is known as parthenogenesis and in the most common type of parthenogenesis the offspring are essentially identical to the mother. This is most often seen in aphids and scale insects.[6]

Life cycle

An insect's life-cycle can be divided into three types:

- **Ametabolous,** no metamorphosis, these insects are primitively wingless where the only difference between adult and nymph is size, e.g. order: Thysanura (silverfish).[4]
- **Hemimetabolous,** or incomplete metamorphosis. The terrestrial young are called nymphs and aquatic young are called naiads. Insect young are usually similar to the adult. Wings appear as buds on the nymphs or early instars. When the last moult is completed the wings expand to the full adult size, e.g. order: Odonata (dragonflies).
- **Holometabolus,** or complete metamorphosis. These insects have a different form in their immature and adult stages, have different behaviours and live in different habitats. The immature form is called larvae and remains similar in form but increases in size. They usually have chewing mouthparts even if the adult form mouth parts suck. At the last larval instar phase the insect forms into a pupa, it doesn't feed and is inactive, and here wing development is initiated, and the adult emerges e.g. order: Lepidoptera (butterflies and moths).[4]

Moulting

As an insect grows it needs to replace the rigid exoskeleton regularly.[2][4] Moulting may occur up to three or four times or, in some insects, fifty times or more during its life.[2] A complex process controlled by hormones, it includes the cuticle of the body wall, the cuticular lining of the tracheae, foregut, hindgut and endoskeletal structures.[2][4]

The stages of molting:

1. **Apolysis**—moulting hormones are released into the haemolymph and the old cuticle separates from the underlying epidermal cells. The epidermis increases in size due to mitosis and then the new cuticle is produced. Enzymes secreted by the epidermal cells digest the old endocuticle, not affecting the old sclerotised exocuticle.
2. **Ecdysis**—this begins with the splitting of the old cuticle, usually starting in the midline of the thorax's dorsal side. The rupturing force is mostly from haemolymph pressure that has been forced into thorax by abdominal muscle contractions caused by the insect swallowing air or water. After this the insect wriggles out of the old cuticle.

3. **Sclerotisation**—after emergence the new cuticle is soft and this a particularly vulnerable time for the insect as its hard protective coating is missing. After an hour or two the exocuticle hardens and darkens. The wings expand by the force of haemolymph into the wing veins.[2][4]

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Beekeeping

Beekeeping (or **apiculture**) is the maintenance of bee colonies, commonly in man-made hives, by humans. Most such bees are honey bees in the genus *Apis*, but other honey-producing bees such as *Melipona* stingless bees are also kept. A beekeeper (or apiarist) keeps bees in order to collect their honey and other products that the hive produce (including beeswax, propolis, flower pollen, bee pollen, and royal jelly), to pollinate crops, or to produce bees for sale to other beekeepers. A location where bees are kept is called an apiary or "bee yard".

Beekeeping, tacuinum sanitatis casanatensis (14th century)

Play media

Beekeeping in Serbia

Contents

History

Early history

Honey seeker depicted on 8,000-year-old cave painting near Valencia, Spain[1]

Depictions of humans collecting honey from wild bees date to 10,000 years ago.[2] Beekeeping in pottery vessels began about 9,000 years ago in North Africa.[3] Domestication of bees is shown in Egyptian art from around 4,500 years ago.[4] Simple hives and smoke were used and honey was stored in jars, some of which were found in the tombs of pharaohs such as Tutankhamun. It wasn't until the 18th century that European understanding of the colonies and biology of bees allowed the construction of the moveable comb hive so that honey could be harvested without destroying the entire colony.

At some point humans began to attempt to maintain colonies of wild bees in artificial hives made from hollow logs, wooden boxes, pottery vessels, and woven straw baskets or "skeps". Traces of beeswax are found in potsherds throughout the Middle East beginning about 7000 BCE.[3]

Honeybees were kept in Egypt from antiquity.[5] On the walls of the sun temple of Nyuserre Ini from the Fifth Dynasty, before 2422 BCE, workers are depicted blowing smoke into hives as they are removing honeycombs.[6] Inscriptions detailing the production of honey are found on the tomb of Pabasa from the Twenty-sixth Dynasty (c. 650 BCE), depicting pouring honey in jars and cylindrical hives.[7] Sealed pots of honey were found in the grave goods of pharaohs such as Tutankhamun.

> I am Shamash-resh-uṣur, the governor of Suhu and the land of Mari. Bees that collect honey, which none of my ancestors had ever seen or brought into the land of Suhu, I brought down from the mountain of the men of Habha, and made them settle in the orchards of the town 'Gabbari-built-it'. They collect honey and wax, and I know how to melt the honey and wax – and the gardeners know too. Whoever comes in the future, may he ask the old men of the town, (who will say) thus: "They are the buildings of Shamash-resh-uṣur, the governor of Suhu, who introduced honey bees into the land of Suhu."
>
> — translated text from stele, (Dalley, 2002)[8]

Stele showing Shamash-resh-uṣur praying to the gods Adad and Ishtar with an inscription about beekeeping in Babylonian cuneiform

In prehistoric Greece (Crete and Mycenae), there existed a system of high-status apiculture, as can be concluded from the finds of hives, smoking pots, honey extractors and other beekeeping paraphernalia in Knossos. Beekeeping was considered a highly valued industry controlled by beekeeping overseers—owners of gold rings depicting apiculture scenes rather than religious ones as they have been reinterpreted recently, contra Sir Arthur Evans.[9]

Archaeological finds relating to beekeeping have been discovered at Rehov, a Bronze and Iron Age archaeological site in the Jordan Valley, Israel.[10] Thirty intact hives, made of straw and unbaked clay, were discovered by archaeologist Amihai Mazar in the ruins of the city, dating from about 900 BCE. The hives were found in orderly rows, three high, in a manner that could have accommodated around 100 hives, held more than 1 million bees and had a potential annual yield of 500 kilograms of honey and 70 kilograms of beeswax, according to Mazar, and are evidence that an advanced honey industry existed in ancient Israel 3,000 years ago.[11][12][13]

In ancient Greece, aspects of the lives of bees and beekeeping are discussed at length by Aristotle. Beekeeping was also documented by the Roman writers Virgil, Gaius Julius Hyginus, Varro, and Columella.

The Beekeepers, 1568, by Pieter Bruegel the Elder

Beekeeping has also been practiced in ancient China since antiquity. In the book "Golden Rules of Business Success" written by Fan Li (or Tao Zhu Gong) during the Spring and Autumn period there are sections describing the art of beekeeping, stressing the importance of the quality of the wooden box used and how this can affect the quality of the honey. The Chinese word for honey (蜜 *mì*, reconstructed Old Chinese pronunciation *mjit) was borrowed from Indo-European proto-Tocharian language, the source of "honey", from proto-Tocharian **ḿət(ə)* (where **ḿ* is palatalized; cf. Tocharian B *mit*), cognate with English *mead*.

The ancient Maya domesticated a separate species of stingless bee. The use of stingless bees is referred to as meliponiculture, named after bees of the tribe Meliponini—such as *Melipona quadrifasciata* in Brazil. This variation of bee keeping still occurs around the world today.[14] For instance, in Australia, the stingless bee *Tetragonula carbonaria* is kept for production of their honey.[15]

Scientific study of honey bees

It was not until the 18th century that European natural philosophers undertook the scientific study of bee colonies and began to understand the complex and hidden world of bee biology. Preeminent among these scientific pioneers were Swammerdam, René Antoine Ferchault de Réaumur, Charles Bonnet, and François Huber. Swammerdam and Réaumur were among the first to use a microscope and dissection to understand the internal biology of honey bees. Réaumur was among the first to construct a glass walled observation hive to better observe activities within hives. He observed queens laying eggs in open cells, but still had no idea of how a queen was fertilized; nobody had ever witnessed the mating of a queen and drone and many theories held that queens were "self-fertile," while others believed that a vapor or "miasma" emanating from the drones fertilized queens without direct physical contact. Huber was the first to prove by observation and experiment that queens are physically inseminated by drones outside the confines of hives, usually a great distance away.

Following Réaumur's design, Huber built improved glass-walled observation hives and sectional hives that could be opened like the leaves of a book. This allowed inspecting individual wax combs and greatly improved direct observation of hive activity. Although he went blind before he was twenty, Huber employed a secretary, François Burnens, to make daily observations, conduct careful experiments, and keep accurate notes over more than twenty years. Huber confirmed that a hive consists of one queen who is the mother of all the female workers and male drones in the colony. He was also the first to confirm that mating with drones takes place outside of hives and that queens are inseminated by a number of successive matings with male drones, high in the air at a great distance from their hive. Together, he and Burnens dissected bees under the microscope and were among the first to describe the ovaries and spermatheca, or sperm store, of queens as well as the penis of male drones. Huber is universally regarded as "the father of modern bee-science" and his "Nouvelles Observations sur Les Abeilles (or "New Observations on Bees") [16] revealed all the basic scientific truths for the biology and ecology of honeybees.

Invention of the movable comb hive


Rural beekeeping in the 16th century

Early forms of honey collecting entailed the destruction of the entire colony when the honey was harvested. The wild hive was crudely broken into, using smoke to suppress the bees, the honeycombs were torn out and smashed up — along with the eggs, larvae and honey they contained. The liquid honey from the destroyed brood nest was strained through a sieve or basket. This was destructive and unhygienic, but for hunter-gatherer societies this did not matter, since the honey was generally consumed immediately and there were always more wild colonies to exploit. But in settled societies the destruction of the bee colony meant the loss of a valuable resource; this drawback made beekeeping both inefficient and something of a "stop and start" activity. There could be no continuity of production and no possibility of selective breeding, since each bee colony was destroyed at harvest time, along with its precious queen.

During the medieval period abbeys and monasteries were centers of beekeeping, since beeswax was highly prized for candles and fermented honey was used to make alcoholic mead in areas of Europe where vines would not grow. The 18th and 19th centuries saw successive stages of a revolution in beekeeping, which allowed the bees themselves to be preserved when taking the harvest.

Intermediate stages in the transition from the old beekeeping to the new were recorded for example by Thomas Wildman in 1768/1770, who described advances over the destructive old skep-based beekeeping so that the bees no longer had to be killed to harvest the honey.[17] Wildman for example fixed a parallel array of wooden bars across the top of a straw hive or skep (with a separate straw top to be fixed on later) "so that there are in all seven bars of deal" [in a 10-inch-diameter (250 mm) hive] "to which the bees fix their combs".[18] He also described using such hives in a multi-storey configuration, foreshadowing the modern use of supers: he described adding (at a proper time) successive straw hives below, and eventually removing the ones above when free of brood and filled with honey, so that the bees could be separately preserved at the harvest for a following season. Wildman also described[19] a further development, using hives with "sliding frames" for the bees to build their comb, foreshadowing more modern uses of movable-comb hives. Wildman's book acknowledged the advances in knowledge of bees previously made by Swammerdam, Maraldi, and de Réaumur—he included a lengthy translation of Réaumur's account of the natural history of bees—and he also described the initiatives of others in designing hives for the preservation of bee-life when taking the harvest, citing in particular reports from Brittany dating from the 1750s, due to Comte de la Bourdonnaye. However, the forerunners of the modern hives with movable frames that are mainly used today are considered the traditional basket top bar (movable comb) hives of Greece, known as “Greek beehives”. The oldest testimony on their use dates back to 1669 although it is probable that their use is more than 3000 years old.[20]

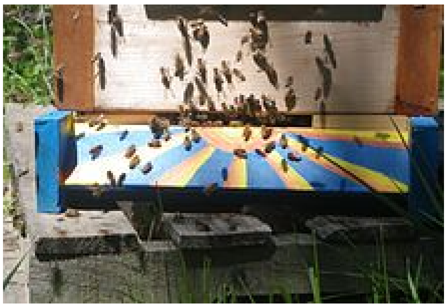
The 19th century saw this revolution in beekeeping practice completed through the perfection of the movable comb hive by the American Lorenzo Lorraine Langstroth. Langstroth was the first person to make practical use of Huber's earlier discovery that there was a specific spatial measurement between the wax combs, later called *the bee space*, which bees do not block with wax, but keep as a free passage. Having determined this bee space (between 5 and 8 mm, or 1/4 to 3/8"), Langstroth then designed a series of wooden frames within a rectangular hive box, carefully maintaining the correct space between successive frames, and found that the bees would build parallel honeycombs in the box without bonding them to each other or to the hive walls. This enables the beekeeper to slide any frame out of the hive for inspection, without harming the bees or the comb, protecting the eggs, larvae and pupae contained within the cells. It also meant that combs containing honey could be gently removed and the honey

Lorenzo Langstroth (1810–1895)

extracted without destroying the comb. The emptied honey combs could then be returned to the bees intact for refilling. Langstroth's book, *The Hive and Honey-bee*, published in 1853, described his rediscovery of the bee space and the development of his patent movable comb hive.

The invention and development of the movable-comb-hive fostered the growth of commercial honey production on a large scale in both Europe and the US (see also Beekeeping in the United States).

Evolution of hive designs



Bees at the hive entrance

Langstroth's design for movable comb hives was seized upon by apiarists and inventors on both sides of the Atlantic and a wide range of moveable comb hives were designed and perfected in England, France, Germany and the United States. Classic designs evolved in each country: Dadant hives and Langstroth hives are still dominant in the US; in France the De-Layens trough-hive became popular and in the UK a British National hive became standard as late as the 1930s although in Scotland the smaller Smith hive is still popular. In some Scandinavian countries and in Russia the traditional trough hive persisted until late in the 20th century and is still kept in some areas. However, the Langstroth and Dadant designs remain ubiquitous in the US and also in many parts of Europe, though Sweden, Denmark, Germany, France and Italy all have their own national hive designs. Regional variations of hive evolved to reflect the climate, floral productivity and the reproductive characteristics of the various subspecies of native honey bee in each bio-region.

Honey-laden honeycomb in a wooden frame

The differences in hive dimensions are insignificant in comparison to the common factors in all these hives: they are all square or rectangular; they all use movable wooden frames; they all consist of a floor, brood-box, honey super, crown-board and roof. Hives have traditionally been constructed of cedar, pine, or cypress wood, but in recent years hives made from injection molded dense polystyrene have become increasingly important.

Hives also use queen excluders between the brood-box and honey supers to keep the queen from laying eggs in cells next to those containing honey intended for consumption. Also, with the advent in the 20th century of mite pests, hive floors are often replaced for part of (or the whole) year with a wire mesh and removable tray.

In 2015 the Flow Hive system was invented in Australia by Cedar Anderson and his father Stuart Anderson[21], allowing honey to be extracted without expensive centrifuge equipment.

Flow Hive 2 with honey pouring into jars

Pioneers of practical and commercial beekeeping

The 19th century produced an explosion of innovators and inventors who perfected the design and production of beehives, systems of management and husbandry, stock improvement by selective breeding, honey extraction and marketing. Preeminent among these innovators were:

Petro Prokopovych used frames with channels in the side of the woodwork; these were packed side by side in boxes that were stacked one on top of the other. The bees traveled from frame to frame and box to box via the channels. The channels were similar to the cut outs in the sides of modern wooden sections[22] (1814).

Jan Dzierżon was the father of modern apiology and apiculture. All modern beehives are descendants of his design.

François Huber did significant discoveries on the life of bees including the mating of queens and their interaction with other members of the hive in spite of his blindness. His work was published as *New Observations on the Natural History of Bees*.

L. L. Langstroth revered as the "father of American apiculture"; no other individual has influenced modern beekeeping practice more than Lorenzo Lorraine Langstroth. His classic book *The Hive and Honey-bee* was published in 1853.

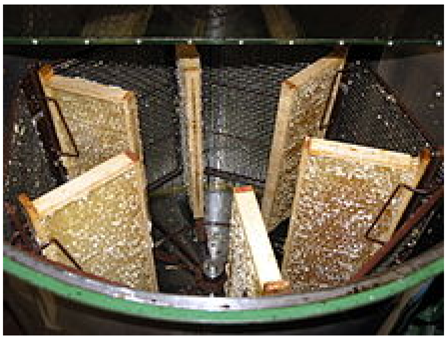
Moses Quinby often termed "the father of commercial beekeeping in the United States", author of *Mysteries of Bee-Keeping Explained*. He invented the Bee smoker in 1873.[23][24]

Amos Root author of the *A B C of Bee Culture*, which has been continuously revised and remains in print. Root pioneered the manufacture of hives and the distribution of bee-packages in the United States.

A. J. Cook author of *The Bee-Keepers' Guide; or Manual of the Apiary*, 1876.

Dr. C.C. Miller was one of the first entrepreneurs to actually make a living from apiculture. By 1878 he made beekeeping his sole business activity. His book, *Fifty Years Among the Bees*, remains a classic and his influence on bee management persists to this day.

Franz Hruschka was an Italian military officer who made one crucial invention that catalyzed the commercial honey industry. In 1865 he invented a simple machine for extracting honey from the comb by means of centrifugal force. His original idea was simply to support combs in a metal framework and then spin them around within a container to collect honey as it was thrown out by centrifugal force. This meant that honeycombs could be returned to a hive undamaged but empty, saving the bees a vast amount of work, time, and materials. This single invention greatly improved the efficiency of honey harvesting and catalysed the modern honey industry.[25]



Honey Extractor

Walter T. Kelley was an American pioneer of modern beekeeping in the early and mid-20th century. He greatly improved upon beekeeping equipment and clothing and went on to manufacture these items as well as other equipment. His company sold via catalog worldwide and his book, *How to Keep Bees & Sell Honey*, an introductory book of apiculture and marketing, allowed for a boom in beekeeping following World War II.

In the U.K. practical beekeeping was led in the early 20th century by a few men, pre-eminently Brother Adam and his Buckfast bee and R.O.B. Manley, author of many titles, including *Honey Production in the British Isles* and inventor of the Manley frame, still universally popular in the U.K. Other notable British pioneers include William Herrod-Hempsall and Gale.

Dr. Ahmed Zaky Abushady (1892–1955), was an Egyptian poet, medical doctor, bacteriologist and bee scientist who was active in England and in Egypt in the early part of the twentieth century. In 1919, Abushady patented a removable, standardized aluminum honeycomb. In 1919 he also founded The Apis Club in Benson, Oxfordshire, and its periodical Bee World, which was to be edited by Annie D. Betts and later by Dr. Eva Crane. The Apis Club was transitioned to the International Bee Research Association (IBRA). Its archives are held in the National Library of Wales. In Egypt in the 1930s, Abushady established The Bee Kingdom League and its organ, The Bee Kingdom.

In India, R. N. Mattoo was the pioneer worker in starting beekeeping with Indian honeybee, (*Apis cerana indica*) in the early 1930s. Beekeeping with European honeybee, (*Apis mellifera*) was started by Dr. A. S. Atwal and his team members, O. P. Sharma and N. P. Goyal in Punjab in the early 1960s. It remained confined to Punjab and Himachal Pradesh up to the late 1970s. Later on in 1982, Dr. R. C. Sihag, working at Haryana Agricultural University, Hisar (Haryana), introduced and established this honeybee in Haryana and standardized its management practices for semi-arid-subtropical climates. On the basis of these practices, beekeeping with this honeybee could be extended to the rest of the country. Now beekeeping with *Apis mellifera* predominates in India.

Traditional beekeeping

Fixed comb hives


Wooden hives in Stripeikiai honeymaking museum, Lithuania

A fixed comb hive is a hive in which the combs cannot be removed or manipulated for management or harvesting without permanently damaging the comb. Almost any hollow structure can be used for this purpose, such as a log gum, skep, wooden box, or a clay pot or tube. Fixed comb hives are no longer in common use in industrialized countries, and are illegal in places that require movable combs to inspect for problems such as varroa and American foulbrood. In many developing countries fixed comb hives are widely used and, because they can be made from any locally available material .


Beekeeping at Kawah Ijen Mountain, Indonesia

Beekeeping using fixed comb hives is an essential part of the livelihoods of many communities in poor countries. The charity Bees for Development recognizes that local skills to manage bees in fixed comb hives[26] are widespread in Africa, Asia, and South America. Internal size of fixed comb hives range from 32.7 liters (2000 cubic inches) typical of the clay tube hives used in Egypt to 282 liters (17209 cubic inches) for the Perone hive. Straw skeps, bee gums, and unframed box hives are unlawful in most US states, as the comb and brood cannot be inspected for diseases. However, skeps are still used for collecting swarms by hobbyists in the UK, before moving them into standard hives. Quinby used box hives to produce so much honey that he saturated the New York market in the 1860s. His writings contain excellent advice for management of bees in fixed comb hives.

Modern beekeeping

Topbar hives

Top bar hives have been widely adopted in Africa where they are used to keep tropical honeybee ecotypes. Their advantages include being light weight, adaptable, easy to harvest honey, and less stressful for the bees. Disadvantages include combs that are fragile and cannot usually be extracted and returned to the bees to be refilled and that they cannot easily be expanded for additional honey storage.

A growing number of amateur beekeepers are adopting various top-bar hives similar to the type commonly found in Africa. Top bar hives were originally used as a traditional beekeeping method in Greece and Vietnam with a history dating back over 2000 years.[13] These hives have no frames and the honey-filled comb is not returned after extraction. Because of this, the production of honey is likely to be somewhat less than that of a frame and super based hive such as Langstroth or Dadant. Top bar hives are mostly kept by people who are more interested in having bees in their garden than in honey production per se. Some of the most well known top-bar hive designs are the Kenyan Top Bar Hive with sloping sides, the Tanzanian Top Bar Hive with straight sides, and Vertical Top Bar Hives, such as the Warre or "People's Hive" designed by Abbe Warre in the mid-1900s.

The initial costs and equipment requirements are typically much less than other hive designs. Scrap wood or #2 or #3 pine can often be used to build a nice hive. Top-bar hives also offer some advantages to interacting with the bees and the amount of weight that must be lifted is greatly reduced. Top-bar hives are being widely used in developing countries in Africa and Asia as a result of the Bees for Development program. Since 2011, a growing number of beekeepers in the U.S. are using various top-bar hives.[27]

Vertical stackable hives

There are three types of vertical stackable hives: hanging or top-access frame, sliding or side-access frame, and top bar.

Hanging frame hives include Langstroth, the British National, Dadant, Layens, and Rose, differing primarily by size or number of frames. The Langstroth was the first successful top-opened hive with movable frames. Many other hive designs are based on the principle of bee space first described by Langstroth, and is a descendant of Jan Dzierzon's Polish hive designs. Langstroth hives are the most common size in the United States and much of the world; the British National is the most common size in the United Kingdom; Dadant and Modified Dadant hives are widely used in France and Italy, and Layens by some beekeepers, where their large size is an advantage. Square Dadant hives–often called 12 frame Dadant or Brother Adam hives–are used in large parts of Germany and other parts of Europe by commercial beekeepers.

Any hanging frame hive design can be built as a sliding frame design. The AZ Hive, the original sliding frame design, integrates hives using Langstroth-sized frames into a honey house so as to streamline the workflow of honey harvest by localization of labor, similar to cellular manufacturing. The honey house can be a portable trailer, allowing the beekeeper to haul the hives to a site and provide pollination services.

Top bar stackable hives simply use top bars instead of full frames. The most common type is the Warre hive, although any hive with hanging frames can be made into a top bar stackable hive by using only the top bar and not the whole frame. This may work less-well with larger frames, where crosscomb and attachment can occur more-readily.

Protective clothing

Most beekeepers also wear some protective clothing. Novice beekeepers usually wear gloves and a hooded suit or hat and veil. Experienced beekeepers sometimes elect not to use gloves because they inhibit delicate manipulations. The face and neck are the most important areas to protect, so most beekeepers wear at least a veil. Defensive bees are attracted to the breath, and a sting on the face can lead to much more pain and swelling than a sting elsewhere, while a sting on a bare hand can usually be quickly removed by fingernail scrape to reduce the amount of venom injected.

The protective clothing is generally light colored (but not colorful) and of a smooth material. This provides the maximum differentiation from the colony's natural predators (such as bears and skunks) which tend to be dark-colored and furry.

'Stings' retained in clothing fabric continue to pump out an alarm pheromone that attracts aggressive action and further stinging attacks. Washing suits regularly, and rinsing gloved hands in vinegar minimizes attraction.

Smoker

Smoke is the beekeeper's third line of defense. Most beekeepers use a "smoker"—a device designed to generate smoke from the incomplete combustion of various fuels. Smoke calms bees; it initiates a feeding response in anticipation of possible hive abandonment due to fire.[28] Smoke also masks alarm pheromones released by guard bees or when bees are squashed in an inspection. The ensuing confusion creates an opportunity for the beekeeper to open the hive and work without triggering a defensive reaction. In addition, when a bee consumes honey the bee's abdomen distends, supposedly making it difficult to make the necessary flexes to sting, though this has not been tested scientifically.

Beekeepers often wear protective clothing to protect themselves from stings

Many types of fuel can be used in a smoker as long as it is natural and not contaminated with harmful substances. These fuels include hessian, twine, burlap, pine needles, corrugated cardboard, and mostly rotten or punky wood. Indian beekeepers, especially in Kerala, often use coconut fibers as they are readily available, safe, and of negligible expense. Some beekeeping supply sources also sell commercial fuels like pulped paper and compressed cotton, or even aerosol cans of smoke. Other beekeepers use sumac as fuel because it ejects lots of smoke and doesn't have an odor.

Some beekeepers are using "liquid smoke" as a safer, more convenient alternative. It is a water-based solution that is sprayed onto the bees from a plastic spray bottle.

Torpor may also be induced by the introduction of chilled air into the hive – while chilled carbon dioxide may have harmful long-term effects.[29]

Effects of stings and of protective measures

Bee smoker with heat shield and hook

Some beekeepers believe that the more stings a beekeeper receives, the less irritation each causes, and they consider it important for safety of the beekeeper to be stung a few times a season. Beekeepers have high levels of antibodies (mainly IgG) reacting to the major antigen of bee venom, phospholipase A2 (PLA).[30] Antibodies correlate with the frequency of bee stings.

The entry of venom into the body from bee-stings may also be hindered and reduced by protective clothing that allows the wearer to remove stings and venom sacs with a simple tug on the clothing. Although the stinger is barbed, a worker bee is less likely to become lodged into clothing than human skin.

If a beekeeper is stung by a bee, there are many protective measures that should be taken in order to make sure the affected area does not become too irritated. The first cautionary step that should be taken following a bee sting is removing the stinger without squeezing the attached venom glands. A quick scrape with a fingernail is effective and intuitive. This step is effective in making sure that the venom injected does not spread, so the side effects of the sting will go away sooner. Washing the affected area with soap and water is also a good way to stop the spread of venom. The last step that needs to be taken is to apply ice or a cold compress to the stung area.[31]

Natural beekeeping

The natural beekeeping movement believes that bee hives are weakened by modern beekeeping and agricultural practices, such as crop spraying, hive movement, frequent hive inspections, artificial insemination of queens, routine medication, and sugar water feeding.

Practitioners of "natural beekeeping" tend to use variations of the top-bar hive, which is a simple design that retains the concept of having a movable comb without the use of frames or a foundation. The horizontal top-bar hive, as championed by Marty Hardison, Michael Bush, Philip Chandler, Dennis Murrell and others, can be seen as a modernization of hollow log hives, with the addition of wooden bars of specific width from which bees hang their combs. Its widespread adoption in recent years can be attributed to the publication in 2007 of *The Barefoot Beekeeper*[32] by Philip Chandler, which challenged many aspects of modern beekeeping and offered the horizontal top-bar hive as a viable alternative to the ubiquitous Langstroth-style movable-frame hive.

The most popular vertical top-bar hive is the Warré hive, based on a design by the French priest Abbé Émile Warré (1867–1951) and popularized by Dr. David Heaf in his English translation of Warré's book *L'Apiculture pour Tous* as *Beekeeping For All*.[33]

Urban or backyard beekeeping

Honey bee in Toronto

Related to natural beekeeping, urban beekeeping is an attempt to revert to a less industrialized way of obtaining honey by utilizing small-scale colonies that pollinate urban gardens. Urban apiculture has undergone a renaissance in the first decade of the 21st century, and urban beekeeping is seen by many as a growing trend.

Some have found that "city bees" are actually healthier than "rural bees" because there are fewer pesticides and greater biodiversity in the urban gardens.[34] Urban bees may fail to find forage, however, and homeowners can use their landscapes to help feed local bee populations by planting flowers that provide nectar and pollen. An environment of year-round, uninterrupted bloom creates an ideal environment for colony reproduction.[35]

Urban beekeepers are testing modern types of beehives, testing for urban contest and ease of use. In 2015 the FlowHive appeared and in 2018 Beeing (https://beeing.it/en/home-your-bees-your-honey/), a hive made in Italy, that allows the beekeeper to extract honey without having contact with the bees.

Indoor beekeeping

Play media

MIT's "Synthetic Apiary" project raises colonies entirely indoors

Modern beekeepers have experimented with raising bees indoors, in a controlled environment or in indoor observation hives. This may be done for reasons of space and monitoring, or in the off-season. In the off-season, large commercial beekeepers may move colonies to "wintering" warehouses, with fixed temperature, light and humidity. This helps the bees remain healthy, but relatively dormant. These relatively dormant or "wintered" bees survive on stored honey, and new bees are not born.[36]

Experiments in raising bees for longer durations indoors have looked into more detailed and varying environment controls. In 2015, MIT's *Synthetic Apiary* project simulated springtime inside a closed environment, for a number of hives over the course of a winter. They provided food sources and simulated long days, and saw activity and reproduction levels comparable to the levels seen outdoors in warm weather. They concluded that such an indoor apiary could be sustained year-round if needed.[37][38]

Bee colonies

Species

There are more than 20,000 species of wild bees.[39] Many species are solitary[40] (e.g., mason bees, leafcutter bees (Megachilidae), carpenter bees and other ground-nesting bees). Many others rear their young in burrows and small colonies (e.g., bumblebees and stingless bees). Some honey bees are wild e.g. the little honeybee (*Apis florea*), giant honeybee (*Apis dorsata*) and rock bee (*Apis laboriosa*). Beekeeping, or apiculture, is concerned with the practical management of the social species of honey bees, which live in large colonies of up to 100,000 individuals. In Europe and America the species universally managed by beekeepers is the Western honey bee (*Apis mellifera*). This species has several sub-species or regional varieties, such as the Italian bee (*Apis mellifera ligustica*), European dark bee (*Apis mellifera mellifera*), and the Carniolan honey bee (*Apis mellifera carnica*). In the tropics, other species of social bees are managed for honey production, including the Asiatic honey bee (*Apis cerana*).

Castes

A colony of bees consists of three castes of bee:

- a queen bee, which is normally the only breeding female in the colony;
- a large number of female worker bees, typically 30,000–50,000 in number;
- a number of male drones, ranging from thousands in a strong hive in spring to very few during dearth or cold season.


Queen bee (center)

The queen is the only sexually mature female in the hive and all of the female worker bees and male drones are her offspring. The queen may live for up to three years or more and may be capable of laying half a million eggs or more in her lifetime. At the peak of the breeding season, late spring to summer, a good queen may be capable of laying 3,000 eggs in one day, more than her own body weight. This would be exceptional however; a prolific queen might peak at 2,000 eggs a day, but a more average queen might lay just 1,500 eggs per day. The queen is raised from a normal worker egg, but is fed a larger amount of royal jelly than a normal worker bee, resulting in a radically different growth and metamorphosis. The queen influences the colony by the production and dissemination of a variety of pheromones or "queen substances". One of these chemicals suppresses the development of ovaries in all the female worker bees in the hive and prevents them from laying eggs.

Mating of queens

The queen emerges from her cell after 15 days of development and she remains in the hive for 3–7 days before venturing out on a mating flight. Mating flight is otherwise known as "nuptial flight". Her first orientation flight may only last a few seconds, just enough to mark the position of the hive. Subsequent mating flights may last from 5 minutes to 30 minutes, and she may mate with a number of male drones on each flight. Over several matings, possibly a dozen or more, the queen receives and stores enough sperm from a succession of drones to fertilize hundreds of thousands of eggs. If she does not manage to leave the hive to mate—possibly due to bad weather or being trapped in part of the hive—she remains infertile and becomes a *drone layer*, incapable of producing female worker bees. Worker bees sometimes kill a non-performing queen and produce another. Without a properly performing queen, the hive is doomed.

Mating takes place at some distance from the hive and often several hundred feet in the air; it is thought that this separates the strongest drones from the weaker ones, ensuring that only the fastest and strongest drones get to pass on their genes.

Worker bees

Most of the bees in a hive are female worker bees. At the height of summer when activity in the hive is frantic and work goes on non-stop, the life of a worker bee may be as short as 6 weeks; in late autumn, when no brood is being raised and no nectar is being harvested, a young bee may live for 16 weeks, right through the winter.

Over the course of their lives, worker bees' duties are dictated by age. For the first few weeks of their lifespan, they perform basic chores within the hive: cleaning empty brood cells, removing debris and other housekeeping tasks, making wax for building or repairing comb, and feeding larvae. Later, they may ventilate the hive or guard the entrance. Older workers leave the hive daily, weather permitting, to forage for nectar, pollen, water, and propolis.

Worker bee

Period	Work activity
Days 1–3	Cleaning cells and incubation
Day 3–6	Feeding older larvae
Day 6–10	Feeding younger larvae
Day 8–16	Receiving nectar and pollen from field bees
Day 12–18	Beeswax making and cell building
Day 14 onwards	Entrance guards; nectar, pollen, water and propolis foraging; robbing other hives

Drones

Drones are the largest bees in the hive (except for the queen), at almost twice the size of a worker bee. Note in the picture that they have much larger eyes than the workers have, presumably to better locate the queen during the mating flight. They do not work, do not forage for pollen or nectar, are unable to sting, and have no other known function than to mate with new queens and fertilize them on their mating flights. A bee colony generally starts to raise drones a few weeks before building queen cells so they can supersede a failing queen or prepare for swarming. When queen-raising for the season is over, bees in colder climates drive drones out of the hive to die, biting and tearing their legs and wings.

Larger drones compared to smaller workers

Differing stages of development

Stage of development	Queen	Worker	Drone
Egg	3 days	3 days	3 days
Larva (successive molts)	8 days	10 days	13 days
Cell Capped	day 8	day 8	day 10
Pupa	4 days	8 days	8 days
Total	15 days	21 days	24 days

Structure of a bee colony

A domesticated bee colony is normally housed in a rectangular hive body, within which eight to ten parallel frames house the vertical plates of honeycomb that contain the eggs, larvae, pupae and food for the colony. If one were to cut a vertical cross-section through the hive from side to side, the brood nest would appear as a roughly ovoid ball spanning 5–8 frames of comb. The two outside combs at each side of the hive tend to be exclusively used for long-term storage of honey and pollen.

Within the central brood nest, a single frame of comb typically has a central disk of eggs, larvae and sealed brood cells that may extend almost to the edges of the frame. Immediately above the brood patch an arch of pollen-filled cells extends from side to side, and above that again a broader arch of honey-filled cells extends to the frame tops. The pollen is protein-rich food for developing larvae, while honey is also food but largely energy rich rather than protein rich. The nurse bees that care for the developing brood secrete a special food called "royal jelly" after feeding themselves on honey and pollen. The amount of royal jelly fed to a larva determines whether it develops into a worker bee or a queen.

Apart from the honey stored within the central brood frames, the bees store surplus honey in combs above the brood nest. In modern hives the beekeeper places separate boxes, called "supers", above the brood box, in which a series of shallower combs is provided for storage of honey. This enables the beekeeper to remove some of the supers in the late summer, and to extract the surplus honey harvest, without damaging the colony of bees and its brood nest below. If all the honey is taken, including the amount of honey needed to survive winter, the beekeeper must replace these stores by feeding the bees sugar or corn syrup in autumn.

Annual cycle of a bee colony

The development of a bee colony follows an annual cycle of growth that begins in spring with a rapid expansion of the brood nest, as soon as pollen is available for feeding larvae. Some production of brood may begin as early as January, even in a cold winter, but breeding accelerates towards a peak in May (in the northern hemisphere), producing an abundance of harvesting bees synchronized to the main nectar flow in that region. Each race of bees times this build-up slightly differently, depending on how the flora of its original region blooms. Some regions of Europe have two nectar flows: one in late spring and another in late August. Other regions have only a single nectar flow. The skill of the beekeeper lies in predicting when the nectar flow will occur in his area and in trying to ensure that his colonies achieve a maximum population of harvesters at exactly the right time.

The key factor in this is the prevention or skillful management of the swarming impulse. If a colony swarms unexpectedly and the beekeeper does not manage to capture the resulting swarm, he is likely to harvest significantly less honey from that hive, since he has lost half his worker bees at a single stroke. If, however, he can use the swarming impulse to breed a new queen but keep all the bees in the colony together, he maximizes his chances of a good harvest. It takes many years of learning and experience to be able to manage all these aspects successfully, though owing to variable circumstances many beginners often achieve a good honey harvest.

Formation of new colonies

Colony reproduction: swarming and supersedure

A swarm about to land

All colonies are totally dependent on their queen, who is the only egg-layer. However, even the best queens live only a few years and one or two years longevity is the norm. She can choose whether or not to fertilize an egg as she lays it; if she does so, it develops into a female worker bee; if she lays an unfertilized egg it becomes a male drone. She decides which type of egg to lay depending on the size of the open brood cell she encounters on the comb. In a small worker cell, she lays a fertilized egg; if she finds a larger drone cell, she lays an unfertilized drone egg.

All the time that the queen is fertile and laying eggs she produces a variety of pheromones, which control the behavior of the bees in the hive. These are commonly called *queen substance*, but there are various pheromones with different functions. As the queen ages, she begins to run out of stored sperm, and her pheromones begin to fail.

Inevitably, the queen begins to falter, and the bees decide to replace her by creating a new queen from one of her worker eggs. They may do this because she has been damaged (lost a leg or an antenna), because she has run out of sperm and cannot lay fertilized eggs (has become a "drone laying queen"), or because her pheromones have dwindled to where they cannot control all the bees in the hive. At this juncture, the bees produce one or more queen cells by modifying existing worker cells that contain a normal female egg. They then pursue one of two ways to replace the queen: **supersedure**, replacing or superseding the queen without swarming, or **swarm cell production**, dividing the hive into two colonies through swarming.

Supersedure is highly valued as a behavioral trait by beekeepers. A hive that supersedes its old queen does not lose any stock. Instead it creates a new queen and the old one fades away or is killed when the new queen emerges. In these hives, the bees produce just one or two queen cells, characteristically in the center of the face of a broodcomb.

Swarm cell production involves creating many queen cells, typically a dozen or more. These are located around the edges of a broodcomb, often at the sides and the bottom.

Once either process has begun, the old queen leaves the hive with the hatching of the first queen cells. She leaves accompanied by a large number of bees, predominantly young bees (wax-secretors), who form the basis of the new hive. Scouts are sent out from the swarm to find suitable hollow trees or rock crevices. As soon as one is found, the entire swarm moves in. Within a matter of hours, they build new wax brood combs, using honey stores that the young bees have filled themselves with before leaving the old hive. Only young bees can secrete wax from special abdominal segments, and this is why swarms tend to contain more young bees. Often a number of virgin queens accompany the first swarm (the "prime swarm"), and the old queen is replaced as soon as a daughter queen mates and begins laying. Otherwise, she is quickly superseded in the new home.


New wax combs between basement joists

Different sub-species of *Apis mellifera* exhibit differing swarming characteristics. In general the more northerly black races are said to swarm less and supersede more, whereas the more southerly yellow and grey varieties are said to swarm more frequently. The truth is complicated because of the prevalence of cross-breeding and hybridization of the sub species.

Factors that trigger swarming

Some beekeepers may monitor their colonies carefully in spring and watch for the appearance of queen cells, which are a dramatic signal that the colony is determined to swarm.


A swarm attached to a branch

This swarm looks for shelter. A beekeeper may capture it and introduce it into a new hive, helping meet this need. Otherwise, it returns to a feral state, in which case it finds shelter in a hollow tree, excavation, abandoned chimney, or even behind shutters.

A small after-swarm has less chance of survival and may threaten the original hive's survival if the number of individuals left is unsustainable. When a hive swarms despite the beekeeper's preventative efforts, a good management practice is to give the reduced hive a couple frames of open brood with eggs. This helps replenish the hive more quickly and gives a second opportunity to raise a queen if there is a mating failure.

Each race or sub-species of honey bee has its own swarming characteristics. Italian bees are very prolific and inclined to swarm; Northern European black bees have a strong tendency to supersede their old queen without swarming. These differences are the result of differing evolutionary pressures in the regions where each sub-species evolved.

Artificial swarming

When a colony accidentally loses its queen, it is said to be "queenless". The workers realize that the queen is absent after as little as an hour, as her pheromones fade in the hive. Instinctively, the workers select cells containing eggs aged less than three days and enlarge these cells dramatically to form "emergency queen cells". These appear similar to large peanut-like structures about an inch long that hang from the center or side of the brood combs. The developing larva in a queen cell is fed differently from an ordinary worker-bee; in addition to the normal honey and pollen, she receives a great deal of royal jelly, a special food secreted by young "nurse bees" from the hypopharyngeal gland. This special food dramatically alters the growth and development of the larva so that, after metamorphosis and pupation, it emerges from the cell as a queen bee. The queen is the only bee in a colony which has fully developed ovaries, and she secretes a pheromone which suppresses the normal development of ovaries in all her workers.

Beekeepers use the ability of the bees to produce new queens to increase their colonies in a procedure called *splitting a colony*. To do this, they remove several brood combs from a healthy hive, taking care to leave the old queen behind. These combs must contain eggs or larvae less than three days old and be covered by young *nurse bees*, which care for the brood and keep it warm. These brood combs and attendant nurse bees are then placed into a small "nucleus hive" with other combs containing honey and pollen. As soon as the nurse bees find themselves in this new hive and realize they have no queen, they set about constructing emergency queen cells using the eggs or larvae they have in the combs with them.

Losses

Diseases

The common agents of disease that affect adult honey bees include fungi, bacteria, protozoa, viruses, parasites, and poisons. The gross symptoms displayed by affected adult bees are very similar, whatever the cause, making it difficult for the apiarist to ascertain the causes of problems without microscopic identification of microorganisms or chemical analysis of poisons.[41] Since 2006 colony losses from colony collapse disorder have been increasing across the world although the causes of the syndrome are, as yet, unknown.[42][43] In the US, commercial beekeepers have been increasing the number of hives to deal with higher rates of attrition.[44]

Parasites

Galleria mellonella and *Achroia grisella* “wax moth” larvae that hatch, tunnel through, and destroy comb that contains bee larvae and their honey stores. The tunnels they create are lined with silk, which entangles and starves emerging bees. Destruction of honeycombs also results in honey leaking and being wasted. A healthy hive can manage wax moths, but weak colonies, unoccupied hives, and stored frames can be decimated.[45]

Small hive beetle *(Aethina tumida)* is native to Africa but has now spread to most continents. It is a serious pest among honey bees unadapted to it.[46]

Varroa destructor, the Varroa mite, is an established pest of two species of honey bee through many parts of the world, and is blamed by many researchers as a leading cause of CCD.[47]

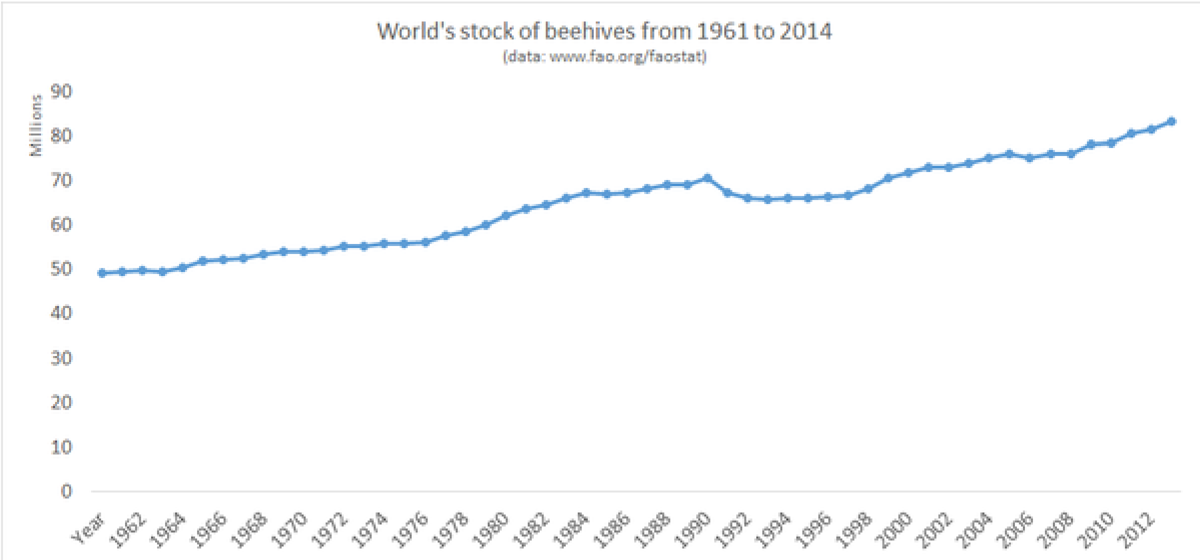
Acarapis woodi, the tracheal mite, infests the trachea of honey bees.

Predators

Most predators prefer not to eat honeybees due to their unpleasant sting, but they still have some predators. These include large animals such as skunks or bears, which are after the honey and brood in the nest as well as the adult bees themselves.[48] Some birds will also eat bees (for example, bee-eaters, which are named for their bee-centric diet), as do some robber flies, such as *Mallophora ruficauda*, which is a pest of apiculture in South America due to its habit of eating workers while they are foraging in meadows.[49]

World apiculture

According to U.N. FAO data (http://www.fao.org/faostat), the world's beehive stock rose from around 50 million in 1961 to around 83 million in 2014, which comes to about 1.3% average annual growth. Average annual growth has accelerated to 1.9% since 2009.



World's stock of beehives from 1961 to 2014

WIKIPEDIA

Sericulture

Sericulture, or **silk farming**, is the cultivation of silkworms to produce silk. Although there are several commercial species of silkworms, *Bombyx mori* (the caterpillar of the domestic silkmoth) is the most widely used and intensively studied silkworm. Silk was believed to have first been produced in China as early as the Neolithic Period. Sericulture has become an important cottage industry in countries such as Brazil, China, France, India, Italy, Japan, Korea, and Russia. Today, China and India are the two main producers, with more than 60% of the world's annual production.

Court Ladies Preparing Newly Woven Silk by Emperor Huizong of Song

Contents

Silkworm and cocoon

History

According to OMKAR text, the discovery of silk production dates to about 2700 BC, although archaeological records point to silk cultivation as early as the Yangshao period (5000–3000 BC).[1] In 1977, a piece of ceramic created 5400–5500 years ago and designed to look like a silkworm was discovered in Nancun, Hebei, providing the earliest known evidence of sericulture.[2] Also, by careful analysis of archaeological silk fibre found on Indus Civilization sites dating back to 2450–2000 BC, it is believed that silk was being used over a wide region of South Asia.[3][4] By about the first half of the 1st century AD, it had reached ancient Khotan,[5] by a series of interactions along the Silk Road. By AD 140, the practice had been established in India.[6] In the 6th century AD, the smuggling of silkworm eggs into the Byzantine Empire led to its establishment in the Mediterranean, remaining a monopoly in the Byzantine Empire for centuries (Byzantine silk). In 1147, during the Second Crusade, Roger II of Sicily (1095–1154) attacked Corinth and Thebes, two important centres of Byzantine silk production, capturing the weavers and their equipment and establishing his own silkworks in Palermo and Calabria,[7] eventually spreading the industry to Western Europe.

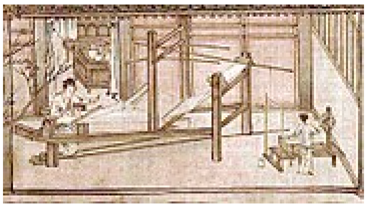
Chinese sericulture process


The silkworms and mulberry leaves are placed on trays.


Twig frames for the silkworms are prepared.


The cocoons are weighed.


The cocoons are soaked and the silk is wound on spools.


The silk is woven using a loom.

Production

The silkworms are fed with mulberry leaves, and after the fourth moult, they climb a twig placed near them and spin their silken cocoons. The silk is a continuous filament comprising fibroin protein, secreted from two salivary glands in the head of each worm, and a gum called sericin, which cements the filaments. The sericin is removed by placing the cocoons in hot water, which frees the silk filaments and readies them for reeling. This is known as the degumming process.[8] The immersion in hot water also kills the silkmoth pupa.

Single filaments are combined to form thread, which is drawn under tension through several guides and wound onto reels. The threads may be plied to form yarn. After drying, the raw silk is packed according to quality.

Stages of production

The stages of production are as follows:

1. The female silkmoth lays 300 to 500 eggs.
2. The silkmoth eggs hatch to form larvae or caterpillars, known as silkworms.
3. The larvae feed on mulberry leaves.
4. Having grown and moulted several times, the silkworm extrudes a silk fibre and forms a net to hold itself.
5. It swings itself from side to side in a figure '8', distributing the saliva that will form silk.
6. The silk solidifies when it contacts the air.
7. The silkworm spins approximately one mile of filament and completely encloses itself in a cocoon in about two or three days. The amount of usable quality silk in each cocoon is small. As a result, about 2,500 silkworms are required to produce a pound of raw silk.[9]
8. The intact cocoons are boiled, killing the silkworm pupa.
9. The silk is obtained by brushing the undamaged cocoon to find the outside end of the filament.
10. The silk filaments are then wound on a reel. One cocoon contains approximately 1,000 yards of silk filament. The silk at this stage is known as raw silk. One thread comprises up to 48 individual silk filaments.

Mahatma Gandhi was critical of silk production based on the Ahimsa philosophy "not to hurt any living thing". He also promoted "Ahimsa silk", made without boiling the pupa to procure the silk and wild silk made from the cocoons of wild and semiwild silkmoths.[10][11] The Human League also criticised sericulture in their early single "Being Boiled". In the early 21st century, the organisation PETA has also campaigned against silk.[12]

The third stage of the silkworm

Silkworms on a modern rotary mountage

Silk cocoons on mountages

Play media

A silk pavilion constructed with silkworms

See also

- Good agricultural practices
- Macclesfield silk museums
- Magnanery
- Silk industry in Azerbaijan
- Silk industry in China

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Shellac

Shellac is a resin secreted by the female lac bug, on trees in the forests of India and Thailand. It is processed and sold as dry flakes (pictured) and dissolved in alcohol to make liquid shellac, which is used as a brush-on colorant, food glaze and wood finish. Shellac functions as a tough natural primer, sanding sealant, tannin-blocker, odour-blocker, stain, and high-gloss varnish. Shellac was once used in electrical applications as it possesses good insulation qualities and it seals out moisture. Phonograph and 78 rpm gramophone records were made of it until they were replaced by vinyl long-playing records from the 1950s onwards.

Some of the many different colors of shellac

From the time it replaced oil and wax finishes in the 19th century, shellac was one of the dominant wood finishes in the western world until it was largely replaced by nitrocellulose lacquer in the 1920s and 1930s.

Shellac in alcohol

Contents

Etymology

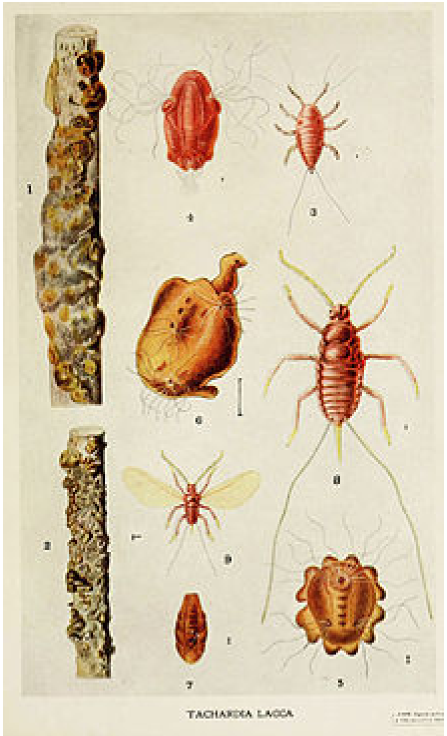
Shellac comes from *shell* and *lac*, a calque of French *laque en écailles*, "lac in thin pieces", later *gomme-laque*, "gum lac".[1] Most European languages (except Romance ones and Greek) have borrowed the word for the substance from English or from the German equivalent *Schellack*.

Production

Shellac is scraped from the bark of the trees where the female lac bug, *Kerria lacca* (order Hemiptera, family Kerriidae, also known as *Laccifer lacca*), secretes it to form a tunnel-like tube as it traverses the branches of the tree. Though these tunnels are sometimes referred to as "cocoons", they are not cocoons in the entomological sense.[2] This insect is in the same superfamily as the insect from which cochineal is obtained. The insects suck the sap of the tree and excrete "sticklac" almost constantly. The least-coloured shellac is produced when the insects feed on the kusum tree (*Schleichera*).

Lac tubes created by *Kerria lacca*

The number of lac bugs required to produce 1 kilogram (2.2 lb) of shellac has variously been estimated as 50,000,[3] 200,000,[4] or 300,000.[5][6] The root word lakh is a unit in Indian numbering system for 100,000 and presumably refers to the huge numbers of insects that swarm on host trees, up to 150 per square inch.[7]



Drawing of the insect *Kerria lacca* and its shellac tubes, by Harold Maxwell-Lefroy, 1909

The raw shellac, which contains bark shavings and lac bugs removed during scraping, is placed in canvas tubes (much like long socks) and heated over a fire. This causes the shellac to liquefy, and it seeps out of the canvas, leaving the bark and bugs behind. The thick, sticky shellac is then dried into a flat sheet and broken into flakes, or dried into "buttons" (pucks/cakes), then bagged and sold. The end-user then crushes it into a fine powder and mixes it with ethyl alcohol before use, to dissolve the flakes and make liquid shellac.

Liquid shellac has a limited shelf life (about 1 year), so is sold in dry form for dissolution before use. Liquid shellac sold in hardware stores is often marked with the production (mixing) date, so the consumer can know whether the shellac inside is still good. Some manufacturers (e.g., Zinsser) have ceased labeling shellac with the production date, but the production date may be discernible from the production lot code. Alternatively, old shellac may be tested to see if it is still usable: a few drops on glass should quickly dry to a hard surface. Shellac that remains tacky for a long time is no longer usable. Storage life depends on peak temperature, so refrigeration extends shelf life.

The thickness (concentration) of shellac is measured by the unit "pound cut", referring to the amount (in pounds) of shellac flakes dissolved in a gallon of denatured alcohol. For example: a 1-lb. cut of shellac is the strength obtained by dissolving one pound of shellac flakes in a gallon of alcohol.[8] Most pre-mixed commercial preparations come at a 3-lb. cut. Multiple thin layers of shellac produce a significantly better end result than a few thick layers. Thick layers of shellac do not adhere to the substrate or to each other well, and thus can peel off with relative ease; in addition, thick shellac will obscure fine details in carved designs in wood and other substrates.

Shellac naturally dries to a high-gloss sheen. For applications where a flatter (less shiny) sheen is desired, products containing amorphous silica,[9] such as "Shellac Flat", may be added to the dissolved shellac.

Shellac naturally contains a small amount of wax (3%–5% by volume), which comes from the lac bug. In some preparations, this wax is removed (the resulting product being called "dewaxed shellac"). This is done for applications where the shellac will be coated with something else (such as paint or varnish), so the topcoat will adhere. Waxy (non-dewaxed) shellac appears milky in liquid form, but dries clear.

Colours and availability

Shellac comes in many warm colours, ranging from a very light blonde ("platina") to a very dark brown ("garnet"), with many varieties of brown, yellow, orange and red in between. The colour is influenced by the sap of the tree the lac bug is living on and by the time of harvest. Historically, the most commonly sold shellac is called "orange shellac", and was used extensively as a combination stain and protectant for wood panelling and cabinetry in the 20th century.

Shellac was once very common anywhere paints or varnishes were sold (such as hardware stores). However, cheaper and more abrasion- and chemical-resistant finishes, such as polyurethane, have almost completely replaced it in decorative residential wood finishing such as hardwood floors, wooden wainscoting plank panelling, and kitchen cabinets. These alternative products, however, must be applied over a stain if the user wants the wood to be coloured; clear or blonde shellac may be applied over a stain without affecting the colour of the finished piece, as a protective topcoat. "Wax over shellac" (an application of buffed-on paste wax over several coats of shellac) is often regarded as a beautiful, if fragile, finish for hardwood floors. Luthiers still use shellac to *French polish* fine acoustic stringed instruments, but it has been replaced by synthetic plastic lacquers and varnishes in many workshops, especially high-volume production environments.[10]

Shellac dissolved in alcohol, typically more dilute than French-Polish, is now commonly sold as "sanding sealer" by several companies. It is used to seal wooden surfaces, often as preparation for a final more durable finish; it reduces the amount of final coating required by reducing its absorption into the wood.

Properties

Shellac is a natural bioadhesive polymer and is chemically similar to synthetic polymers, and thus can be considered a natural form of plastic. It can be turned into a moulding compound when mixed with wood flour and moulded under heat and pressure methods, so it can also be classified as thermoplastic.

A decorative medal made in France in the early 20th century moulded from shellac compound, the same used for phonograph records of the period

Shellac scratches more easily than most lacquers and varnishes, and application is more labour-intensive, which is why it has been replaced by plastic in most areas. But damaged shellac can easily be touched up with another coat of shellac (unlike polyurethane) because the new coat merges with and bonds to the existing coat(s). Shellac is much softer than Urushi lacquer, for instance, which is far superior with regard to both chemical and mechanical resistance.

Shellac is soluble in alkaline solutions such as ammonia, sodium borate, sodium carbonate, and sodium hydroxide, and also in various organic solvents. When dissolved in de-natured alcohol or ethanol, shellac yields a coating of good durability and hardness.

Upon mild hydrolysis shellac gives a complex mix of aliphatic and alicyclic hydroxy acids and their polymers that varies in exact composition depending upon the source of the shellac and the season of collection. The major component of the aliphatic component is aleuritic acid, whereas the main alicyclic component is shellolic acid.[11]

Shellac is UV-resistant, and does not darken as it ages (though the wood under it may do so, as in the case of pine).[4]

History

The earliest written evidence of shellac goes back 3,000 years, but shellac is known to have been used earlier.[4] According to the ancient Indian epic poem, the Mahabharata, an entire palace was built out of dried shellac.[4]

Shellac was in rare use as a dyestuff for as long as there was a trade with the East Indies. Merrifield[12] cites 1220 for the introduction of shellac as an artist's pigment in Spain. Lapis lazuli, an ultramarine pigment from Afghanistan, was already being imported long before this.

The use of overall paint or varnish decoration on large pieces of furniture was first popularised in Venice (then later throughout Italy). There are a number of 13th-century references to painted or varnished cassone, often dowry cassone that were made deliberately impressive as part of dynastic marriages. The definition of varnish is not always clear, but it seems to have been a spirit varnish based on gum benjamin or mastic, both traded around the Mediterranean. At some time, shellac began to be used as well. An article from the *Journal of the American Institute of Conservation* describes using infrared spectroscopy to identify shellac coating on a 16th-century cassone.[13] This is also the period in history where "varnisher" was identified as a distinct trade, separate from both carpenter and artist.

Another use for shellac is sealing wax. Woods's *The Nature and Treatment of Wax and Shellac Seals*[14] discusses the various formulations, and the period when shellac started to be added to the previous beeswax recipes.

The "period of widespread introduction" would seem to be around 1550 to 1650, when the substance moved from being a rarity on highly decorated pieces to being described in the standard texts of the day.

Uses

Historical

In the early- and mid-twentieth century, orange shellac was used as a one-product finish (combination stain and varnish-like topcoat) on decorative wood panelling used on walls and ceilings in homes, particularly in the US. In the American South, use of knotty pine plank panelling covered with orange shellac was once as common in new construction as drywall is today. It was also often used on kitchen cabinets and hardwood floors, prior to the advent of polyurethane.

Until the advent of vinyl, most gramophone records were pressed from shellac compounds.[15][16] From 1921 to 1928, 18,000 tons of shellac were used to create 260 million records for Europe.[7] In the 1930s, it was estimated that half of all shellac was used for gramophone records.[17] Use of shellac for records was common until the 1950s and continued into the 1970s in some non-Western countries.

Until recent advances in technology, shellac (French polish) was the only glue used in the making of ballet dancers' pointe shoes, to stiffen the box (toe area) to support the dancer en pointe. Many manufacturers of pointe shoes still use the traditional techniques, and many dancers use shellac to revive a softening pair of shoes.[18]

Shellac was historically used as a protective coating on paintings.

Sheets of Braille were coated with shellac to help protect them from wear due to being read by hand.

Shellac was used from the mid-nineteenth century to produce small moulded goods such as picture frames, boxes, toilet articles, jewelry, inkwells and even dentures. Advances in plastics have rendered shellac obsolete as a moulding compound.

Shellac (both orange and white varieties) was used both in the field and laboratory to glue and stabilise dinosaur bones until about the mid-1960s. While effective at the time, the long-term negative effects of shellac (being organic in nature) on dinosaur bones and other fossils is debated, and shellac is very rarely used by professional conservators and fossil preparators today.

Shellac was used for fixing inductor, motor, generator and transformer windings. It was applied directly to single-layer windings in an alcohol solution. For multi-layer windings, the whole coil was submerged in shellac solution, then drained and placed in a warm place to allow the alcohol to evaporate. The shellac locked the wire turns in place, provided extra insulation, prevented movement and vibration and reduced buzz and hum. In motors and generators it also helps transfer force generated by magnetic attraction and repulsion from the windings to the rotor or armature. In more recent times, shellac has been replaced in these applications by synthetic resins such as polyester resin. Some applications use shellac mixed with other natural or synthetic resins, such as pine resin or phenol-formaldehyde resin, of which Bakelite is the best known, for electrical use. Mixed with other resins, barium sulfate, calcium carbonate, zinc sulfide, aluminium oxide and/or cuprous carbonate (malachite), shellac forms a component of heat-cured capping cement used to fasten the caps or bases to the bulbs of electric lamps.

Current

It is the central element of the traditional "French polish" method of finishing furniture, fine string instruments, and pianos.

Shellac, edible, is used as a glazing agent on pills (see excipient) and sweets, in the form of *pharmaceutical glaze* (or, *confectioner's glaze*). Because of its acidic properties (resisting stomach acids), shellac-coated pills may be used for a timed enteric or colonic release.[19] Shellac is used as a 'wax' coating on citrus fruit to prolong its shelf/storage life. It is also used to replace the natural wax of the apple, which is removed during the cleaning process.[20] When used for this purpose, it has the food additive E number E904.

Shellac coating applied with either a standard or modified Huon-Stuehrer nozzle, can be economically micro-sprayed onto various smooth sweets, such as chocolate coated peanuts. Irregularities on the surface of the product being sprayed typically result in the formation of unsightly aggregates ("lac-aggs") which precludes the use of this technique on foods such as walnuts or raisins (however, chocolate-coated raisins being smooth surfaced, are able to be sprayed successfully using a modified Huon-Stuehrer nozzle).

Shellac is an odour and stain blocker and so is often used as the base of "solves all problems" primers. Although its durability against abrasives and many common solvents is not very good, shellac provides an excellent barrier against water vapour penetration. Shellac-based primers are an effective sealant to control odours associated with fire damage.

Shellac has traditionally been used as a dye for cotton and, especially, silk cloth in Thailand, particularly in the north-eastern region.[21] It yields a range of warm colours from pale yellow through to dark orange-reds and dark ochre.[22] Naturally dyed silk cloth, including that using shellac, is widely available in the rural northeast, especially in Ban Khwao District, Chaiyaphum province. The Thai name for the insect and the substance is "khrang" (Thai: ครั่ง).

Wood finish

Wood finishing is one of the most traditional and still popular uses of Shellac mixed with solvents or alcohol. This dissolved Shellac liquid, applied to a piece of wood, is an evaporative finish: the alcohol of the shellac mixture evaporates leaving behind a protective film.[23]

Shellac as wood finish is natural and non-toxic in its pure form. A finish made of Shellac is UV-resistant. For water-resistance and durability, it does not keep up with synthetic finishing products.[24]

Because it is compatible with most other finishes, shellac is also used as a barrier or primer coat on wood to prevent the bleeding of resin or pigments into the final finish, or to prevent wood stain from blotching.[25]

Other

Shellac is used:

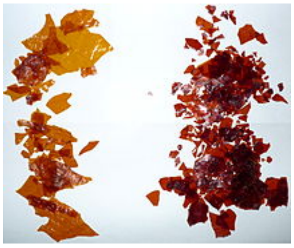
- in the tying of artificial flies for trout and salmon where the shellac was used to seal all trimmed materials at the head of the fly.
- in combination with wax for preserving and imparting a shine to citrus fruits, such as lemons.

- in dental technology, where it is occasionally used in the production of custom impression trays and (partial) denture production.
- as a binder in India ink.
- for cycling as a protective and decorative coating for bicycle handlebar tape,[26] and as a hard-drying adhesive for tubular cycle tyres, particularly for track racing.[27]
- for re-attaching ink sacs when restoring vintage fountain pens, the orange variety preferably.
- for fixing pads to the key-cups of woodwind instruments.
- for Luthier applications, to bind wood fibres down and prevent tear out on the soft spruce soundboards.
- to stiffen and impart water-resistance to felt hats, for wood finishing[28] and as a constituent of *gossamer* (or *goss* for short), a cheesecloth fabric coated in shellac and ammonia solution used in the shell of traditional silk top and riding hats.
- for mounting insects, in the form of a gel adhesive mixture composed of 75% ethyl alcohol.[29]
- as a binder in the fabrication of abrasive wheels,[30] imparting flexibility and smoothness not found in vitrified (ceramic bond) wheels. 'Elastic' bonded wheels typically contain plaster of paris, yielding a stronger bond when mixed with shellac; the mixture of dry plaster powder, abrasive (e.g. corundum/aluminium oxide Al_2O_3), and shellac are heated and the mixture pressed in a mould.
- in fireworks pyrotechnic compositions as a low-temperature fuel, where it allows the creation of pure 'greens' and 'blues'- colours difficult to achieve with other fuel mixes.
- in watchmaking, due to its low melting temperature (about 80-100 °C), shellac is used in most mechanical movements to adjust and adhere pallet stones to the pallet fork and secure the roller jewel to the roller table of the balance wheel. Also for securing small parts to a 'wax chuck' (faceplate) in a watchmakers' lathe.
- in the early twentieth century, it was used to protect some military rifle stocks.[31]
- in Jelly Belly jelly beans, in combination with beeswax to give them their final buff and polish.[32]
- in modern traditional archery, shellac is one of the hot-melt glue/resin products used to attach arrowheads to wooden or bamboo arrow shafts.
- Sanding sealer, is a solution of shellac dissolved in alcohol widely sold to seal sanded surfaces, typically wooden surfaces before a final coat of a more durable finish. Similar to French Polish but more dilute.
- as a topcoat in nail polish (although not all nail polish sold as "shellac" contains shellac, and some nail polish not labelled in this way does)

Gallery

Blonde shellac flakes

Dewaxed Bona (L) and Waxy #1 Orange (R) shellac flakes. The latter—orange shellac—is the traditional shellac used for decades to finish wooden wall paneling, kitchen cabinets and tool handles.



Closeup of Waxy #1 Orange (L) and Dewaxed Bona (R) shellac flakes. The former—orange shellac—is the traditional shellac used for decades to finish wooden wall paneling and kitchen cabinets.

"Quick and dirty" example of a pine board coated with 1-5 coats of Dewaxed Dark shellac (a darker version of traditional orange shellac)

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Horticulture/Biological Pest Control

Biological control of pests and diseases is a method of controlling pests and diseases in agriculture that relies on natural predation rather than introduced chemicals.

Predatory Polistes wasp looking for bollworms or other caterpillars on a cotton plant

Overview

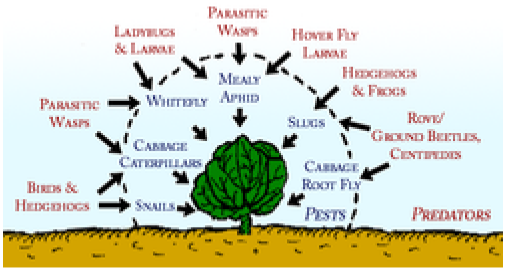

Diagram illustrating the natural enemies of cabbage pests

A key belief of the organic gardener is that biodiversity furthers health. The more variety a landscape has, the more sustainable it is. The organic gardener therefore works to create a system where the insects that are sometimes called pests and the pathogens that cause diseases are not eradicated, but instead are kept at manageable levels by a complex system of checks and balances within a living and vibrant ecosystem. Contrary to more 'conventional' gardening practices which often use chemical methods to kill both useful and harmful garden life forms indiscriminately, this is a holistic approach that seeks to develop an understanding of the webs of interaction between the myriad of organisms that constitute the garden fauna and flora. The organic gardener will often hold the view for example that the eradication of the creatures that are often described as pests is not only not possible, but also undesirable, for without them the beneficial predatory and parasitic insects which depend upon them as food or hosts would not be able to survive.

In a healthy natural woodland where there is little direct human intervention, pest and disease organisms will always be present, but, unless there is a drastic environmental change, will normally kept in a state of equilibrium where they are not able to get out of hand to a level which is detrimental to the overall woodland community. This is the model for which the sensitive organic gardener will strive, but at the same time it is wise to recognise that there will often be some degree of intervention needed to manipulate the natural checks and balances to the gardener's favour, particularly if growing plants for food or ornament which would not normally occur in natural situations. Therefore biological control is about developing a range of techniques that use living organisms to maintain the beneficial equilibria in garden landscapes without causing adverse effects to humans or the wider environment. Of course, introducing exotic insects into any ecosystem entails taking risks of moving further from the intended equilibrium through unexpected interactions.

An important part of the biological gardening approach is to become familiar with the various life forms that inhabit the garden, predators as well as pests, and also their life cycles, patterns of feeding and the habitats that they prefer.

Insects have devised many ways to eat other insects. Predators will directly attack and devour their prey, whilst parasitoids will deposit an egg within another insects body, from which a larva will emerge which will devour the host's innards.

Examples of predators

ladybugs, and in particular their larvae which are active between May and July, are voracious predators of aphids, and will also consume mites, scale insects and small caterpillars. The ladybird is a very familiar beetle with red and black markings, whilst its larvae are initially small and spidery, growing up to 17 mm long. It has a tapering segmented grey/black body with orange/yellow markings nettles in the garden and by leaving hollow stems and some plant debris over-winter so that they can hibernate over winter.


Ladybird larva eating wooly apple aphids

Hoverflies are another very welcome garden predator. Resembling slightly darker bees or wasps, they have characteristic hovering, darting flight patterns. There are over 100 species of hoverfly whose larvae principally feed upon greenfly, one larva devouring up to fifty a day, or 1000 in its lifetime. They also eat fruit tree spider mites and small caterpillars. Adults feed on nectar and pollen, which they require for egg production. Eggs are minute (1 mm), pale yellow white and laid singly near greenfly colonies. Larvae are 8–17 mm long, disguised to resemble bird droppings, they are legless and have no distinct head. Semi-transparent in a range of colours from green, white, brown and black.


Lacewings are available from biocontrol dealers.

Hoverflies can be encouraged by growing attractant flowers such as the poached egg plant *(Limnanthes douglasii)*, marigolds or phacelia throughout the growing season.

Dragonflies are important predators of mosquitoes, both in the water, where the dragonfly nyads eat mosquito larvae, and in the air, where adult dragonflies capture and eat adult mosquitoes. Community-wide mosquito control programs that spray adult mosquitoes also kill dragonflies, thus removing an important biocontrol agent, and can actually increase mosquito populations in the long term.

Other useful garden predators include lacewings, anthrocorid bugs, rove and ground beetles, aphid midge, centipedes, predatory mites, as well as megafauna such as frogs, toads, hedgehogs, slow-worms and birds. Cats and rat terriers kill field mice, rats, June bugs, and birds. Dogs chase away many types of pest animals. Dachshunds are bred specifically to fit inside tunnels underground to kill gophers and rabbits.

Parasitic wasps

A diverse range of wasps lay their eggs on or in the body of an insect host, which is then used as a food for developing wasps. Parasitic wasps take much longer than predators to consume their victims, for if the larvae were to eat too fast they would run out of food before they became adults. Such parasites are very useful in the organic garden, for they are very efficient hunters, always at work searching for pest invaders. As adults they require high energy fuel as they fly from place to place, and feed upon nectar, pollen and sap, therefore planting plenty of flowering plants, particularly buckwheat, umbellifers and composites will encourage their presence.

Three of the most important groups are;

- Ichneumon Flies: (5–10 mm). Prey mainly on caterpillars.
- Braconid Wasps: Tiny wasps (up to 5 mm) attack caterpillars and a wide range of other insects including greenfly. A common parasite of the cabbage white caterpillar- seen as clusters of sulphur yellow cocoons bursting from collapsed caterpillar skin.
- Chalcid Wasps: Among the smallest of insects (<3 mm). Parasitize eggs/larvae of Aphids, Horticulture/Whiteflies, cabbage caterpillars, Scale Insects and strawberry tortrix moth.

Plants to regulate insect pests

Choosing a diverse range of plants for the garden can help to regulate pests in a variety of ways, including;

- Masking the crop plants from pests, depending on the proximity of the companion or intercrop.
- Producing olfactory inhibitors, odors that confuse and deter pests.

Acting as trap plants by providing an alluring food that entices pests away from crops.

- Serving as nursery plants, providing breeding grounds for beneficial insects.
- Providing an alternative habitat, usually in a form of a shelterbelt, hedgerow, or w:beetle bank where beneficial insects can live and reproduce. Nectar-rich plants that bloom for long periods are especially good, as many beneficials are nectivorous during the adult stage, but parasitic or predatory as larvae. A good example of this is the soldier beetle which is frequently found on flowers as an adult, but whose larvae eat aphids, caterpillars, grasshopper eggs, and other beetles.

The following are plants often used in vegetable gardens to deter insects [1]

- **Basil** — Repels flies and mosquitoes.
- **Catnip** — Deters flea beetle.
- **Garlic** — Deters Japanese beetle.
- **Horseradish** — Deters potato bugs.
- **Marigold** — The workhorse of pest deterrents. Discourages Mexian bean beetles, nematodes and others.
- **Mint** — Deters white cabbage moth.
- **Nasturium** — Deters aphids, squash bugs and striped pumpkin beetles.
- **Pot Marigold** — Deters asparagus beetles, tomato worm, and general garden pests.
- **Peppermint** — Repels the white cabbage butterfly.
- **Rosemary** — Deters cabbage moth, bean beetles and carrot fly.
- **Sage** — Deters cabbage moth and carrot fly.
- **Southern Wood** — Deters cabbage moth.
- **Summer Savory** — Deters bean beetles.
- **Tansy** — Deters flying insects, Japanese beetles, striped cucumber beetles, squash bugs and ants.
- **Thyme** — Deters cabbage worm.
- **Wormwood** — Deters animals from garden.

Directly introducing biological controls

Most of the biological controls listed above depend on providing incentives in order to 'naturally' attract beneficial insects to the garden. However there are occasions when biological controls can be directly introduced. Common biocontrol agents include parasitoids, predators, pathogens or weed feeders. This is particularly appropriate in situations such as the greenhouse, a largely artificial environment, and are usually purchased by mail order.

Some biocontrol agents that can be introduced include;

- *Encarsia formosa*. This is a small predatory chaclid wasp which is parasitical on whitefly, a sap-feeding insect which can cause wilting and black sooty moulds. It is most effective when dealing with low level infestations, giving protection over a long period of time. The wasp lays its eggs in young whitefly 'scales', turning them black as the parasite larvae pupates. It should be introduced as soon as possible after the first adult whitefly are seen. Should be used in conjunction with insecticidal soap.
- Red spider mite, another pest found in the greenhouse, can be controlled with the predatory mite *Phytoseilus persimilis*. This is slightly larger than its prey and has an orange body. It develops from egg to adult twice as fast as the red spider mite and once established quickly overcomes infestation.

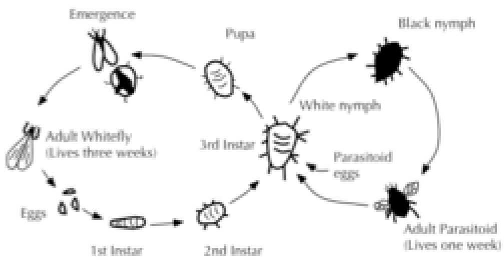

Diagram illustrating the life cycles of Greenhouse whitefly and its parasitoid wasp Encarsia formosa

- A fairly recent development in the control of slugs is the introduction of 'Nemaslug', a microscopic nematode (*Phasmarhabditis hermaphrodita*) which will seek out and Parasitize slugs, reproducing inside them and killing them. The nematode is applied by watering onto moist soil, and gives protection for up to six weeks in optimum conditions, though is mainly effective with small and young slugs under the soil surface.
- A bacterial biological control which can be introduced in order to control butterfly caterpillars is *Bacillus thuringiensis*. This available in sachets of dried spores which are mixed with water and sprayed onto vulnerable plants such as brassicas and fruit trees. The bacterial disease will kill the caterpillars, but leave other insects unharmed. There are strains of *Bt* that are effective against other insect larvae. *Bt israelensis* is effective against mosquito larvae and some midges.
- A biological control being developed for use in the treatment of plant disease is the fungus *Trichoderma viride*. Trichoderma species are free - living fungi that are very common in root ecosystems. This has been used against Dutch Elm disease, and to treat the spread of fungal and bacterial growth on tree wounds. It may also have potential as a means of combating silver leafroo disease.

Economics of biological pest control

Biological control proves to be very successful economically, and even when the method has been less successful, it still produces a benefit-to-cost ratio of 11:1. One study has estimated that a successful biocontrol program returns £32 in benefits for each £1 invested in developing and implementing the program, i.e., a 32:1 benefit-to-cost ratio. The same study had shown that an average chemical pesticide program only returned profits in the ratio of 2.5:1.

See also

- w:Insectary plants

References

1. "Notes on Natural Pest Control for an Organic Garden - DigGood.com". http://www.didgood.com/health/naturalpestcontrol.html.

External links

- Biological Control: A Guide to Natural Enemies in North America (http://www.nysaes.cornell.edu/ent/biocontrol/)
- Beyond Pesticides (http://www.beyondpesticides.org) - Provides information on pesticides and alternatives to their use
- GreenMethods.com (http://www.greenmethods.com) - Extensive biocontrol and IPM information resource

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Biological pest control

Biological control or **biocontrol** is a method of controlling pests such as insects, mites, weeds and plant diseases using other organisms.[1] It relies on predation, parasitism, herbivory, or other natural mechanisms, but typically also involves an active human management role. It can be an important component of integrated pest management (IPM) programs.

Syrphus hoverfly larva (below) feed on aphids (above), making them natural biological control agents.

There are three basic strategies for biological pest control: classical (importation), where a natural enemy of a pest is introduced in the hope of achieving control; inductive (augmentation), in which a large population of natural enemies are administered for quick pest control; and inoculative (conservation), in which measures are taken to maintain natural enemies through regular reestablishment.[2]

Natural enemies of insect pests, also known as biological control agents, include predators, parasitoids, pathogens, and competitors. Biological control agents of plant diseases are most often referred to as antagonists. Biological control agents of weeds include seed predators, herbivores and plant pathogens.

A parasitoid wasp (*Cotesia congregata*) adult with pupal cocoons on its host, a tobacco hornworm (*Manduca sexta*, green background), an example of a hymenopteran biological control agent

Biological control can have side-effects on biodiversity through attacks on non-target species by any of the same mechanisms, especially when a species is introduced without thorough understanding of the possible consequences.

Contents

History

The term "biological control" was first used by Harry Scott Smith at the 1919 meeting of the Pacific Slope Branch of the American Association of Economic Entomologists, in Riverside, California.[3] It was brought into more widespread use by the entomologist Paul H. DeBach (1914–1993) who worked on citrus crop pests throughout his life.[4][5] However, the practice has previously been used for centuries. The first report of the use of an insect species to control an insect pest comes from "Nanfang Caomu Zhuang" (南方草木狀 *Plants of the Southern Regions*) (c. 304 AD), attributed to Western Jin dynasty botanist *Ji Han* (嵇含, 263–307), in which it is mentioned that "*Jiaozhi people sell ants and their nests attached to twigs looking like thin cotton envelopes, the reddish-yellow ant being larger than normal. Without such ants, southern citrus fruits will be severely insect-damaged*".[6] The ants used are known as *huang gan* (*huang* = yellow, *gan* = citrus) ants (*Oecophylla smaragdina*). The practice was later reported by Ling Biao Lu Yi (late Tang Dynasty or Early Five Dynasties), in *Ji Le Pian* by *Zhuang Jisu* (Southern Song Dynasty), in the *Book of Tree Planting* by Yu Zhen Mu (Ming Dynasty), in the book *Guangdong Xing Yu* (17th century), *Lingnan* by Wu Zhen Fang (Qing Dynasty), in *Nanyue Miscellanies* by Li Diao Yuan, and others.[6]

Biological control techniques as we know them today started to emerge in the 1870s. During this decade, in the US, the Missouri State Entomologist C. V. Riley and the Illinois State Entomologist W. LeBaron began within-state redistribution of parasitoids to control crop pests. The first international shipment of an insect as biological control agent was made by Charles V. Riley in 1873, shipping to France the predatory mites *Tyroglyphus phylloxera* to help fight the grapevine phylloxera (*Daktulosphaira vitifoliae*) that was destroying grapevines in France. The United States Department of Agriculture (USDA) initiated research in classical biological control following the establishment of the Division of Entomology in 1881, with C. V. Riley as Chief. The first importation of a parasitoidal wasp into the United States was that of the braconid *Cotesia glomerata* in 1883–1884, imported from Europe to control the invasive cabbage white butterfly, *Pieris rapae*. In 1888–1889 the vedalia beetle, *Rodolia cardinalis*, a lady beetle, was introduced from Australia to California to control the cottony cushion scale, *Icerya purchasi*. This had become a major problem for the newly developed citrus industry in California, but by the end of 1889 the cottony cushion scale population had already declined. This great success led to further introductions of beneficial insects into the US.[7][8]

In 1905 the USDA initiated its first large-scale biological control program, sending entomologists to Europe and Japan to look for natural enemies of the gypsy moth, *Lymantria dispar dispar*, and brown-tail moth, *Euproctis chrysorrhoea*, invasive pests of trees and shrubs. As a result, nine parasitoids (solitary wasps) of gypsy moth, seven of brown-tail moth, and two predators of both moths became established in the US. Although the gypsy moth was not fully controlled by these natural enemies, the frequency, duration, and severity of its outbreaks were reduced and the program was regarded as successful. This program also led to the development of many concepts, principles, and procedures for the implementation of biological control programs.[7][8][9]

Prickly pear cacti were introduced into Queensland, Australia as ornamental plants, starting in 1788. They quickly spread to cover over 25 million hectares of Australia by 1920, increasing by 1 million hectares per year. Digging, burning and crushing all proved ineffective. Two control agents were introduced to help control the spread of the plant, the cactus moth *Cactoblastis cactorum*, and the scale insect *Dactylopius*. Between 1926 and 1931, tens of millions of cactus moth eggs were distributed around Queensland with great success, and by 1932, most areas of prickly pear had been destroyed.[10]

The first reported case of a classical biological control attempt in Canada involves the parasitoidal wasp *Trichogramma minutum*. Individuals were caught in New York State and released in Ontario gardens in 1882 by William Saunders, trained chemist and first Director of the Dominion Experimental Farms, for controlling the invasive currantworm *Nematus ribesii*. Between 1884 and

1908, the first Dominion Entomologist, James Fletcher, continued introductions of other parasitoids and pathogens for the control of pests in Canada.[11]

Cactoblastis cactorum larvae feeding on *Opuntia* prickly pear cacti

Types of biological pest control

There are three basic biological pest control strategies: importation (classical biological control), augmentation and conservation.[12]

Importation

Rodolia cardinalis, the vedalia beetle, was imported from Australia to California in the 19th century, successfully controlling cottony cushion scale.

Importation or classical biological control involves the introduction of a pest's natural enemies to a new locale where they do not occur naturally. Early instances were often unofficial and not based on research, and some introduced species became serious pests themselves.[13]

To be most effective at controlling a pest, a biological control agent requires a colonizing ability which allows it to keep pace with changes to the habitat in space and time. Control is greatest if the agent has temporal persistence, so that it can maintain its population even in the temporary absence of the target species, and if it is an opportunistic forager, enabling it to rapidly exploit a pest population.[14]

Joseph Needham noted a Chinese text dating from 304 AD, *Records of the Plants and Trees of the Southern Regions*, by Hsi Han, which describes mandarin oranges protected by large reddish-yellow citrus ants which attack and kill insect pests of the orange trees. The citrus ant (*Oecophylla smaragdina*)[15] was rediscovered in the 20th century, and since 1958 has been used in China to protect orange groves.[16]

One of the earliest successes in the west was in controlling *Icerya purchasi* (cottony cushion scale) in Australia, using a predatory insect *Rodolia cardinalis* (the vedalia beetle). This success was repeated in California using the beetle and a parasitoidal fly, *Cryptochaetum iceryae*.[17] Other successful cases include the control of *Antonina graminis* in Texas by *Neodusmetia sangwani* in the 1960s.[18]

Damage from *Hypera postica*, the alfalfa weevil, a serious introduced pest of forage, was substantially reduced by the introduction of natural enemies. 20 years after their introduction the population of weevils in the alfalfa area treated for alfalfa weevil in the Northeastern United States remained 75 percent down.[19]

Alligator weed was introduced to the United States from South America. It takes root in shallow water, interfering with navigation, irrigation, and flood control. The alligator weed flea beetle and two other biological controls were released in Florida, greatly reducing the amount of land covered by the plant.[20] Another aquatic weed, the giant salvinia (*Salvinia molesta*) is a serious pest, covering waterways, reducing water flow and harming native species. Control with the salvinia weevil (*Cyrtobagous salviniae*) and the salvinia stem-borer moth (*Samea multiplicalis)* is effective in warm climates,[21][22] and in Zimbabwe, a 99% control of the weed was obtained over a two-year period.[23]

Small commercially reared parasitoidal wasps,[12] *Trichogramma ostriniae*, provide limited and erratic control of the European corn borer (*Ostrinia nubilalis*), a serious pest. Careful formulations of the bacterium *Bacillus thuringiensis* are more effective.[24]

The population of *Levuana iridescens*, the Levuana moth, a serious coconut pest in Fiji, was brought under control by a classical biological control program in the 1920s.[25]

The invasive species *Alternanthera philoxeroides* (alligator weed) was controlled in Florida (U.S.) by introducing alligator weed flea beetle.

Augmentation

Augmentation involves the supplemental release of natural enemies that occur in a particular area, boosting the naturally occurring populations there. In inoculative release, small numbers of the control agents are released at intervals to allow them to reproduce, in the hope of setting up longer-term control, and thus keeping the pest down to a low level, constituting prevention rather than cure. In inundative release, in contrast, large numbers are released in the hope of rapidly reducing a damaging pest population, correcting a problem that has already arisen. Augmentation can be effective, but is not guaranteed to work, and depends on the precise details of the interactions between each pest and control agent.[26]

Hippodamia convergens, the convergent lady beetle, is commonly sold for biological control of aphids.

An example of inoculative release occurs in the horticultural production of several crops in greenhouses. Periodic releases of the parasitoidal wasp, *Encarsia formosa*, are used to control greenhouse whitefly,[27] while the predatory mite *Phytoseiulus persimilis* is used for control of the two-spotted spider mite.[28]

The egg parasite *Trichogramma* is frequently released inundatively to control harmful moths. Similarly, *Bacillus thuringiensis* and other microbial insecticides are used in large enough quantities for a rapid effect.[26] Recommended release rates for *Trichogramma* in vegetable or field crops range from 5,000 to 200,000 per acre (1 to 50 per square metre) per week according to the level of pest infestation.[29] Similarly, nematodes that kill insects (that are entomopathogenic) are released at rates of millions and even billions per acre for control of certain soil-dwelling insect pests.[30]

Conservation

The conservation of existing natural enemies in an environment is the third method of biological pest control.[31] Natural enemies are already adapted to the habitat and to the target pest, and their conservation can be simple and cost-effective, as when nectar-producing crop plants are grown in the borders of rice fields. These provide nectar to support parasitoids and predators of planthopper pests and have been demonstrated to be so effective (reducing pest densities by 10- or even 100-fold) that farmers sprayed 70% less insecticides and enjoyed yields boosted by 5%.[32] Predators of aphids were similarly found to be present in tussock grasses by field boundary hedges in England, but they spread too slowly to reach the centres of fields. Control was improved by planting a metre-wide strip of tussock grasses in field centres, enabling aphid predators to overwinter there.[31]

Cropping systems can be modified to favor natural enemies, a practice sometimes referred to as habitat manipulation. Providing a suitable habitat, such as a shelterbelt, hedgerow, or beetle bank where beneficial insects such as parasitoidal wasps can live and reproduce, can help ensure the survival of populations of natural enemies. Things as simple as leaving a layer of fallen leaves or mulch in place provides a suitable food source for worms and provides a shelter for insects, in turn being a food source for such beneficial mammals as hedgehogs and shrews. Compost piles and stacks of wood can provide shelter for invertebrates and small mammals. Long grass and ponds support amphibians. Not removing dead annuals and non-hardy plants in the autumn allows insects to make use of their hollow stems during winter.[33] In California, prune trees are sometimes planted in grape vineyards to provide an improved overwintering habitat or refuge for a key grape pest parasitoid.[34] The providing of artificial shelters in the form of wooden caskets, boxes or flowerpots is also sometimes undertaken, particularly in gardens, to make a cropped area more attractive to natural enemies. For example, earwigs are natural predators which can be encouraged in gardens by hanging upside-down flowerpots filled with straw or wood wool. Green lacewings can be encouraged by using plastic bottles with an open bottom and a roll of cardboard inside. Birdhouses enable insectivorous birds to nest; the most useful birds can be attracted by choosing an opening just large enough for the desired species.[33]


An inverted flowerpot filled with straw to attract earwigs

In cotton production, the replacement of broad-spectrum insecticides with selective control measures such as Bt cotton can create a more favorable environment for natural enemies of cotton pests due to reduced insecticide exposure risk. Such predators or parasitoids can control pests not affected by the Bt protein. Reduced prey quality and abundance associated increased control from Bt cotton can also indirectly decrease natural enemy populations in some cases, but the percentage of pests eaten or parasitized in Bt and non-Bt cotton are often similar.[35]

Biological control agents

Predators


Predatory lacewings are available from biocontrol dealers.

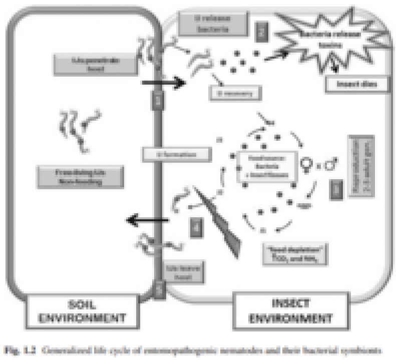
Predators are mainly free-living species that directly consume a large number of prey during their whole lifetime. Given that many major crop pests are insects, many of the predators used in biological control are insectivorous species. Lady beetles, and in particular their larvae which are active between May and July in the northern hemisphere, are voracious predators of aphids, and also consume mites, scale insects and small caterpillars. The spotted lady beetle (*Coleomegilla maculata*) is also able to feed on the eggs and larvae of the Colorado potato beetle (*Leptinotarsa decemlineata*).[36]

The larvae of many hoverfly species principally feed upon aphids, one larva devouring up to 400 in its lifetime. Their effectiveness in commercial crops has not been studied.[37]


Predatory *Polistes* wasp searching for bollworms or other caterpillars on a cotton plant

Several species of entomopathogenic nematode are important predators of insect and other invertebrate pests.[38][39] Entomopathogenic nematodes form a stress–resistant stage known as the infective juvenile. These spread in the soil and infect suitable insect hosts. Upon entering the insect they move to the hemolymph where they recover from their stagnated state of development and release their bacterial symbionts. The bacterial symbionts reproduce and release toxins, which then kill the host insect.[39][40] *Phasmarhabditis hermaphrodita* is a microscopic nematode that kills slugs. Its complex life cycle includes a free-living, infective stage in the soil where it becomes associated with a pathogenic bacteria such as *Moraxella osloensis*. The nematode enters the slug through the posterior mantle region, thereafter feeding and reproducing inside, but it is the bacteria that kill the slug. The nematode is available commercially in Europe and is applied by watering onto moist soil.[41] Entomopathogenic nematodes have a limited shelf life because of their limited resistance to high temperature and dry conditions.[40] The type of soil they are applied to may also limit their effectiveness.[39]

Species used to control spider mites include the predatory mites *Phytoseiulus persimilis*,[42] *Neoseilus californicus*,[43] and *Amblyseius cucumeris*, the predatory midge *Feltiella acarisuga*,[43] and a ladybird *Stethorus punctillum*.[43] The bug *Orius insidiosus* has been successfully used against the two-spotted spider mite and the western flower thrips (*Frankliniella occidentalis*).[44]



Generalized life cycle of entomopathogenic nematodes and their bacterial symbionts.

Predators including *Cactoblastis cactorum* (mentioned above) can also be used to destroy invasive plant species. As another example, the poison hemlock moth (*Agonopterix alstroemeriana)* can be used to control poison hemlock (*Conium maculatum*). During its larval stage, the moth strictly consumes its host plant, poison hemlock, and can exist at hundreds of larvae per individual host plant, destroying large swathes of the hemlock.[45]

For rodent pests, cats are effective biological control when used in conjunction with reduction of "harborage"/hiding locations.[47][48][49] While cats are effective at preventing rodent "population explosions", they are not effective for eliminating pre-existing severe infestations.[49] Barn owls are also sometimes used as biological rodent control.[50] Although there are no quantitative studies of the effectiveness of barn owls for this purpose,[51] they are known rodent predators that can be used in addition to or instead of cats;[52][53] they can be encouraged into an area with nest boxes.[54][55]

The parasitoid wasp *Aleiodes indiscretus* parasitizing a gypsy moth caterpillar, a serious pest of forestry[46]

Parasitoids

Parasitoids lay their eggs on or in the body of an insect host, which is then used as a food for developing larvae. The host is ultimately killed. Most insect parasitoids are wasps or flies, and many have a very narrow host range. The most important groups are the ichneumonid wasps, which mainly use caterpillars as hosts; braconid wasps, which attack caterpillars and a wide range of other insects including aphids; chalcid wasps, which parasitize eggs and larvae of many insect species; and tachinid flies, which parasitize a wide range of insects including caterpillars, beetle adults and larvae, and true bugs.[56] Parasitoids are most effective at reducing pest populations when their host organisms have limited refuges to hide from them.[57]

Parasitoids are among the most widely used biological control agents. Commercially, there are two types of rearing systems: short-term daily output with high production of parasitoids per day, and long-term, low daily output systems.[58] In most instances, production will need to be matched with the appropriate release dates when susceptible host species at a suitable phase of development will be available.[59] Larger production facilities produce on a yearlong basis, whereas some facilities produce only seasonally. Rearing facilities are usually a significant distance from where the agents are to be used in the field, and transporting the parasitoids from the point of production to the point of use can pose problems.[60] Shipping conditions can be too hot, and even vibrations from planes or trucks can adversely affect parasitoids.[58]

Encarsia formosa is a small predatory chalcid wasp which is a parasitoid of whitefly, a sap-feeding insect which can cause wilting and black sooty moulds in glasshouse vegetable and ornamental crops. It is most effective when dealing with low level infestations, giving protection over a long period of time. The wasp lays its eggs in young whitefly 'scales', turning them black as the parasite larvae pupate.[27] *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae) has been introduced to control the glassy-winged sharpshooter *Homalodisca vitripennis* (Hemiptera: Cicadellidae) in French Polynesia and has successfully controlled ~95% of the pest density.[61]

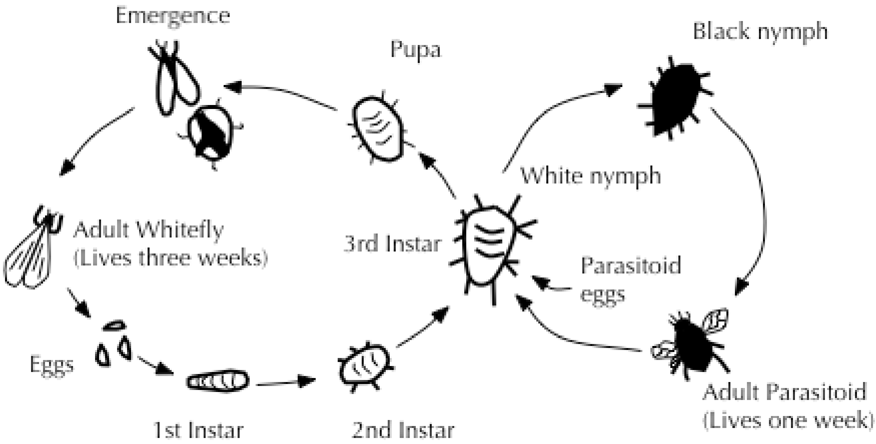
Encarsia formosa, widely used in greenhouse horticulture, was one of the first biological control agents developed.

The eastern spruce budworm is an example of a destructive insect in fir and spruce forests. Birds are a natural form of biological control, but the *Trichogramma minutum*, a species of parasitic wasp, has been investigated as an alternative to more controversial chemical controls.[62]

There are a number of recent studies pursuing sustainable methods for controlling urban cockroaches using parasitic wasps.[63][64] Since most cockroaches remain in the sewer system and sheltered areas which are inaccessible to insecticides, employing active-hunter wasps is a strategy to try and reduce their populations.

Pathogens

Pathogenic micro-organisms include bacteria, fungi, and viruses. They kill or debilitate their host and are relatively host-specific. Various microbial insect diseases occur naturally, but may also be used as biological pesticides.[65] When naturally occurring, these outbreaks are density-dependent in that they generally only occur as insect populations become denser.[66]



Life cycles of greenhouse whitefly and its parasitoid wasp *Encarsia formosa*

Bacteria

Bacteria used for biological control infect insects via their digestive tracts, so they offer only limited options for controlling insects with sucking mouth parts such as aphids and scale insects.[67] *Bacillus thuringiensis*, a soil-dwelling bacterium, is the most widely applied species of bacteria used for biological control, with at least four sub-species used against Lepidopteran (moth, butterfly), Coleopteran (beetle) and Dipteran (true fly) insect pests. The bacterium is available to organic farmers in sachets of dried spores which are mixed with water and sprayed onto vulnerable plants such as brassicas and fruit trees.[68][69] Genes from *B. thuringiensis* have also been incorporated into transgenic crops, making the plants express some of the bacterium's toxins, which are proteins. These confer resistance to insect pests and thus reduce the necessity for pesticide use.[70] If pests develop resistance to the toxins in these crops, *B. thuringiensis* will become useless in organic farming also.[71][69] The bacterium *Paenibacillus popilliae* which causes milky spore disease has been found useful in the control of Japanese beetle, killing the larvae. It is very specific to its host species and is harmless to vertebrates and other invertebrates.[72]

Fungi

Entomopathogenic fungi, which cause disease in insects, include at least 14 species that attack aphids.[73] *Beauveria bassiana* is mass-produced and used to manage a wide variety of insect pests including whiteflies, thrips, aphids and weevils.[74] *Lecanicillium* spp. are deployed against white flies, thrips and aphids. *Metarhizium* spp. are used against pests including beetles, locusts and other grasshoppers, Hemiptera, and spider mites. *Paecilomyces fumosoroseus* is effective against white flies, thrips and aphids; *Purpureocillium lilacinus* is used against root-knot nematodes, and 89 *Trichoderma* species against certain plant pathogens. *Trichoderma viride* has been used against Dutch elm disease, and has shown some effect in suppressing silver leaf, a disease of stone fruits caused by the pathogenic fungus *Chondrostereum purpureum*.[75]

Green peach aphid, a pest in its own right and a vector of plant viruses, killed by the fungus *Pandora neoaphidis* (Zygomycota: Entomophthorales) Scale bar = 0.3 mm.

The fungi *Cordyceps* and *Metacordyceps* are deployed against a wide spectrum of arthropods.[76] *Entomophaga* is effective against pests such as the green peach aphid.[77]

Several members of Chytridiomycota and Blastocladiomycota have been explored as agents of biological control.[78][79] From Chytridiomycota, *Synchytrium solstitiale* is being considered as a control agent of the yellow star thistle (*Centaurea solstitialis*) in the United States.[80]

Viruses

Baculoviruses are specific to individual insect host species and have been shown to be useful in biological pest control. For example, the Lymantria dispar multicapsid nuclear polyhedrosis virus has been used to spray large areas of forest in North America where larvae of the gypsy moth are causing serious defoliation. The moth larvae are killed by the virus they have eaten and die, the disintegrating cadavers leaving virus particles on the foliage to infect other larvae.[81]

A mammalian virus, the rabbit haemorrhagic disease virus was introduced to Australia to attempt to control the European rabbit populations there.[82] It escaped from quarantine and spread across the country, killing large numbers of rabbits. Very young animals survived, passing immunity to their offspring in due course and eventually producing a virus-resistant population.[83] Introduction into New Zealand in the 1990s was similarly successful at first, but a decade later, immunity had developed and populations had returned to pre-RHD levels.[84]

Oomycota

Lagenidium giganteum is a water-borne mold that parasitizes the larval stage of mosquitoes. When applied to water, the motile spores avoid unsuitable host species and search out suitable mosquito larval hosts. This mold has the advantages of a dormant phase, resistant to desiccation, with slow-release characteristics over several years. Unfortunately, it is susceptible to many chemicals used in mosquito abatement programmes.[85]

Competitors

The legume vine *Mucuna pruriens* is used in the countries of Benin and Vietnam as a biological control for problematic *Imperata cylindrica* grass: the vine is extremely vigorous and suppresses neighbouring plants by out-competing them for space and light. *Mucuna pruriens* is said not to be invasive outside its cultivated area.[86] *Desmodium uncinatum* can be used in push-pull farming to stop the parasitic plant, witchweed (*Striga*).[87]

The Australian bush fly, *Musca vetustissima*, is a major nuisance pest in Australia, but native decomposers found in Australia are not adapted to feeding on cow dung, which is where bush flies breed. Therefore, the Australian Dung Beetle Project (1965–1985), led by George Bornemissza of the Commonwealth Scientific and Industrial Research Organisation, released forty-nine species of dung beetle, to reduce the amount of dung and therefore also the potential breeding sites of the fly.[88]

Combined use of parasitoids and pathogens

In cases of massive and severe infection of invasive pests, techniques of pest control are often used in combination. An example is the emerald ash borer, *Agrilus planipennis*, an invasive beetle from China, which has destroyed tens of millions of ash trees in its introduced range in North America. As part of the campaign against it, from 2003 American scientists and the Chinese Academy of Forestry searched for its natural enemies in the wild, leading to the discovery of several parasitoid wasps, namely *Tetrastichus planipennisi*, a gregarious larval endoparasitoid, *Oobius agrili*, a solitary, parthenogenic egg parasitoid, and *Spathius agrili*, a gregarious larval ectoparasitoid. These have been introduced and released into the United States of America as a possible biological control of the emerald ash borer. Initial results for *Tetrastichus planipennisi* have shown promise, and it is now being released along with *Beauveria bassiana*, a fungal pathogen with known insecticidal properties.[89][90][91]

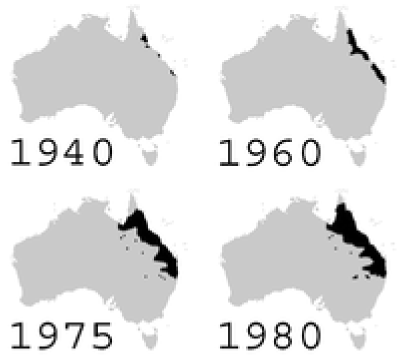
Difficulties

Many of the most important pests are exotic, invasive species that severely impact agriculture, horticulture, forestry and urban environments. They tend to arrive without their co-evolved parasites, pathogens and predators, and by escaping from these, populations may soar. Importing the natural enemies of these pests may seem a logical move but this may have unintended consequences; regulations may be ineffective and there may be unanticipated effects on biodiversity, and the adoption of the techniques may prove challenging because of a lack of knowledge among farmers and growers.[92]

Side effects

Biological control can affect biodiversity[14] through predation, parasitism, pathogenicity, competition, or other attacks on non-target species.[93] An introduced control does not always target only the intended pest species; it can also target native species.[94] In Hawaii during the 1940s parasitic wasps were introduced to control a lepidopteran pest and the wasps are still found there today. This may have a negative impact on the native ecosystem; however, host range and impacts need to be studied before declaring their impact on the environment.[95]

Vertebrate animals tend to be generalist feeders, and seldom make good biological control agents; many of the classic cases of "biocontrol gone awry" involve vertebrates. For example, the cane toad (*Rhinella marina*) was intentionally introduced to Australia to control the greyback cane beetle (*Dermolepida albohirtum*),[96] and other pests of sugar cane. 102 toads were obtained from Hawaii and bred in captivity to increase their numbers until they were released into the sugar cane fields of the tropic north in 1935. It was later discovered that the toads could not jump very high and so were unable to eat the cane beetles which stayed on the upper stalks of the cane plants. However, the toad thrived by feeding on other insects and soon spread very rapidly; it took over native amphibian habitat and brought foreign disease to native toads and frogs, dramatically reducing their populations. Also, when it is threatened or handled, the cane toad releases poison from parotoid glands on its shoulders; native Australian species such as goannas, tiger snakes, dingos and northern quolls that attempted to eat the toad were harmed or killed. However, there has been some recent evidence that native predators are adapting, both physiologically and through changing their behaviour, so in the long run, their populations may recover.[97]



Cane toad (introduced into Australia 1935) spread from 1940 to 1980: it was ineffective as a control agent. Its distribution has continued to widen since 1980.

Rhinocyllus conicus, a seed-feeding weevil, was introduced to North America to control exotic musk thistle (*Carduus nutans*) and Canadian thistle (*Cirsium arvense*). However, the weevil also attacks native thistles, harming such species as the endemic Platte thistle (*Cirsium neomexicanum*) by selecting larger plants (which reduced the gene pool), reducing seed production and ultimately threatening the species' survival.[98] Similarly, the weevil *Larinus planus* was also used to try to control the Canadian thistle, but it damaged other thistles as well.[99][100] This included one species classified as threatened.[101]

The small Asian mongoose (*Herpestus javanicus*) was introduced to Hawaii in order to control the rat population. However, the mongoose was diurnal, and the rats emerged at night; the mongoose therefore preyed on the endemic birds of Hawaii, especially their eggs, more often than it ate the rats, and now both rats and mongooses threaten the birds. This introduction was undertaken without understanding the consequences of such an action. No regulations existed at the time, and more careful evaluation should prevent such releases now.[102]

The sturdy and prolific eastern mosquitofish (*Gambusia holbrooki*) is a native of the southeastern United States and was introduced around the world in the 1930s and '40s to feed on mosquito larvae and thus combat malaria. However, it has thrived at the expense of local species, causing a decline of endemic fish and frogs through competition for food resources, as well as through eating their eggs and larvae.[103] In Australia, control of the mosquitofish is the subject of discussion; in 1989 researchers A. H. Arthington and L. L. Lloyd stated that "biological population control is well beyond present capabilities".[104]

Grower education

A potential obstacle to the adoption of biological pest control measures is that growers may prefer to stay with the familiar use of pesticides. However, pesticides have undesired effects, including the development of resistance among pests, and the destruction of natural enemies; these may in turn enable outbreaks of pests of other species than the ones originally targeted, and on crops at a distance from those treated with pesticides.[105] One method of increasing grower adoption of biocontrol methods involves letting them learn by doing, for example showing them simple field experiments, enabling them to observe the live predation of pests, or demonstrations of parasitised pests. In the Philippines, early season sprays against leaf folder caterpillars were common practice, but growers were asked to follow a 'rule of thumb' of not spraying against leaf folders for the first 30 days after transplanting; participation in this resulted in a reduction of insecticide use by 1/3 and a change in grower perception of insecticide use.[106]

See also

- Beneficial insects
- Biological control of gorse in New Zealand
- Biological pesticide
- Chitosan
- Companion planting
- Insectary plants
- International Organization for Biological Control
- Inundative application
- Japanese beetle
- Mating disruption
- Nematophagous fungus
- Organic gardening
- Organic farming
- Pest control
- Permaculture zone 5
- Sterile insect technique
- Sustainable farming
- Sustainable gardening
- Zero Budget Farming

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Ecosystem services

Ecosystem services are the many and varied benefits that humans freely gain from the natural environment and from properly-functioning ecosystems. Such ecosystems include, for example, agroecosystems, forest ecosystems, grassland ecosystems and aquatic ecosystems. These ecosystems functioning properly provides such things like agricultural produce, timber, and aquatic organisms such as fishes and crabs. Collectively, these benefits are becoming known as 'ecosystem services', and are often integral to the provisioning of clean drinking water, the decomposition of wastes, and the natural pollination of crops and other plants.

Honey bee on Avocado crop. Pollination is just one type of ecosystem service.

While scientists and environmentalists have discussed ecosystem services implicitly for decades, the Millennium Ecosystem Assessment (MA) in the early 2000s popularized this concept.[1] There, ecosystem services are grouped into four broad categories: *provisioning*, such as the production of food and water; *regulating*, such as the control of climate and disease; *supporting*, such as nutrient cycles and oxygen production; and *cultural*, such as spiritual and recreational benefits. To help inform decision-makers, many ecosystem services are being assigned economic values.

Upland bog in Wales, forming the official source of the River Severn. Healthy bogs sequester carbon, hold back water thereby reducing flood risk, and supply cleaned water better than degraded habitats do.

Social forestry in Andhra Pradesh, India, providing fuel, soil protection, shade and even well-being to travellers.

Contents

History

While the notion of human dependence on Earth's ecosystems reaches to the start of *Homo sapiens*' existence, the term 'natural capital' was first coined by E.F. Schumacher in 1973 in his book *Small is Beautiful* [2]. Recognition of how ecosystems could provide complex services to humankind date back to at least Plato (c. 400 BC) who understood that deforestation could lead to soil erosion and the drying of springs.[3] Modern ideas of ecosystem services probably began when Marsh challenged in 1864 the idea that Earth's natural resources are unbounded by pointing out changes in soil fertility in the Mediterranean.[4] It was not until the late 1940s that three key authors—Henry Fairfield Osborn, Jr,[5] William Vogt,[6] and Aldo Leopold [7]—promoted recognition of human dependence on the environment.

In 1956, Paul Sears drew attention to the critical role of the ecosystem in processing wastes and recycling nutrients.[8] In 1970, Paul Ehrlich and Rosa Weigert called attention to "ecological systems" in their environmental science textbook[9] and "the most subtle and dangerous threat to man's existence... the potential destruction, by man's own activities, of those ecological systems upon which the very existence of the human species depends".

The term "**environmental services**" was introduced in a 1970 report of the *Study of Critical Environmental Problems*,[10] which listed services including insect pollination, fisheries, climate regulation and flood control. In following years, variations of the term were used, but eventually 'ecosystem services' became the standard in scientific literature.[11]

The ecosystem services concept has continued to expand and includes socio-economic and conservation objectives, which are discussed below. A history of the concepts and terminology of ecosystem services as of 1997, can be found in Daily's book "Nature's Services: Societal Dependence on Natural Ecosystems".[3]

While Gretchen Daily's original definition distinguished between ecosystem goods and ecosystem services, Robert Costanza and colleagues' later work and that of the Millennium Ecosystem Assessment lumped all of these together as ecosystem services.[12][13]

Definition

Per the 2006 Millennium Ecosystem Assessment (MA), ecosystem services are "the benefits people obtain from ecosystems". The MA also delineated the four categories of ecosystem services—supporting, provisioning, regulating and cultural—discussed below.

By 2010, there had evolved various working definitions and descriptions of ecosystem services in the literature.[14] To prevent double counting in ecosystem services audits, for instance, The Economics of Ecosystems and Biodiversity (TEEB) replaced "Supporting Services" in the MA with "Habitat Services" and "ecosystem functions", defined as "a subset of the interactions between ecosystem structure and processes that underpin the capacity of an ecosystem to provide goods and services".[15]

Categorization

The Millennium Ecosystem Assessment (MA) report 2005 defines *Ecosystem services* as benefits people obtain from ecosystems and distinguishes four categories of ecosystem services, where the so-called supporting services are regarded as the basis for the services of the other three categories.[1]

Detritivores like this dung beetle help to turn animal wastes into organic material that can be reused by primary producers.

Supporting services

These include services such as nutrient cycling, primary production, soil formation, habitat provision and pollination.[16] These services make it possible for the ecosystems to continue providing services such as food supply, flood regulation, and water purification. Slade et al [17] outline the situation where a greater number of species would maximise more ecosystem services

Provisioning services

- food (including seafood and game), crops, wild foods, and spices
- raw materials (including lumber, skins, fuel wood, organic matter, fodder, and fertilizer)
- genetic resources (including crop improvement genes, and health care)
- water purity
- biogenic minerals
- medicinal resources (including pharmaceuticals, chemical models, and test and assay organisms)
- energy (hydropower, biomass fuels)
- ornamental resources (including fashion, handicraft, jewelry, pets, worship, decoration and souvenirs like furs, feathers, ivory, orchids, butterflies, aquarium fish, shells, etc.)

Regulating services

- Carbon sequestration and climate regulation
- Predation regulates prey populations
- Waste decomposition and detoxification
- Purification of water and air
- pest and disease control

Cultural services

- cultural (including use of nature as motif in books, film, painting, folklore, national symbols, architect, advertising, etc.)
- spiritual and historical (including use of nature for religious or heritage value or natural)
- recreational experiences (including ecotourism, outdoor sports, and recreation)

- science and education (including use of natural systems for school excursions, and scientific discovery)
- Therapeutic (including Ecotherapy, social forestry and animal assisted therapy)

There is discussion as to how the concept of **cultural ecosystem services** can be operationalized. A good review of approaches in landscape aesthetics, cultural heritage, outdoor recreation, and spiritual significance to define and assess cultural values of our environment so that they fit into the ecosystem services approach is given by Daniel et al.[18] who vote for models that explicitly link ecological structures and functions with cultural values and benefits. There also is a fundamental *critique* of the concept of cultural ecosystem services that builds on three arguments:[19]

1. Pivotal cultural values attaching to the natural/cultivated environment rely on an area's unique character that cannot be addressed by methods that use universal scientific parameters to determine ecological structures and functions.
2. If a natural/cultivated environment has symbolic meanings and cultural values the object of these values are not ecosystems but shaped phenomena like mountains, lakes, forests, and, mainly, symbolic landscapes.[20]
3. Those cultural values do result not from properties produced by ecosystems but are the product of a specific way of seeing within the given cultural framework of symbolic experience.[21]

Common International Classification of Ecosystem Services (CICES)

The **Common International Classification of Ecosystem Services (CICES)** is a classification scheme developed to accounting systems (like National counts etc.), in order to avoid double-counting of Suporting Services with others Provisioning and Regulating Services.

https://cices.eu/

Examples

The following examples illustrate the relationships between humans and natural ecosystems through the services derived from them:

- In New York City, where the quality of drinking water had fallen below standards required by the U.S. Environmental Protection Agency (EPA), authorities opted to restore the polluted Catskill Watershed that had previously provided the city with the ecosystem service of water purification. Once the input of sewage and pesticides to the watershed area was reduced, natural abiotic processes such as soil absorption and filtration of chemicals, together with biotic recycling via root systems and soil microorganisms, water quality improved to levels that met government standards. The cost of this investment in natural capital was estimated between $1–1.5 billion, which contrasted dramatically with the estimated $6–8 billion cost of constructing a water filtration plant plus the $300 million annual running costs.[22]
- Pollination of crops by bees is required for 15–30% of U.S. food production; most large-scale farmers import non-native honey bees to provide this service. One study [23] reports that in California's agricultural region, it was found that wild bees alone could provide partial or complete pollination services or enhance the services provided by honey bees through behavioral interactions. However, intensified agricultural practices can quickly erode pollination services through the loss of species. The remaining species are unable to compensate this. The results of this study also indicate that the proportion of chaparral and oak-woodland habitat available for wild bees within 1–2 km of a farm can stabilize and enhance the provision of pollination services. The presence of such ecosystem elements functions almost like an insurance policy for farmers.
- In watersheds of the Yangtze River (China), spatial models for water flow through different forest habitats were created to determine potential contributions for hydroelectric power in the region. By quantifying the relative value of ecological parameters (vegetation-soil-slope complexes), researchers were able to estimate the annual economic benefit of maintaining forests in the watershed for power services to be 2.2 times that if it were harvested once for timber.[24]
- In the 1980s, mineral water company Vittel (now a brand of Nestlé Waters) faced a critical problem. Nitrates and pesticides were entering the company's springs in northeastern France. Local farmers had intensified agricultural practices and cleared native vegetation that previously had filtered water before it seeped into the aquifer used by Vittel. This contamination threatened the company's right to use the "natural mineral water" label under French law.[25] In response to this business risk, Vittel developed an incentive package for farmers to improve their agricultural practices and consequently reduce water pollution that had affected Vittel's product. For example, Vittel provided subsidies and free technical assistance to farmers in exchange for farmers' agreement to enhance

pasture management, reforest catchments, and reduce the use of agrochemicals. This is an example of a payment for ecosystem services program.[26]

- It was counted that to plant 15 000 ha new woodland in the UK, if we consider only the value of timber, it would cost £79 000 000 which is more than the benefit of £65 000 000. If, however, we include all other benefits the trees in lowland could provide (like soil stabilization, wind deflection, recreation, food production, air purification, carbon storage, wildlife habitat, fuel production, cooling, flood prevention), the costs will increase due to displacing the profitable farmland (would be around £231 000 000) but will be overweight by benefits of £546 000 000.[27]
- In Europe, various projects are implemented in order to define the values of concrete ecosystems and to implement this concept into decision making process. For example, "LIFE Viva grass" project aims to do this with grasslands in Baltics.[28]

Ecology

Understanding of ecosystem services requires a strong foundation in ecology, which describes the underlying principles and interactions of organisms and the environment. Since the scales at which these entities interact can vary from microbes to landscapes, milliseconds to millions of years, one of the greatest remaining challenges is the descriptive characterization of energy and material flow between them. For example, the area of a forest floor, the detritus upon it, the microorganisms in the soil and characteristics of the soil itself will all contribute to the abilities of that forest for providing ecosystem services like carbon sequestration, water purification, and erosion prevention to other areas within the watershed. Note that it is often possible for multiple services to be bundled together and when benefits of targeted objectives are secured, there may also be ancillary benefits—the same forest may provide habitat for other organisms as well as human recreation, which are also ecosystem services.

The complexity of Earth's ecosystems poses a challenge for scientists as they try to understand how relationships are interwoven among organisms, processes and their surroundings. As it relates to human ecology, a suggested research agenda [23] for the study of ecosystem services includes the following steps:

1. identification of *ecosystem service providers* (*ESP*s)—species or populations that provide specific ecosystem services—and characterization of their functional roles and relationships;
2. determination of community structure aspects that influence how ESPs function in their natural landscape, such as compensatory responses that stabilize function and non-random extinction sequences which can erode it;
3. assessment of key environmental (abiotic) factors influencing the provision of services;
4. measurement of the spatial and temporal scales ESPs and their services operate on.

Recently, a technique has been developed to improve and standardize the evaluation of ESP functionality by quantifying the relative importance of different species in terms of their efficiency and abundance.[29] Such parameters provide indications of how species respond to changes in the environment (i.e. predators, resource availability, climate) and are useful for identifying species that are disproportionately important at providing ecosystem services. However, a critical drawback is that the technique does not account for the effects of interactions, which are often both complex and fundamental in maintaining an ecosystem and can involve species that are not readily detected as a priority. Even so, estimating the functional structure of an ecosystem and combining it with information about individual species traits can help us understand the resilience of an ecosystem amidst environmental change.

Many ecologists also believe that the provision of ecosystem services can be stabilized with biodiversity. Increasing biodiversity also benefits the variety of ecosystem services available to society. Understanding the relationship between biodiversity and an ecosystem's stability is essential to the management of natural resources and their services.

Redundancy hypothesis

The concept of ecological redundancy is sometimes referred to as *functional compensation* and assumes that more than one species performs a given role within an ecosystem.[30] More specifically, it is characterized by a particular species increasing its efficiency at providing a service when conditions are stressed in order to maintain aggregate stability in the ecosystem.[31]

However, such increased dependence on a compensating species places additional stress on the ecosystem and often enhances its susceptibility to subsequent disturbance. The redundancy hypothesis can be summarized as "species redundancy enhances ecosystem resilience".[32]

Another idea uses the analogy of rivets in an airplane wing to compare the exponential effect the loss of each species will have on the function of an ecosystem; this is sometimes referred to as *rivet popping*.[33] If only one species disappears, the loss of the ecosystem's efficiency as a whole is relatively small; however, if several species are lost, the system essentially collapses—similar to an airplane that lost too many rivets. The hypothesis assumes that species are relatively specialized in their roles and that their ability to compensate for one another is less than in the redundancy hypothesis. As a result, the loss of any species is critical to the performance of the ecosystem. The key difference is the rate at which the loss of species affects total ecosystem functioning.

Portfolio effect

A third explanation, known as the *portfolio effect*, compares biodiversity to stock holdings, where diversification minimizes the volatility of the investment, or in this case, the risk of instability of ecosystem services.[34] This is related to the idea of *response diversity* where a suite of species will exhibit differential responses to a given environmental perturbation. When considered together, they create a stabilizing function that preserves the integrity of a service.[35]

Several experiments have tested these hypotheses in both the field and the lab. In ECOTRON, a laboratory in the UK where many of the biotic and abiotic factors of nature can be simulated, studies have focused on the effects of earthworms and symbiotic bacteria on plant roots.[33] These laboratory experiments seem to favor the rivet hypothesis. However, a study on grasslands at Cedar Creek Reserve in Minnesota supports the redundancy hypothesis, as have many other field studies.[36]

Economics

Sustainable urban drainage pond near housing in Scotland. The filtering and cleaning of surface and waste water by natural vegetation is a form of ecosystem service.

There are questions regarding the environmental and economic values of ecosystem services.[37] Some people may be unaware of the environment in general and humanity's interrelatedness with the natural environment, which may cause misconceptions. Although environmental awareness is rapidly improving in our contemporary world, ecosystem capital and its flow are still poorly understood, threats continue to impose, and we suffer from the so-called 'tragedy of the commons'.[38] Many efforts to inform decision-makers of current versus future costs and benefits now involve organizing and translating scientific knowledge to economics, which articulate the consequences of our choices in comparable units of impact on human well-being.[39] An especially challenging aspect of this process is that interpreting ecological information collected from one spatial-temporal scale does not necessarily mean it can be applied at another; understanding the dynamics of ecological processes relative to ecosystem services is essential in aiding economic decisions.[40] Weighting factors such as a service's irreplaceability or bundled services can also allocate economic value such that goal attainment becomes more efficient.

The economic valuation of ecosystem services also involves social communication and information, areas that remain particularly challenging and are the focus of many researchers.[41] In general, the idea is that although individuals make decisions for any variety of reasons, trends reveal the aggregative preferences of a society, from which the economic value of services can be inferred and assigned. The six major methods for valuing ecosystem services in monetary terms are:[42]

- Avoided cost: Services allow society to avoid costs that would have been incurred in the absence of those services (e.g. waste treatment by wetland habitats avoids health costs)

- Replacement cost: Services could be replaced with man-made systems (e.g. restoration of the Catskill Watershed cost less than the construction of a water purification plant)
- Factor income: Services provide for the enhancement of incomes (e.g. improved water quality increases the commercial take of a fishery and improves the income of fishers)
- Travel cost: Service demand may require travel, whose costs can reflect the implied value of the service (e.g. value of ecotourism experience is at least what a visitor is willing to pay to get there)
- Hedonic pricing: Service demand may be reflected in the prices people will pay for associated goods (e.g. coastal housing prices exceed that of inland homes)
- Contingent valuation: Service demand may be elicited by posing hypothetical scenarios that involve some valuation of alternatives (e.g. visitors willing to pay for increased access to national parks)

A peer-reviewed study published in 1997 estimated the value of the world's ecosystem services and natural capital to be between US$16–54 trillion per year, with an average of US$33 trillion per year.[43] However, Salles (2011) indicates 'The total value of biodiversity is infinite, so having debate about what is the total value of nature is actually pointless because we can't live without it'.

Management and policy

Although monetary pricing continues with respect to the valuation of ecosystem services, the challenges in policy implementation and management are significant and multitudinous. The administration of common pool resources is a subject of extensive academic pursuit.[44][45][46][47][48] From defining the problems to finding solutions that can be applied in practical and sustainable ways, there is much to overcome. Considering options must balance present and future human needs, and decision-makers must frequently work from valid but incomplete information. Existing legal policies are often considered insufficient since they typically pertain to human health-based standards that are mismatched with necessary means to protect ecosystem health and services. To improve the information available, one suggestion has involved the implementation of an *Ecosystem Services Framework* (ESF[49]), which integrates the biophysical and socio-economic dimensions of protecting the environment and is designed to guide institutions through multidisciplinary information and jargon, helping to direct strategic choices.

Novel and expedient methods are needed to deal with managing Earth's ecosystem services. Local to regional collective management efforts might be considered appropriate for services like crop pollination or resources like water.[23][44] Another approach that has become increasingly popular over the last decade is the marketing of ecosystem services protection. Payment and trading of services is an emerging worldwide small-scale solution where one can acquire credits for activities such as sponsoring the protection of carbon sequestration sources or the restoration of ecosystem service providers. In some cases, banks for handling such credits have been established and conservation companies have even gone public on stock exchanges, defining an evermore parallel link with economic endeavors and opportunities for tying into social perceptions.[39] However, crucial for implementation are clearly defined land rights, which is often lacking in many developing countries.[50] In particular, many forest-rich developing countries suffering deforestation experience conflict between different forest stakeholders.[50] In addition, concerns for such global transactions include inconsistent compensation for services or resources sacrificed elsewhere and misconceived warrants for irresponsible use. Another approach has been focused on protecting ecosystem service 'hotspots'. Recognition that the conservation of many ecosystem services aligns with more traditional conservation goals (i.e. biodiversity) has led to the suggested merging of objectives for maximizing their mutual success. This may be particularly strategic when employing networks that permit the flow of services across landscapes, and might also facilitate securing the financial means to protect services through a diversification of investors.[51][52]

For example, in recent years there has been interest in the valuation of ecosystem services provided by shellfish production and restoration.[53] A keystone species, low in the food chain, bivalve shellfish such as oysters support a complex community of species by performing a number of functions essential to the diverse array of species that surround them. There is also increasing recognition that some shellfish species may impact or control many ecological processes; so much so that they are included on the list of "ecosystem engineers"—organisms that physically, biologically or chemically modify the environment around them in ways that influence the health of other organisms.[54] Many of the ecological functions and processes performed or affected by shellfish contribute to human well-being by providing a stream of valuable ecosystem services over time by filtering out particulate materials and potentially mitigating water quality issues by controlling excess nutrients in the water.

Ecosystem-based adaptation (EbA)

Ecosystem-based adaptation or EbA is an emerging strategy for community development and environmental management that seeks to use an ecosystem services framework to help communities adapt to the effects of climate change. The Convention on Biological Diversity currently defines Ecosystem-Based Adaptation as "the use of biodiversity and ecosystem services to help people adapt to the adverse effects of climate change", which includes the use of "sustainable management, conservation and restoration of ecosystems, as part of an overall adaptation strategy that takes into account the multiple social, economic and cultural co-benefits for local communities".[55]

In 2001, the Millennium Ecosystem Assessment announced that humanity's impact on the natural world was increasing to levels never before seen, and that the degradation of the planet's ecosystems would become a major barrier to achieving the Millennium Development Goals. In recognition of this fact, Ecosystem-Based Adaptation seeks to use the restoration of ecosystems as a stepping-stone to improving the quality of life in communities experiencing the impacts of climate change. Specifically, this involves the restoration of ecosystems that provide the community with essential services, such as the provisioning of food and water and protection from storm surges and flooding. EbA interventions typically combine elements of both climate change mitigation and adaptation to global warming to help address the community's current and future needs.[56]

Collaborative planning between scientists, policy makers, and community members is an essential element of Ecosystem-Based Adaptation. By drawing on the expertise of outside experts and local residents alike, EbA seeks to develop unique solutions to unique problems, rather than simply replicating past projects.[55]

Estuarine and coastal ecosystem services

Ecosystem services are defined as the gains acquired by humankind from surroundings ecosystems. Four different types of ecosystem services have been distinguished by the scientific body: regulating services, provisioning services, cultural services and supporting services. An ecosystem does not necessarily offer all four types of services simultaneously; but given the intricate nature of any ecosystem, it is usually assumed that humans benefit from a combination of these services. The services offered by diverse types of ecosystems (forests, seas, coral reefs, mangroves, etc.) differ in nature and in consequence. In fact, some services directly affect the livelihood of neighboring human populations (such as fresh water, food or aesthetic value, etc.) while other services affect general environmental conditions by which humans are indirectly impacted (such as climate change, erosion regulation or natural hazard regulation, etc.).[57]

Estuarine and coastal ecosystems are both marine ecosystems. An estuary is defined as the area in which a river meets the sea or the ocean. The waters surrounding this area are predominantly salty waters or brackish waters; and the incoming river water is dynamically motioned by the tide. An estuary strip may be covered by populations of reed (or similar plants) and/or sandbanks (or similar form or land).

A coastal ecosystem occurs in areas where the sea or ocean waters meet the land.

Regulating services

Regulating services are the "benefits obtained from the regulation of ecosystem processes".[58] In the case of coastal and estuarine ecosystems, these services include climate regulation, waste treatment and disease control and natural hazard regulation.

Climate regulation

Both the biotic and abiotic ensembles of marine ecosystems play a role in climate regulation. They act as sponges when it comes to gases in the atmosphere, retaining large levels of CO_2 and other greenhouse gases (methane and nitrous oxide). Marine plants also use CO_2 for photosynthesis purposes and help in reducing the atmospheric CO_2. The oceans and seas absorb the heat from the atmosphere and redistribute it through the means of water currents, and atmospheric processes, such as evaporation and the reflection of light allow for the cooling and warming of the overlying atmosphere. The ocean temperatures are thus imperative to the regulation of the atmospheric temperatures in any part of the world: "without the ocean, the Earth would be unbearably hot during the daylight hours and frigidly cold, if not frozen, at night".[59]

Waste treatment and disease regulation

Another service offered by marine ecosystem is the treatment of wastes, thus helping in the regulation of diseases. Wastes can be diluted and detoxified through transport across marine ecosystems; pollutants are removed from the environment and stored, buried or recycled in marine ecosystems: "Marine ecosystems break down organic waste through microbial communities that filter water, reduce/limit the effects of eutrophication, and break down toxic hydrocarbons into their basic components such as carbon dioxide, nitrogen, phosphorus, and water".[59] The fact that waste is diluted with large volumes of water and moves with water currents leads to the regulation of diseases and the reduction of toxics in seafood.

Buffer zones

Coastal and estuarine ecosystems act as buffer zones against natural hazards and environmental disturbances, such as floods, cyclones, tidal surges and storms. The role they play is to "[absorb] a portion of the impact and thus [lessen] its effect on the land".[59] Wetlands, for example, and the vegetation it supports – trees, root mats, etc. – retain large amounts of water (surface water, snowmelt, rain, groundwater) and then slowly releases them back, decreasing the likeliness of floods.[60] Mangrove forests protect coastal shorelines from tidal erosion or erosion by currents; a process that was studied after the 1999 cyclone that hit India. Villages that were surrounded with mangrove forests encountered less damages than other villages that weren't protected by mangroves.[61]

Provisioning Services

Provisioning services consist of all "the products obtained from ecosystems". Marine ecosystems provide people with: wild & cultured seafood, fresh water, fiber & fuel and biochemical & genetic resources.

Marine products

Humans consume a large number of products originating from the seas, whether as a nutritious product or for use in other sectors: "More than one billion people worldwide, or one-sixth of the global population, rely on fish as their main source of animal protein. In 2000, marine and coastal fisheries accounted for 12 per cent of world food production".[62] Fish and other edible marine products – primarily fish, shellfish, roe and seaweeds – constitute for populations living along the coast the main elements of the local cultural diets, norms and traditions. A very pertinent example would be sushi, the national food of Japan, which consists mostly of different types of fish and seaweed.

Fresh water

Water bodies that are not highly concentrated in salts are referred to as 'fresh water' bodies. Fresh water may run through lakes, rivers and streams, to name a few; but it is most prominently found in the frozen state or as soil moisture or buried deep underground. Fresh water is not only important for the survival of humans, but also for the survival of all the existing species of animals, plants.

Raw materials

Marine creatures provide us with the raw materials needed for the manufacturing of clothing, building materials (lime extracted from coral reefs), ornamental items and personal-use items (luffas, art and jewelry): "The skin of marine mammals for clothing, gas deposits for energy production, lime (extracted from coral reefs) for building construction, and the timber of mangroves and coastal forests for shelter are some of the more familiar uses of marine organisms. Raw marine materials are utilized for non-essential goods as well, such as shells and corals in ornamental items".[62] Humans have also referred to processes within marine environments for the production of renewable energy: using the power of waves – or tidal power – as a source of energy for the powering of a turbine, for example. Oceans and seas are used as sites for offshore oil and gas installations, offshore wind farms.

Biochemical and genetic resources

Biochemical resources are compounds extracted from marine organisms for use in medicines, pharmaceuticals, cosmetics and other biochemical products. Genetic resources are the genetic information found in marine organisms that would later on be used for animal and plant breeding and for technological advances in the biological field. These resources are either directly taken out from an organism – such as fish oil as a source of omega3 –, or used as a model for innovative man-made products: "such as the construction of fiber optics technology based on the properties of sponges. ... Compared to terrestrial products, marine-sourced products tend to be more highly bioactive, likely due to the fact that marine organisms have to retain their potency despite being diluted in the surrounding sea-water".[62]

Cultural services

Cultural services relate to the non-material world, as they benefit the benefit recreational, aesthetic, cognitive and spiritual activities, which are not easily quantifiable in monetary terms.

Inspirational

Marine environments have been used by many as an inspiration for their works of art, music, architecture, traditions... Water environments are spiritually important as a lot of people view them as a means for rejuvenation and change of perspective. Many also consider the water as being a part of their personality, especially if they have lived near it since they were kids: they associate it to fond memories and past experiences. Living near water bodies for a long time results in a certain set of water activities that become a ritual in the lives of people and of the culture in the region.

Recreation and tourism

Sea sports are very popular among coastal populations: surfing, snorkeling, whale watching, kayaking, recreational fishing...a lot of tourists also travel to resorts close to the sea or rivers or lakes to be able to experience these activities, and relax near the water.

Science and education

A lot can be learned from marine processes, environments and organisms – that could be implemented into our daily actions and into the scientific domain. Although much is still yet to still be known about the ocean world: "by the extraordinary intricacy and complexity of the marine environment and how it is influenced by large spatial scales, time lags, and cumulative effects".[59]

Beach accommodated into a recreational area.

Supporting services

Supporting services are the services that allow for the other ecosystem services to be present. They have indirect impacts on humans that last over a long period of time. Several services can be considered as being both supporting services and regulating/cultural/provisioning services.

Nutrient cycling

Nutrient cycling is the movement of nutrients through an ecosystem by biotic and abiotic processes.[63] The ocean is a vast storage pool for these nutrients, such as carbon, nitrogen and phosphorus. The nutrients are absorbed by the basic organisms of the marine food web and are thus transferred from one organism to the other and from one ecosystem to the other. Nutrients are recycled through the life cycle of organisms as they die and decompose, releasing the nutrients into the neighboring environment. "The service of nutrient cycling eventually impacts all other ecosystem services as all living things require a constant supply of nutrients to survive".[59]

Biologically mediated habitats

Biologically mediated habitats are defined as being the habitats that living marine structures offer to other organisms.[64] These need not to be designed for the sole purpose of serving as a habitat, but happen to become living quarters whilst growing naturally. For example, coral reefs and mangrove forests are home to numerous species of fish, seaweed and shellfish... The importance of these habitats is that they allow for interactions between different species, aiding the provisioning of marine goods and services. They are also very important for the growth at the early life stages of marine species (breeding and bursary spaces), as they serve as a food source and as a shelter from predators.

Primary production


Coral and other living organisms serve as habitats for many marine species.

Primary production refers to the production of organic matter, i.e., chemically bound energy, through processes such as photosynthesis and chemosynthesis. The organic matter produced by primary producers forms the basis of all food webs. Further, it generates oxygen (O2), a molecule necessary to sustain animals and humans.[65][66][67][68] On average, a human consumes about 550 liter of oxygen per day, whereas plants produce 1,5 liter of oxygen per 10 grams of growth.[69]

Businessworld

Ecosystem services degradation can pose a number of risks to corporate performance as well as provide business opportunities through ecosystem restoration and enhancement. Risks and opportunities include:

- ***Operational***
  - Risks such as higher costs for freshwater due to scarcity or lower output for hydroelectric facilities due to siltation
  - Opportunities such as increasing water-use efficiency or building an on-site wetland to circumvent the need for new water treatment infrastructure
- ***Regulatory and legal***
  - Risks such as new fines, government regulations, or lawsuits from local communities that lose ecosystem services due to corporate activities
  - Opportunities such as engaging governments to develop policies and incentives to protect or restore ecosystems that provide services a company needs
- ***Reputational***

- Risks such as retail companies being targeted by nongovernmental organization campaigns for purchasing wood or paper from sensitive forests

Opportunities such as implementing and communicating sustainable purchasing, operating, or investment practices in order to differentiate corporate brands.

- ***Market and product***
  - Risks such as customers switching to other suppliers that offer products with lower ecosystem impacts or governments implementing new sustainable procurement policies
  - Opportunities such as launching new products and services that reduce customer impacts on ecosystems or participating in emerging markets for carbon sequestration and watershed protection other products
- ***Financing***
  - Risks such as banks implementing more rigorous lending requirements for corporate loans
  - Opportunities such as banks offering more favorable loan terms or investors taking positions in companies supplying products and services that improve resource use efficiency or restore degraded ecosystems

Many companies are not fully aware of the extent of their dependence and impact on ecosystems and the possible ramifications. Likewise, environmental management systems and environmental due diligence tools are more suited to handle "traditional" issues of pollution and natural resource consumption. Most focus on environmental impacts, not dependence. Several newly developed tools and methodologies can help the private sector value and assess ecosystem services. These include Our Ecosystem,[70] the Corporate Ecosystem Services Review (ESR),[71] Artificial Intelligence for Ecosystem Services (ARIES),[72] the Natural Value Initiative (NVI)[73] and InVEST (Integrated Valuation of Ecosystem Services & Tradeoffs) [74]

Land use change decisions

Ecosystem services decisions require making complex choices at the intersection of ecology, technology, society and the economy. The process of making ecosystem services decisions must consider the interaction of many types of information, honor all stakeholder viewpoints, including regulatory agencies, proposal proponents, decision makers, residents, NGOs, and measure the impacts on all four parts of the intersection. These decisions are usually spatial, always multi-objective, and based on uncertain data, models, and estimates. Often it is the combination of the best science combined with the stakeholder values, estimates and opinions that drive the process.[75]

One analytical study modeled the stakeholders as agents to support water resource management decisions in the Middle Rio Grande basin of New Mexico. This study focused on modeling the stakeholder inputs across a spatial decision, but ignored uncertainty.[76] Another study used Monte Carlo methods to exercise econometric models of landowner decisions in a study of the effects of land-use change. Here the stakeholder inputs were modeled as random effects to reflect the uncertainty.[77] A third study used a Bayesian decision support system to both model the uncertainty in the scientific information Bayes Nets and to assist collecting and fusing the input from stakeholders. This study was about siting wave energy devices off the Oregon Coast, but presents a general method for managing uncertain spatial science and stakeholder information in a decision making environment.[78] Remote sensing data and analyses can be used to assess the health and extent of land cover classes that provide ecosystem services, which aids in planning, management, monitoring of stakeholders' actions, and communication between stakeholders.[79]

In Baltic countries scientists, nature conservationists and local authorities are implementing integrated planning approach for grassland ecosystems (http://vivagrass.eu/about-the-project/). They are developing Integrated Planning Tool that will be based on GIS (geographic information system) technology and put online that will help for planners to choose the best grassland management solution for concrete grassland. It will look holistically at the processes in the countryside and help to find best grassland management solutions by taking into account both natural and socioeconomic factors of the particular site.

See also

- Blue carbon
- Biodiversity banking
- Controlled Ecological Life Support System
- Diversity-function debate
- Earth Economics
- Ecological goods and services
- Environmental finance
- Existence value
- Forest farming
- Environmental and economic benefits of having indigenous peoples tend land
- Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
- Mitigation banking
- Natural Capital
- Non-timber forest product
- Oxygen cycle
- Rangeland Management
- Soil functions
- Spaceship Earth
- Nature Based Solutions

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Insects as food

Insects as food or **edible insects** are insect species used for human consumption, e.g., whole or as an ingredient in processed food products such as burger patties, pasta, or snacks. The cultural and biological process of eating insects (by humans as well as animals) is described as entomophagy.

Whole, fried edible insects as street food in Germany

Contents

Edible insects

Frequently consumed insect species

Estimates of numbers of edible insect species consumed globally range from 1,000 to 2,000.[1] These species include 235 butterflies and moths, 344 beetles, 313 ants, bees and wasps, 239 grasshoppers, crickets and cockroaches, 39 termites, and 20 dragonflies, as well as cicadas.[2] Which species are consumed varies by region due to differences in environment, ecosystems, and climate.

The table below lists the top five insect orders consumed by humans worldwide, retrieved from *Edible Insects: Future Prospects for Food and Feed Security* by Arnold van Huis, Joost Van Itterbeeck, Harmke Klunder, Esther Mertens, Afton Halloran, Giulia Muir and Paul Vantomme.[3]

Order of insect	Common name	Consumption rate worldwide by human population (%)
Coleoptera	Beetles	31
Lepidoptera	Butterflies, moths	18
Hymenoptera	Bees, wasps, ants	14
Orthoptera	Grasshoppers, locusts, crickets	13
Hemiptera	Cicadas, leafhoppers, planthoppers	10

For a list of edible insects consumed locally see: List of edible insects by country.

Edible insects for industrialized mass production

In Western markets such as Europe and North America, academics as well as large-scale insect food producers such as *Entomofarms* in Canada, *Aspire Food Group* in the United States,[4] *Protifarm* in the Netherlands, and *Bühler Group* in Switzerland, focus on four insects species suitable for human consumption as well as industrialized mass production:[5]

- House cricket (*Acheta domesticus*)
- European migratory locust (*Locusta migratoria*)
- Mealworms (*Tenebrio molitor*) as larvae
- Lesser mealworms (*Alphitobius diaperinus*) as larvae, mostly marketed under the term buffalo worms.

Freeze-dried house crickets as food (or food ingredient)

Mealworms as food (or food ingredient)

Buffalo worms as food (or ingredient)

Nutritional profile

Insects are nutrient efficient compared to other meat sources. Insects such as crickets are a complete protein and contain a useful amount, comparable with protein from soybeans, though less than in casein (found in foods such as cheese).[6] They have dietary fiber and include mostly unsaturated fat and contain some vitamins, such as vitamin B12[7], riboflavin and vitamin A, and essential minerals.[8][9]

Freeze-dried mealworms and buffalo worms (lesser mealworm)

Locusts contain between 8 and 20 milligrams of iron for every 100 grams of raw locust. Beef on the other hand contains roughly 6 milligrams of iron in the same amount of meat. Crickets as well are very efficient in terms of nutrients. For every 100 grams of substance crickets contain 12.9 grams of protein, 121 calories, and 5.5 grams of fat. Beef contains more protein containing 23.5 grams in 100 grams of substance, but also has roughly 3 times the calories, and four times the amount of fat as crickets do in 100 grams. So, per 100 grams of substance, crickets contain only half the nutrients of beef, except for iron. High levels of iron are implicated in bowel cancer[10] and heart disease.[11]

Nutritional value per 100 g	**Mealworms (*Tenebrio molitor*)**	**Buffalo worms (*Alphitobius diaperinus*)**	**House crickets (*Acheta domesticus*)**	**Migratory locust (*Locusta migratoria*)**
Energy	550 kcal / 2303 KJ	484 kcal/ 2027 KJ	458 kcal/ 1918 KJ	559 kcal/ 2341 KJ
Fat Of which saturated fatty acids	37,2 g 9 g	24,7 g 8 g	18,5 g 7 g	38,1 g 13,1 g
Carbohydrates Of which sugars	5,4 g 0 g	6,7 g 0 g	0 g 0 g	1,1 g 0 g
Protein	45,1 g	56,2 g	69,1 g	48,2 g
Salt	0,37 g	0,38 g	1,03 g	0,43 g

Farming, production, and processing

Edible insects are raised as livestock in specialized insect farms. In North American as well as European countries such as the Netherlands or Belgium, insects are produced under strict food law and hygiene standard for human consumption.


Crickets being raised for human consumption

Several variables apply, such as temperature, humidity, feed, water sources, housing, depending on the insect species. The insects are raised from eggs to larvae status (mealworms, lesser mealworms) or to their mature form (crickets, locusts), and then killed, in industrialized insect farms by lowering the temperature.[12][13] After that the insects are freeze-dried and packed whole, or pulverized to insect powder (insect flour), to be processed in other food products such as bakery products, or snacks.

Aside from nutritional composition and digestibility, insects are also selected for ease of rearing by the producer. This includes susceptibility to disease, efficiency of feed conversion, developmental rate and generational turnover.[14]

Insect food products

The following processed food products are produced by several producers in North America, Canada, and the EU:

- *Insect flour*: Pulverized, freeze-dried insects (e.g., cricket flour).
- *Insect burger*: Hamburger patties made from insect powder / insect flour (mainly from worms or from house cricket) and further ingredients.[15]
- *Insect fitness bars*: Protein bars containing insect powder (mostly house crickets).
- *Insect pasta*: Pasta made of wheat flour, fortified with insect flour (house crickets or mealworms).
- *Insect bread* (Finnish *Sirkkaleipä*): Bread baked with insect flour (mostly house crickets).[16]

Insect burger made by Essento containing mealworms

Fusilli made of cricket flour

Snack made of cricket flour

Food safety

Challenges and safety concerns

In spite of all the advantages that insect protein are provided, there are some potential challenges caused by production and safety concerns.

Mass production in the insect industry is a concern due to a lack of technology and funds to efficiently harvest, and produce insects. The machinery would have to house proper enclosure for each life cycle of the insect as well as the temperature control as that is key for insect development.[17]

The industry also has to consider the shelf life of insects in comparison to animal products as that some can have food safety concerns. Insects have the capability of accumulating potential hazards, such as contaminants, pathogens, the concentration of heavy metals, allergens, and pesticides etc.[18]

Table below combined the data from two studies[19][20] published in Comprehensive Reviews in Food Science and Food Safety, and summarized the potential hazards of the top five insect species consumed by humans.

Insect order	Common name	Hazard category	Potential hazard
Coleoptera	Beetle	Chemical	Oromones
			Cyanogentic substances
			Heavy metal contamination
Lepidoptera	Silkworm	Allergic	
		Chemical	Thiaminase
	Honeycomb moth	Microbial	High bacterial count
		Chemical	Cyanogentic substances
Hymenoptera	Ant	Chemical	Antinutritional factors (tannin, phytate)
Orthoptera	House cricket	Microbial	High bacterial count
Hemiptera		Parasitical	Chagas disease
Diptera	Black soldier fly	Parasitical	Myiasis

Hazards in insects that are shown above can be controlled by various ways. Allergic hazard can be labelled on the package to avoid consumption by allergy susceptible consumers. Selective farming can be used to minimize chemical hazard, whereas microbial and parasitical hazard can be controlled by cooking processes.[21]

Regulation and authorisation

Switzerland

On 1 May 2017, Switzerland has approved the following insect species as food:[22]

- House cricket (*Acheta domesticus*)
- European locust (*Locusta migratoria*)
- Mealworms (*Tenebrio molitor*) as larvae

Under certain conditions, these may be offered to consumers as whole animals, pulverized, or processed in food products.

EU

In the EU, insects fall within the definition of novel food as food ingredients isolated from animals, given by the European Commission. Parts of insects, e.g., legs, wings, or heads, as well as whole insects, fall within this definition.[23] Dossiers for several insects species are currently under review by the European Food Safety Authority. In August 2018, EFSA published a risk profile for the house cricket as food.[24]

Awareness

The World Edible Insect Day, being held on 23 October, was introduced by Belgian entrepreneur Chris Derudder in 2015 to raise awareness globally for the consumption of edible insects, with a focus on Europe, North America, and Australia.[25]

See also

- Insectivore

Footnotes

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Insects in medicine

Insects have long been used in medicine, both traditional and modern, sometimes with little evidence of their effectiveness. For the purpose of the article, and in line with custom, medicinal uses of other arthropods such as spiders are included.

Maggot debridement therapy on a wound on a diabetic foot

Contents

Traditional and alternative uses

The medicinal uses of insects and other arthropods worldwide have been reviewed by Meyer-Rochow [1], who provides examples of all major insect groups,spiders, worms and molluscs and discusses their potential as suppliers of bioactive components. Using insects (and spiders) to treat various maladies and injuries has a long tradition and, having stood the test of time, can be effective and provide results. However, sometimes folk-medicinal "logic" was based on the Doctrine of Signatures = "let likes be cured by likes"and had, if any at all, little more than a psychological effect. For example, to treat cases of constipation, dung beetles were prescribed; to slim down stick insects were thought to help; hairy tarantulas seemed the right treatment for hair loss and fat grubs resembling the swollen limb caused by the parasite Wucheria bancrofti were expected to help the elephantiasis sufferer. An organism bearing parts that resemble human body parts, animals, or other objects, was thought to have useful relevance to those parts, animals or objects. So, for example, the femurs of grasshoppers, which were said to resemble the human liver, were used to treat liver ailments by the indigenous peoples of Mexico.[2] This doctrine is common throughout traditional and alternative medicine, but is most prominent where medical traditions are broadly accepted, as in traditional Chinese medicine and Ayurveda, and less by community and family based medicine, as is more common in parts of Africa.

Traditional Chinese medicine

Traditional Chinese medicine includes the use of herbal medicine, acupuncture, massage, exercise, and dietary therapy. It is a typical component of modern medical care throughout East Asia and in some parts of Southeast Asia (such as Thailand). Insects are very commonly incorporated as part of the herbal medicine component of traditional Chinese medicine, and their medical properties and applications are broadly accepted and agreed upon. Some brief examples follow:

The Chinese Black Mountain Ant, *Polyrhachis vicina*, is supposed to act as a cure all and is widely used, especially by the elderly. It is said to prolong life, to have anti-aging properties, to replenish Qi, and to increase virility and fertility. Recent interest in the ants' medicinal qualities has led to British researchers to study the extract's potential to serve as a cancer-fighting agent.[3] Chinese Black Mountain Ant extract is typically consumed mixed with wine.

India and Ayurveda

Ayurveda is ancient traditional Indian treatment almost universally incorporated alongside Western medicine as a typical component of medical treatment in India. Although Ayurvedic medicine is often effective, doses can be inconsistent, and may sometimes be contaminated with toxic heavy metals.[4] Some brief examples to follow:

Termite is said to cure a variety of diseases, both specific and vague. Typically the mound or a portion of the mound is dug up and the termites and the architectural components of the mound are together ground into a paste which is then applied topically to the affected areas or, more rarely, mixed with water and consumed.[5] This treatment was said to cure ulcers, rheumatic diseases, and anemia.[4] It was also suggested to be a general pain reliever and health improver.[4]

The Jatropha Leaf Miner, a lepidopteran which feeds preferentially on *Jatropha*, is an example of a major insect agricultural pest which is also a medicinal remedy.[5] The larvae, which are also the form of the insect with the greatest economic impact on agriculture, are harvested, boiled, and mashed into a paste which is administered topically and is said to induce lactation, reduce fever, and soothe gastrointestinal tracts.[5]

Africa

Unlike China and India, the traditional insect medicine of Africa is extremely variable. It is largely regional, with few, if any, major agreements on which insects are useful as treatments for which ailments.[5] Most insect medicinal treatments are passed on through communities and families, rather than being taught in university settings, as Traditional Chinese Medicine and Ayurveda sometimes are; furthermore, most traditional medicine practices necessitate a person in a "healer" role.[5] Some brief examples to follow:

Grasshopper is both commonly eaten as a delicacy and an excellent source of protein *and* is consumed for medicinal purposes.[5] These insects are typically collected, dried in the sun, and then ground into a powder.[5] The powder can then be turned into a paste when mixed with water and ash and applied to the forehead to alleviate the pain of violent headaches.[5] Additionally, the headaches themselves can be prevented by a "healer" inserting the paste under the skin at the nape of the afflicted person's neck.[5]

Termites are also used in parts of Africa much like they are in India.[4] Parts of the mound are dug up, boiled, and turned into a paste, which can then be applied to external wounds to prevent infection or consumed to treat internal hemorrhages.[5] termites are used not only as a form of medicine, but also as a medical device. If a "healer" wants to insert a medicine subcutaneously, they will often spread that medicine on the skin of the patient, and then agitate a termite and place the insect on the skin of the patient.[5] When the termite bites, its mandibles effectively serve as an injection device.[5]

Americas

The Americas were more highly influenced by the Doctrine of Signatures than China, India, or Africa, most likely because of their colonial history with Europe. The majority of insect use in medicine is associated with Central America and parts of South America, rather than North America, and most of it is based on the medical techniques of indigenous peoples.[2] Currently, insect medicine is practiced much more rarely than in China, India, or Africa, though it is still relatively common in rural areas with large indigenous populations.[2] Some examples to follow:

Chapulines, or grasshoppers, are commonly consumed as a toasted regional dish in some parts of Mexico, but they are also used medicinally.[2] They are said to serve as diuretic to treat kidney diseases, to reduce swelling, and to relieve the pain of intestinal disorders when they are consumed.[2] However, there are some risks associated with consuming chapulines, as they are known to harbor nematodes which may be transmitted to humans upon consumption.

Much like the termites of Africa, ants were sometimes used as medicinal devices by the indigenous peoples of Central America.[2] The soldier cast of the Army ant would be collected and used as living sutures by Mayans.[2] This involved agitating an ant and holding its mandibles up to the wound edges; when it bit down, the thorax and abdomen were removed, leaving the head holding the wound together.[2] The ant's salivary gland secretions were reputed to have antibiotic properties.[2] The venom of the Red harvester ant was used to treat rheumatism, arthritis, and poliomyelitis via the immunological reaction produced by its sting. This technique, in which ants are allowed to sting afflicted areas in a controlled manner, is still used in some arid rural areas of Mexico.[2]

The silkworm, *Bombyx mori*, was also commonly consumed both as a regional food and for medicinal purposes in Central America after it was brought to the New World by the Spanish and Portuguese.[2] Only the immatures are consumed. Boiled pupae were eaten to treat apoplexy, aphasy, bronchitis, pneumonia, convulsions, hemorrhages, and frequent urination.[2] The excrement produced by the larvae is also eaten to improve circulation and alleviate the symptoms of cholera (intense vomiting and diarrhea).[2]

Honey bee products

Honey bee products are used medicinally across Asia, Europe, Africa, Australia, and the Americas, despite the fact that the honey bee was not introduced to the Americas until the colonization by Spain and Portugal. They are by far the most common medical insect product, both historically and currently.[5]

Honey is the most frequently referenced medical bee material. It can be applied to skin to treat excessive scar tissue, rashes, and burns,[6] and can be applied as a poultice to eyes to treat infection.[4] It is also consumed for digestive problems and as a general health restorative, and can be heated and consumed to treat head colds, cough, throat infections, laryngitis, tuberculosis, and lung diseases.[2]

Additionally, apitoxin, or honey bee venom, can be applied via direct stings to relieve arthritis, rheumatism, polyneuritis, and asthma.[2] Propolis, a resinous, waxy mixture collected by honeybees and used as a hive insulator and sealant, is often consumed by menopausal women because of its high hormone content, and it is said to have antibiotic, anesthetic, and anti-inflammatory properties.[2] Royal jelly is used to treat anemia, gastrointestinal ulcers, arteriosclerosis, hypo- and hypertension, and inhibition of sexual libido.[2] Finally Bee bread, or bee pollen, is eaten as a generally health restorative, and is said to help treat both internal and external infections.[2] All of these honey bee products are regularly produced and sold, especially online and in health food stores, though none are yet approved by the FDA.

Modern scientific uses

Though insects were widely used throughout history for medical treatment on nearly every continent, relatively little medical entomological research has been conducted since the revolutionary advent of antibiotics. Heavy reliance on antibiotics, coupled with discomfort with insects in Western culture limited the field of insect pharmacology until the rise of antibiotic resistant infections sparked pharmaceutical research to explore new resources. Arthropods represent a rich and largely unexplored source of new medicinal compounds.[7]

Maggot therapy

Maggot therapy is the intentional introduction of live, disinfected blow fly larvae (maggots) into soft tissue wounds to selectively clean out the necrotic tissue. This helps to prevent infection; it also speeds healing of chronically infected wounds and ulcers.[8] Military surgeons since classical antiquity noticed that wounds which had been left untreated for several days, and which had become infested with maggots, healed better than wounds not so infested.[9] Maggots secrete several chemicals that kill microbes, including allantoin, urea, phenylacetic acid, phenylacetaldehyde, calcium carbonate, proteolytic enzymes, and many others.[10]

Maggots were used for wound healing by the Maya and by indigenous Australians. More recently, they were used in Renaissance Europe, in the Napoleonic Wars, the American Civil War, and in the First and Second World Wars.[11][12] It continues to be used in military medicine.[13]

Apitherapy

Apitherapy is the medical use of honeybee products such as honey, pollen, bee bread, propolis, royal jelly and bee venom. One of the major peptides in bee venom, called Melittin, has the potential to treat inflammation in sufferers of Rheumatoid arthritis and Multiple sclerosis. Melittin blocks the expression of inflammatory genes, thus reducing swelling and pain. It is administered by direct insect sting, or intramuscular injections. Bee products demonstrate a wide array of antimicrobial factors and in laboratory studies and have been shown to kill antibiotic resistant bacteria, pancreatic cancer cells, and many other infectious microbes.[14]

Blister beetle and Spanish fly

Spanish fly is an emerald-green beetle, *Lytta vesicatoria*, in the blister beetle family (Meloidae). It and other such species were used in preparations offered by traditional apothecaries. The insect is the source of the terpenoid cantharidin, a toxic blistering agent once used as an aphrodisiac.[15][16]

Blood-feeding insects

Many blood-feeding insects like ticks, horseflies, and mosquitoes inject multiple bioactive compounds into their prey. These insects have been used by practitioners of Eastern Medicine for hundreds of years to prevent blood clot formation or thrombosis.[17] However, modern medical research has only recently begun to investigate the drug development potential of blood-feeding insect saliva. These compounds in the saliva of blood feeding insects are capable of increasing the ease of blood feeding by preventing coagulation of platelets around the wound and provide protection against the host’s immune response. Currently, over 1280 different protein families have been associated with the saliva of blood feeding organisms.[18] This diverse range of compounds may include:[14][19]

- inhibitors of platelet aggregation, ADP, arachidonic acid, thrombin, and PAF.
- anticoagulants
- vasodilators
- vasoconstrictors
- antihistamines
- sodium channel blockers
- complement inhibitors
- pore formers
- inhibitors of angiogenesis
- anaesthetics
- AMPs and microbial pattern recognition molecules.
- Parasite enhancers/activators

Currently, some preliminary progress has been made with investigation of the therapeutic properties of tick anticoagulant peptide (TAP) and Ixolaris a novel recombinant tissue factor pathway inhibitor (TFPI) from the salivary gland of the tick, *Ixodes scapularis*.[20] Additionally, Ixolaris, a tissue factor inhibitor has been shown to block primary tumor growth and angiogenesis in a glioblastoma model.[21] Despite the strong potential of these compounds for use as anticoagulants or immunomodulating drugs no modern medicines, developed from the saliva of blood-sucking insects, are currently on the market.[14]

Arachnids

Like plants and insects, arachnids have also been used for thousands of years in traditional medical practices. Recent scientific research in natural bioactive factors has increased, leading to a renewed interest in venom components in many animals. In 1993 Margatoxin was synthesized from the venom of the *Centruroides margaritatus* the Central American bark scorpion. It is a peptide that selectively inhibits voltage-dependent potassium channels. Patented by Merck, it has the potential to prevent neointimal hyperplasia, a common cause of bypass graft failure.[22]

In addition to medical uses of arachnid defense compounds, a great amount of research has recently been directed toward the synthesis and use of spider silk as a scaffolding for ligament generation. Spider silk is an ideal material for the synthesis of medical skin grafts or ligament implants because it is one of the strongest known natural fibers and triggers little immune response in animals. Spider silk may also be used to make fine sutures for stitching nerves or eyes to heal with little scarring. Medical uses of spider silk is not a new idea. Spider silks have been used for thousands of years to fight infection and heal wounds. Efforts to produce industrial quantities and qualities of spider silk in transgenic goat milk are underway.[23][24]

Psychoactive scorpions

Recent news reports[25] claim that use of scorpions for psychoactive purposes is gaining in popularity in Asia. Heroin addicts in Afghanistan are purported to smoke dried scorpions or use scorpion stings to get high when heroin is not available. The 'scorpion sting craze' has also increased in India with a decreasing availability of other drugs and alcohol available to youth.[26] Young people are reportedly flocking to highway sides where they can purchase scorpion stings that after several minutes of intense pain, supposedly produce a six- to eight-hour feeling of wellbeing.[27]

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Human interactions with insects

Human interactions with insects include both a wide variety of uses, whether practical such as for food, textiles, and dyestuffs, or symbolic, as in art, music, and literature, and negative interactions including serious damage to crops and extensive efforts to eliminate insect pests.

The "Spanish fly", *Lytta vesicatoria*, has been considered to have medicinal, aphrodisiac, and other properties.

Academically, the interaction of insects and society has been treated in part as **cultural entomology**, dealing mostly with "advanced" societies, and in part as **ethnoentomology**, dealing mostly with "primitive" societies, though the distinction is weak and not based on theory. Both academic disciplines explore the parallels, connections and influence of insects on human populations, and vice versa. They are rooted in anthropology and natural history, as well as entomology, the study of insects. Other cultural uses of insects, such as biomimicry, do not necessarily lie within these academic disciplines.

More generally, people make a wide range of uses of insects, both practical and symbolic. On the other hand, attitudes to insects are often negative, and extensive efforts are made to kill them. The widespread use of insecticides has failed to exterminate any insect pest, but has caused resistance to commonly-used chemicals in a thousand insect species.

Practical uses include as food, in medicine, for the valuable textile silk, for dyestuffs such as carmine, in science, where the fruit fly is an important model organism in genetics, and in warfare, where insects were successfully used in the Second World War to spread disease in enemy populations. One insect, the honey bee, provides honey, pollen, royal jelly, propolis and an anti-inflammatory peptide, melittin; its larvae too are eaten in some societies. Medical uses of insects include maggot therapy for wound debridement. Over a thousand protein families have been identified in the saliva of blood-feeding insects; these may provide useful drugs such as anticoagulants, vasodilators, antihistamines and anaesthetics.

Symbolic uses include roles in art, in music (with many songs featuring insects), in film, in literature, in religion, and in mythology. Insect costumes are used in theatrical productions and worn for parties and carnivals.

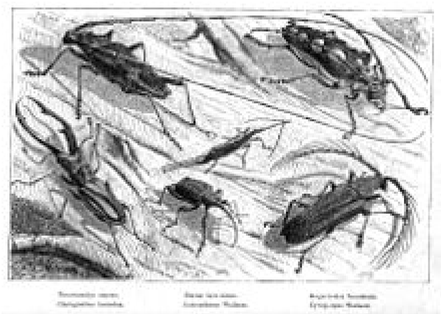
Contents

Context

Culture

Culture consists of the social behaviour and norms found in human societies and transmitted through social learning. Cultural universals in all human societies include expressive forms like art, music, dance, ritual, religion, and technologies like tool usage, cooking, shelter, and clothing. The concept of material culture covers physical expressions such as technology, architecture and art, whereas immaterial culture includes principles of social organization, mythology, philosophy, literature, and science.[1] This article describes the roles played by insects in human culture so defined.

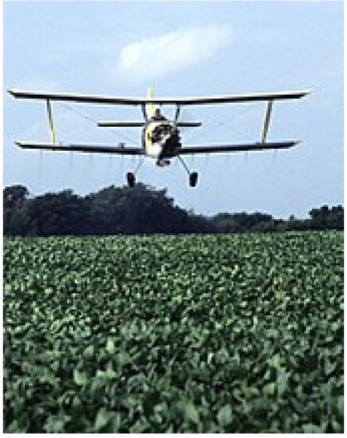
Cultural entomology and ethnoentomology



"Remarkable Beetles Found at Simunjon, Borneo": Alfred Russel Wallace was a pioneer of ethnoentomology.

Ethnoentomology developed from the 19th century with early works by authors such as Alfred Russel Wallace (1852) and Henry Walter Bates (1862). Hans Zinsser's classic *Rats, Lice and History* (1935) showed that insects were an important force in human history. Writers like William Morton Wheeler, Maurice Maeterlinck, and Jean Henri Fabre described insect life and communicated their meaning to people "with imagination and brilliance". Frederick Simon Bodenheimer's *Insects as Human Food* (1951) drew attention to the scope and potential of entomophagy, and showed a positive aspect of insects. Food is the most studied topic in ethnoentomology, followed by medicine and beekeeping.[2]

In 1968, Erwin Schimitschek claimed cultural entomology as a branch of insect studies, in a review of the roles insects played in folklore and culture including religion, food, medicine and the arts.[3] In 1984, Charles Hogue covered the field in English and from 1994 to 1997, Hogue's *The Cultural Entomology Digest* served as a forum on the field.[4][5] Hogue argued that "Humans spend their intellectual energies in three basic areas of activity: surviving, using practical learning (the application of technology); seeking pure knowledge through inductive mental processes (science); and pursuing enlightenment to taste a pleasure by aesthetic exercises that may be referred to as the 'humanities.' Entomology has long been concerned with survival (economic entomology) and scientific study (academic entomology), but the branch of investigation that addresses the influence of insects (and other terrestrial Arthropoda, including arachnids and myriapods) in literature, language, music, the arts, interpretive history, religion, and recreation has only become recognized as a distinct field" through Schimitschek's work.[3][6][7] Hogue set out the boundaries of the field by saying: "The narrative history of the science of entomology is not part of cultural entomology, while the influence of insects on general history would be considered cultural entomology."[8] He added: "Because the term "cultural" is narrowly defined, some aspects normally included in studies of human societies are excluded."[8]



Fighting insects: an agricultural aircraft applies low-insecticide bait to kill western corn rootworms.

Darrell Addison Posey, noting that the boundary between cultural entomology and ethnoentomology is difficult to draw, cites Hogue as limiting cultural entomology to the influence of insects on "the essence of humanity as expressed in the arts and humanities". Posey notes further that cultural anthropology is usually restricted to the study of "advanced", industrialised, and literate societies, whereas ethnoentomology studies "the entomological concerns of 'primitive' or 'noncivilized' societies". Posey states at once that the division is artificial, complete with an unjustified us/them bias.[2] Brian Morris similarly criticises the way that anthropologists treat non-Western attitudes to nature as monadic and spiritualist, and contrast this "in gnostic fashion" with a simplistic treatment of Western, often 17th-century, mechanistic attitude. Morris considers this "quite unhelpful, if not misleading", and offers instead his own research into the multiple ways that the people of Malawi relate to insects and other animals: "pragmatic, intellectual, realist, practical, aesthetic, symbolic and sacramental."[9]

Benefits and costs

Insect ecosystem services

Pollination, here by a bee on an avocado crop, is an ecosystem service.

The Millennium Ecosystem Assessment (MEA) report 2005 defines ecosystem services as benefits people obtain from ecosystems, and distinguishes four categories, namely provisioning, regulating, supporting, and cultural. A fundamental tenet is that a few species of arthropod are well understood for their influence on humans (such as honeybees, ants, mosquitoes, and spiders). However, insects offer ecological goods and services.[10] The Xerces Society calculates the economic impact of four ecological services rendered by insects: pollination, recreation (i.e. "the importance of bugs to hunting, fishing, and wildlife observation, including bird-watching"), dung burial, and pest control. The value has been estimated at $153 billion worldwide.[11] As the ant expert[12] E. O. Wilson observed: "If all mankind were to disappear, the world would regenerate back to the rich state of equilibrium that existed ten thousand years ago. If insects were to vanish, the environment would collapse into chaos."[13] A *Nova* segment on the American Public Broadcasting Service framed the relationship with insects in an urban context: "We humans like to think that we run the world. But even in the heart of our great cities, a rival superpower thrives ... These tiny creatures live all around us in vast numbers, though we hardly even notice them. But in many ways, it is they who really run the show.[14] *The Washington Post* stated: "We are flying blind in many aspects of preserving the environment, and that's why we are so surprised when a species like the honeybee starts to crash, or an insect we don't want, the Asian tiger mosquito or the fire ant, appears in our midst. In other words: Start thinking about the bugs."[15]

Pests and propaganda

Human attitudes toward insects are often negative, reinforced by sensationalism in the media.[16] This has produced a society that attempts to eliminate insects from daily life.[17] For example, nearly 75 million pounds of broad-spectrum insecticides are manufactured and sold each year for use in American homes and gardens. Annual revenues from insecticide sales to homeowners exceeded $450 million in 2004. Out of the roughly a million species of insects described so far, not more than 1,000 can be regarded as serious pests, and less than 10,000 (about 1%) are even occasional pests.[17] Yet not one species of insect has been permanently eradicated through the use of pesticides. Instead, at least 1,000 species have developed field resistance to pesticides, and extensive harm has been done to beneficial insects including pollinators such as bees.[18]

In the war against the potato beetle, East German Young Pioneers were urged to collect and kill Colorado beetles.

During the Cold War, the Warsaw Pact countries launched a widespread war against the potato beetle, blaming the introduction of the species from America on the CIA, demonising the species in propaganda posters, and urging children to gather the beetles and kill them.[19]

Practical uses

As food

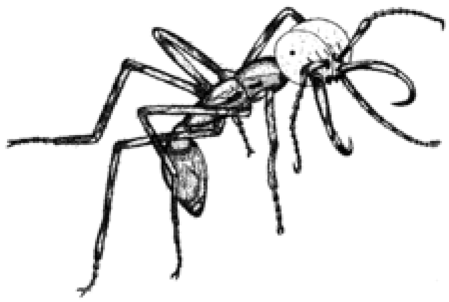
Witchetty grubs were prized as food by Australian aborigines.

Entomophagy is the eating of insects. Many edible insects are considered a culinary delicacy in some societies around the world, and Frederick Simon Bodenheimer's *Insects as Human Food* (1951) drew attention to the scope and potential of entomophagy, but the practice is uncommon and even taboo in other societies. Sometimes insects are considered suitable only for the poor in the third world, but in 1975 Victor Meyer-Rochow suggested that insects could help ease global future food shortages and advocated a change in western attitudes towards cultures in which insects were appreciated as a food item.[20] P. J. Gullan and P. S. Cranston felt that the remedy for this may be marketing of insect dishes as suitably exotic and costly to make them acceptable. They also note that some societies in sub-Saharan Africa prefer caterpillars to beef, while Chakravorty et al. (2011)[21] point out that food insects (highly appreciated in North-East India) are more expensive than meat. The economics, i.e., the costs involved collecting food insects and the money earned through the sale of such insects, have been studied in a Laotian setting by Meyer-Rochow et al. (2008).[22] In Mexico, ant larvae and corixid water boatman eggs are sought out as a form of caviar by gastronomes. In Guangdong, water beetles fetch a high enough price for these insects to be farmed. Especially high prices are fetched in Thailand for the giant water bug *Lethocerus indicus*.[23]

Insects used in food include honey bee larvae and pupae,[24][25] mopani worms,[26] silkworms,[27] Maguey worms,[28] Witchetty grubs,[29] crickets,[30] grasshoppers[31] and locusts.[32] In Thailand, there are 20,000 farmers rearing crickets, producing some 7,500 tons per year.[33]

In medicine

Insects have been used medicinally in cultures around the world, often according to the Doctrine of Signatures. Thus, the femurs of grasshoppers, which were said to resemble the human liver, were used to treat liver ailments by the indigenous peoples of Mexico.[34] The doctrine was applied in both Traditional Chinese Medicine (TCM) and in Ayurveda. TCM uses arthropods for various purposes; for example, centipede is used to treat tetanus, seizures, and convulsions,[35] while the Chinese Black Mountain Ant, *Polyrhachis vicina*, is used as a cure all, especially by the elderly, and extracts have been examined as a possible anti-cancer agent.[36] Ayurveda uses insects such as Termite for conditions such as ulcers, rheumatic diseases, anaemia, and pain. The Jatropha leaf miner's larvae are used boiled to induce lactation, reduce fever, and soothe the gastrointestinal tract.[21][37] In contrast, the traditional insect medicine of Africa is local and unformalised.[37] The indigenous peoples of Central America used a wide variety of insects medicinally. Mayans used Army ant soldiers as living sutures.[34] The venom of the Red harvester ant was used to cure rheumatism, arthritis, and poliomyelitis via the immune reaction produced by its sting.[34] Boiled *silkworm* pupae were taken to treat apoplexy, aphasy, bronchitis, pneumonia, convulsions, haemorrhages, and frequent urination.[34]



Army ants were used by the Mayans as living sutures, their powerful jaws holding a wound closed.

Honey bee products are used medicinally in apitherapy across Asia, Europe, Africa, Australia, and the Americas, despite the fact that the honey bee was not introduced to the Americas until the colonization by Spain and Portugal. They are by far the most common medical insect product both historically and currently, and the most frequently referenced of these is honey.[37] It can be applied to skin to treat excessive scar tissue, rashes, and burns,[38] and as an eye poultice to treat infection.[21] Honey is taken for digestive problems and as a general health restorative. It is taken hot to treat colds, cough, throat infections, laryngitis, tuberculosis, and lung diseases.[34] Apitoxin (honey bee venom) is applied via direct stings to relieve arthritis, rheumatism, polyneuritis, and asthma.[34] Propolis, a resinous, waxy mixture collected by honeybees and used as a hive insulator and sealant, is often consumed by menopausal women because of its high hormone content, and it is said to have antibiotic, anesthetic, and anti-inflammatory properties.[34] Royal jelly is used to treat anaemia, gastrointestinal ulcers, arteriosclerosis, hypo- and hypertension, and inhibition of sexual libido.[34] Finally bee bread, or bee pollen, is eaten as a generally health restorative, and is said to help treat both internal and external infections.[34] One of the major peptides in bee venom, melittin, has the potential to treat inflammation in sufferers of rheumatoid arthritis and multiple sclerosis.[39]

The rise of antibiotic resistant infections has sparked pharmaceutical research for new resources, including into arthropods.[40]

Maggot therapy uses blowfly larvae to perform wound-cleaning debridement.[41]

Cantharidin, the blister-causing oil found in several families of beetles described by the vague common name Spanish fly has been used as an aphrodisiac in some societies.[39]

Blood-feeding insects like ticks, horseflies, and mosquitoes inject multiple bioactive compounds into their prey. These insects have long been used by practitioners of Eastern Medicine to prevent blood clot formation or thrombosis, suggesting possible applications in scientific medicine.[42] Over 1280 protein families have been associated with the saliva of blood feeding organisms, including inhibitors of platelet aggregation, ADP, arachidonic acid, thrombin, PAF, anticoagulants, vasodilators, vasoconstrictors, antihistamines, sodium channel blockers, complement inhibitors, pore formers, inhibitors of angiogenesis, anaesthetics, AMPs and microbial pattern recognition molecules, and parasite enhancers/activators.[39][43][44][45]

In science and technology

Insects play an important role in biological research. Because of its small size, short generation time and high fecundity, the common fruit fly *Drosophila melanogaster* was selected as a model organism for studies of the genetics of higher eukaryotes. *D. melanogaster* has been an essential part of studies into principles like genetic linkage, interactions between genes, chromosomal genetics, evolutionary developmental biology, animal behaviour and evolution. Because genetic systems are well conserved among eukaryotes, understanding basic cellular processes like DNA replication or transcription in fruit flies helps scientists to understand those processes in other eukaryotes, including humans.[46] The genome of *D. melanogaster* was sequenced in 2000, reflecting the fruit fly's important role in biological research. 70% of the fly genome is similar to the human genome, supporting the Darwinian theory of evolution from a single origin of life.[47]

Cochineal scale insects being collected from a prickly pear in Central America. Illustration by José Antonio de Alzate y Ramírez, 1777

Some hemipterans are used to produce dyestuffs such as carmine (also called cochineal). The scale insect *Dactylopius coccus* produces the brilliant red-coloured carminic acid to deter predators. Up to 100,000 scale insects are needed to make a kilogram (2.2 lbs) of cochineal dye.[48][49]

The common fruitfly *Drosophila melanogaster* is one of the most widely used model organisms in biological research.

A similarly enormous number of lac bugs are needed to make a kilogram of shellac, a brush-on colourant and wood finish.[50] Additional uses of this traditional product include the waxing of citrus fruits to extend their shelf-life, and the coating of pills to moisture-proof them, provide slow-release or mask the taste of bitter ingredients.[51]

Kermes is a red dye from the dried bodies of the females of a scale insect in the genus *Kermes*, primarily *Kermes vermilio*. *Kermes* are native to the Mediterranean region, living on the sap of the kermes oak. They were used as a red dye by the ancient Greeks and Romans. The kermes dye is a rich red, and has good colour fastness in silk and wool.[52][53][54][55][56]

Insect attributes are sometimes mimicked in architecture, as at the Eastgate Centre, Harare, which uses passive cooling, storing heat in the morning and releasing it in the warm parts of the day.[57] The target of this piece of biomimicry is the structure of the mounds of termites such as *Macrotermes michaelseni* which effectively cool the nests of these social insects.[58][59] The properties of the Namib desert beetle's exoskeleton, in particular its wing-cases (elytra) which have bumps with hydrophilic (water-attracting) tips and hydrophobic (water-shedding) sides, have been mimicked in a film coating designed for the British Ministry of Defence, to capture water in arid regions.[60][61]

Target for biomimicry research: the Namib desert beetle, *Stenocara gracilipes*, channels water from fog down its wings.

In textiles

Silkworms, the caterpillars and pupae of the moth *Bombyx mori*, have been reared to produce silk in China from the Neolithic Yangshao period onwards, c. 5000 BC.[62][63] Production spread to India by 140 AD.[64] The caterpillars are fed on mulberry leaves. The cocoon, produced after the fourth moult, is covered with a continuous filament of the silk protein, fibroin, gummed together with sericin. In the traditional process, the gum is removed by soaking in hot water, and the silk is then unwound from the cocoon and reeled. Filaments are spun together to make silk thread.[65] Commerce in silk between China and countries to its west began in ancient times, with silk known from an Egyptian mummy of 1070 BC, and later to the ancient Greeks and Romans. The silk road leading west from China was opened in the 2nd century AD, helping to drive trade in silk and other goods.[66]

In warfare

The use of insects for warfare may have been attempted in the Middle Ages or earlier, but was first systematically researched by several nations during the 20th century. It was put into practice by the Japanese army's Unit 731 in attacks on China during the Second World War, killing almost 500,000 Chinese people with fleas infected with plague and flies infected with cholera.[67][68] Also in the Second World War, the Germans explored the use of Colorado beetles to destroy enemy potato crops.[69] During the Cold War, the US Army considered using yellow fever mosquitoes to attack Soviet cities.[67]

Court Ladies Preparing Newly Woven Silk, Song dynasty, 1100–1133

Symbolic uses

In mythology and folklore

Insects have appeared in mythology around the world from ancient times. Among the insect groups featuring in myths are the bee, butterfly, cicada, fly, dragonfly, praying mantis and scarab beetle. Scarab beetles held religious and cultural symbolism in Old Egypt, Greece and some shamanistic Old World cultures. The ancient Chinese regarded cicadas as symbols of rebirth or immortality.[23][70] In the *Homeric Hymn to Aphrodite*, the goddess Aphrodite retells the legend of how Eos, the goddess of the dawn, requested Zeus to let her lover Tithonus live forever as an immortal.[71] Zeus granted her request, but, because Eos forgot to ask him to also make Tithonus ageless, Tithonus never died, but he did grow old.[71] Eventually, he became so tiny and shriveled that he turned into the first cicada.[71]

Gold plaques embossed with winged bee goddesses, perhaps the Thriai, found at Camiros Rhodes, dated to the 7th century BC.

In an ancient Sumerian poem, a fly helps the goddess Inanna when her husband Dumuzid is being chased by *galla* demons.[72] Flies also appear on Old Babylonian seals as symbols of Nergal, the god of death[72] and fly-shaped lapis lazuli beads were often worn by many different cultures in ancient Mesopotamia, along with other kinds of fly-jewellery.[72] The Akkadian *Epic of Gilgamesh* contains allusions to dragonflies, signifying the impossibility of immortality.[23][70]

Amongst the Arrernte Aborigines of Australia, honey ants and witchety grubs served as personal clan totems. In the case of the San bushmen of the Kalahari, it is the praying mantis which holds much cultural significance including creation and zen-like patience in waiting.[23][70]:9

Woolly bear caterpillar larva of the isabella tiger moth, *Pyrrharctia isabella*, is celebrated in the annual Woollybear Festival of the American Great Lakes.

Insects feature in folklore around the world. In China, farmers traditionally regulated their crop planting according to the Awakening of the Insects, when temperature shifts and monsoon rains bring insects out of hibernation. Most "awakening" customs are related to eating snacks like pancakes, parched beans, pears, and fried corn, symbolizing harmful insects in the field.[73]

In the Great Lakes region of the United States, there is an annual Woollybear Festival that has been celebrated for over 40 years. The larvae of the species *Pyrrharctia isabella* (commonly known as the isabella tiger moth), with their 13 distinct segments of black and reddish brown, have the reputation in common folklore of being able to forecast the coming winter weather.[74]

There is a common misconception that cockroaches are serious vectors of disease, but while they can carry bacteria they do not travel far, and have no bite or sting.[75][76] Their shells contain a protein, arylphorin, implicated in asthma and other respiratory conditions.[77]

Shoen Uemura - firefly, a sign of summer in Japan

Many people believe the urban myth that the daddy longlegs (Opiliones) has the most poisonous bite in the spider world, but that the fangs are too small to penetrate human skin. This is untrue on several counts. None of the known species of harvestmen have venom glands; their chelicerae are not hollowed fangs but grasping claws that are typically very small and definitely not strong enough to break human skin.[78][79]

In Japan, the emergence of fireflies and rhinoceros beetles signify the anticipated changing of the seasons.[80]

In religion

In the Brazilian Amazon, members of the Tupí–Guaraní language family have been observed using *Pachycondyla commutata* ants during female rite-of-passage ceremonies, and prescribing the sting of *Pseudomyrmex* spp. for fevers and headaches.[81]

Scarab with separate wings, c. 712-342 BC.

The red harvester ant *Pogonomyrmex californicus* has been widely used by natives of Southern California and Northern Mexico for hundreds of years in ceremonies conducted to help tribe members acquire spirit helpers through hallucination. During the ritual, young men are sent away from the tribe and consume large quantities of live, unmasticated ants under the supervision of an elderly member of the tribe. Ingestion of ants should lead to a prolonged state of unconsciousness, where dream helpers appear and serve as allies to the dreamer for the rest of his life.[82]

In art

Radha and Krishna in Rasamanjari by Bhanudatta, Basohli, c. 1670. Opaque watercolour and gold on paper, with applied beetlewing fragments

Both the symbolic form and the actual body of insects have been used to adorn humans in ancient and modern times. A recurrent theme for ancient cultures in Europe and the Near East regarded the sacred image of a bee or human with insect features. Often referred to as the bee "goddess", these images were found in gems and stones. An onyx gem from Knossos (ancient Crete) dating to approximately 1500 BC illustrates a Bee goddess with bull horns above her head. In this instance, the figure is surrounded by dogs with wings, most likely representing Hecate and Artemis – gods of the underworld, similar to the Egyptian gods Akeu and Anubis.[83]

Beetlewing art is an ancient craft technique using iridescent beetle wings practiced traditionally in Thailand, Myanmar, India, China and Japan. Beetlewing pieces are used as an adornment to paintings, textiles and jewelry. Different species of metallic wood-boring beetle wings were used depending on the region, but traditionally the most valued were those from beetles belonging to the genus Sternocera. The practice comes from across Asia and Southeast Asia, especially Thailand, Myanmar, Japan, India and China. In Thailand beetlewings were preferred to decorate clothing (shawls and Sabai cloth) and jewellery in former court circles.[84]

The Canadian entomologist Charles Howard Curran's 1945 book, *Insects of the Pacific World*, noted women from India and Sri Lanka, who kept $1\frac{1}{2}$ inch (38 mm) long, iridescent greenish coppery beetles of the species *Chrysochroa ocellata* as pets. These living jewels were worn on festive occasions, probably with a small chain attached to one leg anchored to the clothing to prevent escape. Afterwards, the insects were bathed, fed, and housed in decorative cages. Living jewelled beetles have also been worn and kept as pets in Mexico.[85]

A Dragon-fly, Two Moths, a Spider and Some Beetles, With Wild Strawberries by Jan van Kessel, 17th century. Wasp beetle, top left; clouded border moth, top right; migrant hawker dragonfly and cardinal beetle, centre left; magpie moth, centre right; cockchafer, lower left.

Butterflies have long inspired humans with their life cycle, color, and ornate patterns. The novelist Vladimir Nabokov was also a renowned butterfly expert. He published and illustrated many butterfly species, stating:

> I discovered in nature the nonutilitarian delights that I sought in art. Both were a form of magic, both were games of intricate enchantment and deception.[86]

It was the aesthetic complexity of insects that led Nabokov to reject natural selection.[87][88]

The naturalist Ian MacRae writes of butterflies:

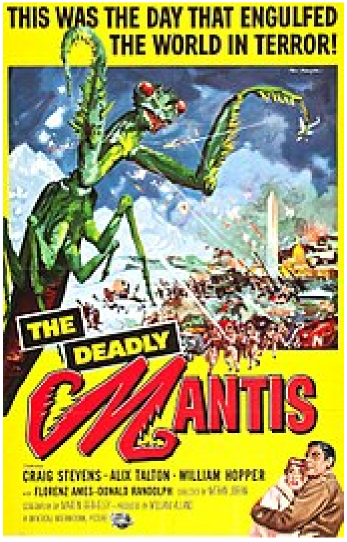
> the animal is at once awkward, flimsy, strange, bouncy in flight, yet beautiful and immensely sympathetic; it is painfully transient, albeit capable of extreme migrations and transformations. Images and phrases such as "kaleidoscopic instabilities," "oxymoron of similarities," "rebellious rainbows," "visible darkness" and "souls of stone" have much in common. They bring together the two terms of a conceptual contradiction, thereby facilitating the mixing of what should be discrete and mutually exclusive categories ... In positing such questions, butterfly science, an inexhaustible, complex, and finely nuanced field, becomes not unlike the human imagination, or the field of literature itself. In the natural history of the animal, we begin to sense its literary and artistic possibilities.[89]

The photographer Kjell Sandved spent 25 years documenting all 26 characters of the Latin alphabet using the wing patterns of butterflies and moths as *The Butterfly Alphabet*.[90]

In 2011, the artist Anna Collette created over 10,000 individual ceramic insects at Nottingham Castle, "Stirring the Swarm". Reviews of the exhibit offered a compelling narrative for cultural entomology: "the unexpected use of materials, dark overtones, and the straightforward impact of thousands of tiny multiples within the space. The exhibition was at once both exquisitely beautiful and deeply repulsive, and this strange duality was fascinating."[91][92]

In literature and film

The Ancient Greek playwright Aeschylus has a gadfly pursue and torment Io, a maiden associated with the moon, watched constantly by the eyes of the herdsman Argus, associated with all the stars: "Io: Ah! Hah! Again the prick, the stab of gadfly-sting! O earth, earth, hide, the hollow shape—Argus—that evil thing—the hundred-eyed." William Shakespeare, inspired by Aeschylus, has Tom o'Bedlam in *King Lear*, "Whom the foul fiend hath led through fire and through flame, through ford and whirlpool, o'er bog and quagmire", driven mad by the constant pursuit.[93] In *Antony and Cleopatra*, Shakespeare similarly likens Cleopatra's hasty departure from the Actium battlefield to that of a cow chased by a gadfly.[94] H. G. Wells introduced giant wasps in his 1904 novel *The Food of the Gods and How It Came to Earth*,[95] making use of the newly discovered growth hormones to lend plausibility to his science fiction.[96] Lafcadio Hearn's essay *Butterflies* analyses the treatment of the butterfly in Japanese literature, both prose and poetry. He notes that these often allude to Chinese tales, such as of the young woman that the butterflies took to be a flower. He translates 22 Japanese haiku poems about butterflies, including one by the haiku master Matsuo Bashō, said to suggest happiness in springtime: "Wake up! Wake up!—I will make thee my comrade, thou sleeping butterfly."[97]



Poster for the 1957 film *The Deadly Mantis*

The novelist Vladimir Nabokov was the son of a professional lepidopterist, and was interested in butterflies himself.[98] He wrote his novel *Lolita* while travelling on his annual butterfly-collection trips in the western United States.[99] He eventually became a leading lepidopterist. This is reflected in his fiction, where for example *The Gift* devotes two whole chapters (of five) to the tale of a father and son on a butterfly expedition.[100]

Horror films involving insects, sometimes called "big bug movies", include the pioneering 1954 *Them!*, featuring giant ants mutated by radiation, and the 1957 *The Deadly Mantis*.[101][102][103]

The Far Side, a newspaper cartoon, has been used by professor of Michael Burgett as a teaching tool in his entomology class; *The Far Side* and its author Gary Larson have been acknowledged by biologist Dale H. Clayton his colleague for "the enormous contribution" Larson has made to their field through his cartoons.[104][105]

In music

The "Flight of the Bumblebee" was written by Nikolai Rimsky-Korsakov, in 1899–1900, as part of his opera, *The Tale of Tsar Saltan*. The piece is one of the most recognizable pieces in classical composition. The bumblebee in the story is a prince who has been transformed into an insect so that he can fly off to visit his father.[106][107][108] The play upon which the opera was based – written by Alexandr Pushkin – originally had two more insect themes: the Flight of the Mosquito and the Flight of the Fly.[109]

The Hungarian composer Béla Bartók explained in his diary that he was attempting to depict the desperate attempts to escape of a fly caught in a cobweb in his piece *From the Diary of a Fly, for piano (Mikrokosmos Vol. 6/142)*.[110]

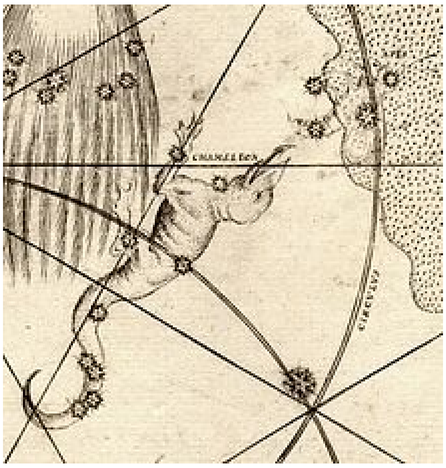
The jazz musician and philosophy professor David Rothenberg plays duets with singing insects including cicadas, crickets, and beetles.[111]

In astronomy and cosmology

In astronomy, constellations named after arthropods include the zodiacal Scorpius, the scorpion,[112][113] and Musca, the fly, also known as Apis, the bee, in the deep southern sky. Musca, the only recognised insect constellation, was named by Petrus Plancius in 1597.[114]

"The Bug Nebula", also called "The Butterfly Nebula", is a more recent discovery. Known as NGC 6302 is one of the brightest and most popular stars in the universe – popular in that its features draw the attention of a lot of researchers. It happens to be located in the Scorpius constellation. It is perfectly bipolar, and until recently, the central star was unobservable, clouded by gas, but estimated to be one of the hottest in the galaxy – 200,000 degrees Fahrenheit, perhaps 35 times hotter than our Sun.[115][116]

The honey bee played a central role in the cosmology of the Mayan people. The stucco figure at the temples of Tulum known as "Ah Mucen Kab" – the Diving Bee God – bears resemblance to the insect in the Codex Tro-Cortesianus identified as a bee. Such reliefs might have indicated towns and villages that produce honey. Modern Mayan authorities say the figure also have a connection to modern cosmology. Mayan mythology expert Migel Angel Vergara relates that the Mayans held a belief that bees came from Venus, the "Second Sun." The relief might be indicative of another "insect deity", that of Xux Ex, the Mayan "wasp



The constellation Musca (as Apis) is upper right. Detail from Johann Bayer's *Uranometria*, 1603

star."[117] The Mayan embodied Venus in the form of the god Kukulkán (also known as or related to Gukumatz and Quetzalcoatl in other parts of Mexico), Quetzalcoatl is a Mesoamerican deity whose name in Nahuatl means "feathered serpent". The cult was the first Mesoamerican religion to transcend the old Classic Period linguistic and ethnic divisions. This cult facilitated communication and peaceful trade among peoples of many different social and ethnic backgrounds.[118] Although the cult was originally centered on the ancient city of Chichén Itzá in the modern Mexican state of Yucatán, it spread as far as the Guatemalan highlands.[119]

The Butterfly Nebula, NGC 6302

In costumes

Bee and other insect costumes are worn in a variety of countries for parties, carnivals and other celebrations.[120][121]

A bee costume for a Mardi Gras celebration

Ovo is an insect-themed production by the world renowned Canadian entertainment company Cirque du Soleil. The show looks at the world of insects and its biodiversity where they go about their daily lives until a mysterious egg appears in their midst, as the insects become awestruck about this iconic object that represents the enigma and cycles of their lives. The costuming was a fusion of arthropod body types blended with superhero armour. Liz Vandal, the lead costume designer, has a special affinity for the world of the insect:[122]

> When I was just a kid I put rocks down around the yard near the fruit trees and I lifted them regularly to watch the insects who had taken up residence underneath them. I petted caterpillars and let butterflies into the house. So when I learned that OVO was inspired by insects, I immediately knew that I was in a perfect position to pay tribute to this majestic world with my costumes. All insects are beautiful and perfect; it is what they evoke for each of us that changes our perception of them."[122]

The Webby award-winning video series *Green Porno* was created to showcase the reproductive habits of insects. Jody Shapiro and Rick Gilbert were responsible for translating the research and concepts that Isabella Rossellini envisioned into the paper and paste costumes which directly contribute to the series' unique visual style. The film series was driven by the creation of costumes to translate scientific research into "something visual and how to make it comical."[123]

See also

- Arthropods in culture
- Birds in culture
- Plants in culture

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Arthropods in culture

Culture consists of the social behaviour and norms in human societies transmitted through social learning.[1] Arthropods play many roles in human culture, including as food, in art, in stories, and in mythology and religion. Many of these concern insects, which are important both economically and symbolically, from the work of honeybees to the scarabs of Ancient Egypt. Other arthropods with cultural significance include crustaceans such as crabs, lobsters, and crayfish, which are popular subjects in art, especially still lifes, and arachnids such as spiders and scorpions, whose venom has medical applications. The crab and the scorpion are astrological signs of the zodiac.

Crayfish and Two Shrimps by Utagawa Hiroshige, 1835-1845

Contents

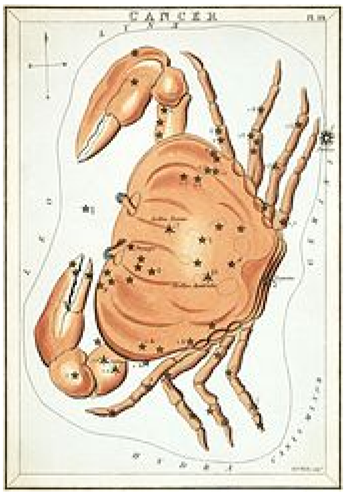
Overview

Culture consists of the social behaviour and norms found in human societies and transmitted through social learning. Cultural universals in all human societies include expressive forms like art, music, dance, ritual, religion, and technologies like tool usage, cooking, shelter, and clothing. The concept of material culture covers physical expressions such as technology, architecture and art, whereas immaterial culture includes principles of social organization, mythology, philosophy, literature, and science.[1] This article describes the roles played by arthropods in human culture.

Gold plaques embossed with winged bee goddesses, perhaps the Thriai, found at Camiros Rhodes, dated to the 7th century B.C.

The arthropods are a phylum of animals with jointed legs; they include the insects, arachnids such as spiders, myriapods, and crustaceans.[2] Insects play many roles in culture including their direct use as food,[3] in medicine,[4] for dyestuffs,[5] and in science, where the common fruit fly *Drosophila melanogaster* serves as a model organism for work in genetics and developmental biology.[6]

As food



The constellation of Cancer, the crab, from Urania's Mirror, c. 1825

Crustaceans are an important source of food, providing nearly 10,700,000 tons in 2007; the vast majority of this output is of decapods: crabs, lobsters, shrimps, crayfish, and prawns. Over 60% by weight of all crustaceans caught for consumption are shrimp and prawns, and nearly 80% is produced in Asia, with China alone producing nearly half the world's total. Non-decapod crustaceans are not widely consumed, with only 118,000 tons of krill being caught, despite krill having one of the greatest biomasses on the planet.[7][8]

Crabs make up 20% of all marine crustaceans caught, farmed, and consumed worldwide, amounting to 1.5 million tonnes annually. One species, *Portunus trituberculatus*, accounts for one-fifth of that total. Other commercially important taxa include *Portunus pelagicus*, several species in the genus *Chionoecetes*, the blue crab (*Callinectes sapidus*), *Charybdis* spp., *Cancer pagurus*, the Dungeness crab (*Metacarcinus magister*), and *Scylla serrata*, each of which yields more than 20,000 tonnes annually.[9]

Lobsters are caught using baited, one-way traps with a colour-coded marker buoy to mark cages. Lobster is fished in water between 2 and 900 metres (1 and 500 fathoms), although some lobsters live at 3,700 metres (2,000 fathoms). Cages are of plastic-coated galvanised steel or wood. A lobster fisher may tend as many as 2,000 traps. Around 2000, owing to overfishing and high demand, lobster aquaculture expanded.[10] As of 2008, no lobster aquaculture operation had achieved commercial success, mainly because lobsters eat each other (cannibalism) and the growth of the species is slow.[11]

Spiders are sometimes used as food. Cooked tarantula spiders are considered a delicacy in Cambodia,[12] and by the Piaroa Indians of southern Venezuela – provided the highly irritant hairs, the spiders' main defence system, are removed first.[13]

Cooked tarantula spiders are a delicacy in Cambodia.

In science and engineering

Insects feature in a variety of ways in biomimicry, where for example the cooling system of termite mounds has been imitated in architecture.[14]

Spider venoms may be a less polluting alternative to conventional pesticides, as they are deadly to insects but the great majority are harmless to vertebrates. Australian funnel web spiders are a promising source, as most of the world's insect pests have had no opportunity to develop any immunity to their venom, and funnel web spiders thrive in captivity and are easy to "milk". It may be possible to target specific pests by engineering genes for the production of spider toxins into viruses that infect species such as cotton bollworms.[15]

Because spider silk is both light and strong, attempts are being made to produce it in goats' milk and in the leaves of plants, by means of genetic engineering.[16][17]

In medicine

The Ch'ol Maya use a beverage created from the tarantula *Brachypelma vagans* for a condition they term 'tarantula wind', the symptoms of which include chest pain, asthma and coughing. The peptide GsMtx-4, found in the venom, has been studied for possible use in cardiac arrhythmia, muscular dystrophy, and glioma.[18] Possible medical uses for other spider venoms have been investigated for the treatment of cardiac arrhythmia,[19] Alzheimer's disease,[20] strokes,[21] and erectile dysfunction.[22]

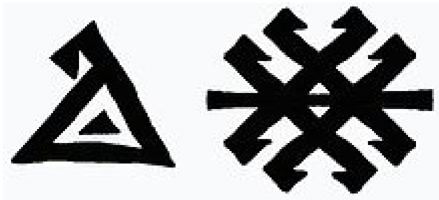
In folklore, mythology and religion

Moche ceramic spider, c. 300 AD

Arthropods appear in folklore, in mythology,[23] and in religion.[24] Since Insects in mythology and in religion are covered elsewhere, this section focuses on other arthropods.

Both the constellation Cancer and the astrological sign Cancer are named after the crab, and depicted as a crab. William Parsons, 3rd Earl of Rosse drew the Crab Nebula in 1848 and noticed its similarity to the animal; the Crab pulsar lies at the centre of the nebula.[25] The Moche people of ancient Peru worshipped nature, especially the sea,[26] and often depicted crabs in their art.[27] In Greek mythology, Karkinos was a crab that came to the aid of the Lernaean Hydra as it battled Heracles. One of Rudyard Kipling's *Just So Stories*, *The Crab that Played with the Sea*, tells the story of a gigantic crab who made the waters of the sea go up and down, like the tides.[28]

In the Japanese fairy tale "My Lord Bag of Rice", the warrior Fujiwara no Hidesato slays a giant centipede, Ōmukade, to help a dragon princess.[29]



Scorpion motif is often woven into Turkish kilim flatweave carpets, for protection from their sting (2 examples).

Spiders have been depicted in stories, mythologies and the arts of many cultures for centuries.[30] They have symbolized patience due to their hunting technique of setting webs and waiting for prey, as well as mischief and malice due to their venomous bites.[31] The Italian tarantella is a dance supposedly to rid the young woman of the lustful effects of a bite by the tarantula wolf spider, *Lycosa tarantula*.[32] Web-spinning caused the association of the spider with creation myths, as they seem to produce their own worlds.[33] Dreamcatchers are depictions of spiderwebs. The Moche people of ancient Peru worshipped nature,[34] emphasising animals and often depicting spiders in their art.[35]

The scorpion appeared as the astrological sign *Scorpio*, in the twelve signs of the Zodiac, created by Babylonian astronomers during the Chaldean period, around 600 BC.[36] In South Africa and South Asia, the scorpion is a significant animal culturally, appearing as a motif in art, especially in Islamic art in the Middle East.[37] A scorpion motif is often woven into Turkish kilim flatweave carpets, for protection from their sting.[38] The scorpion is perceived both as an embodiment of evil and a protective force that counters evil, such as a dervish's powers to combat evil.[37] In another context, the scorpion portrays human sexuality.[37] Scorpions are used in folk medicine in South Asia especially in antidotes for scorpion stings.[37] In ancient Egypt the goddess Serket was often depicted as a scorpion, one of several goddesses who protected the Pharaoh.[39]

In art, literature, and music

Insects feature in art,[40] in literature, in film,[41] and in music.

The "Lobster Quadrille", also known as "The Mock Turtle's Song", is a song recited by the Mock Turtle in *Alice's Adventures in Wonderland*, chapters 9 and 10, accompanied by a dance.[42]

The surrealist artist Salvador Dali created a sculpture called *Lobster Telephone* with the crustacean in place of the traditional handset, resting in the cradle above the dial.[43] The Surrealist filmmaker Luis Buñuel used scorpions in his 1930 classic *L'Age d'or* (*The Golden Age*).[44]

Lewis Carroll's lobster, drawn by Sir John Tenniel, 1869

Crustaceans in Roman mosaic in the 'House of the Dancing Faun', Pompeii (by 79 AD)

Still Life with Crab, Shrimps and Lobster, Clara Peeters, c. 1600

Pronk *Still life with lobster*, Jasper Geeraerts, 1650–1654

Le Crabe by William-Adolphe Bouguereau, 1869

The Lobster by Samuel Peploe, c. 1903

Illustration from *The Water-Babies* by Charles Kingsley, illustrated by Warwick Goble (d. 1943)

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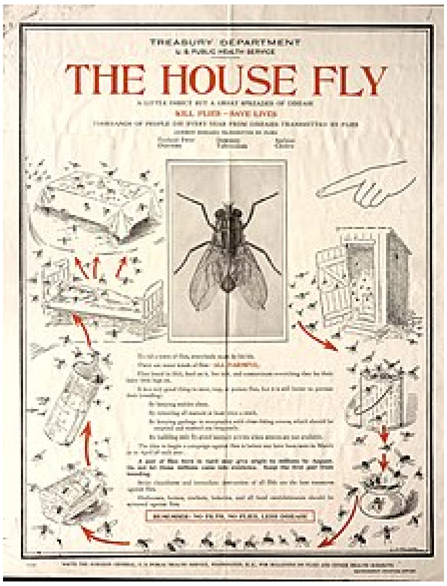
List of common household pests

This is a **list of common household pests** – undesired animals that have a history of living, invading, causing damage, eating human foods, acting as disease vectors or causing other harms in human habitation.



The house fly is found all over the world where humans live and so is the most widely distributed insect.[1]

Contents

Mammals

- Mice
  - Field mice
  - House mice
- Rats
  - Black rats
  - Brown rats
  - Wood rats
  - Cotton rats

Invertebrates

- Ants
  - Argentine ants
  - Carpenter ants
  - Fire ants
  - Odorous house ants
  - Pharaoh ants
  - Thief ants
- Bed bugs[2]
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  - Woodworms
    - Death watch beetles
    - Furniture beetles
  - Weevils
    - Maize weevil
    - Rice weevil
  - Carpet beetles

        - Fur beetles
        - Varied carpet beetles
    - Spider beetles
    - Mealworm beetles
- Centipedes
    - House centipedes
- Cockroaches
    - Brown-banded cockroaches
    - German cockroaches
    - American cockroaches
    - Oriental cockroaches
- Dust mites[3]
- Earwigs
- Crickets
    - House crickets
- Flies
    - Bottle flies
        - Blue bottle flies
        - Green bottle flies
    - House flies[1]
    - Fruit flies
- Mosquitoes
- Moths
    - Almond moths
    - Indianmeal moths
    - Clothes moths
    - Gypsy moths
        - Common clothes moths
    - Brown house moths
- Paper Lice
- Red spiders
- Silverfish
- Woodlice
- Termites[4]
    - Dampwood termites
    - Subterranean termites

See also

- Home-stored product entomology
- List of notifiable diseases
- Noxious weed
- Pest (organism)

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Entomophagy


Deep-fried insects on sale at a food stall in Bangkok, Thailand

Entomophagy (/ˌɛntəˈmɒfədʒi/, from Greek ἔντομον *éntomon*, 'insect', and φαγεῖν *phagein*, 'to eat') describes the practice of **eating insects** by humans (as well as by non-human species).

The eggs, larvae, pupae, and adults of certain insects have been eaten by humans from prehistoric times to the present day.[1] Around 3,000 ethnic groups practice entomophagy.[2] Human insect-eating is common to cultures in most parts of the world, including Central and South America, Africa, Asia, Australia, and New Zealand. Eighty percent of the world's nations eat insects of 1,000 to 2,000 species.[3][4] In some societies, primarily western nations, entomophagy is uncommon or taboo.[5][6][7][8][9][10] Today, insect eating is uncommon in North America and Europe, but insects remain a popular food elsewhere, and some companies are trying to introduce insects as food into Western diets.[11] FAO has registered some 1,900 edible insect species and estimates that there were, in 2005, some two billion insect consumers worldwide. They suggest eating insects as a possible solution to environmental degradation caused by livestock production.[12]

Contents

Definition

Entomophagy is sometimes defined broadly also to cover the eating of arthropods other than insects, including arachnids and myriapods.[13] Insects and arachnids eaten around the world include crickets, cicadas, grasshoppers, ants, various beetle grubs (such as mealworms, the larvae of the darkling beetle),[14] various species of caterpillar (such as bamboo worms, mopani worms, silkworms and waxworms), scorpions and tarantulas. There are over 1,900 known species of arthropods which are edible for humans.[15]


Mealworms presented in a bowl for human consumption

Recent assessments of the potential of large-scale entomophagy have led some experts to suggest insects as a potential alternative protein source to conventional livestock, citing possible benefits including greater efficiency, lower resource use, increased food security, and environmental and economic sustainability.[16][17][18][19]

In non-humans

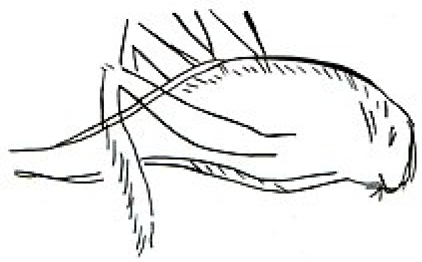
Insects,[20] nematodes[21] and fungi[22] that obtain their nutrition from insects are sometimes termed entomophagous, especially in the context of biological control applications. These may also be more specifically classified into predators, parasites or parasitoids, while viruses, bacteria and fungi that grow on or inside insects may also be termed "entomopathogenic" (see also entomopathogenic fungi).


Entomophagy among animals: The giant anteater is a mammal specialized in eating insects

History

Before humans had tools to hunt or farm, insects may have represented an important part of their diet. Evidence has been found analyzing coprolites from caves in the US and Mexico. Coprolites in caves in the Ozark Mountains were found to contain ants, beetle larvae, lice, ticks, and mites.[24] Evidence suggests that evolutionary precursors of *Homo sapiens* were also entomophagous. Insectivory also features to various degrees amongst extant primates, such as marmosets and tamarins,[25] and some researchers suggest that the earliest primates were nocturnal, arboreal insectivores.[6] Similarly, most extant apes are insectivorous to some degree.[26][27][28]

Cave paintings in Altamira, north Spain, which have been dated from about 30,000 to 9,000 BC, depict the collection of edible insects and wild bee nests, suggesting a possibly entomophagous society.[24] Cocoons of wild silkworm (*Triuncina religiosae*) were found in ruins in Shanxi Province of China, from 2,000 to 2,500 years BC. The cocoons were discovered with large holes in them, suggesting the pupae were eaten.[24] Many ancient entomophagy practices have changed little over time compared with other agricultural practices, leading to the development of modern traditional entomophagy.[24]



Carving of Cave grasshopper on animal bone discovered in the Magdalenian grotto of Les Trois Frères indicates a possible link with food magic.[23]

Eating insects in human cultures

Traditional cultures

Many cultures embrace the eating of insects. Edible insects have long been used by ethnic groups in Asia,[29][30][31][32][33][34][35] Africa, Mexico and South America as cheap and sustainable sources of protein. Up to 2,086 species are eaten by 3,071 ethnic groups in 130 countries.[4] The species include 235 butterflies and moths, 344 beetles, 313 ants, bees and wasps, 239 grasshoppers, crickets and cockroaches, 39 termites, and 20 dragonflies, as well as cicadas.[36] Insects are known to be eaten in 80 percent of the world's nations.[3]

Indonesian *botok tawon*, spiced bee larvae steamed in banana leaf package.

The leafcutter ant *Atta laevigata* is traditionally eaten in some regions of Colombia and northeast Brazil. In southern Africa, the widespread moth *Gonimbrasia belina*'s large caterpillar, the *mopani* or *mopane worm*, is a source of food protein. In Australia, the witchetty grub is eaten by the indigenous population. The grubs of *Hypoderma tarandi*, a reindeer parasite, were part of the traditional diet of the Nunamiut people.[37] *Udonga montana* is a pentatomid bug that has periodic population outbreaks and is eaten in northeastern India.[38]

Traditionally several ethnic groups in Indonesia are known to consume insects—especially grasshoppers, crickets, termites, the larvae of the sago palm weevil, and bee. In Java and Kalimantan, grasshoppers and crickets are usually lightly battered and deep fried in palm oil as a crispy *kripik* or *rempeyek* snack.[39] In Banyuwangi, East Java, there is a specialty *botok* called *botok tawon* (honeybee botok), which is beehives that contains bee larvae, being seasoned in spices and shredded coconut, wrapped inside a banana leaf package and steamed.[40] Dayak tribes of Kalimantan, also Moluccans and Papuan tribes in Eastern Indonesia, are known to consumes *ulat sagu* (lit. 'sagoo caterpillar') or larvae of sago palm weevil. This protein-rich larvae is considered as a delicacy in Papua, eaten both roasted or uncooked.[41]

In Thailand, certain insects are also consumed, especially in northern provinces. Traditional markets in Thailand often have stalls selling deep-fried grasshoppers, cricket (*ching rit*), bee larvae, silkworm (*non mai*), ant eggs (*khai mot*) and termites.[42][43]

The use of insects as an ingredient in traditional foodstuffs in places such as Hidalgo in Mexico has been on a large enough scale to cause their populations to decline.[44]

Western culture

Eating insects has not been adopted as a widespread practice in the West; however, there is a popular current trend towards the consumption of insects.[45] By 2011, a few restaurants in the Western world regularly served insects. For example, two places in Vancouver, British Columbia, Canada, offer cricket-based items. Vij's Restaurant has parathas that are made from roasted crickets that are ground into a powder or meal.[46] Its sister restaurant, Rangoli Restaurant, offers pizza that was made by sprinkling whole roasted crickets on naan dough.[46][47] Aspire Food Group was the first large-scale industrialized intensive farming entomophagy company in North America, using automated machinery in a 25,000-square-foot warehouse dedicated to raising organically-grown house crickets for human consumption.[48]

At Safeco Field, the home stadium of the baseball team the Seattle Mariners, grasshoppers are a popular novelty snack, selling in high volumes since they were introduced to the stadium's concessions stands in 2017.

Cultural taboo


Casu marzu is a traditional Sardinian sheep milk cheese that contains insect larvae.

Within Western culture, entomophagy (barring some food additives, such as carmine and shellac) is seen as taboo.[49] There are some exceptions. Casu marzu, for example, also called casu modde, casu cundhídu, or in Italian formaggio marcio, is a cheese made in Sardinia notable for being riddled with live insect larvae. Casu marzu means 'rotten cheese' in Sardinian language and is known colloquially as maggot cheese. A scene in the Italian film *Mondo Cane* (1962) features an insect banquet for shock effect, and a scene from *Indiana Jones and the Temple of Doom* features insects as part of a similar banquet for shock factor. Western avoidance of entomophagy coexists with the consumption of other invertebrates such as molluscs and the insects' close arthropod relatives crustaceans, and is not based on taste or food value.[49]

Some schools of Islamic jurisprudence consider scorpions haram, but eating locusts as halal. Others prohibit all animals that creep, including insects.[50][51]

Within Judaism, most insects are not considered kosher, with the disputed exception of a few species of "kosher locust" which are accepted by certain communities.[52]

Public health nutritionist Alan Dangour has argued that large-scale entomophagy in Western culture faces "extremely large" barriers, which are "perhaps currently even likely to be insurmountable."[53] There is widespread disgust at entomophagy in the West, the image of insects being "unclean and disease-carrying"; there have been certain notable individual exceptions, for example the celebrity Angelina Jolie has been widely pictured cooking and eating arthropod "bugs" including a spider and a scorpion, but there is little sign that this is anything other than a case of a single celebrity trying to experience a wider global perspective, nor that Jolie herself eats insects as a primary part of her diet, as opposed to experimentally or for the publicity value inherent in such an activity.[54] The anthropologist Marvin Harris has suggested that the eating of insects is taboo in cultures that have other protein sources which require more work to obtain, such as poultry or cattle, though there are cultures which feature both animal husbandry and entomophagy. Examples can be found in Botswana, South Africa and Zimbabwe where strong cattle-raising traditions co-exist with entomophagy of insects like the mopane worm. In addition, people in cultures where entomophagy is common are not indiscriminate in their choice of insects, as Thai consumers of insects perceive edible insects not consumed within their culture in a similar way as Western consumers.[55]

Advantages of eating insects

Food security


Deep-fried crickets

The major role of entomophagy in human food security is well-documented.[18] While more attention is needed to fully assess the potential of edible insects, they provide a natural source of essential carbohydrates, proteins, fats, minerals and vitamins, offering an opportunity to bridge the gap in protein consumption between poor and wealthy nations and also to lighten the ecological footprint.[18] Many insects contain abundant stores of lysine, an amino acid deficient in the diets of many people who depend heavily on grain.[56] Some argue that the combination of increasing land use pressure, climate change, and food grain shortages due to the use of corn as a biofuel feedstock will cause serious challenges for attempts to meet future protein demand.[17]

Fried beetles in Lao cuisine

The first publication to suggest that edible insects could ease the problems of global food shortages was by Meyer-Rochow in 1975.[57] Insects as food and feed have emerged as an especially relevant issue in the 21st century due to the rising cost of animal protein, food and feed insecurity, environmental pressures, population growth and increasing demand for protein among the middle classes.[58] At the 2013 International Conference on Forests for Food Security and Nutrition,[59] the Food and Agriculture Organization of the United Nations released a publication titled *Edible insects - Future prospects for food and feed security* describing the contribution of insects to food security.[58] It shows the many traditional and potential new uses of insects for direct human consumption and the opportunities for and constraints to farming them for food and feed. It examines the body of research on issues such as insect nutrition and food safety, the use of insects as animal feed, and the processing and preservation of insects and their products.

Fried silk worm pupae sold by a street vendor in Jinan, China, one with a bite taken out of it

Small-scale insect farming / Minilivestock

The intentional cultivation of insects and edible arthropods for human food, referred to as "minilivestock", is now emerging in animal husbandry as an ecologically sound concept. Several analyses have found insect farming to be a more environmentally friendly alternative to traditional animal livestocking.[16][60]

In Thailand, two types of edible insects (cricket and palm weevil larvae) are commonly farmed in the north and south respectively.[61] Cricket-farming approaches throughout the northeast are similar and breeding techniques have not changed much since the technology was introduced 15 years ago. Small-scale cricket farming, involving a small number of breeding tanks, is rarely found today and most of the farms are medium- or large-scale enterprises. Community cooperatives of cricket farmers have been established to disseminate information on technical farming, marketing and business issues, particularly in northeastern and northern Thailand. Cricket farming has developed into a significant animal husbandry sector and is the main source of income for a number of farmers. In 2013, there are approximately 20,000 farms operating 217,529 rearing pens.[61] Total production over the last six years (1996-2011) has averaged around 7,500 tonnes per year.

In the Western world, agricultural technology companies such as Tiny Farms[62] have been founded with the aim of modernizing insect rearing techniques, permitting the scale and efficiency gains required for insects to displace other animal proteins in the human food supply. The first domestic insect farm, LIVIN Farms Hive, has recently been successfully Kickstarted and will allow for the production of 200-500g of mealworms per week, a step toward a more distributed domestic production system.

Therapeutic foods

In 2012, Dr. Aaron T. Dossey announced that his company, All Things Bugs, had been named a Grand Challenges Explorations winner by the Bill & Melinda Gates Foundation.[63] Grand Challenges Explorations provides funding to individuals with ideas for new approaches to public health and development. The research project is titled "Good Bugs: Sustainable Food for Malnutrition in Children".[63] Director of pediatric nutrition at the University of Alabama at Birmingham Frank Franklin has argued that since low calories and low protein are the main causes of death for approximately five million children annually, insect protein formulated into a ready-to-use therapeutic food similar to Nutriset's Plumpy'Nut could have potential as a relatively inexpensive solution to malnutrition.[53] In 2009, Dr. Vercruysse from Ghent University in Belgium has proposed that insect protein can be used to generate hydrolysates, exerting both ACE inhibitory and antioxidant activity, which might be incorporated as a multifunctional ingredient into functional foods. Additionally, edible insects can provide a good source of unsaturated fats, thereby helping to reduce coronary disease.[2]

Indigenous cultivation

Edible insects can provide economic, nutritional, and ecological advantages to the indigenous populations that raise them.[64] For instance, the mopane worm of South Africa provides a "flagship taxon" for the conservation of mopane woodlands. Some researchers have argued that edible insects provide a unique opportunity for insect conservation by combining issues of food security and forest conservation through a solution which includes appropriate habitat management and recognition of local traditional knowledge and enterprises.[64] Cultures in Africa have developed unique interactions with insects as a result of their traditional ecological management practices and customs. However, senior FAO forestry officer Patrick Durst claims that "Among forest managers, there is very little knowledge or appreciation of the potential for managing and harvesting insects sustainably. On the other hand, traditional forest-dwellers and forest-dependent people often possess remarkable knowledge of the insects and their management."[65]

Similarly, Julieta Ramos-Elorduy has stated that rural populations, who primarily "search, gather, fix, commercialize and store this important natural resource", do not exterminate the species which are valuable to their lives and livelihoods.[4] According to the FAO, many experts see income opportunities for rural people involved in cultivation. However, adapting food technology and safety standards to insect-based foods would enhance these prospects by providing a clear legal foundation for insect-based foods.[65]

Pest harvesting

Some researchers have proposed entomophagy as a solution to policy incoherence created by traditional agriculture, by which conditions are created which favor a few insect species, which then multiply and are termed "pests".[17] In parts of Mexico, the grasshopper *Sphenarium purpurascens* is controlled by its capture and use as food. Such strategies allow decreased use of pesticide and create a source of income for farmers totaling nearly US$3000 per family. Environmental impact aside, some argue that pesticide use is inefficient economically due to its destruction of insects which may contain up to 75 percent animal protein in order to save crops containing no more than 14 percent protein.[17]

Larvae of the sago palm weevil, (*Rhynchophorus ferrugineus*), a serious pest of date, coconut and oil palms, is a delicacy in Papua New Guinea and eastern Indonesia.

Environmental benefits

The methods of matter assimilation and nutrient transport used by insects make insect cultivation a more efficient method of converting plant material into biomass than rearing traditional livestock. More than 10 times more plant material is needed to produce one kilogram of meat than one kilogram of insect biomass.[17] The spatial usage and water requirements are only a fraction of that required to produce the same mass of food with cattle farming. Production of 150g of grasshopper meat requires very little water, while cattle requires 3290 liters to produce the same amount of beef.[66] This indicates that lower natural resource use and ecosystem strain could be expected from insects at all levels of the supply chain.[17] Edible insects also display much faster growth and breeding cycles than traditional livestock. An analysis of the carbon intensity of five edible insect species conducted at the University of Wageningen, Netherlands found that "the average daily gain (ADG) of the five insect species studied was 4.0-19.6 percent, the minimum value of this range being close to the 3.2% reported for pigs, whereas the maximum value was 6 times higher. Compared to cattle (0.3%), insect ADG values were much higher." Additionally, all insect species studied produced much lower amounts of ammonia than conventional livestock, though further research is needed to determine the long-term impact. The authors conclude that insects could serve as a more environmentally friendly source of dietary protein.[67]

Economic benefits

Insects generally have a higher food conversion efficiency than more traditional meats, measured as efficiency of conversion of ingested food, or ECI.[68] While many insects can have an energy input to protein output ratio of around 4:1, raised livestock has a ratio closer to 54:1.[69] This is partially due to the fact that feed first needs to be grown for most traditional livestock. Additionally, endothermic (warm-blooded) vertebrates need to use a significantly greater amount of energy just to stay warm whereas ectothermic (cold-blooded) plants or insects do not.[66] An index which can be used as a measure is the Efficiency of conversion of ingested food to body substance: for example, only 10% of ingested food is converted to body substance by beef cattle, versus 19–31% by silkworms and 44% by German cockroaches. Studies concerning the house cricket (*Acheta domesticus*) provide further evidence for the efficiency of insects as a food source. When reared at 30 °C or more and fed a diet of equal quality to the diet used to rear conventional livestock, crickets showed a food conversion twice as efficient as pigs and broiler chicks, four times that of sheep, and six times higher than steers when losses in carcass trim and dressing percentage are counted.[24]

Insects reproduce at a faster rate than beef animals. A female cricket can lay from 1,200 to 1,500 eggs in three to four weeks, while for beef the ratio is four breeding animals for each market animal produced. This gives house crickets a true food conversion efficiency almost 20 times higher than beef.[24]


Mexican *chapulines*

Nutritional benefits

Insects such as crickets are a complete protein and contain a more useful amount, comparable with protein from soybeans, though less than in casein (found in foods such as cheese).[70] They have dietary fiber and include mostly unsaturated fat and contain some vitamins[71] and essential minerals.[72][73]

Impacts of animal agriculture

According to the United Nations Food and Agriculture Organization (FAO), animal agriculture makes a "very substantial contribution" to climate change, air pollution, land, soil and water degradation, land use concerns, deforestation and the reduction of biodiversity.[74] The high growth and intensity of animal agriculture has caused ecological damage worldwide; with meat production predicted to double from now to 2050, maintaining the status quo's environmental impact would demand a 50 percent reduction of impacts per unit of output. As the FAO states, animal livestock "emerges as one of the top two or three most significant contributors to the most serious environmental problems, at every scale from local to global."[74] Some researchers argue that establishing sustainable production systems will depend upon a large-scale replacement of traditional livestock with edible insects; such a shift would require a major change in Western perceptions of edible insects, pressure to conserve remaining habitats, and an economic push for food systems that incorporate insects into the supply chain.[19]

Greenhouse gas emission

In total, the emissions of the livestock sector account for 18 percent of total anthropogenic greenhouse gas emissions,[16] a greater share than the transportation sector.[74] Using the ratio between body growth realized and carbon production as an indicator of environmental impact, conventional agriculture practices entail substantial negative impacts as compared to entomophagy.[16] The University of Wageningen analysis found that the CO_2 production per kilogram of mass gain for the five insect species studied was 39-129% that of pigs and 12-54% that of cattle. This finding corroborates existing literature on the higher feed conversion efficiency of insects as compared to mammalian livestock. For four of the five species studied, GHG emission was "much lower than documented for pigs when expressed per kg of mass gain and only around 1% of the GHG emission for ruminants."[16]

Land use

Animal livestock is the largest anthropogenic user of land.[74] 26 percent of the Earth's ice-free terrestrial surface is occupied by grazing, while feedcrop production amounts to 33 percent of total arable land. Livestock production accounts for 70 percent of all agricultural land and 30 percent of the planet's land surface. According to the Food and Agriculture Organization, livestock activity such as overgrazing, erosion, and soil compaction, has been the primary cause of the degradation of 20 percent of the world's pastures and rangeland.[74] Animal livestock is responsible for 64 percent of man-made ammonia emissions, which contribute significantly to acid rain.[74] By extension, animal waste contributes to environmental pollution through nitrification and acidification of soil.[16]

Water pollution

According to the Food and Agriculture Organization, 64 percent of the world's population is expected to live in water-stressed basins by 2025. A reassessment of human usage and treatment of water resources will likely become necessary in order to meet growing population needs.[74] The FAO argues that the livestock sector is a major source of water pollution and loss of freshwater resources:

> The livestock sector [...] is probably the largest sectoral source of water pollution, contributing to eutrophication, "dead" zones in coastal areas, degradation of coral reefs, human health problems, emergence of antibiotic resistance and many others. The major sources of pollution are from animal wastes, antibiotics and hormones, chemicals from tanneries, fertilizers and pesticides used for feedcrops, and sediments from eroded pastures. Global figures are not available but in the United States, with the world's fourth largest land area, livestock are responsible for an estimated 55 percent of erosion and sediment, 37 percent of pesticide use, 50 percent of antibiotic use, and a third of the loads of nitrogen and phosphorus into freshwater resources. Livestock also affect the replenishment of freshwater by compacting soil, reducing infiltration, degrading the banks of watercourses, drying up floodplains and lowering water tables.[74]

Potential as alternative pet food

There is potential for insects to be used as a protein source in insect based pet food. Novel protein sources have possible benefits for pets with sensitive gastrointestinal tracts or food allergies, as the proteins are not recognized by the animal's body, and therefore are less likely to cause irritation.[75] Insects have also been shown to have a high palatability to both companion and livestock animals.[76] They have a good amino acid profile, and also contain many essential nutrients for companion animals. Insects have also been shown to have a high digestibility in pets.[77] There have been studies done evaluating the protein quality of commonly used insects and their nutrient values in comparison to traditional pet food protein.[78]

Disadvantages

Spoilage

Spore forming bacteria can spoil both raw and cooked insect protein, threatening to cause food poisoning. While edible insects must be processed with care, simple methods are available to prevent spoilage. Boiling before refrigeration is recommended; drying, acidification, or use in fermented foods also seem promising.[79]

Toxicity

In general, many insects are herbivorous and less problematic than omnivores. Cooking is advisable in ideal circumstances since parasites of concern may be present. But pesticide use can make insects unsuitable for human consumption. Herbicides can accumulate in insects through bioaccumulation. For example, when locust outbreaks are treated by spraying, people can no longer eat them. This may pose a problem since edible plants have been consumed by the locusts themselves.[24]

In some cases, insects may be edible regardless of their toxicity. In the Carnia region of Italy, moths of the Zygaenidae family have been eaten by children despite their potential toxicity. The moths are known to produce hydrogen cyanide precursors in both larvae and adults. However, the crops of the adult moths contain cyanogenic chemicals in extremely low quantities along with high concentrations of sugar, making *Zygaena* a convenient supplementary source of sugar during the early summer. The moths are very common and easy to catch by hand, and the low cyanogenic content makes *Zygaena* a minimally risky seasonal delicacy.[80]

Cases of lead poisoning after consumption of chapulines were reported by the California Department of Health Services in November 2003.[81] Adverse allergic reactions are also a possible hazard.[82]

Promotion and policy instruments

The Food and Agriculture Organization has displayed an interest in developing entomophagy on multiple occasions. In 2008, the FAO organized a conference to "discuss the potential for developing insects in the Asia and Pacific region.".[65] According to Durst, FAO efforts in entomophagy will focus on regions in which entomophagy has been historically accepted but has recently experienced a decline in popularity.

In 2011, the European Commission issued a request for reports on the current use of insects as food, with the promise that reports from each European Union member state would serve to inform legislative proposals for the new process for insect foods.[83] According to NPR, the European Union is investing more than 4 million dollars to research entomophagy as a human protein source.[84]

See also

- Insects in medicine
- Kunga cake
- Taboo food and drink
- *Man Eating Bugs: The Art and Science of Eating Insects* (book)
- *The Eat-A-Bug Cookbook* (book)
- Sustainable agriculture
- Human interactions with insects

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Cockroach

Cockroaches are insects of the order Blattodea, which also includes termites. About 30 cockroach species out of 4,600 are associated with human habitats. About four species are well known as pests.

The cockroaches are an ancient group, dating back at least as far as the Carboniferous period, some 320 million years ago. Those early ancestors however lacked the internal ovipositors of modern roaches. Cockroaches are somewhat generalized insects without special adaptations like the sucking mouthparts of aphids and other true bugs; they have chewing mouthparts and are likely among the most primitive of living neopteran insects. They are common and hardy insects, and can tolerate a wide range of environments from Arctic cold to tropical heat. Tropical cockroaches are often much bigger than temperate species, and, contrary to popular belief, extinct cockroach relatives and 'roachoids' such as the Carboniferous *Archimylacris* and the Permian *Apthoroblattina* were not as large as the biggest modern species.

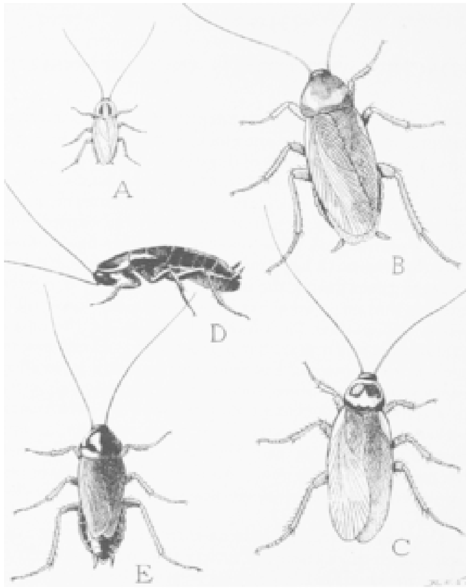
Some species, such as the gregarious German cockroach, have an elaborate social structure involving common shelter, social dependence, information transfer and kin recognition. Cockroaches have appeared in human culture since classical antiquity. They are popularly depicted as dirty pests, though the great majority of species are inoffensive and live in a wide range of habitats around the world.

Cockroach

Temporal range: 145–0 Ma

PreЄ Є O S D C P T J K PgN

Cretaceous–recent



Common household cockroaches

A) German cockroach

B) American cockroach

C) Australian cockroach

D&E) Oriental cockroach (♀ & ♂)

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Superorder:	Dictyoptera
Order:	Blattodea

Families

Blaberidae
Blattidae
Corydiidae
Cryptocercidae
Ectobiidae
Lamproblattidae
Nocticolidae
Tryonicidae

Contents

Taxonomy and evolution

A 40- to 50-million-year-old cockroach in Baltic amber (Eocene)

Cockroaches are members of the order Blattodea, which includes the termites, a group of insects once thought to be separate from cockroaches. Currently, 4,600 species and over 460 genera are described worldwide.[1][2] The name "cockroach" comes from the Spanish word for cockroach, *cucaracha*, transformed by 1620s English folk etymology into "cock" and "roach".[3] The scientific name derives from the Latin *blatta*, "an insect that shuns the light", which in classical Latin was applied to not only cockroaches, but also mantids.[4][5]

Historically, the name Blattaria was used largely interchangeably with the name Blattodea, but whilst the former name was used to refer to 'true' cockroaches exclusively, the latter also includes the termites. The current catalogue of world cockroach species uses the name Blattodea for the group.[1] Another name, Blattoptera, is also sometimes used.[6] The earliest cockroach-like fossils ("blattopterans" or "roachids") are from the Carboniferous period 320 million years ago, as are fossil roachoid nymphs.[7][8][9]

Since the 19th century, scientists believed that cockroaches were an ancient group of insects that had a Devonian origin, according to one hypothesis.[10] Fossil roachoids that lived during that time differ from modern cockroaches in having long external ovipositors and are the ancestors of mantises, as well as modern blattodeans. As the body, hind wings and mouthparts are not preserved in fossils frequently, the relationship of these roachoids and modern cockroaches remains disputed. The first fossils of modern cockroaches with internal ovipositors appeared in the early Cretaceous. A recent phylogenetic analysis suggests that cockroaches originated at least in the Jurassic.[10]

The evolutionary relationships of the Blattodea (cockroaches and termites) shown in the cladogram are based on Eggleton, Beccaloni & Inward (2007).[11] The cockroach families Lamproblattidae and Tryonicidae are not shown but are placed within the superfamily Blattoidea. The cockroach families Corydiidae and Ectobiidae were previously known as the Polyphagidae and Blattellidae.[12]

- Dictyoptera
  - **Blattodea**
    - Blattoidea
      - Termitoidea (Termites)
        - Termitidae
        - Rhinotermitidae
        - Kalotermitidae
        - Termopsidae
        - Hodotermitidae
        - Mastotermitidae
      - Cryptocercoidae
        - Cryptocercidae (brown-hooded cockroaches)
      - Blattidae (Oriental, American and other cockroaches)
    - Blaberoidea
      - Blaberidae (Giant cockroaches)
      - Ectobiidae (part)
      - Ectobiidae (part)
    - Corydioidea
      - Corydiidae (Sand cockroaches, etc)
      - Nocticolidae (Cave cockroaches, etc)

Mantodea (Mantises)

Termites were previously regarded as a separate order Isoptera to cockroaches. However, recent genetic evidence strongly suggests that they evolved directly from 'true' cockroaches, and many authors now place them as an "epifamily" of Blattodea.[11] This evidence supported a hypothesis suggested in 1934 that termites are closely related to the wood-eating cockroaches (genus *Cryptocercus*). This hypothesis was originally based on similarity of the symbiotic gut flagellates in termites regarded as living fossils and wood-eating cockroaches.[13] Additional evidence emerged when F. A. McKittrick (1965) noted similar morphological characteristics between some termites and cockroach nymphs.[14] The similarities among these cockroaches and termites have led some scientists to reclassify termites as a single family, the Termitidae, within the order Blattodea.[11][15] Other scientists have taken a more conservative approach, proposing to retain the termites as the Termitoidea, an epifamily within the order. Such measure preserves the classification of termites at family level and below.[16]

Description


Domino cockroach *Therea petiveriana*, normally found in India

Most species of cockroach are about the size of a thumbnail, but several species are bigger. The world's heaviest cockroach is the Australian giant burrowing cockroach *Macropanesthia rhinoceros*, which can reach 9 cm (3.5 in) in length and weigh more than 30 g (1.1 oz).[17] Comparable in size is the Central American giant cockroach *Blaberus giganteus*, which grows to a similar length.[18] The longest cockroach species is *Megaloblatta longipennis*, which can reach 97 mm (3.8 in) in length and 45 mm (1.8 in) across.[19] A Central and South American species, *Megaloblatta blaberoides*, has the largest wingspan of up to 185 mm (7.3 in).[20]

Cockroaches are generalized insects, with few special adaptations, and may be among the most primitive living neopteran insects. They have a relatively small head and a broad, flattened body, and most species are reddish-brown to dark brown. They have large compound eyes, two ocelli, and long, flexible antennae. The mouthparts are on the underside of the head and include generalized chewing mandibles, salivary glands and various touch and taste receptors.[21]


Head of *Periplaneta americana*

The body is divided into a thorax of three segments and a ten-segmented abdomen. The external surface has a tough exoskeleton which contains calcium carbonate and protects the inner organs and provides attachment to muscles. It is coated with wax to repel water. The wings are attached to the second and third thoracic segments. The tegmina, or first pair of wings, are tough and protective, lying as a shield on top of the membranous hind wings, which are used in flight. All four wings have branching longitudinal veins, and multiple cross-veins.[22]

The three pairs of legs are sturdy, with large coxae and five claws each.[22] They are attached to each of the three thoracic segments. The front legs are the shortest and the hind legs the longest, providing the main propulsive power when the insect runs.[21] The spines on the legs were earlier considered to be sensory, but observations of the insect's gait on sand and wire meshes have demonstrated that they help in locomotion on difficult terrain. The structures have been used as inspiration for robotic legs.[23][24]

The abdomen has ten segments, each with a pair of spiracles for respiration. Segment ten bears a pair of cerci, a pair of anal styles, the anus and the external genitalia. Males have an aedeagus through which they secrete sperm during copulation and females have spermathecae for storing sperm and an ovipositor through which the ootheca is laid.[21]

Distribution and habitat

Cockroaches are abundant throughout the world and live in a wide range of environments, especially in the tropics and subtropics.[25] Cockroaches can withstand extremely cold temperatures, allowing them to live in the Arctic. Some species are capable of surviving temperatures of −188 °F (−122 °C) by manufacturing an antifreeze made out of glycerol.[26] In North America, 50 species separated into five families are found throughout the continent.[25] 450 species are found in Australia.[27] Only about four widespread species are commonly regarded as pests.[28][29]

Cockroaches occupy a wide range of habitats. Many live in leaf litter, among the stems of matted vegetation, in rotting wood, in holes in stumps, in cavities under bark, under log piles and among debris. Some live in arid regions and have developed mechanisms to survive without access to water sources. Others are aquatic, living near the surface of water bodies, including bromeliad phytotelmata, and diving to forage for food. Most of these respire by piercing the water surface with the tip of the abdomen which acts as a snorkel, but some carry a bubble of air under their thoracic shield when they submerge. Others live in the forest canopy where they may be one of the main types of invertebrate present. Here they may hide during the day in crevices, among dead leaves, in bird and insect nests or among epiphytes, emerging at night to feed.[30]

Behavior


A cockroach soon after ecdysis

Cockroaches are social insects; a large number of species are either gregarious or inclined to aggregate, and a slightly smaller number exhibit parental care.[31] It used to be thought that cockroaches aggregated because they were reacting to environmental cues, but it is now believed that pheromones are involved in these behaviors. Some species secrete these in their feces with gut microbial symbionts being involved, while others use glands located on their mandibles. Pheromones produced by the cuticle may enable cockroaches to distinguish between different populations of cockroach by odor. The behaviors involved have been studied in only a few species, but German cockroaches leave fecal trails with an odor gradient.[31] Other cockroaches follow such trails to discover sources of food and water, and where other cockroaches are hiding. Thus, cockroaches have emergent behavior, in which group or swarm behavior emerges from a simple set of individual interactions.[32]

Daily rhythms may also be regulated by a complex set of hormonal controls of which only a small subset have been understood. In 2005, the role of one of these proteins, pigment dispersing factor (PDF), was isolated and found to be a key mediator in the circadian rhythms of the cockroach.[33]

Pest species adapt readily to a variety of environments, but prefer warm conditions found within buildings. Many tropical species prefer even warmer environments. Cockroaches are mainly nocturnal[34] and run away when exposed to light. An exception to this is the Asian cockroach, which flies mostly at night but is attracted to brightly lit surfaces and pale colors.[35]

Collective decision-making

Gregarious cockroaches display collective decision-making when choosing food sources. When a sufficient number of individuals (a "quorum") exploits a food source, this signals to newcomer cockroaches that they should stay there longer rather than leave for elsewhere.[36] Other mathematical models have been developed to explain aggregation dynamics and conspecific recognition.[37][38]

Cooperation and competition are balanced in cockroach group decision-making behavior.[32]

Cockroaches appear to use just two pieces of information to decide where to go, namely how dark it is and how many other cockroaches there are. A study used specially-scented roach-sized robots that appear to the roaches as real to demonstrate that once there are enough insects in a place to form a critical mass, the roaches accepted the collective decision on where to hide, even if this was an unusually lit place.[39]

Social behavior

When reared in isolation, German cockroaches show behavior that is different from behavior when reared in a group. In one study, isolated cockroaches were less likely to leave their shelters and explore, spent less time eating, interacted less with conspecifics when exposed to them, and took longer to recognize receptive females. Because these changes occurred in many contexts, the authors suggested them as constituting a behavioral syndrome. These effects might have been due either to reduced metabolic and developmental rates in isolated individuals or the fact that the isolated individuals hadn't had a training period to learn about what others were like via their antennae.[40]

Individual American cockroaches appear to have consistently different "personalities" regarding how they seek shelter. In addition, group personality is not simply the sum of individual choices, but reflects conformity and collective decision-making.[41][42]

The gregarious German and American cockroaches have elaborate social structure, chemical signalling, and "social herd" characteristics. Lihoreau and his fellow researchers stated:[32]

> The social biology of domiciliary cockroaches ... can be characterized by a common shelter, overlapping generations, non-closure of groups, equal reproductive potential of group members, an absence of task specialization, high levels of social dependence, central place foraging, social information transfer, kin recognition, and a meta-population structure.[32]

Sounds

Some species make a hissing noise while other cockroaches make a chirping noise. The Madagascar hissing cockroach produces its sound through the modified spiracles on the fourth abdominal segment. Several different hisses are produced, including disturbance sounds, produced by adults and larger nymphs; and aggressive, courtship and copulatory sounds produced by adult males.[43] *Henschoutedenia epilamproides* has a stridulatory organ between its thorax and abdomen, but the purpose of the sound produced is unclear.[44]

Several Australian species practice acoustic and vibration behavior as an aspect of courtship. They have been observed producing hisses and whistles from air forced through the spiracles. Furthermore, in the presence of a potential mate, some cockroaches tap the substrate in a rhythmic, repetitive manner. Acoustic signals may be of greater prevalence amongst perching species, particularly those that live on low vegetation in Australia's tropics.[45]

Biology

Digestive tract

Cockroaches are generally omnivorous; the American cockroach (*Periplaneta americana*), for example, feeds on a great variety of foodstuffs including bread, fruit, leather, starch in book bindings, paper, glue, skin flakes, hair, dead insects and soiled clothing.[46] Many species of cockroach harbor in their gut symbiotic protozoans and bacteria which are able to digest cellulose. In many species, these symbionts may be essential if the insect is to utilize cellulose; however, some species secrete cellulase in their saliva, and the wood-eating cockroach, *Panesthia cribrata*, is able to survive indefinitely on a diet of crystallized cellulose while being free of micro-organisms.[47]

The similarity of these symbionts in the genus *Cryptocercus* to those in termites are such that these cockroaches have been suggested to be more closely related to termites than to other cockroaches,[48] and current research strongly supports this hypothesis about their relationships.[49] All species studied so far carry the obligate mutualistic endosymbiont bacterium *Blattabacterium*, with the exception of *Nocticola australiensise*, an Australian cave-dwelling species without eyes, pigment or wings, which recent genetic studies indicate is a very primitive cockroach.[50][51] It had previously been thought that all five families of cockroach were descended from a common ancestor that was infected with *B. cuenoti*. It may be that *N. australiensise* subsequently lost its symbionts, or alternatively this hypothesis will need to be re-examined.[51]

Tracheae and breathing

Like other insects, cockroaches breathe through a system of tubes called tracheae which are attached to openings called spiracles on all body segments. When the carbon dioxide level in the insect rises high enough, valves on the spiracles open and carbon dioxide diffuses out and oxygen diffuses in. The tracheal system branches repeatedly, the finest tracheoles bringing air directly to each cell, allowing gaseous exchange to take place.[52]

While cockroaches do not have lungs as do vertebrates, and can continue to respire if their heads are removed, in some very large species, the body musculature may contract rhythmically to forcibly move air in and out of the spiracles; this may be considered a form of breathing.[52]

Reproduction

Cockroaches use pheromones to attract mates, and the males practice courtship rituals, such as posturing and stridulation. Like many insects, cockroaches mate facing away from each other with their genitalia in contact, and copulation can be prolonged. A few species are known to be parthenogenetic, reproducing without the need for males.[22]

Female cockroaches are sometimes seen carrying egg cases on the end of their abdomens; the German cockroach holds about 30 to 40 long, thin eggs in a case called an ootheca. She drops the capsule prior to hatching, though live births do occur in rare instances. The egg capsule may take more than five hours to lay and is initially bright white in color. The eggs are hatched from the combined pressure of the hatchlings gulping air. The hatchlings are initially bright white nymphs and continue inflating themselves with air, becoming harder and darker within about four hours. Their transient white stage while hatching and later while molting has led to claims of albino cockroaches.[22] Development from eggs to adults takes three to four months. Cockroaches live up to a year, and the female may produce up to eight egg cases in a lifetime; in favorable conditions, she can produce 300 to 400 offspring. Other species of cockroaches, however, can produce far more eggs; in some cases a female needs to be impregnated only once to be able to lay eggs for the rest of her life.[22]

The female usually attaches the egg case to a substrate, inserts it into a suitably protective crevice, or carries it about until just before the eggs hatch. Some species, however, are ovoviviparous, keeping the eggs inside their body, with or without an egg case, until they hatch. At least one genus, *Diploptera*, is fully viviparous.[22]

Cockroaches have incomplete metamorphosis, meaning that the nymphs are generally similar to the adults, except for undeveloped wings and genitalia. Development is generally slow, and may take a few months to over a year. The adults are also long-lived, and have survived for as much as four years in the laboratory.[22]

3 millimeter cockroach nymph

Female *Periplaneta fuliginosa* with ootheca

Empty ootheca

American cockroach oothecae

Hardiness

Cockroaches are among the hardiest insects. Some species are capable of remaining active for a month without food and are able to survive on limited resources, such as the glue from the back of postage stamps.[53] Some can go without air for 45 minutes. Japanese cockroach (*Periplaneta japonica*) nymphs, which hibernate in cold winters, survived twelve hours at −5 °C to −8 °C in laboratory experiments.[54]

Experiments on decapitated specimens of several species of cockroach found a variety of behavioral functionality remained, including shock avoidance and escape behavior, although many insects other than cockroaches are also able to survive decapitation, and popular claims of the longevity of headless cockroaches do not appear to be based on published research.[55][56] The severed head is able to survive and wave its antennae for several hours, or longer when refrigerated and given nutrients.[56]

It is popularly suggested that cockroaches will "inherit the earth" if humanity destroys itself in a nuclear war. Cockroaches do indeed have a much higher radiation resistance than vertebrates, with the lethal dose perhaps six to 15 times that for humans. However, they are not exceptionally radiation-resistant compared to other insects, such as the fruit fly.[57]

The cockroach's ability to withstand radiation better than human beings can be explained through the cell cycle. Cells are most vulnerable to the effects of radiation when they are dividing. A cockroach's cells divide only once each time it molts, which is weekly at most in a juvenile roach. Since not all cockroaches would be molting at the same time, many would be unaffected by an acute burst of radiation, although lingering radioactive fallout would still be harmful.[52]

Relationship with humans

In research and education

Cockroaches in research: *Periplaneta americana* in an electrophysiology experiment

Because of their ease of rearing and resilience, cockroaches have been used as insect models in the laboratory, particularly in the fields of neurobiology, reproductive physiology and social behavior.[31] The cockroach is a convenient insect to study as it is large and simple to raise in a laboratory environment. This makes it suitable both for research and for school and undergraduate biology studies. It can be used in experiments on topics such as learning, sexual pheromones, spatial orientation, aggression, activity rhythms and the biological clock, and behavioral ecology.[58] Research conducted in 2014 suggests that humans fear cockroaches the most, even more than mosquitoes, due to an evolutionary aversion.[59]

As pests

The Blattodea include some thirty species of cockroaches associated with humans; these species are atypical of the thousands of species in the order.[60] They feed on human and pet food and can leave an offensive odor.[61] They can passively transport pathogenic microbes on their body surfaces, particularly in environments such as hospitals.[62][63] Cockroaches are linked with allergic reactions in humans.[64][65] One of the proteins that trigger allergic reactions is tropomyosin.[66] These allergens are also linked with asthma.[67] About 60% of asthma patients in Chicago are also sensitive to cockroach allergens. Studies similar to this have been done globally and all the results are similar. Cockroaches can live for a few days up to a month without food, so just because no cockroaches are visible in a home does not mean they are not there. Approximately 20-48% of homes with no visible sign of cockroaches have detectable cockroach allergens in dust.[68]

Cockroaches can burrow into human ears, causing pain and hearing loss.[69][70] They may be removed with forceps, possibly after first drowning with olive oil.[71][72][73]

Control

Many remedies have been tried in the search for control of the major pest species of cockroaches, which are resilient and fast-breeding. Household chemicals like sodium bicarbonate (baking soda) have been suggested, without evidence for their effectiveness.[74] Garden herbs including bay, catnip, mint, cucumber, and garlic have been proposed as repellents.[75] Poisoned bait containing hydramethylnon or fipronil, and boric acid powder is effective on adults.[76] Baits with egg killers are also quite effective at reducing the cockroach population. Alternatively, insecticides containing deltamethrin or pyrethrin are very effective.[76] In Singapore and Malaysia, taxi drivers use pandan leaves to repel cockroaches in their vehicles.[77]

Few parasites and predators are effective for biological control of cockroaches. Parasitoidal wasps such as *Ampulex* wasps sting nerve ganglia in the cockroach's thorax, temporarily paralyzing the victim, allowing the wasp to deliver an incapacitating sting into the cockroach's brain. The wasp clips the antennae with its mandibles and drinks some hemolymph before dragging the prey to a burrow, where an egg (rarely two) is laid on it.[78] The wasp larva feeds on the subdued living cockroach.[79][80] Another wasp which is considered a promising candidate for biological control is the ensign wasp *Evania appendigaster* which attacks cockroach oothecae to lay a single egg inside.[81][82] Ongoing research is still developing technologies allowing for mass-rearing these wasps for application releases.[83][84]

Cockroaches can be trapped in a deep, smooth-walled jar baited with food inside, placed so that cockroaches can reach the opening, for example with a ramp of card or twigs on the outside. An inch or so of water or stale beer (by itself a cockroach attractant) in the jar can be used to drown any insects thus captured. The method works well with the American cockroach, but less so with the German cockroach.[85]

A study conducted by scientists at Purdue University concluded that the most common cockroaches in the US, Australia and Europe were able to develop a “cross resistance” to multiple types of pesticide. This contradicted previous understanding that the animals can develop resistance against one pesticide at a time.[86] The scientists suggested that cockroaches will no longer be easily controlled using a diverse spectrum of chemical pesticides and that a mix of other means, such as traps and better sanitation, will need to be employed.[87]

As food

Although considered disgusting in Western culture, cockroaches are eaten in many places around the world.[88][89] Whereas household pest cockroaches may carry bacteria and viruses, cockroaches bred under laboratory conditions can be used to prepare nutritious food.[90] In Mexico and Thailand, the heads and legs are removed, and the remainder may be boiled, sautéed, grilled, dried or diced.[88] In China, cockroaches have become popular as medicine and cockroach farming is rising with over 100 farms.[91] The cockroaches are fried twice in a wok of hot oil, which makes them crispy with soft innards that are like cottage cheese.[92][93] Fried cockroaches are ground and sold as pills for stomach, heart and liver diseases.[94] A cockroach recipe from Formosa (Taiwan) specifies salting and frying cockroaches after removing the head and entrails.[95]

In traditional and homeopathic medicine

In China, cockroaches are raised in large quantities for medicinal purposes.[96]

Two species of cockroach were used in homeopathic medicine in the 19th century.[97]

Conservation

While a small minority of cockroaches are associated with human habitats and viewed as repugnant by many people, a few species are of conservation concern. The Lord Howe Island wood-feeding cockroach (*Panesthia lata*) is listed as endangered by the New South Wales Scientific Committee, but the cockroach may be extinct on Lord Howe Island itself. The introduction of rats, the spread of Rhodes grass (*Chloris gayana*) and fires are possible reasons for their scarcity.[98] Two species are currently listed as endangered and critically endangered by the IUCN Red List, *Delosia ornata* and *Nocticola gerlachi*.[99][100] Both cockroaches have a restricted distribution and are threatened by habitat loss and rising sea levels. Only 600 *Delosia ornata* adults and 300 nymphs are known to exist, and these are threatened by a hotel development. No action has been taken to save the two cockroach species, but protecting their natural habitats may prevent their extinction. In the former Soviet Union, cockroach populations have been declining at an alarming rate; this may be exaggerated, or the phenomenon may be temporary or cyclic.[101] One species of roach, *Simandoa conserfariam*, is considered extinct in the wild.

Cultural depictions

Cockroaches were known and considered repellent but useful in medicines in Classical times. An insect named in Greek "σίλφη" (*silphe*) has been identified with the cockroach. It is mentioned by Aristotle, saying that it sheds its skin; it is described as foul-smelling in Aristophanes' play *Peace*; Euenus called it a pest of book collections, being "page-eating, destructive, black-bodied" in his *Analect*. Virgil named the cockroach "Lucifuga" ("one that avoids light"). Pliny the Elder recorded the use of "Blatta" in various medicines; he describes the insect as disgusting, and as seeking out dark corners to avoid the light.[102][103] Dioscorides recorded the use of the "Silphe", ground up with oil, as a remedy for earache.[103]

Madagascar hissing cockroaches kept as pets

Lafcadio Hearn (1850–1904) asserted that "For tetanus cockroach tea is given. I do not know how many cockroaches go to make up the cup; but I find that faith in this remedy is strong among many of the American population of New Orleans. A poultice of boiled cockroaches is placed over the wound." He adds that cockroaches are eaten, fried with garlic, for indigestion.[104]

Several cockroach species, such as *Blaptica dubia*, are raised as food for insectivorous pets.[105] A few cockroach species are raised as pets, most commonly the giant Madagascar hissing cockroach, *Gromphadorhina portentosa*.[106] Whilst the hissing cockroaches may be the most commonly kept species, there are many species that are kept by cockroach enthusiasts; there is even a specialist society: the Blattodea Culture Group (BCG), which was a thriving organisation for about 15 years although now appears to be dormant.[107] The BCG provided a source of literature for people interested in rearing cockroaches which was otherwise limited to either scientific papers, or general insect books, or books covering a variety of exotic pets; in the absence of an inclusive book one member published *Introduction to Rearing Cockroaches* which still appears to be the only book dedicated to rearing cockroaches.[108]

Cockroaches have been used for space tests. A cockroach given the name Nadezhda was sent into space by Russian scientists as part of a Foton-M mission, during which she mated, and later became the first terrestrial animal to produce offspring that had been conceived in space.[109]

Because of their long association with humans, cockroaches are frequently referred to in popular culture. In Western culture, cockroaches are often depicted as dirty pests.[110][111] In a 1750–1752 journal, Peter Osbeck noted that cockroaches were frequently seen and found their way to the bakeries, after the sailing ship *Gothenburg* ran aground and was destroyed by rocks.[112]

Donald Harington's satirical novel *The Cockroaches of Stay More* (Harcourt, 1989) imagines a community of "roosterroaches" in a mythical Ozark town where the insects are named after their human counterparts. Madonna has famously quoted, "I am a survivor. I am like a cockroach, you just can't get rid of me."[113] An urban legend maintains that cockroaches are immortal.[114]

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Housefly

The **housefly** (*Musca domestica*) is a fly of the suborder Cyclorrhapha. It is believed to have evolved in the Cenozoic era, possibly in the Middle East, and has spread all over the world as a commensal of humans. It is the most common fly species found in houses. Adults are grey to black, with four dark, longitudinal lines on the thorax, slightly hairy bodies, and a single pair of membranous wings. They have red eyes, set farther apart in the slightly larger female.

The female housefly usually mates only once and stores the sperm for later use. She lays batches of about 100 eggs on decaying organic matter such as food waste, carrion, or feces. These soon hatch into legless white larvae, known as maggots. After 2 to 5 days of development, these metamorphose into reddish-brown pupae, about 8 mm (0.3 in) long. Adult flies normally live for 2 to 4 weeks, but can hibernate during the winter. The adults feed on a variety of liquid or semiliquid substances, as well as solid materials which have been softened by their saliva. They can carry pathogens on their bodies and in their faeces, contaminate food, and contribute to the transfer of food-borne illnesses, while, in numbers, they can be physically annoying. For these reasons, they are considered pests.

Houseflies have been used in the laboratory in research into aging and sex determination. Flies appear in literature from Ancient Greek myth and Aesop's *The Impertinent Insect* onwards. Authors sometimes choose the fly to speak of the brevity of life, as in William Blake's 1794 poem "The Fly", which deals with mortality subject to uncontrollable circumstances.

Housefly

Conservation status	
Not evaluated (IUCN 3.1)	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Diptera
Section:	Schizophora
Family:	Muscidae
Genus:	*Musca*
Species:	***M. domestica***
Binomial name	
Musca domestica Linnaeus, 1758	
Subspecies	

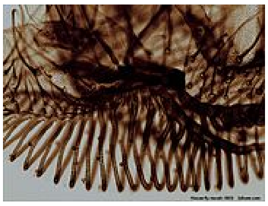
- *M. d. calleva* Walker, 1849
- *M. d. domestica* Linnaeus, 1758

Contents

Description

Head of a female housefly with two large compound eyes and three ocelli

Adult houseflies are usually 6 to 7 mm (0.24 to 0.28 in) long with a wingspan of 13 to 15 mm (0.5 to 0.6 in). The females tend to be larger winged than males, while males have relatively longer legs. Females tend to vary more in size[1] and there is geographic variation with larger individuals in higher latitudes.[2] The head is strongly convex in front and flat and slightly conical behind. The pair of large compound eyes almost touch in the male, but are more widely separated in the female. They have three simple eyes (ocelli) and a pair of short antennae.[3] Flies process visual information around seven times more quickly than humans, enabling them to identify and avoid attempts to catch or swat them, since they effectively see the human's movements in slow motion with their higher flicker fusion rate.[4][5]

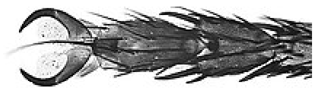


Mouthparts, showing the pseudotracheae, semitubular grooves (dark parallel bands) used for sucking up liquid food

The mouthparts are specially adapted for a liquid diet; the mandibles and maxillae are reduced and not functional, and the other mouthparts form a retractable, flexible proboscis with an enlarged, fleshy tip, the labellum. This is a sponge-like structure that is characterised by many grooves, called pseudotracheae, which suck up fluids by capillary action.[6][7] It is also used to distribute saliva to soften solid foods or collect loose particles.[8] Houseflies have chemoreceptors, organs of taste, on the tarsi of their legs, so they can identify foods such as sugars by walking over them.[9] Flies are often seen cleaning their legs by rubbing them together, enabling the chemoreceptors to taste afresh whatever they walk on next.[10] At the end of each leg is a pair of claws, and below them are two adhesive pads, pulvilli, enabling the fly to walk up smooth walls and ceilings using Van der Waals forces. The claws help the fly to unstick the foot for the next step. Flies walk with a common gait on horizontal and vertical surfaces with three legs in contact with the surface and three in movement. On inverted surfaces, they alter the gait to keep four feet stuck to the surface.[11] Flies land on a ceiling by flying straight towards it; just before landing, they make a half roll and point all six legs at the surface, absorbing the shock with the front legs and sticking a moment later with the other four.[12]

Wing, under 250x magnification

The thorax is a shade of gray, sometimes even black, with four dark, longitudinal bands of even width on the dorsal surface. The whole body is covered with short hairs. Like other Diptera, houseflies have only one pair of wings; what would be the hind pair is reduced to small halteres that aid in flight stability. The wings are translucent with a yellowish tinge at their base. Characteristically, the medial vein (M1+2 or fourth long vein) shows a sharp upward bend. Each wing has a lobe at the back, the calypter, covering the haltere. The abdomen is gray or yellowish with a dark stripe and irregular dark markings at the side. It has 10 segments which bear spiracles for respiration. In males, the ninth segment bears a pair of claspers for copulation, and the 10th bears anal cerci in both sexes.[3][13]



Micrograph of tarsus of leg, showing claws and bristles including the central one between the two pulvilli known as the empodium

A variety of species around the world appear similar to the housefly, such as the lesser house fly, *Fannia canicularis*; the stable fly, *Stomoxys calcitrans*;[13] and other members of the genus *Musca* such as *M. vetustissima*, the Australian bush fly and several closely related taxa that include *M. primitiva*, *M. shanghaiensis*, *M. violacea*, and *M. varensis*.[14] The systematic identification of species may require the use of region-specific taxonomic keys and can require dissections of the male reproductive parts for confirmation.[15][16]

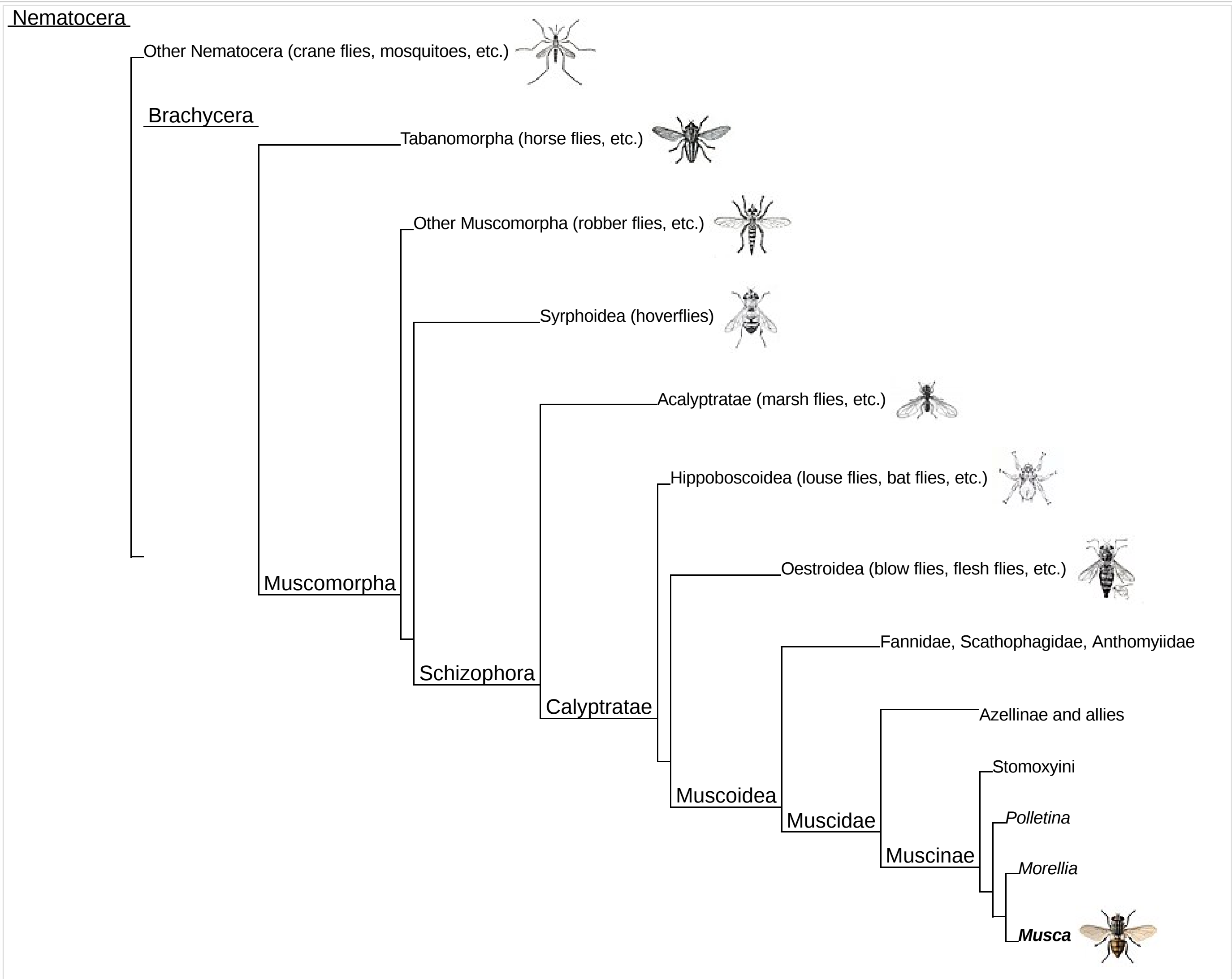
Distribution

The housefly is probably the insect with the widest distribution in the world; it is largely associated with humans and has accompanied them around the globe. It is present in the Arctic, as well as in the tropics, where it is abundant. It is present in all populated parts of Europe, Asia, Africa, Australasia, and the Americas.[3]

Evolution and taxonomy

Though the order of flies (Diptera) is much older, true houseflies are believed to have evolved in the beginning of the Cenozoic era.[17] The housefly's superfamily, Muscoidea, is most closely related to the Oestroidea (blow flies, flesh flies and allies), and more distantly to the Hippoboscoidea (louse flies, bat flies and allies). They are thought to have originated in the southern Palearctic region, particularly the Middle East. Because of their close, commensal relationship with humans, they probably owe their worldwide dispersal to co-migration with humans.[18]

The housefly was first described as *Musca domestica* in 1758 based on the common European specimens by the Swedish botanist and zoologist Carl Linnaeus in his *Systema naturae* and continues to be classified under that name.[19] A more detailed description was given in 1776 by the Danish entomologist Johan Christian Fabricius in his *Genera Insectorum*.[3]



Cladogram showing higher level classification[20][21][22] and position of *Musca* within the family Muscidae based on Couri and Carvalho 2003.[23]

Life cycle


Houseflies mating

Each female housefly can lay up to 500 eggs in her lifetime, in several batches of about 75 to 150. The eggs are white and are about 1.2 mm (0.05 in) in length, and they are deposited by the fly in a suitable place, usually dead and decaying organic matter, such as food waste, carrion, or faeces. Within a day, larvae (maggots) hatch from the eggs; they live and feed where they were laid. They are pale-whitish, 3 to 9 mm (0.12 to 0.35 in) long, thinner at the mouth end, and legless.[13] Larval development takes from two weeks, under optimal conditions, to 30 days or more in cooler conditions. The larvae avoid light; the interiors of heaps of animal manure provide nutrient-rich sites and ideal growing conditions, warm, moist, and dark.[13]

Larva and adult, by Amedeo John Engel Terzi (1872–1956)

At the end of their third instar, the larvae crawl to a dry, cool place and transform into pupae. The pupal case is cylindrical with rounded ends, about 1.2 mm (0.05 in) long, and formed from the last shed larval skin. It is yellowish at first, darkening through red and brown to nearly black as it ages. Pupae complete their development in two to six days at 35 °C (95 °F), but may take 20 days or more at 14 °C (57 °F).[13]

When metamorphosis is complete, the adult fly emerges from the pupa. To do this, it uses the ptilinum, an eversible pouch on its head, to tear open the end of the pupal case. The adult housefly lives from two weeks to a month in the wild, or longer in benign laboratory conditions. Having emerged from the pupa, it ceases to grow; a small fly is not necessarily a young fly, but is instead the result of getting insufficient food during the larval stage.[13]

Male houseflies are sexually mature after 16 hours and females after 24. Females produce a pheromone, (Z)-9-tricosene (muscalure). This cuticular hydrocarbon is not released into the air and males sense it only on contact with females;[12] it has found use as in pest control, for luring males to fly traps.[24][25] The male initiates the mating by bumping into the female, in the air or on the ground, known as a "strike". He climbs on to her thorax, and if she is receptive, a courtship period follows, in which the female vibrates her wings and the male strokes her head. The male then reverses onto her abdomen and the female pushes her ovipositor into his genital opening; copulation, with sperm transfer, lasts for several minutes. Females normally mate only once and then reject further advances from males, while males mate multiple times.[26] A volatile semiochemical that is deposited by females on their eggs attracts other gravid females and leads to clustered egg deposition.[27]

The larvae depend on warmth and sufficient moisture to develop; generally, the warmer the temperature, the faster they grow. In general, fresh swine and chicken manures present the best conditions for the developing larvae, reducing the larval period and increasing the size of the pupae. Cattle, goat, and horse manures produce fewer, smaller pupae, while fully composted swine manure, with a water content under 40%, produces none at all.[28] Pupae can range from about 8.0 to 20 milligrams (0.0003 to 0.0007 ounces) under different conditions.[29]

The lifecycle can be completed in seven to 10 days under optimal conditions, but may take up to two months in adverse circumstances. In temperate regions, 12 generations may occur per year, and in the tropics and subtropics, more than 20.[13]

Ecology


Housefly pupae killed by parasitoid wasp larvae: Each pupa has one hole through which a single adult wasp has emerged; the wasp larvae fed on the housefly larvae.

Houseflies play an important ecological role in breaking down and recycling organic matter. Adults are mainly carnivorous; their primary food is animal matter, carrion, and faeces, but they also consume milk, sugary substances, and rotting fruit and vegetables. Solid foods are softened with saliva before being sucked up.[7] They can be opportunistic blood feeders.[30] Houseflies have a mutualistic relationship with the bacterium *Klebsiella oxytoca*, which can live on the surface of housefly eggs and deter fungi which compete with the fly larvae for nutrients.[31]

Adult houseflies are diurnal and rest at night. If inside a building after dark, they tend to congregate on ceilings, beams, and overhead wires, while out of doors, they crawl into foliage or long grass, or rest in shrubs and trees or on wires.[13] In cooler climates, some houseflies hibernate in winter, choosing to do so in cracks and crevices, gaps in woodwork, and the folds of curtains. They arouse in the spring when the weather warms up, and search out a place to lay their eggs.[32]

Houseflies have many predators, including birds, reptiles, amphibians, various insects, and spiders. The eggs, larvae, and pupae have many species of stage-specific parasites and parasitoids. Some of the more important are the parasitic wasps *Muscidifurax uniraptor* and *Spalangia cameroni*; these lay their eggs in the fly larvae tissue and their offspring complete their development before the adult flies can emerge from the pupae.[13] Hister beetles feed on housefly larvae in manure heaps and the predatory mite *Macrocheles muscae domesticae* consumes housefly eggs, each mite eating 20 eggs per day.[33]

Houseflies sometimes carry phoretic (nonparasitic) passengers, including mites such as *Macrocheles muscaedomesticae*[34] and the pseudoscorpion *Lamprochernes chyzeri*.[35]

The pathogenic fungus *Entomophthora muscae* causes a fatal disease in houseflies. After infection, the fungal hyphae grow throughout the body, killing the fly in about five days. Infected flies have been known to seek high temperatures that could suppress the growth of the fungus. Affected females tend to be more attractive to males, but the fungus-host interactions have not been fully understood.[36] The housefly also acts as the alternative host to the parasitic nematode *Habronema muscae* that attacks horses.[37]

Relationship with humans

Flies are a nuisance, disturbing people at leisure and at work, but they are disliked principally because of their habits of contaminating foodstuffs. They alternate between breeding and feeding in dirty places with feeding on human foods, during which process they soften the food with saliva and deposit their feces, creating a health hazard.[38] However, fly larvae are as nutritious as fish meal, and could be used to convert waste to feed for fish and livestock.[39]

Housefly killed by the pathogenic fungus *Entomophthora muscae*

Flies have been used in art and artefacts in many cultures. In 16th- and 17th-century European vanitas paintings, flies sometimes occur as *memento mori*. They may also be used for other effects as in the Flemish painting, the *Master of Frankfurt* (1496). Fly amulets were popular in ancient Egypt.[40][41]

As a disease vector

Housefly lapping up food from a plate

Houseflies can fly for several miles from their breeding places,[42] carrying a wide variety of organisms on their hairs, mouthparts, vomitus, and faeces. Parasites carried include cysts of protozoa, e.g. *Entamoeba histolytica* and *Giardia lamblia* and eggs of helminths, e.g., *Ascaris lumbricoides, Trichuris trichiura, Hymenolepis nana*, and *Enterobius vermicularis*.[43] Houseflies do not serve as a secondary host or act as a reservoir of any bacteria of medical or veterinary importance, but they do serve as mechanical vectors to over 100 pathogens, such as those causing typhoid, cholera, salmonellosis,[44] bacillary dysentery,[45] tuberculosis, anthrax, ophthalmia,[46] and pyogenic cocci, making them especially problematic in hospitals and during outbreaks of certain diseases.[43] Disease-causing organisms on the outer surface of the fly may survive for a few hours, but those in the crop or gut can be viable for several days.[38] Usually, too few bacteria are on the external surface of the flies (except perhaps for *Shigella*) to cause infection, so the main routes to human infection are through the fly's regurgitation and defecation.[47]

In the early 20th century, Canadian public health workers believed that the control of flies was important in controlling the spread of tuberculosis. A "swat that fly" contest was held for children in Montreal in 1912.[48] Flies were targeted in 1916, when a polio epidemic broke out in the eastern United States. The belief that fly control was key to disease control continued, with extensive use of insecticidal spraying, well until the mid-1950s, declining only after the introduction of Salk's vaccine.[49] In China, Mao Zedong's Four Pests Campaign between 1958 and 1962 exhorted the people to catch and kill flies, along with rats, mosquitoes and sparrows.[50]

In warfare

During the Second World War, the Japanese worked on entomological warfare techniques under Shirō Ishii. Japanese Yagi bombs developed at Pingfan consisted of two compartments, one with houseflies and another with a bacterial slurry that coated the flies prior to release. *Vibrio cholerae*, which causes cholera, was the bacterium of choice, and was used in China in Baoshan in 1942, and in northern Shandong in 1943. Baoshan had been used by the Allies and bombing produced epidemics that killed 60,000 people in the initial stages reaching a radius of 200 km, which finally took a toll of 200,000 victims. The Shandong attack killed 210,000; the occupying Japanese troops had been vaccinated in advance.[51]

Philadelphia Department of Health poster warning the public of fly hazards (*c.* 1942)

In waste management

The ability of housefly larvae to feed and develop in a wide range of decaying organic matter is important for recycling of nutrients in nature. This could be exploited to combat ever-increasing amounts of waste.[52] Housefly larvae can be mass-reared in a controlled manner in animal manure, reducing the bulk of waste and minimizing environmental risks of its disposal.[53][54] Harvested maggots may be used as feed for animal nutrition.[54][55]

Control

Detail of a 1742 painting by Frans van der Mijn that uses a fly in a Renaissance allegory of touch theme

Flies can be controlled, at least to some extent, by physical, chemical, or biological means. Physical controls include screening with small mesh or the use of vertical strips of plastic or strings of beads in doorways to prevent entry of flies into buildings. Fans to create air movement or air barriers in doorways can deter flies from entering, and food premises often use fly-killing devices; sticky fly papers hanging from the ceiling are effective,[47] but electric "bug zappers" should not be used directly above food-handling areas because of scattering of contaminated insect parts.[56] Another approach is the elimination as far as possible of potential breeding sites. Keeping garbage in lidded containers and collecting it regularly and frequently, prevents any eggs laid from developing into adults. Unhygienic rubbish tips are a prime fly-breeding site, but if garbage is covered by a layer of soil, preferably daily, this can be avoided.[47]

Insecticides can be used. Larvicides kill the developing larvae, but large quantities may need to be used to reach areas below the surface. Aerosols can be used in buildings to "zap" flies, but outside applications are only temporarily effective. Residual sprays on walls or resting sites have a longer-lasting effect.[47] Many strains of housefly have become immune to the most commonly used insecticides.[57][58]

Several means of biological pest control have been investigated. These include the introduction of another species, the black soldier fly (*Hermetia illucens*), whose larvae compete with those of the housefly for resources.[59] The introduction of dung beetles to churn up the surface of a manure heap and render it unsuitable for breeding is another approach.[59] Augmentative biological control by releasing parasitoids can be used, but flies breed so fast that the natural enemies are unable to keep up.[60]

In science

The ease of culturing houseflies, and the relative ease of handling them when compared to the fruit fly *Drosophila*, have made them useful as model organism for use in laboratories. The American entomologist Vincent Dethier, in his humorous *To Know A Fly* (1962), pointed out that as a laboratory animal, houseflies did not trouble anyone sensitive to animal cruelty. Houseflies have a small number of chromosomes, haploid six or diploid 12.[61] Because the somatic tissue of the housefly consists of long-lived postmitotic cells, it can be used as an informative model system for understanding cumulative age-related cellular alterations. Oxidative DNA damage 8-hydroxydeoxyguanosine in houseflies was found in one study to increase with age and reduce life expectancy supporting the hypothesis that oxidative molecular damage is a causal factor in senescence (aging).[62][63][64]

The housefly is an object of biological research, partly for its variable sex-determination mechanism. Although a wide variety of sex-determination mechanisms exists in nature (e.g. male and female heterogamy, haplodiploidy, environmental factors), the way sex is determined is usually fixed within a species. The housefly is, however, thought to exhibit multiple mechanisms for sex determination, such as male heterogamy (like most insects and mammals), female heterogamy (like birds), and maternal control over offspring sex. This is because a male-determining gene (*Mdmd*) can be found on most or all housefly chromosomes.[65] Sexual differentiation is controlled as in other insects by an ancient developmental switch, doublesex, which is regulated by the transformer protein in many different insects.[66] *Mdmd* causes male development by negatively regulating *transformer*. There is also a female-determining allele of *transformer* that is not sensitive to the negative regulation of *Mdmd*.[67]

William Blake's illustration of "The Fly" in *Songs of Innocence and of Experience*, 1794

The antimicrobial peptides produced by housefly maggots are of pharmacological interest.[68]

In the 1970s, the aircraft modeller Frank Ehling constructed miniature balsa-wood aircraft powered by live houseflies.[69] Studies of tethered flies have helped in the understanding of insect vision, sensory perception, and flight control.[70]

In literature

The Impertinent Insect is a group of five fables, sometimes ascribed to Aesop, concerning an insect, in one version a fly, which puffs itself up to seem important. In the Biblical fourth plague of Egypt, flies represent death and decay, while the Philistine god Beelzebub's name may mean "lord of the flies".[71] In Greek mythology, Myiagros was a god who chased away flies during the sacrifices to Zeus and Athena; Zeus sent a fly to bite Pegasus, causing Bellerophon to fall back to Earth when he attempted to ride the winged steed to Mount Olympus.[72] In the traditional Navajo religion, Big Fly is an important spirit being.[73][74][75]

William Blake's 1794 poem "The Fly", part of his collection *Songs of Experience*, deals with the insect's mortality, subject to uncontrollable circumstances, just like humans.[76] Emily Dickinson's 1855 poem "I Heard a Fly Buzz When I Died" speaks of flies in the context of death.[77] In William Golding's 1954 novel *Lord of the Flies*, the fly is however a symbol of the children involved.[78]

Ogden Nash's humorous two-line 1942 poem "God in His wisdom made the fly/And then forgot to tell us why." indicates the debate about the value of biodiversity, given that even those considered by humans as pests have their place in the world's ecosystems.[79]

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Cricket (insect)

Crickets (also known as "**true crickets**"), of the family **Gryllidae**, are insects related to bush crickets, and, more distantly, to grasshoppers. The Gryllidae have mainly cylindrical bodies, round heads, and long antennae. Behind the head is a smooth, robust pronotum. The abdomen ends in a pair of long cerci; females have a long, cylindrical ovipositor. The hind legs have enlarged femora, providing power for jumping. The front wings are adapted as tough, leathery elytra, and some crickets chirp by rubbing parts of these together. The hind wings are membranous and folded when not in use for flight; many species, however, are flightless. The largest members of the family are the bull crickets, *Brachytrupes*, which are up to 5 cm (2 in) long.

More than 900 species of crickets are described; the Gryllidae are distributed all around the world except at latitudes 55° or higher, with the greatest diversity being in the tropics. They occur in varied habitats from grassland, bushes, and forests to marshes, beaches, and caves. Crickets are mainly nocturnal, and are best known for the loud, persistent, chirping song of males trying to attract females, although some species are mute. The singing species have good hearing, via the tympana on the tibiae of the front legs.

Crickets often appear as characters in literature. The Talking Cricket features in Carlo Collodi's 1883 children's book, *The Adventures of Pinocchio*, and in films based on the book. The eponymous insect is central to Charles Dickens's 1845 *The Cricket on the Hearth*, as is the chirping insect in George Selden's 1960 *The Cricket in Times Square*. Crickets are celebrated in poems by William Wordsworth, John Keats, and Du Fu. They are kept as pets in countries from China to Europe, sometimes for cricket fighting. Crickets are efficient at converting their food into body mass, making them a candidate for food production. They are used as human food in Southeast Asia, where they are sold deep-fried in markets as snacks. They are also used to feed carnivorous pets and zoo animals. In Brazilian folklore, crickets feature as omens of various events.

Cricket

Temporal range: Triassic–Recent

PreЄ Є O S D C P T J K PgN

[1]

Juvenile *Gryllus campestris*

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Orthoptera
Suborder:	Ensifera
Superfamily:	Grylloidea
Family:	Gryllidae Laicharting, 1781[2]

Subfamilies

See Taxonomy section

Synonyms[2]

- *Gryllides* Laicharting, 1781

Contents

- *Paragryllidae* Desutter-Grandcolas, 1987

Description

African field cricket *Gryllus bimaculatus*

Crickets are small to medium-sized insects with mostly cylindrical, somewhat vertically flattened bodies. The head is spherical with long slender antennae arising from cone-shaped scapes (first segments) and just behind these are two large compound eyes. On the forehead are three ocelli (simple eyes). The pronotum (first thoracic segment) is trapezoidal in shape, robust, and well-sclerotinized. It is smooth and has neither dorsal or lateral keels (ridges).[3]

At the tip of the abdomen is a pair of long cerci (paired appendages on rearmost segment), and in females, the ovipositor is cylindrical, long and narrow, smooth and shiny. The femora (third segments) of the back pair of legs are greatly enlarged for jumping. The tibiae (fourth segments) of the hind legs are armed with a number of moveable spurs, the arrangement of which is characteristic of each species. The tibiae of the front legs bear one or more tympani which are used for the reception of sound.[3]

The wings lie flat on the body and are very variable in size between species, being reduced in size in some crickets and missing in others. The fore wings are elytra made of tough chitin, acting as a protective shield for the soft parts of the body and in males, bear the stridulatory organs for the production of sound. The hind pair is membranous, folding fan-wise under the fore wings. In many species, the wings are not adapted for flight.[1]

The largest members of the family are the 5 cm (2 in)-long bull crickets (*Brachytrupes*) which excavate burrows a metre or more deep. The tree crickets (Oecanthinae) are delicate white or pale green insects with transparent fore wings, while the field crickets (Gryllinae) are robust brown or black insects.[1]

Distribution and habitat

Crickets have a cosmopolitan distribution, being found in all parts of the world with the exception of cold regions at latitudes higher than about 55° North and South. They have colonised many large and small islands, sometimes flying over the sea to reach these locations, or perhaps conveyed on floating timber or by human activity. The greatest diversity occurs in tropical locations, such as in Malaysia, where 88 species were heard chirping from a single location near Kuala Lumpur. A greater number than this could have been present because some species are mute.[1]

Crickets are found in many habitats. Members of several subfamilies are found in the upper tree canopy, in bushes, and among grasses and herbs. They also occur on the ground and in caves, and some are subterranean, excavating shallow or deep burrows. Some make home in rotting wood, and certain beach-dwelling species can run and jump over the surface of water.[1]

Biology

Defence

Crickets are relatively defenceless, soft-bodied insects. Most species are nocturnal and spend the day hidden in cracks, under bark, inside curling leaves, under stones or fallen logs, in leaf litter, or in the cracks in the ground that develop in dry weather. Some excavate their own shallow holes in rotting wood or underground and fold in their antennae to conceal their presence. Some of these burrows are temporary shelters, used for a single day, but others serve as more permanent residences and places for mating and laying eggs. Crickets burrow by loosening the soil with the mandibles and then carrying it with the limbs, flicking it backwards with the hind legs or pushing it with the head.[4]

Other defensive strategies are the use of camouflage, fleeing, and aggression. Some species have adopted colourings, shapes, and patterns that make it difficult for predators that hunt by sight to detect them. They tend to be dull shades of brown, grey, and green that blend into their background, and desert species tend to be pale. Some species can fly, but the mode of flight tends to be clumsy, so the most usual response to danger is to scuttle away to find a hiding place.[4]

Chirping

Most male crickets make a loud chirping sound by stridulation (scraping two specially textured limbs together). The stridulatory organ is located on the tegmen, or fore wing, which is leathery in texture. A large vein runs along the centre of each tegmen, with comb-like serrations on its edge forming a file-like structure, and at the rear edge of the tegmen is a scraper. The tegmina are held at an angle to the body and rhythmically raised and lowered which causes the scraper on one wing to rasp on the file on the other. The central part of the tegmen contains the "harp", an area of thick, sclerotinized membrane which resonates and amplifies the volume of sound, as does the pocket of air between the tegmina and the body wall. Most female crickets lack the necessary adaptations to stridulate, so make no sound.[5]

A male *Gryllus* cricket chirping: Its head faces its burrow; the leathery fore wings (tegmina; singular "tegmen") are raised (clear of the more delicate hind wings) and are being scraped against each other (stridulation) to produce the song. The burrow acts as a resonator, amplifying the sound.

Several types of cricket songs are in the repertoire of some species. The calling song attracts females and repels other males, and is fairly loud. The courting song is used when a female cricket is near and encourages her to mate with the caller. A triumphal song is produced for a brief period after a successful mating, and may reinforce the mating bond to encourage the female to lay some eggs rather than find another male.[6] An aggressive song is triggered by contact chemoreceptors on the antennae that detect the presence of another male cricket.[7]

Crickets chirp at different rates depending on their species and the temperature of their environment. Most species chirp at higher rates the higher the temperature is (about 62 chirps a minute at 13 °C (55 °F) in one common species; each species has its own rate). The relationship between temperature and the rate of chirping is known as Dolbear's law. According to this law, counting the number of chirps produced in 14 seconds by the snowy tree cricket, common in the United States, and adding 40 will approximate the temperature in degrees Fahrenheit.[6]

0:00 / 0:00

The calling song of a field cricket

In 1975, Dr. William H. Cade discovered that the parasitic tachinid fly *Ormia ochracea* is attracted to the song of the cricket, and uses it to locate the male to deposit her larvae on him. It was the first known example of a natural enemy that locates its host or prey using the mating signal.[8] Since then, many species of crickets have been found to be carrying the same parasitic fly, or related species. In response to this selective pressure, a mutation leaving males unable to chirp was observed amongst a population of *Teleogryllus oceanicus* on the Hawaiian island of Kauai, enabling these crickets to elude their parasitoid predators.[9] A different mutation with the same effect was also discovered on the neighboring island of Oahu (ca. 100 miles (160 km) away).[10] Recently, new "purring" males of the same species in Hawaii are able to produce a novel auditory sexual signal that can be used to attract females while greatly reducing the likelihood of parasitoid attack from the fly.[11]

Flight

Some species, such as the ground crickets (Nemobiinae), are wingless; others have small fore wings and no hind wings (*Copholandrevus*), others lack hind wings and have shortened fore wings in females only, while others are macropterous, with the hind wings longer than the fore wings. In *Teleogryllus*, the proportion of macropterous individuals varies from very low to 100%. Probably, most species with hind wings longer than fore wings engage in flight.[3]

Some species, such as *Gryllus assimilis*, take off, fly, and land efficiently and well, while other species are clumsy fliers.[1] In some species, the hind wings are shed, leaving wing stumps, usually after dispersal of the insect by flight. In other species, they may be pulled off and consumed by the cricket itself or by another individual, probably providing a nutritional boost.[12]

Gryllus firmus exhibits wing polymorphism; some individuals have fully functional, long hind wings and others have short wings and cannot fly. The short-winged females have smaller flight muscles, greater ovarian development, and produce more eggs, so the polymorphism adapts the cricket for either dispersal or reproduction. In some long-winged individuals, the flight muscles deteriorate during adulthood and the insect's reproductive capabilities improve.[13]

Diet

Two adult domestic crickets, *Acheta domestica*, feeding on carrot

Captive crickets are omnivorous; when deprived of their natural diet, they accept a wide range of organic foodstuffs. Some species are completely herbivorous, feeding on flowers, fruit, and leaves, with ground-based species consuming seedlings, grasses, pieces of leaf, and the shoots of young plants. Others are more predatory and include in their diet invertebrate eggs, larvae, pupae, moulting insects, scale insects, and aphids.[14] Many are scavengers and consume various organic remains, decaying plants, seedlings, and fungi.[15] In captivity, many species have been successfully reared on a diet of ground, commercial dry dog food, supplemented with lettuce and aphids.[14]

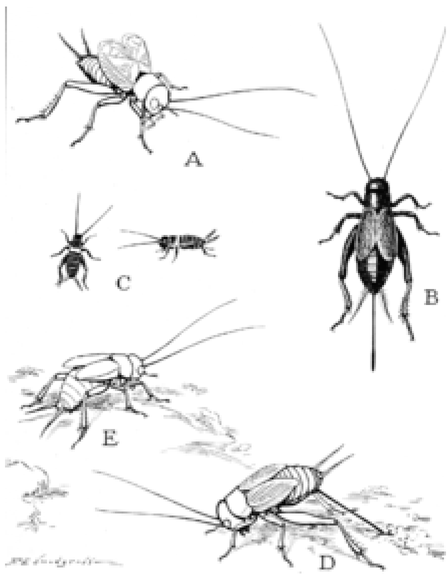
Crickets have relatively powerful jaws, and several species have been known to bite humans.[16]

Reproduction and lifecycle

Male crickets establish their dominance over each other by aggression. They start by lashing each other with their antennae and flaring their mandibles. Unless one retreats at this stage, they resort to grappling, at the same time each emitting calls that are quite unlike those uttered in other circumstances. When one achieves dominance, it sings loudly, while the loser remains silent.[17]

Females are generally attracted to males by their calls, though in nonstridulatory species, some other mechanism must be involved. After the pair has made antennal contact, a courtship period may occur during which the character of the call changes. The female mounts the male and a single spermatophore is transferred to the external genitalia of the female. Sperm flows from this into the female's oviduct over a period of a few minutes or up to an hour, depending on species. After copulation, the female may remove or eat the spermatophore; males may attempt to prevent this with various ritualised behaviours. The female may mate on several occasions with different males.[18]

Most crickets lay their eggs in the soil or inside the stems of plants, and to do this, female crickets have a long, needle-like or sabre-like egg-laying organ called an ovipositor. Some ground-dwelling species have dispensed with this, either depositing their eggs in an underground chamber or pushing them into the wall of a burrow.[1] The short-tailed cricket (*Anurogryllus*) excavates a burrow with chambers and a defecating area, lays its eggs in a pile on a chamber floor, and after the eggs have hatched, feeds the juveniles for about a month.[19]



Various instars of *Gryllus assimilis*, by Robert Evans Snodgrass, 1930

Crickets are hemimetabolic insects, whose lifecycle consists of an egg stage, a larval or nymph stage that increasingly resembles the adult form as the nymph grows, and an adult stage. The egg hatches into a nymph about the size of a fruit fly. This passes through about 10 larval stages, and with each successive moult, it becomes more like an adult. After the final moult, the genitalia and wings are fully developed, but a period of maturation is needed before the cricket is ready to breed.[20]

Inbreeding avoidance

Some species of cricket are polyandrous. In *Gryllus bimaculatus,* the females select and mate with multiple viable sperm donors, preferring novel mates.[21] Female *Teleogryllus oceanicus* crickets from natural populations similarly mate and store sperm from multiple males.[22] Female crickets exert a postcopulatory fertilization bias in favour of unrelated males to avoid the genetic consequences of inbreeding. Fertilization bias depends on the control of sperm transport to the sperm storage organs. The inhibition of sperm storage by female crickets can act as a form of cryptic female choice to avoid the severe negative effects of inbreeding.[23] Controlled-breeding experiments with the cricket *Gryllus firmus* demonstrated inbreeding depression, as nymphal weight and early fecundity declined substantially over the generations'[24] this was caused as expected by an increased frequency of homozygous combinations of deleterious recessive alleles.[24][25]

Predators, parasites, and pathogens

Crickets have many natural enemies and are subject to various pathogens and parasites. They are eaten by large numbers of vertebrate and invertebrate predators and their hard parts are often found during the examination of animal intestines.[4] Mediterranean house geckos (*Hemidactylus turcicus*) have learned that although a calling decorated cricket (*Gryllodes supplicans*) may be safely positioned in an out-of-reach burrow, female crickets attracted to the call can be intercepted and eaten.[17]


Crickets are reared as food for pets and zoo animals like this baboon spider, *Pterinochilus murinus*, emerging from its den to feed.

The entomopathogenic fungus *Metarhizium anisopliae* attacks and kills crickets and has been used as the basis of control in pest populations.[4] The insects are also affected by the cricket paralysis virus, which has caused high levels of fatalities in cricket-rearing facilities.[26] Other fatal diseases that have been identified in mass-rearing establishments include *Rickettsia* and three further viruses. The diseases may spread more rapidly if the crickets become cannibalistic and eat the corpses.[4]

Red parasitic mites sometimes attach themselves to the dorsal region of crickets and may greatly affect them.[4] The horsehair worm *Paragordius varius* is an internal parasite and can control the behaviour of its cricket host and cause it to enter water, where the parasite continues its lifecycle and the cricket likely drowns.[27] The larvae of the sarcophagid fly *Sarcophaga kellyi* develop inside the body cavity of field crickets.[28] Female parasitic wasps of *Rhopalosoma* lay their eggs on crickets, and their developing larvae gradually devour their hosts. Other wasps in the family Scelionidae are egg parasitoids, seeking out batches of eggs laid by crickets in plant tissues in which to insert their eggs.[4]

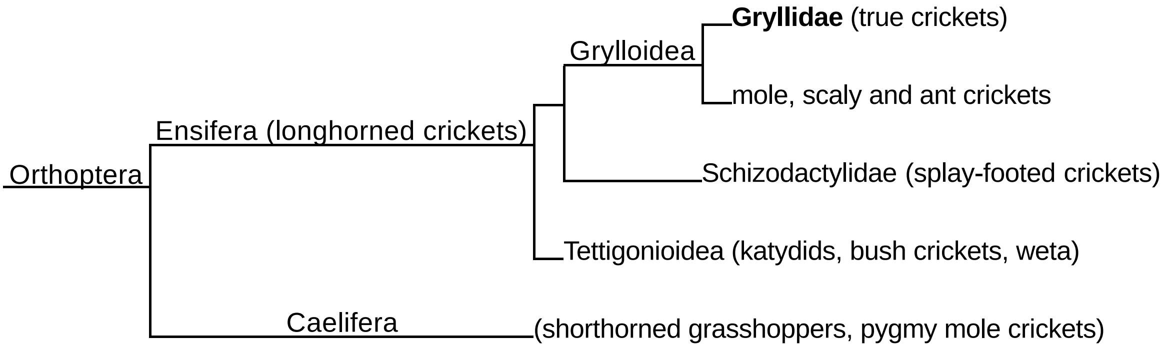
The fly *Ormia ochracea* has very acute hearing and targets calling male crickets. It locates its prey by ear and then lays its eggs nearby. The developing larvae burrow inside any crickets with which they come in contact and in the course of a week or so, devour what remains of the host before pupating.[29] In Florida, the parasitic flies were only present in the autumn, and at that time of year, the males sang less but for longer periods. A trade-off exists for the male between attracting females and being parasitized.[30]

Phylogeny and taxonomy

The phylogenetic relationships of the Gryllidae, summarized by Darryl Gwynne in 1995 from his own work (using mainly anatomical characteristics) and that of earlier authors,[a] are shown in the following cladogram, with the Orthoptera divided into two main groups, Ensifera (crickets *sensu lato*) and Caelifera (grasshoppers). Fossil Ensifera are found from the late Carboniferous period (300 Mya) onwards,[31][32] and the true crickets, Gryllidae, from the Triassic period (250 to 200 Mya).[1]


Fossil cricket from the Cretaceous of Brazil

Cladogram after Gwynne, 1995:[31]



A phylogenetic study by Jost & Shaw in 2006 using sequences from 18S, 28S, and 16S rRNA supported the monophyly of Ensifera. Most ensiferan families were also found to be monophyletic, and the superfamily Gryllacridoidea was found to include Stenopelmatidae, Anostostomatidae, Gryllacrididae and Lezina. Schizodactylidae and Grylloidea were shown to be sister taxa, and Rhaphidophoridae and Tettigoniidae were found to be more closely related to Grylloidea than had previously been thought. The authors stated that "a high degree of conflict exists between the molecular and morphological data, possibly indicating that much homoplasy is present in Ensifera, particularly in acoustic structures." They considered that tegmen stridulation and tibial tympanae are ancestral to Ensifera and have been lost on multiple occasions, especially within the Gryllidae.[33]

Subfamilies

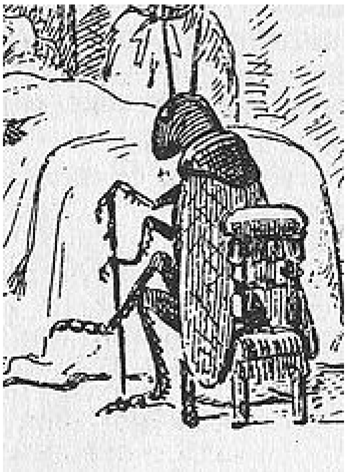
More than 900 species of Gryllidae (true crickets) are known.[34][b] The family is divided into these subfamily groups, subfamilies, and extinct genera (not placed within the subfamilies):[35]

- Subfamily group Gryllinae Laicharting, 1781 – common or field crickets
  - Gryllinae Laicharting, 1781
  - Gryllomiminae Gorochov, 1986
  - Gryllomorphinae Saussure, 1877
  - Gryllospeculinae † Gorochov, 1985
  - Itarinae Shiraki, 1930
  - Landrevinae Gorochov, 1982
  - Sclerogryllinae Gorochov, 1985
- Subfamily group Podoscirtinae
  - Euscyrtinae Gorochov, 1985
  - Hapithinae Gorochov, 1986
  - Pentacentrinae Saussure, 1878
  - Podoscirtinae Saussure, 1878 – anomalous crickets
- Subfamily group Phalangopsinae
  - Cachoplistinae Saussure, 1877
  - Paragryllinae Desutter-Grandcolas, 1987
  - Phalangopsinae Blanchard, 1845 – spider crickets
  - Phaloriinae Gorochov, 1985
  - Pteroplistinae Chopard, 1936
- Subfamily Eneopterinae Saussure, 1893 – bush crickets (American usage), not to be confused with the Tettigoniidae (katydids or bush crickets)
- Subfamily Oecanthinae Blanchard, 1845 – tree crickets
- Subfamily unplaced: extinct
  - Genus *Gryllidium* † Westwood, 1854
  - Genus *Liaonemobius* † Ren, 1998
  - Genus *Lithogryllites* † Cockerell, 1908
  - Genus *Menonia* † George, 1936
  - Genus *Nanaripegryllus* † Martins-Neto, 2002

In human culture

Folklore and myth

The folklore and mythology surrounding crickets is extensive.[36] The singing of crickets in the folklore of Brazil and elsewhere is sometimes taken to be a sign of impending rain, or of a financial windfall. In Álvar Núñez Cabeza de Vaca's chronicles of the Spanish conquest of the Americas, the sudden chirping of a cricket heralded the sighting of land for his crew, just as their water supply had run out.[37] In Caraguatatuba, Brazil, a black cricket in a room is said to portend illness; a gray one, money; and a green one, hope.[37] In Alagoas state, northeast Brazil, a cricket announces death, thus it is killed if it chirps in a house.[38] In Barbados, a loud cricket means money is coming in; hence, a cricket must not be killed or evicted if it chirps inside a house. However, another type of cricket that is less noisy forebodes illness or death.[39]



Il Grillo Parlante (The Talking Cricket) illustrated by Enrico Mazzanti for Carlo Collodi's 1883 children's book "Le avventure di Pinocchio" (*The Adventures of Pinocchio*)

In literature

Illustration for Charles Dickens's 1883 *Cricket on the Hearth* by Fred Barnard

Crickets feature as major characters in novels and children's books. Charles Dickens's 1845 novella *The Cricket on the Hearth*, divided into sections called "Chirps", tells the story of a cricket which chirps on the hearth and acts as a guardian angel to a family.[40] Carlo Collodi's 1883 children's book "Le avventure di Pinocchio" (*The Adventures of Pinocchio*) featured "Il Grillo Parlante" (The Talking Cricket) as one of its characters.[41] George Selden's 1960 children's book *The Cricket in Times Square* tells the story of Chester the cricket from Connecticut who joins a family and their other animals, and is taken to see Times Square in New York.[42] The story, which won the Newbery Honor,[43] came to Selden on hearing a real cricket chirp in Times Square.[44]

Souvenirs entomologiques, a book written by the French entomologist Jean-Henri Fabre, devotes a whole chapter to the cricket, discussing its construction of a burrow and its song-making. The account is mainly of the field cricket, but also mentions the Italian cricket.[45]

Crickets have from time to time appeared in poetry. William Wordsworth's 1805 poem *The Cottager to Her Infant* includes the couplet "The kitten sleeps upon the hearth, The crickets long have ceased their mirth".[46] John Keats's 1819 poem *Ode to Autumn* includes the lines "Hedge-crickets sing; and now with treble soft / The redbreast whistles from a garden-croft".[47] The Chinese Tang dynasty poet Du Fu (712–770) wrote a poem that in the translation by J. P. Seaton begins "House cricket ... Trifling thing. And yet how his mournful song moves us. Out in the grass his cry was a tremble, But now, he trills beneath our bed, to share his sorrow."[48]

As pets and fighting animals

Crickets are kept as pets and are considered good luck in some countries; in China, they are sometimes kept in cages or in hollowed-out gourds specially created in novel shapes.[49] The practice was common in Japan for thousands of years; it peaked in the 19th century, though crickets are still sold at pet shops.[50] It is also common to have them as caged pets in some European countries, particularly in the Iberian Peninsula. Cricket fighting is a traditional Chinese pastime that dates back to the Tang dynasty (618–907). Originally an indulgence of emperors, cricket fighting later became popular among commoners.[51] The dominance and fighting ability of males does not depend on strength alone; it has been found that they become more aggressive after certain pre-fight

Meiji period cricket holder in the form of a *norimono* palanquin, c. 1850 experiences such as isolation, or when defending a refuge. Crickets forced to fly for a short while will afterwards fight for two to three times longer than they otherwise would.[52]

As food

Deep-fried house crickets (*Acheta domesticus*) at a market in Thailand

In the southern part of Asia including Cambodia, Laos, Thailand, and Vietnam, crickets are commonly eaten as a snack, prepared by deep frying the soaked and cleaned insects.[53] In Thailand, there are 20,000 farmers rearing crickets, with an estimated production of 7,500 tons per year[54] and United Nation's FAO has implemented a project in Laos to improve cricket farming and consequently food security.[55] The food conversion efficiency of house crickets (*Acheta domesticus*) is 1.7, some five times higher than that for beef cattle, and if their fecundity is taken into account, 15 to 20 times higher.[56][57]

A cricket flour energy bar with the equivalent of approximately 40 crickets in each bar.

Cricket flour can be used as an additive to consumer foods such as pasta, bread, crackers, and cookies. The cricket flour is being used in protein bars, pet foods, livestock feed, nutraceuticals, and other industrial uses. The United Nations says the use of insect protein, such as cricket flour, could be critical in feeding the growing population of the planet while being less damaging to the environment.[58]

Crickets are also reared as food for carnivorous zoo animals, laboratory animals, and pets.[4][59] They may be "gut loaded" with additional minerals, such as calcium, to provide a balanced diet for predators such as tree frogs (Hylidae).[60]

Common expressions

By the 19th century "cricket" and "crickets" were in use as euphemisms for using Christ as an interjection. The addition of "Jiminy" (a variation of "Gemini"), sometimes shortened to "Jimmy" created the expressions "Jiminy Cricket!" or "Jimmy Crickets!" as less blasphemous alternatives to exclaiming "Jesus Christ!"[61]

By the end of the 20th century the sound of chirping crickets came to represent quietude in literature, theatre and film. From this sentiment arose expressions equating "crickets" with silence altogether, particularly when a group of assembled people makes no noise. These expressions have grown from the more descriptive, "so quiet that you can hear crickets," to simply saying , "crickets" as shorthand for "complete silence."[62]

In popular culture

Cricket characters feature in the Walt Disney animated movies *Pinocchio* (1940), where Jiminy Cricket becomes the title character's conscience, and in *Mulan* (1998), where Cri-kee is carried in a cage as a symbol of luck, in the Asian manner. The Crickets was the name of Buddy Holly's rock and roll band;[63] Holly's home town baseball team in the 1990s was called the Lubbock Crickets.[64] *Cricket* is the name of a US children's literary magazine founded in 1973; it uses a cast of insect characters.[65] The sound of crickets is often used in media to emphasize silence, often for comic effect after an awkward joke, in a similar manner to tumbleweed.[66]

Notes

Jiminy Cricket, from Walt Disney's movie *Pinocchio* (1940)

a. Gwynne cites Ander 1939, Zeuner 1939, Judd 1947, Key 1970, Ragge 1977 and Rentz 1991 as supporting the two-part scheme (Ensifera, Caelifera) in his 1995 paper.[31]

b. Some groups in the Ensifera may be called crickets *sensu lato*, including the Rhaphidophoridae – cave or camel crickets; Stenopelmatidae – Jerusalem or sand crickets; Mogoplistidae – scaly crickets; Gryllotalpidae – mole crickets; Anabrus – mormon crickets; Myrmecophilidae – ant crickets; and Tettigoniidae – katydids or bush crickets.

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Beetle

Beetles are a group of insects that form the order **Coleoptera**, in the superorder Endopterygota. Their front pair of wings are hardened into wing-cases, elytra, distinguishing them from most other insects. The Coleoptera, with about 400,000 species, is the largest of all orders, constituting almost 40% of described insects and 25% of all known animal life-forms; new species are discovered frequently. The largest of all families, the Curculionidae (weevils), with some 83,000 member species, belongs to this order. Found in almost every habitat except the sea and the polar regions, they interact with their ecosystems in several ways: beetles often feed on plants and fungi, break down animal and plant debris, and eat other invertebrates. Some species are serious agricultural pests, such as the Colorado potato beetle, while others such as Coccinellidae (ladybirds or ladybugs) eat aphids, scale insects, thrips, and other plant-sucking insects that damage crops.

Beetles typically have a particularly hard exoskeleton including the elytra, though some such as the rove beetles have very short elytra while blister beetles have softer elytra. The general anatomy of a beetle is quite uniform and typical of insects, although there are several examples of novelty, such as adaptations in water beetles which trap air bubbles under the elytra for use while diving. Beetles are endopterygotes, which means that they undergo complete metamorphosis, with a series of conspicuous and relatively abrupt changes in body structure between hatching and becoming adult after a relatively immobile pupal stage. Some, such as stag beetles, have a marked sexual dimorphism, the males possessing enormously enlarged mandibles which they use to fight other males. Many beetles are aposematic, with bright colours and patterns warning of their toxicity, while others are harmless Batesian mimics of such insects. Many beetles, including those that live in sandy places, have effective camouflage.

Beetles are prominent in human culture, from the sacred scarabs of ancient Egypt to beetlewing art and use as pets or fighting insects for entertainment and gambling. Many beetle groups are brightly and attractively coloured making them objects of collection and decorative displays. Over 300 species are used as food, mostly as larvae; species widely consumed include mealworms and rhinoceros beetle larvae. However, the major impact of beetles on human life is as agricultural, forestry, and horticultural pests. Serious pests include the boll weevil of cotton, the Colorado potato beetle, the coconut hispine beetle, and the mountain pine beetle. Most beetles, however, do not cause economic damage and many, such as the lady beetles and dung beetles are beneficial by helping to control insect pests.

Beetle

Temporal range: 318–0 Ma

PreЄ Є O S D C P T J K PgN

Late Carboniferous–Holocene

Clockwise from top left: female golden stag beetle (*Lamprima aurata*), rhinoceros beetle (*Megasoma* sp.), long nose weevil (*Rhinotia hemistictus*), cowboy beetle (*Chondropyga dorsalis*), and a species of *Amblytelus*.

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
(unranked):	Endopterygota
Order:	Coleoptera Linnaeus, 1758

Suborders

- Adephaga
- Archostemata
- Myxophaga
- Polyphaga
- †Protocoleoptera[1]

See subgroups of the order Coleoptera

Contents

Etymology

The name of the taxonomic order, Coleoptera, comes from the Greek *koleopteros* (κολεόπτερος), given to the group by Aristotle for their elytra, hardened shield-like forewings, from *koleos*, sheath, and *pteron*, wing. The English name beetle comes from the Old English word *bitela*, little biter, related to *bītan* (to bite),[2][3] leading to Middle English *betylle*.[4] Another Old English name for beetle is *ċeafor*, chafer, used in names such as cockchafer, from the Proto-Germanic **kebrô* ("beetle"; compare German *Käfer*, Dutch *kever*).[5]

Coleoptera at the Staatliches Museum für Naturkunde Karlsruhe, Germany

Distribution and diversity

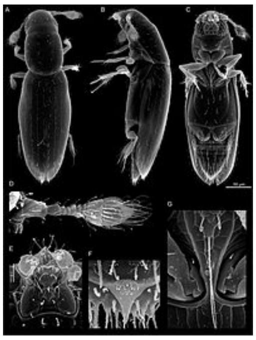
Beetles are by far the largest order of insects: the roughly 400,000 species make up about 40% of all insect species so far described, and about 25% of all animals.[1][6][7][8][9][10] A 2015 study provided four independent estimates of the total number of beetle species, giving a mean estimate of some 1.5 million with a "surprisingly narrow range"[11] spanning all four estimates from a minimum of 0.9 to a maximum of 2.1 million beetle species. The four estimates made use of host-specificity relationships (1.5 to 1.9 million), ratios with other taxa (0.9 to 1.2 million), plant:beetle ratios (1.2 to 1.3), and extrapolations based on body size by year of description (1.7 to 2.1 million).[11][12]

Beetles are found in nearly all habitats, including freshwater and coastal habitats, wherever vegetative foliage is found, from trees and their bark to flowers, leaves, and underground near roots - even inside plants in galls, in every plant tissue, including dead or decaying ones.[13] Tropical forest canopies have a large and diverse fauna of beetles,[14] including Carabidae,[15] Chrysomelidae,[16] and Scarabaeidae.[17]

The heaviest beetle, indeed the heaviest insect stage, is the larva of the goliath beetle, *Goliathus goliatus*, which can attain a mass of at least 115 g (4.1 oz) and a length of 11.5 cm (4.5 in). Adult male goliath beetles are the heaviest beetle in its adult stage, weighing 70–100 g (2.5–3.5 oz) and measuring up to 11 cm (4.3 in).[18] Adult elephant beetles, *Megasoma elephas* and *Megasoma actaeon* often reach 50 g (1.8 oz) and 10 cm (3.9 in).[19]

The longest beetle is the Hercules beetle *Dynastes hercules*, with a maximum overall length of at least 16.7 cm (6.6 in) including the very long pronotal horn. The smallest recorded beetle and the smallest free-living insect (as of 2015), is the featherwing beetle *Scydosella musawasensis* which may measure as little as 325 μm in length.[20]

Titan beetle, *Titanus giganteus*, a tropical longhorn, is one of the largest and heaviest insects in the world.

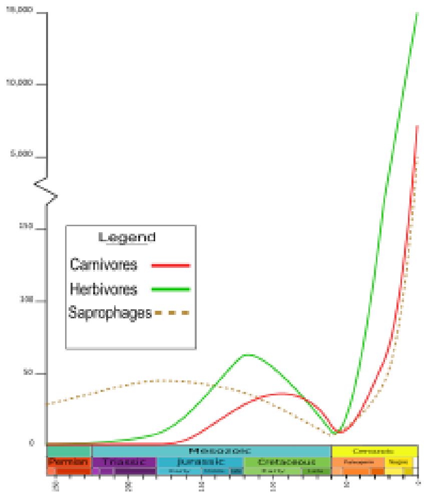


Scydosella musawasensis, the smallest known beetle: scale bar (right) is 50 μm.

Hercules beetle, *Dynastes hercules ecuatorianus*, the longest of all beetles

Evolution

Late Paleozoic



Beetle genera were mainly saprophages (detritivores) in the Permian and Triassic. During the Jurassic, herbivorous and then carnivorous genera became more common. In the Cenozoic, genera at all three trophic levels became far more numerous.

The oldest known fossil insect that unequivocally resembles a Coleopteran is from the Lower Permian Period about 270 million years ago (mya), though these members of the family Tshekardocoleidae have 13-segmented antennae, elytra with more fully developed venation and more irregular longitudinal ribbing, and abdomen and ovipositor extending beyond the apex of the elytra. In the Permian–Triassic extinction event at the end of the Permian, some 30% of all insect species became extinct, so the fossil record of insects only includes beetles from the Lower Triassic 220 mya. Around this time, during the Late Triassic, fungus-feeding species such as Cupedidae appear in the fossil record. In the stages of the Upper Triassic, alga-feeding insects such as Triaplidae and Hydrophilidae begin to appear, alongside predatory water beetles. The first weevils, including the Obrienidae, appear alongside the first rove beetles (Staphylinidae), which closely resemble recent species.[21] Some entomologists are sceptical that such early insects are so closely related to present-day species, arguing that this is extremely unlikely; for example, the structure of the metepisternum suggests that the Obrienidae could be Archostemata, not weevils at all, despite fossils with weevil-like snouts.[22]

In 2009, a fossil beetle was described from the Pennsylvanian of Mazon Creek, Illinois, pushing the origin of the beetles to an earlier date, 318 to 299 mya.[23] Fossils from this time have been found in Asia and Europe, for instance in the red slate fossil beds of Niedermoschel near Mainz, Germany.[24] Further fossils have been found in Obora, Czech Republic and Tshekarda in the Ural mountains, Russia.[25] However, there are only a few fossils from North America before the middle Permian, although both Asia and North America had been united to Euramerica. The first discoveries from North America made in the Wellington formation of Oklahoma were published in 2005 and 2008.[21][26]

As a consequence of the Permian–Triassic extinction event, the fossil record of insects is scant, including beetles from the Lower Triassic.[27] However, there are a few exceptions, such as in Eastern Europe. At the Babiy Kamen site in the Kuznetsk Basin, numerous beetle fossils were discovered, including entire specimens of the infraorders Archostemata (e.g. Ademosynidae, Schizocoleidae), Adephaga (e.g., Triaplidae, Trachypachidae) and Polyphaga (e.g. Hydrophilidae, Byrrhidae, Elateroidea).[28] However, species from the families Cupedidae and Schizophoroidae are not present at this site, whereas they dominate at other fossil sites from the Lower Triassic such as Khey-Yaga, Russia, in the Korotaikha Basin.[21]

Jurassic

During the Jurassic (210 to 145 mya), there was a dramatic increase in the diversity of beetle families,[21] including the development and growth of carnivorous and herbivorous species. The Chrysomeloidea diversified around the same time, feeding on a wide array of plant hosts from cycads and conifers to angiosperms.[29] Close to the Upper Jurassic, the Cupedidae decreased, but the diversity of the early plant-eating species increased. Most recent plant-eating beetles feed on flowering plants or angiosperms, whose success contributed to a doubling of plant-eating species during the Middle Jurassic. However, the increase of the number of beetle families during the Cretaceous does not correlate with the increase of the number of angiosperm species.[30] Around the same time, numerous primitive weevils (e.g. Curculionoidea) and click beetles (e.g. Elateroidea) appeared. The first jewel beetles (e.g. Buprestidae) are present, but they remained rare until the Cretaceous.[31][32][33] The first scarab beetles were not coprophagous but presumably fed on rotting wood with the help of fungus; they are an early example of a mutualistic relationship.

There are more than 150 important fossil sites from the Jurassic, the majority in Eastern Europe and North Asia. Outstanding sites include Solnhofen in Upper Bavaria, Germany,[34] Karatau in South Kazakhstan,[35] the Yixian formation in Liaoning, North China,[36] as well as the Jiulongshan formation and further fossil sites in Mongolia. In North America there are only a few sites with fossil records of insects from the Jurassic, namely the shell limestone deposits in the Hartford basin, the Deerfield basin and the Newark basin.[21][37]

Cretaceous

The Cretaceous saw the fragmenting of the southern landmass, with the opening of the southern Atlantic Ocean and the isolation of New Zealand, while South America, Antarctica, and Australia grew more distant.[29] The diversity of Cupedidae and Archostemata decreased considerably. Predatory ground beetles (Carabidae) and rove beetles (Staphylinidae) began to distribute into different patterns; the Carabidae predominantly occurred in the warm regions, while the Staphylinidae and click beetles (Elateridae) preferred temperate climates. Likewise, predatory species of Cleroidea and Cucujoidea hunted their prey under the bark of trees together with the jewel beetles (Buprestidae). The diversity of jewel beetles increased rapidly, as they were the primary consumers of wood,[38] while longhorn beetles (Cerambycidae) were rather rare: their diversity increased only towards the end of the Upper Cretaceous.[21] The first coprophagous beetles are from the Upper Cretaceous[39] and may have lived on the excrement of herbivorous dinosaurs.[40] The first species where both larvae and adults are adapted to an aquatic lifestyle are found. Whirligig beetles (Gyrinidae) were moderately diverse, although other early beetles (e.g. Dytiscidae) were less, with the most widespread being the species of Coptoclavidae, which preyed on aquatic fly larvae.[21]

Many fossil sites worldwide contain beetles from the Cretaceous. Most are in Europe and Asia and belong to the temperate climate zone during the Cretaceous.[36] Lower Cretaceous sites include the Crato fossil beds in the Araripe basin in the Ceará, North Brazil, as well as overlying Santana formation; the latter was near the equator at that time. In Spain, important sites are near Montsec and Las Hoyas. In Australia, the Koonwarra fossil beds of the Korumburra group, South Gippsland, Victoria, are noteworthy. Major sites from the Upper Cretaceous include Kzyl-Dzhar in South Kazakhstan and Arkagala in Russia.[21]

Cenozoic

Beetle fossils are abundant in the Cenozoic; by the Quaternary (up to 1.6 mya), fossil species are identical to living ones, while from the Late Miocene (5.7 mya) the fossils are still so close to modern forms that they are most likely the ancestors of living species. The large oscillations in climate during the Quaternary caused beetles to change their geographic distributions so much that current location gives little clue to the biogeographical history of a species. It is evident that geographic isolation of populations must often have been broken as insects moved under the influence of changing climate, causing mixing of gene pools, rapid evolution, and extinctions, especially in middle latitudes.[42]

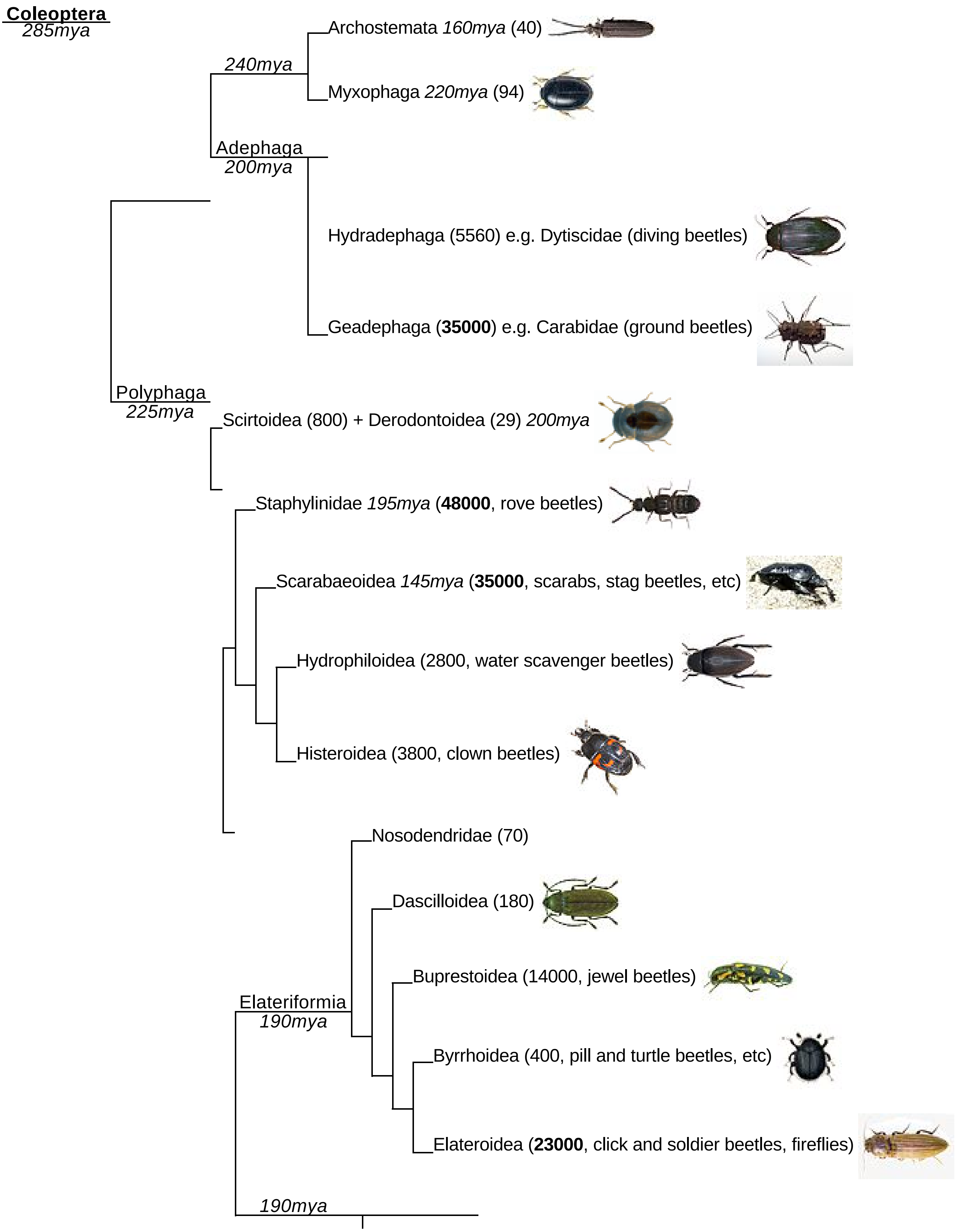
Fossil buprestid beetle from the Eocene (50 mya) Messel pit, which retains its structural color[41]

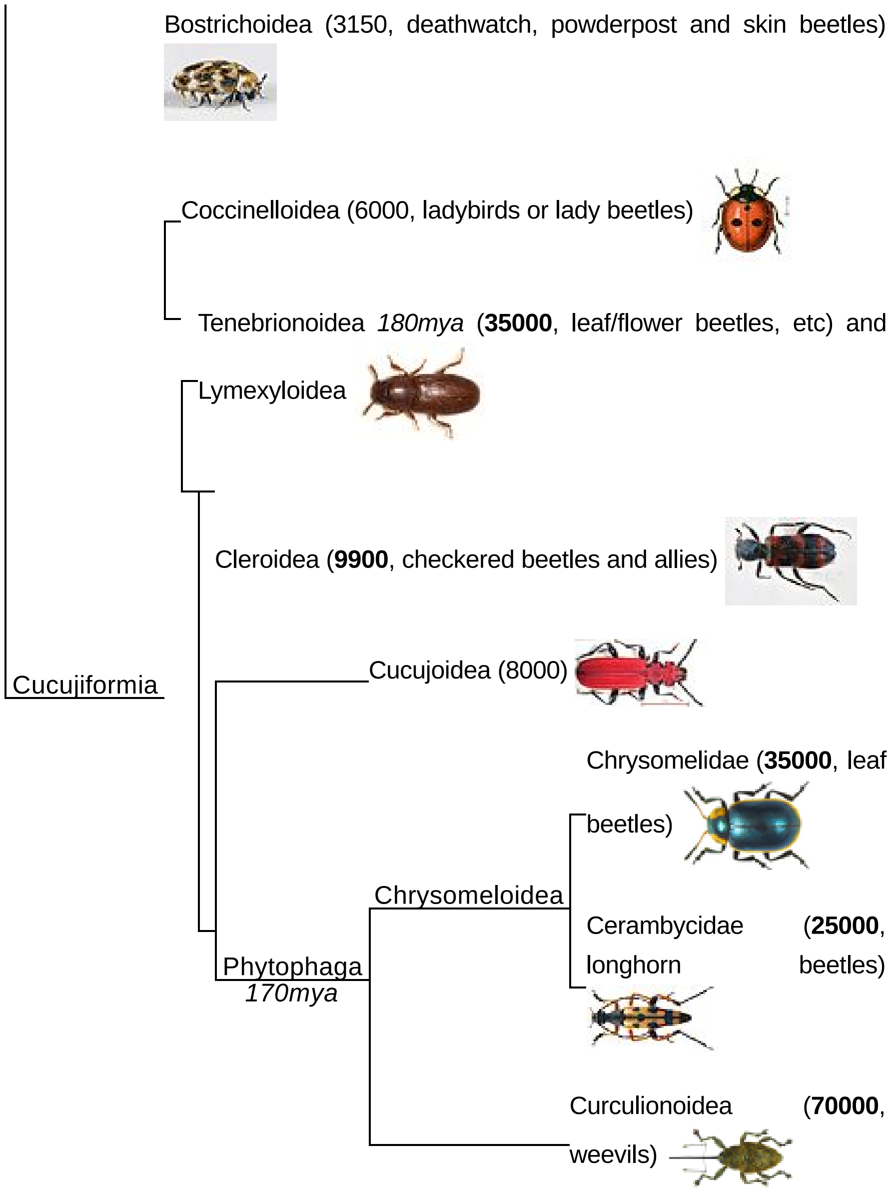
Phylogeny

The very large number of beetle species poses special problems for classification. Some families contain tens of thousands of species, and need to be divided into subfamilies and tribes. This immense number led the evolutionary biologist J. B. S. Haldane to quip, when some theologians asked him what could be inferred about the mind of the Creator from the works of His Creation, "An inordinate fondness for beetles".[43] Polyphaga is the largest suborder, containing more than 300,000 described species in more than 170 families, including rove beetles (Staphylinidae), scarab beetles (Scarabaeidae), blister beetles (Meloidae), stag beetles (Lucanidae) and true weevils (Curculionidae).[9][44] These polyphagan beetle groups can be identified by the presence of cervical sclerites (hardened parts of the head used as points of attachment for muscles) absent in the other suborders.[45] Adephaga contains about 10 families of largely predatory beetles, includes ground beetles (Carabidae), water beetles (Dytiscidae) and whirligig beetles (Gyrinidae). In these insects, the testes are tubular and the first abdominal sternum (a plate of the exoskeleton) is divided by the hind coxae (the basal joints of the beetle's legs).[46] Archostemata contains four families of mainly wood-eating beetles, including reticulated beetles (Cupedidae) and the telephone-pole beetle.[47] The Archostemata have an exposed plate called the metatrochantin in front of the basal segment or coxa of the hind leg.[48] Myxophaga contains about 65 described species in four families, mostly very small, including Hydroscaphidae and the genus *Sphaerius*.[49] The myxophagan beetles are small and mostly alga-feeders. Their mouthparts are characteristic in lacking galeae and having a mobile tooth on their left mandible.[50]

The consistency of beetle morphology, in particular their possession of elytra, has long suggested that Coleoptera is monophyletic, though there have been doubts about the arrangement of the suborders, namely the Adephaga, Archostemata, Myxophaga and Polyphaga within that clade.[51][29][52][53][54] The twisted-wing parasites, Strepsiptera, are thought to be a sister group to the beetles, having split from them in the Early Permian.[53][55][56][57]

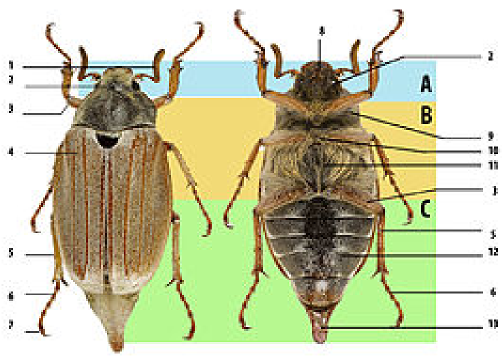
Molecular phylogenetic analysis confirms that the Coleoptera are monophyletic. Duane McKenna et al. (2015) used eight nuclear genes for 367 species from 172 of 183 Coleopteran families. They split the Adephaga into 2 clades, Hydradephaga and Geadephaga, broke up the Cucujoidea into 3 clades, and placed the Lymexyloidea within the Tenebrionoidea. The Polyphaga appear to date from the Triassic. Most extant beetle families appear to have arisen in the Cretaceous.[57] The cladogram is based on McKenna (2015).[57] The number of species in each group (mainly superfamilies) is shown in parentheses, and boldface if over 10,000.[58] English common names are given where possible. Dates of origin of major groups are shown in italics in millions of years ago (mya).[58]





External morphology

Beetles are generally characterized by a particularly hard exoskeleton and hard forewings (elytra) not usable for flying. Almost all beetles have mandibles that move in a horizontal plane. The mouthparts are rarely suctorial, though they are sometimes reduced; the maxillae always bear palps. The antennae usually have 11 or fewer segments, except in some groups like the Cerambycidae (longhorn beetles) and the Rhipiceridae (cicada parasite beetles). The coxae of the legs are usually located recessed within a coxal cavity. The genitalic structures are telescoped into the last abdominal segment in all extant beetles. Beetle larvae can often be confused with those of other endopterygote groups.[48] The beetle's exoskeleton is made up of numerous plates, called sclerites, separated by thin sutures. This design provides armored defenses while maintaining flexibility. The general anatomy of a beetle is quite uniform, although specific organs and appendages vary greatly in appearance and function between the many families in the order. Like all insects, beetles' bodies are divided into three sections: the head, the thorax, and the abdomen.[7] Because there are so many species, identification is quite difficult, and



Beetle body structure, using cockchafer. A: head, B: thorax, C: abdomen. 1: antenna, 2: compound eye, 3: femur, 4: elytron (wing cover), 5: tibia, 6: tarsus, 7: claws, 8: mouthparts, 9: prothorax, 10: mesothorax, 11: metathorax, 12: abdominal sternites, 13: pygidium.

relies on attributes including the shape of the antennae, the tarsal formulae[a] and shapes of these small segments on the legs, the mouthparts, and the ventral plates (sterna, pleura, coxae). In many species accurate identification can only be made by examination of the unique male genitalic structures.[59]

Head

The head, having mouthparts projecting forward or sometimes downturned, is usually heavily sclerotized and is sometimes very large.[6] The eyes are compound and may display remarkable adaptability, as in the case of the aquatic whirligig beetles (Gyrinidae), where they are split to allow a view both above and below the waterline. A few Longhorn beetles (Cerambycidae) and weevils as well as some fireflies (Rhagophthalmidae) [60] have divided eyes, while many have eyes that are notched, and a few have ocelli, small, simple eyes usually farther back on the head (on the vertex); these are more common in larvae than in adults.[61] The anatomical organization of the compound eyes may be modified and depends on whether a species is primarily crepuscular, or diurnally or nocturnally active.[62] Ocelli are found in the adult carpet beetle (Dermestidae), some rove beetles (Omaliinae), and the Derodontidae.[61]


Polyphylla fullo has distinctive fan-like antennae, one of several distinct forms for the appendages among beetles.

Beetle antennae are primarily organs of sensory perception and can detect motion, odour and chemical substances,[63] but may also be used to physically feel a beetle's environment. Beetle families may use antennae in different ways. For example, when moving quickly, tiger beetles may not be able to see very well and instead hold their antennae rigidly in front of them in order to avoid obstacles.[64] Certain Cerambycidae use antennae to balance, and blister beetles may use them for grasping. Some aquatic beetle species may use antennae for gathering air and passing it under the body whilst submerged. Equally, some families use antennae during mating, and a few species use them for defence. In the cerambycid *Onychocerus albitarsis*, the antennae have venom injecting structures used in defence, which is unique among arthropods.[65] Antennae vary greatly in form, sometimes between the sexes, but are often similar within any given family. Antennae may be clubbed, threadlike, angled, shaped like a string of beads, comb-like (either on one side or both, bipectinate), or toothed. The physical variation of antennae is important for the identification of many beetle groups. The Curculionidae have elbowed or geniculate antennae. Feather like flabellate antennae are a restricted form found in the Rhipiceridae and a few other families. The Silphidae have a capitate antennae with a spherical head at the tip. The Scarabaeidae typically have lamellate antennae with the terminal segments extended into long flat structures stacked together. The Carabidae typically have thread-like antennae. The antennae arises between the eye and the mandibles and in the Tenebrionidae, the antennae rise in front of a notch that breaks the usually circular outline of the compound eye. They are segmented and usually consist of 11 parts, the first part is called the scape and the second part is the pedicel. The other segments are jointly called the flagellum.[63][66][67]

Beetles have mouthparts like those of grasshoppers. The mandibles appear as large pincers on the front of some beetles. The mandibles are a pair of hard, often tooth-like structures that move horizontally to grasp, crush, or cut food or enemies (see defence, below). Two pairs of finger-like appendages, the maxillary and labial palpi, are found around the mouth in most beetles, serving to move food into the mouth. In many species, the mandibles are sexually dimorphic, with those of the males enlarged enormously compared with those of females of the same species.[6]

Thorax

The thorax is segmented into the two discernible parts, the pro- and pterothorax. The pterothorax is the fused meso- and metathorax, which are commonly separated in other insect species, although flexibly articulate from the prothorax. When viewed from below, the thorax is that part from which all three pairs of legs and both pairs of wings arise. The abdomen is everything posterior to the thorax.[7] When viewed from above, most beetles appear to have three clear sections, but this is deceptive: on the beetle's upper surface, the middle section is a hard plate called the pronotum, which is only the front part of the thorax; the back part of the thorax is concealed by the beetle's wings. This further segmentation is usually best seen on the abdomen.[68]

Legs

The multisegmented legs end in two to five small segments called tarsi. Like many other insect orders, beetles have claws, usually one pair, on the end of the last tarsal segment of each leg. While most beetles use their legs for walking, legs have been variously adapted for other uses. Aquatic beetles including the Dytiscidae (diving beetles), Haliplidae, and many species of Hydrophilidae, the legs, often the last pair, are modified for swimming, typically with rows of long hairs. Male diving beetles have suctorial cups on their forelegs that they use to grasp females.[69] Other beetles have fossorial legs widened and often spined for digging. Species with such adaptations are found among the scarabs, ground beetles, and clown beetles (Histeridae). The hind legs of some beetles, such as flea beetles (within Chrysomelidae) and flea weevils (within Curculionidae), have enlarged femurs that help them leap.[70]

Acilius sulcatus, a diving beetle with hind legs adapted as swimming limbs

Wings

Checkered beetle *Trichodes alvearius* taking off, showing the hard elytra (forewings adapted as wing-cases) held stiffly away from the flight wings

The forewings of beetles are not used for flight, but form elytra which cover the hind part of the body and protect the hindwings. The elytra are usually hard shell-like structures which must be raised to allow the hind wings to move for flight.[71] However, in the soldier beetles (Cantharidae), the elytra are soft, earning this family the name of leatherwings.[72] Other soft wing beetles include the net-winged beetle *Calopteron discrepans*, which has brittle wings that rupture easily in order to release chemicals for defence.[73]

Beetles' flight wings are crossed with veins and are folded after landing, often along these veins, and stored below the elytra. A fold (*jugum*) of the membrane at the base of each wing is characteristic.[71] Some beetles have lost the ability to fly. These include some ground beetles (Carabidae) and some true weevils (Curculionidae), as well as desert- and cave-dwelling species of other families. Many have the two elytra fused together, forming a solid shield over the abdomen. In a few families, both the ability to fly and the elytra have been lost, as in the glow-worms (Phengodidae), where the females resemble larvae throughout their lives.[74] The presence of elytra and wings does not always indicate that the beetle will fly. For example, the tansy beetle walks between habitats despite being physically capable of flight.[75]

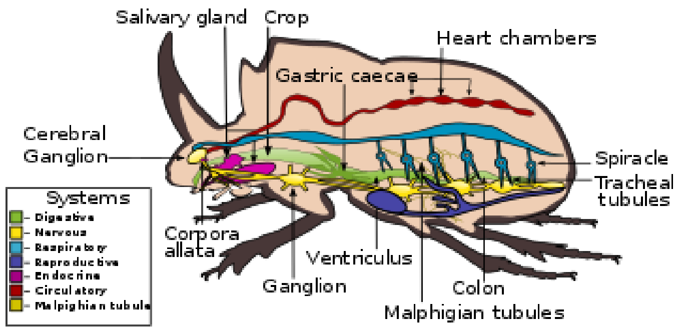
Abdomen

The abdomen is the section behind the metathorax, made up of a series of rings, each with a hole for breathing and respiration, called a spiracle, composing three different segmented sclerites: the tergum, pleura, and the sternum. The tergum in almost all species is membranous, or usually soft and concealed by the wings and elytra when not in flight. The pleura are usually small or hidden in some species, with each pleuron having a single spiracle. The sternum is the most widely visible part of the abdomen, being a more or less sclerotized segment. The abdomen itself does not have any appendages, but some (for example, Mordellidae) have articulating sternal lobes.[76]

Anatomy and physiology

Digestive system

The digestive system of beetles is primarily adapted for a herbivorous diet. Digestion takes place mostly in the anterior midgut, although in predatory groups like the Carabidae, most digestion occurs in the crop by means of midgut enzymes. In the Elateridae, the larvae are liquid feeders that extraorally digest their food by secreting enzymes.[7] The alimentary canal basically consists of a short, narrow pharynx, a widened expansion, the crop, and a poorly developed gizzard. This is followed by the midgut, that varies in dimensions between species, with a large amount of cecum, and the hindgut, with varying lengths. There are typically four to six Malpighian tubules.[6]



A beetle's body systems

Nervous system

The nervous system in beetles contains all the types found in insects, varying between different species, from three thoracic and seven or eight abdominal ganglia which can be distinguished to that in which all the thoracic and abdominal ganglia are fused to form a composite structure.[7]

Respiratory system


Dytiscus spiracles (right) on upper side of abdomen, normally covered by the elytra, are in contact with an air bubble when the beetle dives.

Like most insects, beetles inhale air, for the oxygen it contains, and exhale carbon dioxide, via a tracheal system. Air enters the body through spiracles, and circulates within the haemocoel in a system of tracheae and tracheoles, through whose walls the gases can diffuse.[7]

Diving beetles, such as the Dytiscidae, carry a bubble of air with them when they dive. Such a bubble may be contained under the elytra or against the body by specialized hydrophobic hairs. The bubble covers at least some of the spiracles, permitting air to enter the tracheae.[7] The function of the bubble is not only to contain a store of air but to act as a physical gill. The air that it traps is in contact with oxygenated water, so as the animal's consumption depletes the oxygen in the bubble, more oxygen can diffuse in to replenish it.[77] Carbon dioxide is more soluble in water than either oxygen or nitrogen, so it readily diffuses out faster than in. Nitrogen is the most plentiful gas in the bubble, and the least soluble, so it constitutes a relatively static component of the bubble and acts as a stable medium for respiratory gases to accumulate in and pass through. Occasional visits to the surface are sufficient for the beetle to re-establish the constitution of the bubble.[78]

Circulatory system

Like other insects, beetles have open circulatory systems, based on hemolymph rather than blood. As in other insects, a segmented tube-like heart is attached to the dorsal wall of the hemocoel. It has paired inlets or *ostia* at intervals down its length, and circulates the hemolymph from the main cavity of the haemocoel and out through the anterior cavity in the head.[79]

Specialized organs

Different glands are specialized for different pheromones to attract mates. Pheromones from species of Rutelinae are produced from epithelial cells lining the inner surface of the apical abdominal segments; amino acid-based pheromones of Melolonthinae are produced from eversible glands on the abdominal apex. Other species produce different types of pheromones. Dermestids produce esters, and species of Elateridae produce fatty acid-derived aldehydes and acetates.[7] To attract a mate, fireflies (Lampyridae) use modified fat body cells with transparent surfaces backed with reflective uric acid crystals to produce light by bioluminescence. Light production is highly efficient, by oxidation of luciferin catalyzed by enzymes (luciferases) in the presence of adenosine triphosphate (ATP) and oxygen, producing oxyluciferin, carbon dioxide, and light.[7]

Tympanal organs or hearing organs consist of a membrane (tympanum) stretched across a frame backed by an air sac and associated sensory neurons, are found in two families.[80] Several species of the genus *Cicindela* (Carabidae) have hearing organs on the dorsal surfaces of their first abdominal segments beneath the wings; two tribes in the Dynastinae (within the Scarabaeidae) have hearing organs just beneath their pronotal shields or neck membranes. Both families are sensitive to ultrasonic frequencies, with strong evidence indicating they function to detect the presence of bats by their ultrasonic echolocation.[7]

Reproduction and development

Beetles are members of the superorder Endopterygota, and accordingly most of them undergo complete metamorphosis. The typical form of metamorphosis in beetles passes through four main stages: the egg, the larva, the pupa, and the imago or adult. The larvae are commonly called grubs and the pupa sometimes is called the chrysalis. In some species, the pupa may be enclosed in a cocoon constructed by the larva towards the end of its final instar. Some beetles, such as typical members of the families Meloidae and Rhipiphoridae, go further, undergoing hypermetamorphosis in which the first instar takes the form of a triungulin.[81]

Mating


Punctate flower chafers (*Neorrhina punctata*, Scarabaeidae) mating

Some beetles have intricate mating behaviour. Pheromone communication is often important in locating a mate. Different species use different pheromones. Scarab beetles such as the Rutelinae use pheromones derived from fatty acid synthesis, while other scarabs such as the Melolonthinae use amino acids and terpenoids. Another way beetles find mates is seen in the fireflies (Lampyridae) which are bioluminescent, with abdominal light-producing organs. The males and females engage in a complex dialogue before mating; each species has a unique combination of flight patterns, duration, composition, and intensity of the light produced.[7]

Before mating, males and females may stridulate, or vibrate the objects they are on. In the Meloidae, the male climbs onto the dorsum of the female and strokes his antennae on her head, palps, and antennae. In *Eupompha*, the male draws his antennae along his longitudinal vertex. They may not mate at all if they do not perform the precopulatory ritual.[7] This mating behaviour may be different amongst dispersed populations of the same species. For example, the mating of a Russian population of tansy beetle (*Chysolina graminis*) is preceded by an elaborate ritual involving the male tapping the female's eyes, pronotum and antennae with its antennae, which is not evident in the population of this species in the United Kingdom.[82]

Competition can play a part in the mating rituals of species such as burying beetles (*Nicrophorus*), the insects fighting to determine which can mate. Many male beetles are territorial and fiercely defend their territories from intruding males. In such species, the male often has horns on the head or thorax, making its body length greater than that of a female. Copulation is generally quick, but in some cases lasts for several hours. During copulation, sperm cells are transferred to the female to fertilize the egg.[6]

Life cycle

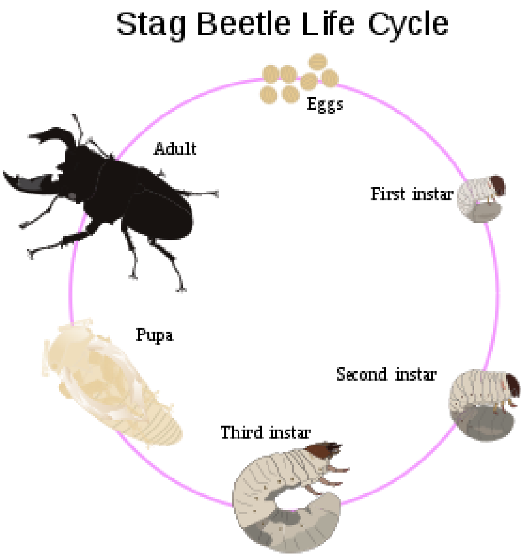
Egg

Essentially all beetles lay eggs, though some myrmecophilous Aleocharinae and some Chrysomelinae which live in mountains or the subarctic are ovoviviparous, laying eggs which hatch almost immediately. Beetle eggs generally have smooth surfaces and are soft, though the Cupedidae have hard eggs. Eggs vary widely between species: the eggs tend to be small in species with many instars (larval stages), and in those that lay large numbers of eggs. A female may lay from several dozen to several thousand eggs during her lifetime, depending on the extent of parental care. This ranges from the simple laying of eggs under a leaf, to the parental care provided by scarab beetles, which house, feed and protect their young. The Attelabidae roll leaves and lay their eggs inside the roll for protection.[7][83]

Larva

The larva is usually the principal feeding stage of the beetle life cycle. Larvae tend to feed voraciously once they emerge from their eggs. Some feed externally on plants, such as those of certain leaf beetles, while others feed within their food sources. Examples of internal feeders are most Buprestidae and longhorn beetles. The larvae of many beetle families are predatory like the adults (ground beetles, ladybirds, rove beetles). The larval period varies between species, but can be as long as several years. The larvae of skin beetles undergo a degree of reversed development when starved, and later grow back to the previously attained level of maturity. The cycle can be repeated many times (see Biological immortality).[84] Larval morphology is highly varied amongst species, with well-developed and sclerotized heads, distinguishable thoracic and abdominal segments (usually the tenth, though sometimes the eighth or ninth).[6]

Scarabaeiform larva of Hercules beetle



The life cycle of the stag beetle includes three instars.

Beetle larvae can be differentiated from other insect larvae by their hardened, often darkened heads, the presence of chewing mouthparts, and spiracles along the sides of their bodies. Like adult beetles, the larvae are varied in appearance, particularly between beetle families. Beetles with somewhat flattened, highly mobile larvae include the ground beetles and rove beetles; their larvae are described as campodeiform. Some beetle larvae resemble hardened worms with dark head capsules and minute legs. These are elateriform larvae, and are found in the click beetle (Elateridae) and darkling beetle (Tenebrionidae) families. Some elateriform larvae of click beetles are known as wireworms. Beetles in the Scarabaeoidea have short, thick larvae described as scarabaeiform, more commonly known as grubs.[85]

All beetle larvae go through several instars, which are the developmental stages between each moult. In many species, the larvae simply increase in size with each successive instar as more food is consumed. In some cases, however, more dramatic changes occur. Among certain beetle families or genera, particularly those that exhibit parasitic lifestyles, the first instar (the planidium) is highly mobile to search out a host, while the following instars are more sedentary and remain on or within their host. This is known as hypermetamorphosis; it occurs in the Meloidae, Micromalthidae, and Ripiphoridae.[86] The blister beetle *Epicauta vittata* (Meloidae), for example, has three distinct larval stages. Its first stage, the triungulin, has longer legs to go in search of the eggs of grasshoppers. After feeding for a week it moults to the second stage, called the caraboid stage, which resembles the larva of a carabid beetle. In another week it moults and assumes the appearance of a scarabaeid larva – the scarabaeidoid stage. Its penultimate larval stage is the pseudo-pupa or the coarcate larva, which will overwinter and pupate until the next spring.[87]

The larval period can vary widely. A fungus feeding staphylinid *Phanerota fasciata* undergoes three moults in 3.2 days at room temperature while *Anisotoma* sp. (Leiodidae) completes its larval stage in the fruiting body of slime mold in 2 days and possibly represents the fastest growing beetles. Dermestid beetles, *Trogoderma inclusum* can remain in an extended larval state under unfavourable conditions, even reducing their size between moults. A larva is reported to have survived for 3.5 years in an enclosed container.[7]

Pupa and adult

As with all endopterygotes, beetle larvae pupate, and from these pupae emerge fully formed, sexually mature adult beetles, or imagos. Pupae never have mandibles (they are adecticous). In most pupae, the appendages are not attached to the body and are said to be exarate; in a few beetles (Staphylinidae, Ptiliidae etc.) the appendages are fused with the body (termed as obtect pupae).[6]

Adults have extremely variable lifespans, from weeks to years, depending on the species.[6][48] Some wood-boring beetles can have extremely long life-cycles. It is believed that when furniture or house timbers are infested by beetle larvae, the timber already contained the larvae when it was first sawn up. A birch bookcase 40 years old released adult *Eburia quadrigeminata* (Cerambycidae), while *Buprestis aurulenta* and other Buprestidae have been documented as emerging as much as 51 years after manufacture of wooden items.[88]

Behaviour

Locomotion

Photinus pyralis, firefly, in flight

The ivory-marked beetle, *Eburia quadrigeminata*, may live up to 40 years inside the hardwoods on which the larva feeds.

The elytra allow beetles to both fly and move through confined spaces, doing so by folding the delicate wings under the elytra while not flying, and folding their wings out just before takeoff. The unfolding and folding of the wings is operated by muscles attached to the wing base; as long as the tension on the radial and cubital veins remains, the wings remain straight. In some day-flying species (for example, Buprestidae, Scarabaeidae), flight does not include large amounts of lifting of the elytra, having the metathorac wings extended under the lateral elytra margins.[7] The altitude reached by beetles in flight varies. One study investigating the flight altitude of the ladybird species *Coccinella septempunctata* and *Harmonia axyridis* using radar showed that, whilst the majority in flight over a single location were at 150–195 m above ground level, some reached altitudes of over 1100 m.[89]

Many rove beetles have greatly reduced elytra, and while they are capable of flight, they most often move on the ground: their soft bodies and strong abdominal muscles make them flexible, easily able to wriggle into small cracks.[90]

Aquatic beetles use several techniques for retaining air beneath the water's surface. Diving beetles (Dytiscidae) hold air between the abdomen and the elytra when diving. Hydrophilidae have hairs on their under surface that retain a layer of air against their bodies. Adult crawling water beetles use both their elytra and their hind coxae (the basal segment of the back legs) in air retention, while whirligig beetles simply carry an air bubble down with them whenever they dive.[91]

Communication

Beetles have a variety of ways to communicate, including the use of pheromones. The mountain pine beetle emits a pheromone to attract other beetles to a tree. The mass of beetles are able to overcome the chemical defenses of the tree. After the tree's defenses have been exhausted, the beetles emit an anti-aggregation pheromone. This species can stridulate to communicate,[92] but others may use sound to defend themselves when attacked.[93]

Parental care

A dung beetle rolling dung

Parental care is found in a few families[94] of beetle, perhaps for protection against adverse conditions and predators.[7] The rove beetle *Bledius spectabilis* lives in salt marshes, so the eggs and larvae are endangered by the rising tide. The maternal beetle patrols the eggs and larvae, burrowing to keep them from flooding and asphyxiating, and protects them from the predatory carabid beetle *Dicheirotrichus gustavi* and from the parasitoidal wasp *Barycnemis blediator*, which kills some 15% of the larvae.[95]

Burying beetles are attentive parents, and participate in cooperative care and feeding of their offspring. Both parents work to bury small animal carcass to serve as a food resource for their young and build a brood chamber around it. The parents prepare the carcass and protect it from competitors and from early decomposition. After their eggs hatch, the parents keep the larvae clean of fungus and bacteria and help the larvae feed by regurgitating food for them.[96]

Some dung beetles provide parental care, collecting herbivore dung and laying eggs within that food supply, an instance of mass provisioning. Some species do not leave after this stage, but remain to safeguard their offspring.[97]

Most species of beetles do not display parental care behaviors after the eggs have been laid.[98]

Subsociality, where females guard their offspring, is well-documented in two families of Chrysomelidae, Cassidinae and Chrysomelinae.[99][100][101][102][103]

Eusociality

Eusociality involves cooperative brood care (including brood care of offspring from other individuals), overlapping generations within a colony of adults, and a division of labour into reproductive and non-reproductive groups.[104] Few organisms outside Hymenoptera exhibit this behavior; the only beetle to do so is the weevil *Austroplatypus incompertus*.[105] This Australian species lives in horizontal networks of tunnels, in the heartwood of *Eucalyptus* trees. It is one of more than 300 species of wood-boring Ambrosia beetles which distribute the spores of ambrosia fungi.[106] The fungi grow in the beetles' tunnels, providing food for the beetles and their larvae; female offspring remain in the tunnels and maintain the fungal growth, probably never reproducing.[106][105] Cooperative brood care is also found in the bess beetles (Passalidae) where the larvae feed on the semi-digested faeces of the adults.[107]

Feeding

Hycleus sp. (Meloidae) feeding on the petals of *Ipomoea carnea*

Beetles are able to exploit a wide diversity of food sources available in their many habitats. Some are omnivores, eating both plants and animals. Other beetles are highly specialized in their diet. Many species of leaf beetles, longhorn beetles, and weevils are very host-specific, feeding on only a single species of plant. Ground beetles and rove beetles (Staphylinidae), among others, are primarily carnivorous and catch and consume many other arthropods and small prey, such as earthworms and snails. While most predatory beetles are generalists, a few species have more specific prey requirements or preferences.[108]

Decaying organic matter is a primary diet for many species. This can range from dung, which is consumed by coprophagous species (such as certain scarab beetles in the Scarabaeidae), to dead animals, which are eaten by necrophagous species (such as the carrion beetles, Silphidae). Some beetles found in dung and carrion are in fact predatory. These include members of the Histeridae and Silphidae, preying on the larvae of coprophagous and necrophagous insects.[109] Many beetles feed under bark, some feed on wood while others feed on fungi growing on wood or leaf-litter. Some beetles have special mycangia, structures for the transport of fungal spores.[110]

Ecology

Anti-predator adaptations

A camouflaged longhorn beetle, *Ecyrus dasycerus*

Beetles, both adults and larvae, are the prey of many animal predators including mammals from bats to rodents, birds, lizards, amphibians, fishes, dragonflies, robberflies, reduviid bugs, ants, other beetles, and spiders.[111][112] Beetles use a variety of anti-predator adaptations to defend themselves. These include camouflage and mimicry against predators that hunt by sight, toxicity, and defensive behaviour.

Camouflage

Camouflage is common and widespread among beetle families, especially those that feed on wood or vegetation, such as leaf beetles (Chrysomelidae, which are often green) and weevils. In some species, sculpturing or various coloured scales or hairs cause beetles such as the avocado weevil *Heilipus apiatus* to resemble bird dung or other inedible objects.[111] Many beetles that live in sandy environments blend in with the coloration of that substrate.[113]

Mimicry and aposematism

Clytus arietis (Cerambycidae), a Batesian mimic of wasps

Some longhorn beetles (Cerambycidae) are effective Batesian mimics of wasps. Beetles may combine coloration with behavioural mimicry, acting like the wasps they already closely resemble. Many other beetles, including ladybirds, blister beetles, and lycid beetles secrete distasteful or toxic substances to make them unpalatable or poisonous, and are often aposematic, where bright or contrasting coloration warn off predators; many beetles and other insects mimic these chemically protected species.[114]

Blister beetles such as *Hycleus* have brilliant aposematic coloration, warning of their toxicity.

The bloody-nosed beetle, *Timarcha tenebricosa*, defending itself by releasing a droplet of noxious red liquid (base of leg, on right)

Chemical defense is important in some species, usually being advertised by bright aposematic colours. Some Tenebrionidae use their posture for releasing noxious chemicals to warn off predators. Chemical defences may serve purposes other than just protection from vertebrates, such as protection from a wide range of microbes. Some species sequester chemicals from the plants they feed on, incorporating them into their own defenses.[113]

Other species have special glands to produce deterrent chemicals. The defensive glands of carabid ground beetles produce a variety of hydrocarbons, aldehydes, phenols, quinones, esters, and acids released from an opening at the end of the abdomen. African carabid beetles (for example, *Anthia* and *Thermophilum* – *Thermophilum* is sometimes included within *Anthia*) employ the same chemicals as ants: formic acid.[114] Bombardier beetles have well-developed pygidial glands that empty from the sides of the intersegment membranes between the seventh and eighth abdominal segments. The gland is made of two containing chambers, one for hydroquinones and hydrogen peroxide, the other holding hydrogen peroxide and catalase enzymes. These chemicals mix and result in an explosive ejection, reaching a temperature of around 100 °C (212 °F), with the breakdown of hydroquinone to hydrogen, oxygen, and quinone. The oxygen propels the noxious chemical spray as a jet that can be aimed accurately at predators.[7]

Other defences

Large ground-dwelling beetles such as Carabidae, the rhinoceros beetle and the longhorn beetles defend themselves using strong mandibles, or heavily sclerotised (armored) spines or horns to deter or fight off predators.[113] Many species of weevil that feed out in the open on leaves of plants react to attack by employing a drop-off reflex. Some combine it with thanatosis, in which they close up their appendages and "play dead".[115] The click beetles (Elateridae) can suddenly catapult themselves out of danger by releasing the energy stored by a click mechanism, which consists of a stout spine on the prosternum and a matching groove in the mesosternum.[111] Some species startle an attacker by producing sounds through a process known as stridulation.[93]

Parasitism

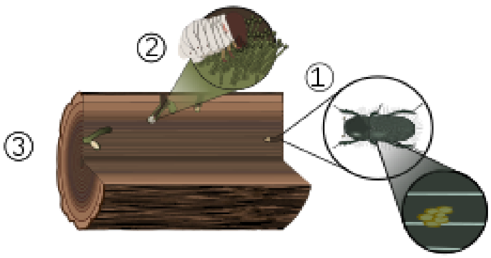
A few species of beetles are ectoparasitic on mammals. One such species, *Platypsyllus castoris*, parasitises beavers (*Castor* spp.). This beetle lives as a parasite both as a larva and as an adult, feeding on epidermal tissue and possibly on skin secretions and wound exudates. They are strikingly flattened dorsoventrally, no doubt as an adaptation for slipping between the beavers' hairs. They are wingless and eyeless, as are many other ectoparasites.[116] Others are kleptoparasites of other invertebrates, such as the small hive beetle (*Aethina tumida*) that infests honey bee nests,[117] while many species are parasitic inquilines or commensal in the nests of ants.[118] A few groups of beetles are primary parasitoids of other insects, feeding off of, and eventually killing their hosts.[119]

Pollination

Beetle-pollinated flowers are usually large, greenish or off-white in color, and heavily scented. Scents may be spicy, fruity, or similar to decaying organic material. Beetles were most likely the first insects to pollinate flowers. Most beetle-pollinated flowers are flattened or dish-shaped, with pollen easily accessible, although they may include traps to keep the beetle longer. The plants' ovaries are usually well protected from the biting mouthparts of their pollinators. The beetle families that habitually pollinate flowers are the Buprestidae, Cantharidae, Cerambycidae, Cleridae, Dermestidae, Lycidae, Melyridae, Mordellidae, Nitidulidae and Scarabaeidae.[120] Beetles may be particularly important in some parts of the world such as semiarid areas of southern Africa and southern California[121] and the montane grasslands of KwaZulu-Natal in South Africa.[122]

An Israeli Copper Flower-Chafer (*Protaetia cuprea ignicollis*) pollinating a crown daisy (*Glebionis coronaria*)

Mutualism



1: Adult ambrosia beetle burrows into wood and lays eggs, carrying fungal spores in its mycangia.
2: Larva feeds on fungus, which digests wood, removing toxins, to mutual benefit.
3: Larva pupates.

Mutualism is well known in a few beetles, such as the ambrosia beetle, which partners with fungi to digest the wood of dead trees. The beetles excavate tunnels in dead trees in which they cultivate fungal gardens, their sole source of nutrition. After landing on a suitable tree, an ambrosia beetle excavates a tunnel in which it releases spores of its fungal symbiont. The fungus penetrates the plant's xylem tissue, digests it, and concentrates the nutrients on and near the surface of the beetle gallery, so the weevils and the fungus both benefit. The beetles cannot eat the wood due to toxins, and uses its relationship with fungi to help overcome the defenses of its host tree in order to provide nutrition for their larvae.[123] Chemically mediated by a bacterially produced polyunsaturated peroxide,[124] this mutualistic relationship between the beetle and the fungus is coevolved.[123][125]

Tolerance of extreme environments

Beetle found in Thar Desert

About 90% of beetle species enter a period of adult diapause, a quiet phase with reduced metabolism to tide unfavourable environmental conditions. Adult diapause is the most common form of diapause in Coleoptera. To endure the period without food (often lasting many months) adults prepare by accumulating reserves of lipids, glycogen, proteins and other substances needed for resistance to future hazardous changes of environmental conditions. This diapause is induced by signals heralding the arrival of the unfavourable season; usually the cue is photoperiodic. Short (decreasing) day length serves as a signal of approaching winter and induces winter diapause (hibernation).[126] A study of hibernation in the Arctic beetle *Pterostichus brevicorni* showed that the body fat levels of adults were highest in autumn with the alimentary canal filled with food, but empty by the end of January. This loss of body fat was a gradual process, occurring in combination with dehydration.[127]

All insects are poikilothermic,[128] so the ability of a few beetles to live in extreme environments depends on their resilience to unusually high or low temperatures. The bark beetle *Pityogenes chalcographus* can survive −39 °C whilst overwintering beneath tree bark;[129] the Alaskan beetle *Cucujus clavipes puniceus* is able to withstand −58 °C; its larvae may survive −100 °C.[130] At these low temperatures, the formation of ice crystals in internal fluids is the biggest threat to survival to beetles, but this is prevented through the production of antifreeze proteins that stop water molecules from grouping together. The low temperatures experienced by *Cucujus clavipes* can be survived through their deliberate dehydration in conjunction with the antifreeze proteins. This concentrates the antifreezes several fold.[131] The hemolymph of the mealworm beetle *Tenebrio molitor* contains several antifreeze proteins.[132] The Alaskan beetle *Upis ceramboides* can survive −60 °C: its cryoprotectants are xylomannan, a molecule consisting of a sugar bound to a fatty acid,[133] and the sugar-alcohol, threitol.[134]

Conversely, desert dwelling beetles are adapted to tolerate high temperatures. For example, the Tenebrionid beetle *Onymacris rugatipennis* can withstand 50 °C.[135] Tiger beetles in hot, sandy areas are often whitish (for example, *Habroscelimorpha dorsalis*), to reflect more heat than a darker colour would. These beetles also exhibits behavioural adaptions to tolerate the heat: they are able to stand erect on their tarsi to hold their bodies away from the hot ground, seek shade, and turn to face the sun so that only the front parts of their heads are directly exposed.[136]

The fogstand beetle of the Namib Desert, *Stenocara gracilipes* is able to survive by collecting water from fog on its back.

The fogstand beetle of the Namib Desert, *Stenocara gracilipes*, is able to collect water from fog, as its elytra have a textured surface combining hydrophilic (water-loving) bumps and waxy, hydrophobic troughs. The beetle faces the early morning breeze, holding up its abdomen; droplets condense on the elytra and run along ridges towards their mouthparts. Similar adaptations are found in several other Namib desert beetles such as *Onymacris unguicularis*.[137]

Some terrestrial beetles that exploit shoreline and floodplain habitats have physiological adaptations for surviving floods. In the event of flooding, adult beetles may be mobile enough to move away from flooding, but larvae and pupa often cannot. Adults of *Cicindela togata* are unable to survive immersion in water, but larvae are able to survive a prolonged period, up to 6 days, of anoxia during floods. Anoxia tolerance in the larvae may have been sustained by switching to anaerobic metabolic pathways or by reducing metabolic rate.[138] Anoxia tolerance in the adult Carabid beetle *Pelophilia borealis* was tested in laboratory conditions and it was found that they could survive a continuous period of up to 127 days in an atmosphere of 99.9% nitrogen at 0 °C.[139]

Migration

Many beetle species undertake annual mass movements which are termed as migrations. These include the pollen beetle *Meligethes aeneus*[140] and many species of coccinellids.[141] These mass movements may also be opportunistic, in search of food, rather than seasonal. A 2008 study of an unusually large outbreak of Mountain Pine Beetle (*Dendroctonus ponderosae*) in British Columbia found that beetles were capable of flying 30–110 km per day in densities of up to 18, 600 beetles per hectare.[142]

Relationship to humans

In ancient cultures

ḫpr
in hieroglyphs

Several species of dung beetle, especially the sacred scarab, *Scarabaeus sacer*, were revered in Ancient Egypt.[143][144] The hieroglyphic image of the beetle may have had existential, fictional, or ontologic significance.[145] Images of the scarab in bone, ivory, stone, Egyptian faience, and precious metals are known from the Sixth Dynasty and up to the period of Roman rule. The scarab was of prime significance in the funerary cult of ancient Egypt.[146] The scarab was linked to Khepri, the god of the rising sun, from the supposed resemblance of the rolling of the dung ball by the beetle to the rolling of the sun by the god.[143] Some of ancient Egypt's neighbors adopted the scarab motif for seals of varying types. The best-known of these are the Judean LMLK seals, where eight of 21 designs contained scarab beetles, which were used exclusively to stamp impressions on storage jars during the reign of Hezekiah.[147] Beetles are mentioned as a symbol of the sun, as in ancient Egypt, in Plutarch's 1st century *Moralia*.[148] The Greek Magical Papyri of the 2nd century BC to the 5th century AD describe scarabs as an ingredient in a spell.[149]

A scarab in the Valley of the Kings

Pliny the Elder discusses beetles in his *Natural History*,[150] describing the stag beetle: "Some insects, for the preservation of their wings, are covered with a erust (elytra) – the beetle, for instance, the wing of which is peculiarly fine and frail. To these insects a sting has been denied by Nature; but in one large kind we find horns of a remarkable length, two-pronged at the extremities, and forming pincers, which the animal closes when it is its intention to bite."[151][152] The stag beetle is recorded in a Greek myth by Nicander and recalled by Antoninus Liberalis in which Cerambus[b] is turned into a beetle: "He can be seen on trunks and has hook-teeth, ever moving his jaws together. He is black, long and has hard wings like a great dung beetle".[153] The story concludes with the comment that the beetles were used as toys by young boys, and that the head was removed and worn as a pendant.[152][154]

As pests

Cotton boll weevil

About 75% of beetle species are phytophagous in both the larval and adult stages. Many feed on economically important plants and stored plant products, including trees, cereals, tobacco, and dried fruits.[6] Some, such as the boll weevil, which feeds on cotton buds and flowers, can cause extremely serious damage to agriculture. The boll weevil crossed the Rio Grande near Brownsville, Texas, to enter the United States from Mexico around 1892,[155] and had reached southeastern Alabama by 1915. By the mid-1920s, it had entered all cotton-growing regions in the US, traveling 40 to 160 miles (60–260 km) per year. It remains the most destructive cotton pest in North America. Mississippi State University has estimated, since the boll weevil entered the United States, it has cost cotton producers about $13 billion, and in recent times about $300 million per year.[155]

The bark beetle, elm leaf beetle and the Asian longhorned beetle (*Anoplophora glabripennis*)[156] are among the species that attack elm trees. Bark beetles (Scolytidae) carry Dutch elm disease as they move from infected breeding sites to healthy trees. The disease has devastated elm trees across Europe and North America.[157]

Some species of beetle have evolved immunity to insecticides. For example, the Colorado potato beetle, *Leptinotarsa decemlineata*, is a destructive pest of potato plants. Its hosts include other members of the Solanaceae, such as nightshade, tomato, eggplant and capsicum, as well as the potato. Different populations have between them developed resistance to all major classes of insecticide.[158] The Colorado potato beetle was evaluated as a tool of entomological warfare during World War II, the idea being to use the beetle and its larvae to damage the crops of enemy nations.[159] Germany tested its Colorado potato beetle weaponisation program south of Frankfurt, releasing 54,000 beetles.[160]

Larvae of the Colorado potato beetle, *Leptinotarsa decemlineata*, a serious crop pest

The death watch beetle, *Xestobium rufovillosum* (Ptinidae), is a serious pest of older wooden buildings in Europe. It attacks hardwoods such as oak and chestnut, always where some fungal decay has taken or is taking place. The actual introduction of the pest into buildings is thought to take place at the time of construction.[161]

Other pests include the coconut hispine beetle, *Brontispa longissima*, which feeds on young leaves, seedlings and mature coconut trees, causing serious economic damage in the Philippines.[162] The mountain pine beetle is a destructive pest of mature or weakened lodgepole pine, sometimes affecting large areas of Canada.[163]

As beneficial resources

Beetles can be beneficial to human economics by controlling the populations of pests. The larvae and adults of some species of lady beetles (Coccinellidae) feed on aphids that are pests. Other lady beetles feed on scale insects, whitefly and mealybugs.[164] If normal food sources are scarce, they may feed on small caterpillars, young plant bugs, or honeydew and nectar.[165] Ground beetles (Carabidae) are common predators of many insect pests, including fly eggs, caterpillars, and wireworms.[166] Ground beetles can help to control weeds by eating their seeds in the soil, reducing the need for herbicides to protect crops.[167] The effectiveness of some species in reducing certain

Coccinella septempunctata, a predatory beetle beneficial to agriculture

plant populations has resulted in the deliberate introduction of beetles in order to control weeds. For example, the genus *Zygogramma* is native to North America but has been used to control *Parthenium hysterophorus* in India and *Ambrosia artemisiifolia* in Russia.[168][169]

Dung beetles (Scarabidae) have been successfully used to reduce the populations of pestilent flies, such as *Musca vetustissima* and *Haematobia exigua* which are serious pests of cattle in Australia.[170] The beetles make the dung unavailable to breeding pests by quickly rolling and burying it in the soil, with the added effect of improving soil fertility, tilth, and nutrient cycling.[171] The Australian Dung Beetle Project (1965–1985), introduced species of dung beetle to Australia from South Africa and Europe to reduce populations of *Musca vetustissima*, following successful trials of this technique in Hawaii.[170] The American Institute of Biological Sciences reports that dung beetles save the United States cattle industry an estimated US$380 million annually through burying above-ground livestock feces.[172]

The Dermestidae are often used in taxidermy and in the preparation of scientific specimens, to clean soft tissue from bones.[173] Larvae feed on and remove cartilage along with other soft tissue.[174][175]

As food and medicine

Mealworms in a bowl for human consumption

Beetles are the most widely eaten insects, with about 344 species used as food, usually at the larval stage.[176] The mealworm (the larva of the darkling beetle) and the rhinoceros beetle are among the species commonly eaten.[177] A wide range of species is also used in folk medicine to treat those suffering from a variety of disorders and illnesses, though this is done without clinical studies supporting the efficacy of such treatments.[178]

As biodiversity indicators

Due to their habitat specificity, many species of beetles have been suggested as suitable as indicators, their presence, numbers, or absence providing a measure of habitat quality. Predatory beetles such as the tiger beetles (Cicindelidae) have found scientific use as an indicator taxon for measuring regional patterns of biodiversity. They are suitable for this as their taxonomy is stable; their life history is well described; they are large and simple to observe when visiting a site; they occur around the world in many habitats, with species specialised to particular habitats; and their occurrence by species accurately indicates other species, both vertebrate and invertebrate.[179] According to the habitats, many other groups such as the rove beetles in human-modified habitats, dung beetles in savannas[180] and saproxylic beetles in forests[181] have been suggested as potential indicator species.[182]

In art and adornment

Zopheridae in jewellery at the Texas A&M University Insect Collection

Many beetles have beautiful and durable elytra that have been used as material in arts, with beetlewing the best example.[183] Sometimes, they are incorporated into ritual objects for their religious significance. Whole beetles, either as-is or encased in clear plastic, are made into objects ranging from cheap souvenirs such as key chains to expensive fine-art jewellery. In parts of Mexico, beetles of the genus *Zopherus* are made into living brooches by attaching costume jewelry and golden chains, which is made possible by the incredibly hard elytra and sedentary habits of the genus.[184]

In entertainment

Pendant watch in shape of beetle, Switzerland 1850-1900 gold, diamond, enamel

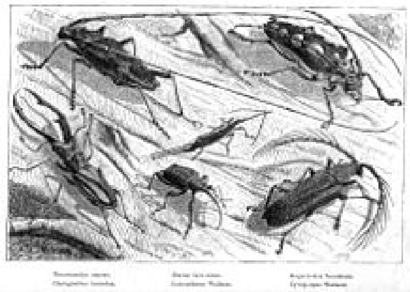
Fighting beetles are used for entertainment and gambling. This sport exploits the territorial behavior and mating competition of certain species of large beetles. In the Chiang Mai district of northern Thailand, male *Xylotrupes* rhinoceros beetles are caught in the wild and trained for fighting. Females are held inside a log to stimulate the fighting males with their pheromones.[185] These fights may be competitive and involve gambling both money and property.[186] In South Korea the Dytiscidae species *Cybister tripunctatus* is used in a roulette-like game.[187]

Beetles are sometimes used as instruments: the Onabasulu of Papua New Guinea historically used the weevil *Rhynchophorus ferrugineus* as a musical instrument by letting the human mouth serve as a variable resonance chamber for the wing vibrations of the live adult beetle.[186]

As pets

Some species of beetle are kept as pets, for example diving beetles (Dytiscidae) may be kept in a domestic fresh water tank.[188]

In Japan the practice of keeping horned rhinoceros beetles (Dynastinae) and stag beetles (Lucanidae) is particularly popular amongst young boys.[189] Such is the popularity in Japan that vending machines dispensing live beetles were developed in 1999, each holding up to 100 stag beetles.[190][191]



"Remarkable Beetles Found at Simunjon, Borneo".[c] A few of the 2000 species of beetle collected by Alfred Russel Wallace in Borneo

As things to collect

Beetle collecting became extremely popular in the Victorian era.[192] The naturalist Alfred Russel Wallace collected (by his own count) a total of 83,200 beetles during the eight years described in his 1869 book *The Malay Archipelago*, including 2,000 species new to science.[193]

As inspiration for technologies

Several coleopteran adaptations have attracted interest in biomimetics with possible commercial applications. The bombardier beetle's powerful repellent spray has inspired the development of a fine mist spray technology, claimed to have a low carbon impact compared to aerosol sprays.[194] Moisture harvesting behavior by the Namib desert beetle (*Stenocara gracilipes*) has inspired a self-filling water bottle which utilises hydrophilic and hydrophobic materials to benefit people living in dry regions with no regular rainfall.[195]

Living beetles have been used as cyborgs. A Defense Advanced Research Projects Agency funded project implanted electrodes into *Mecynorhina torquata* beetles, allowing them to be remotely controlled via a radio receiver held on its back, as proof-of-concept for surveillance work.[196] Similar technology has been applied to enable a human operator to control the free-flight steering and walking gaits of *Mecynorhina torquata* as well as graded turning and backward walking of *Zophobas morio*.[197][198][199]

In conservation

Since beetles form such a large part of the world's biodiversity, their conservation is important, and equally, loss of habitat and biodiversity is essentially certain to impact on beetles. Many species of beetles have very specific habitats and long life cycles that make them vulnerable. Some species are highly threatened while others are already feared extinct.[200] Island species tend to be more susceptible as in the case of *Helictopleurus undatus* of Madagascar which is thought to have gone extinct during the late 20th century.[201] Conservationists have attempted to arouse a liking for beetles with flagship species like the stag beetle, *Lucanus cervus*,[202] and tiger beetles (Cicindelidae). In Japan the Genji firefly, *Luciola cruciata*, is extremely popular, and in South Africa the Addo elephant dung beetle offers promise for broadening ecotourism beyond the big five tourist mammal species. Popular dislike of pest beetles, too, can be turned into public interest in insects, as can unusual ecological adaptations of species like the fairy shrimp hunting beetle, *Cicinis bruchi*.[203]

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Bed bug

Bed bugs are a type of insect that feed on human blood, usually at night.[7] Their bites can result in a number of health impacts including skin rashes, psychological effects and allergic symptoms.[5] Bed bug bites may lead to skin changes ranging from invisible to small areas of redness to prominent blisters.[1][2] Symptoms may take between minutes to days to appear and itchiness is generally present.[2] Some individuals may feel tired or have a fever.[2] Typically, uncovered areas of the body are affected and often three bites occur in a row.[2] Bed bugs bites are not known to transmit any infectious disease.[5][7] Complications may rarely include areas of dead skin or vasculitis.[2]

Bed bug bites are caused primarily by two species of insects of the *Cimex* type: *Cimex lectularius* (the common bed bug) and *Cimex hemipterus*, primarily in the tropics.[3] Their size ranges between 1 and 7 mm.[7] They spread by crawling between nearby locations or by being carried within personal items.[2] Infestation is rarely due to a lack of hygiene but is more common in high-density areas.[2][8] Diagnosis involves both finding the bugs and the occurrence of compatible symptoms.[5] Bed bugs spend much of their time in dark, hidden locations like mattress seams or cracks in the wall.[2]

Treatment is directed towards the symptoms.[2] Eliminating bed bugs from the home is often difficult, partly because bed bugs can survive up to a year without feeding.[2] Repeated treatments of a home may be required.[2] These treatments may include heating the room to 50 °C (122 °F) for more than 90 minutes, frequent vacuuming, washing clothing at high temperatures, and the use of various pesticides.[2]

Bed bugs occur in all regions of the globe.[7] Rates of infestations are relatively common, following an increase since the 1990s.[3][4][6] The exact causes of this increase are unclear; theories including increased human travel, more frequent exchange of second-hand furnishings, a greater focus on control of other pests, and increasing resistance to pesticides.[4] Bed bugs have been known human parasites for thousands of years.[2]

Bed bugs	
Other names	Cimicosis, bed bug bites, bedbugs, bed bug infestation

An adult bed bug (*Cimex lectularius*) with the typical flattened oval shape

Specialty	Family medicine, dermatology
Symptoms	None to prominent blisters, itchy[1][2]
Usual onset	Minutes to days after the bite[2]
Causes	*Cimex* (primarily *Cimex lectularius* and *Cimex hemipterus*)[3]
Risk factors	Travel, second-hand furnishings[4]
Diagnostic method	Based on finding bed bugs and symptoms[5]
Differential diagnosis	Allergic reaction, scabies, dermatitis herpetiformis[2]
Treatment	Symptomatic, bed bug eradication[2]
Medication	Antihistamines, corticosteroids[2]
Frequency	Relatively common[6]

Contents

Signs and symptoms

Skin


Bedbug bites

Individual responses to bites vary, ranging from no visible effect (in about 20–70%),[3][5] to small macular spots, to prominent wheals and bullae formations along with intense itching that may last several days.[5] The bites often occur in a line. A central spot of bleeding may also occur due to the release of anticoagulants in the bug's saliva.[4]

Symptoms may not appear until some days after the bites have occurred.[5] Reactions often become more brisk after multiple bites due to possible sensitization to the salivary proteins of the bed bug.[3] The skin reaction usually occurs in the area of the bite which is most commonly the arms, shoulders and legs as they are more frequently exposed at night.[5] Numerous bites may lead to an erythematous rash or urticaria.[5]

Psychological

Serious infestations and chronic attacks can cause anxiety, stress, and insomnia.[5] Development of refractory delusional parasitosis is possible, as a person develops an overwhelming obsession with bed bugs.[9]

Other

A number of other symptoms may occur from either the bite of the bed bugs or from their exposure. Anaphylaxis from the injection of serum and other nonspecific proteins has been rarely documented.[5][10] Due to each bite taking a tiny amount of blood, chronic or severe infestation may lead to anemia.[5] Bacterial skin infection may occur due to skin break down from scratching.[5][11] Systemic poisoning may occur if the bites are numerous.[12] Exposure to bed bugs may trigger an asthma attack via the effects of airborne allergens although evidence of this association is limited.[5] There is no evidence that bed bugs transmit infectious diseases[5][7] even though they appear physically capable of carrying pathogens and this possibility has been investigated.[3][5] The bite itself may be painful thus resulting in poor sleep and worse work performance.[5]


Bedbug bites

Similar to humans, pets can also be bitten by bed bugs. The signs left by the bites are the same as in case of people and cause identical symptoms (skin irritation, scratching etc).

Insect

Bed bug infestations are primarily the result of two species of insects from genus *Cimex*: *Cimex lectularius* (the common bed bug) and *Cimex hemipterus*.[3] These insects feed exclusively on blood and may survive a year without eating.[3] Adult *Cimex* are light brown to reddish-brown, flat, oval, and have no hind wings. The front wings are vestigial and reduced to pad-like structures. Adults grow to 4–5 mm (0.16–0.20 in) long and 1.5–3 mm (0.059–0.118 in) wide.

An adult bed bug is about 4 to 5 mm long.

Bed bugs have five immature nymph life stages and a final sexually mature adult stage.[13] They shed their skins through ecdysis at each stage, discarding their outer exoskeleton.[14] Newly hatched nymphs are translucent, lighter in color, and become browner as they moult and reach maturity. Bed bugs may be mistaken for other insects, such as booklice, small cockroaches, or carpet beetles; however, when warm and active, their movements are more ant-like, and like most other true bugs, they emit a characteristic disagreeable odor when crushed.

Bed bugs are obligatory bloodsuckers. They have mouth parts that saw through the skin and inject saliva with anticoagulants and painkillers. Sensitivity of humans varies from extreme allergic reaction to no reaction at all (about 20%). The bite usually produces swelling with no red spot, but when many bugs feed on a small area, reddish spots may appear after the swelling subsides.[15] Bedbugs prefer exposed skin, preferably the face, neck, and arms of a sleeping person.

Bed bugs are attracted to their hosts primarily by carbon dioxide, secondarily by warmth, and also by certain chemicals.[4][16][17][18] *Cimex lectularius* only feeds every five to seven days, which suggests that it does not spend the majority of its life searching for a host. When a bed bug is starved, it leaves its shelter and searches for a host. It returns to its shelter after successful feeding or if it encounters exposure to light.[19] *Cimex lectularius* aggregate under all life stages and mating conditions. Bed bugs may choose to aggregate because of predation, resistance to desiccation, and more opportunities to find a mate. Airborne pheromones are responsible for aggregations.[20]

Spread

Infestation is rarely caused by a lack of hygiene.[8] Transfer to new places is usually in the personal items of the human they feed upon.[3] Dwellings can become infested with bed bugs in a variety of ways, such as:

- Bugs and eggs inadvertently brought in from other infested dwellings on a visiting person's clothing or luggage;
- Infested items (such as furniture especially beds or couches, clothing, or backpacks) brought in a home or business;
- Proximity of infested dwellings or items, if easy routes are available for travel, e.g. through ducts or false ceilings;
- Wild animals (such as bats or birds)[21][22] that may also harbour bed bugs or related species such as the bat bug;
- People visiting an infested area (e.g. dwelling, means of transport, entertainment venue, or lodging) and carrying the bugs to another area on their clothing, luggage, or bodies. Bedbugs are increasingly found in air travel.[23]

Though bed bugs will opportunistically feed on pets, they do not live or travel on the skin of their hosts, and pets are not believed to be a factor in their spread.[24]

Diagnosis

A definitive diagnosis of health effects due to bed bugs requires a search for and finding of the insect in the sleeping environment as symptoms are not sufficiently specific.[5] Bed bugs classically form a line of bites colloquially referred to as "breakfast, lunch, and dinner" and rarely feed in the armpit or behind the knee which may help differentiate it from other biting insects.[4] If the number in a house is large a pungent sweet odor may be described.[4] There are specially trained dogs that can detect this smell.[2]

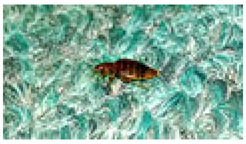
Detection

Bed bugs can exist singly, but tend to congregate once established. Although strictly parasitic, they spend only a tiny fraction of their lifecycles physically attached to hosts. Once a bed bug finishes feeding, it relocates to a place close to a known host, commonly in or near beds or couches in clusters of adults, juveniles, and eggs—which entomologists call harborage areas or simply harborages to which the insect returns after future feedings by following chemical trails. These places can vary greatly in format, including luggage, inside of vehicles, within furniture, among bedside clutter—even inside electrical sockets and nearby laptop computers. Bed bugs may also nest near animals that have nested within a dwelling, such as bats, birds,[22] or rodents. They are also capable of surviving on domestic cats and dogs, though humans are the preferred host of *C. lectularius*.[25]

Bed bugs can also be detected by their characteristic smell of rotting raspberries.[26] Bed bug detection dogs are trained to pinpoint infestations, with a possible accuracy rate between 11% and 83%.[6] Homemade detectors have been developed.[27][28]

Eggs and two adults found inside a dresser

Fecal spot



Bed bug on carpet

Differential diagnosis

Other possible conditions with which these conditions can be confused include scabies, gamasoidosis, allergic reactions, mosquito bites, spider bites, chicken pox and bacterial skin infections.[5]

Prevention

To prevent bringing home bed bugs, travelers are advised to take precautions after visiting an infested site: generally, these include checking shoes on leaving the site, changing clothes outside the house before entering, and putting the used clothes in a clothes dryer outside the house. When visiting a new lodging, it is advised to check the bed before taking suitcases into the sleeping area, and putting the suitcase on a raised stand to make bedbugs less likely to crawl in. An extreme measure would be putting the suitcase in the tub. Clothes should be hung up or left in the suitcase, and never left on the floor.[29] The founder of a company dedicated to bedbug extermination said that 5% of hotel rooms he books into were infested. He advised people never to sit down on public transport; check office chairs, plane seats, and hotel mattresses; and monitor and vacuum home beds once a month.[30]

Management

Treatment requires keeping the person from being repeatedly bitten and possible symptomatic use of antihistamines and corticosteroids (either topically or systemically).[5] There however is no evidence that medications improve outcomes and symptoms usually resolve without treatment in 1–2 weeks.[3][4]

Avoiding repeated bites can be difficult, since it usually requires eradicating bed bugs from a home or workplace; eradication frequently requires a combination of pesticide and non-pesticide approaches.[3] Pesticides that have historically been found to be effective include pyrethroids, dichlorvos and malathion.[4] Resistance to pesticides has increased significantly over time and there are concerns of negative health effects from their use.[3] Mechanical approaches, such as vacuuming up the insects and heat-treating or wrapping mattresses have been recommended.[3]

Once established, bed bugs are extremely difficult to get rid of.[3] This frequently requires a combination of nonpesticide approaches and the use of insecticides.[3][4]

Mechanical approaches, such as vacuuming up the insects and heat-treating or wrapping mattresses, are effective.[3][6] An hour at a temperature of 45 °C (113 °F) or over, or two hours at less than −17 °C (1 °F) kills them.[6] This may include a domestic clothes drier for fabric or a commercial steamer. Bed bugs and their eggs will die on contact when exposed to surface temperatures above 180 °F (82 °C) and a steamer can reach well above 230 °F (110 °C).[15][31] A study found 100% mortality rates for bed bugs exposed to temperatures greater than 50 °C (122 °F) for more than 2 minutes. The study recommended maintaining temperatures of above 48 °C (118 °F) for more than 20 min to effectively kill all life stages of bed bugs, and because in practice treatment times of 6 to 8 hours are used to account for cracks and indoor clutter.[32] This method is expensive and has caused fires.[6][15] Starving bedbugs is not effective, as they can survive without eating for 100 to 300 days, depending on temperature.[6]

It was stated in 2012 that no truly effective insecticides were available.[6] Insecticides that have historically been found effective include pyrethroids, dichlorvos, and malathion.[4] Resistance to pesticides has increased significantly in recent decades, and harm to health from their use is of concern.[3] The carbamate insecticide propoxur is highly toxic to bed bugs, but it has potential toxicity to children exposed to it, and the US Environmental Protection Agency has been reluctant to approve it for indoor use.[33] Boric acid, occasionally applied as a safe indoor insecticide, is not effective against bed bugs[34] because they do not groom.[35]

Epidemiology

Bed bugs occur around the world.[36] Before the 1950s about 30% of houses in the United States had bedbugs.[2] Rates of infestation in developed countries, while decreasing from the 1930s to the 1980s, have increased dramatically since the 1980s.[3][4][36] This is believed to be partly due to the use of DDT to kill cockroaches.[37] The invention of the vacuum cleaner and simplification of furniture design may have also played a role.[37] Others believe it might simply be the cyclical nature of the organism.[38]

The dramatic increase in bedbug populations in the developed world, which began in the 1980s, is thought to be due to greater foreign travel, increased immigration from the developing world to the developed world, more frequent exchange of second-hand furnishings among homes, a greater focus on control of other pests, resulting in neglect of bed bug countermeasures, and increasing bedbug resistance to pesticides.[4][39] Lower cockroach populations due to insecticide use may have aided bed bugs' resurgence, since cockroaches are known to sometimes predate them.[40] Bans on DDT and other potent pesticides may have also contributed.[41][42]

The U.S. National Pest Management Association reported a 71% increase in bed bug calls between 2000 and 2005.[43] The number of reported incidents in New York City alone rose from 500 in 2004 to 10,000 in 2009.[44] In 2013, Chicago was listed as the number 1 city in the United States for bedbug infestations.[45] As a result, the Chicago City Council passed a bed bug control ordinance to limit their spread. Additionally, bed bugs are reaching places in which they never established before, such as southern South America.[46][47]

The rise in infestations has been hard to track because bed bugs are not an easily identifiable problem and is one that people prefer not to discuss. Most of the reports are collected from pest-control companies, local authorities, and hotel chains.[48] Therefore, the problem may be more severe than is currently believed.[49]

Species

The common bed bug (*C. lectularius*) is the species best adapted to human environments. It is found in temperate climates throughout the world. Other species include *Cimex hemipterus*, found in tropical regions, which also infests poultry and bats, and *Leptocimex boueti*, found in the tropics of West Africa and South America, which infests bats and humans. *Cimex pilosellus* and *Cimex pipistrella* primarily infest bats, while *Haematosiphon inodora*, a species of North America, primarily infests poultry.[50]

History

Cimicidae the ancestor of modern bed bugs first emerged approximately 115 million years ago, more than 30 million years before bats, their previously presumed initial host first appeared. From unknown ancestral hosts, a variety of different lineages evolved which specialized in either bats or birds. The common (*C. lectularius*) and tropical bed bug (*C. hemipterus*), split 40 million years before *Homo* evolution. Humans became hosts to bed bugs through host specialist extension (rather than switching) on three separate occasions.[51][52]

Bed bugs were mentioned in ancient Greece as early as 400 BC, and were later mentioned by Aristotle. Pliny's *Natural History*, first published *circa* AD 77 in Rome, claimed bed bugs had medicinal value in treating ailments such as snake bites and ear infections. Belief in the medicinal use of bed bugs persisted until at least the 18th century, when Guettard recommended their use in the treatment of hysteria.[53]

Bed bugs were first mentioned in Germany in the 11th century, in France in the 13th century, and in England in 1583,[54] though they remained rare in England until 1670. Some in the 18th century believed bed bugs had been brought to London with supplies of wood to rebuild the city after the Great Fire of London (1666). Giovanni Antonio Scopoli noted their presence in Carniola (roughly equivalent to present-day Slovenia) in the 18th century.[55][56]

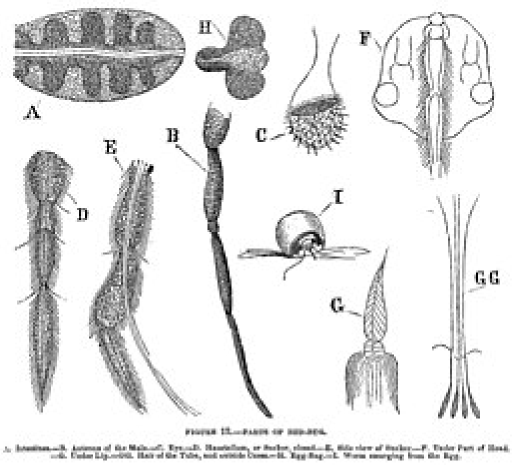
Traditional methods of repelling and/or killing bed bugs include the use of plants, fungi, and insects (or their extracts), such as black pepper;[57] black cohosh (*Actaea racemosa*); *Pseudarthria hookeri*; *Laggera alata* (Chinese *yángmáo cǎo* | 羊毛草);[15] *Eucalyptus saligna* oil;[58][59] henna (*Lawsonia inermis* or camphire);[60] "infused oil of *Melolontha vulgaris*" (presumably cockchafer); fly agaric (*Amanita muscaria*); tobacco; "heated oil of Terebinthina" (i.e. true turpentine); wild mint (*Mentha arvensis*); narrow-leaved pepperwort (*Lepidium ruderale*); *Myrica* spp. (e.g. bayberry); Robert geranium (*Geranium robertianum*); bugbane (*Cimicifuga* spp.); "herb and seeds of *Cannabis*"; "opulus" berries (possibly maple or European cranberrybush); masked hunter bugs (*Reduvius personatus*), "and many others".[61]

1870s–1890s advertisement for a bed bug exterminator. It reads "Use Getz cockroach and bed bug exterminators, sold by all druggists."

In the mid-19th century, smoke from peat fires was recommended as an indoor domestic fumigant against bed bugs.[62]

Dusts have been used to ward off insects from grain storage for centuries, including plant ash, lime, dolomite, certain types of soil, and diatomaceous earth or Kieselguhr.[63] Of these, diatomaceous earth in particular has seen a revival as a nontoxic (when in amorphous form) residual pesticide for bed bug abatement. While diatomaceous earth often performs poorly, silica gel may be effective.[64][65]

Basket-work panels were put around beds and shaken out in the morning in the UK and in France in the 19th century. Scattering leaves of plants with microscopic hooked hairs around a bed at night, then sweeping them up in the morning and burning them, was a technique reportedly used in Southern Rhodesia and in the Balkans.[66]



1860 engraving of bed bug parts: *A*. Intestines – *B*. Antenna of the male – *C*. Eye – *D*. Haustellum, or sucker, closed – *E*. Side view of sucker – *F*. Under part of head – *G*. Under lip – *GG*. Hair of the tube, and outside cases – *H*. Egg-bag – *I*. Larva emerging from the eggs

Bean leaves have been used historically to trap bedbugs in houses in Eastern Europe. The trichomes on the bean leaves capture the insects by impaling the feet (tarsi) of the insects. The leaves are then destroyed.[67]

20th century

Before the mid-20th century, bed bugs were very common. According to a report by the UK Ministry of Health, in 1933, all the houses in many areas had some degree of bed bug infestation.[48] The increase in bed bug populations in the early 20th century has been attributed to the advent of electric heating, which allowed bed bugs to thrive year-round instead of only in warm weather.[68]

Bed bugs were a serious problem at US military bases during World War II.[69] Initially, the problem was solved by fumigation, using Zyklon Discoids that released hydrogen cyanide gas, a rather dangerous procedure.[69] Later, DDT was used to good effect.[69]

The decline of bed bug populations in the 20th century is often credited to potent pesticides that had not previously been widely available.[70] Other contributing factors that are less frequently mentioned in news reports are increased public awareness and slum clearance programs that combined pesticide use with steam disinfection, relocation of slum dwellers to new housing, and in some cases also follow-up inspections for several months after relocated tenants moved into their new housing.[68]

Society and culture

Legal action

Bed bugs are an increasing cause for litigation.[71] Courts have, in some cases, exacted large punitive damage judgments on some hotels.[72][73][74] Many of New York City's Upper East Side homeowners have been afflicted, but they tend to remain publicly silent in order not to ruin their property values and be seen as suffering a blight typically associated with the lower classes.[75] Local Law 69 in New York City requires owners of buildings with three or more units to provide their tenants and potential tenants with reports of bedbug history in each unit. They must also prominently post these listings and reports in their building.[76]

Literature

- "Good night, sleep tight, don't let the bed bugs bite," is a traditional saying.[77]
- *The Bedbug* (Russian: Клоп, Klop) is a play by Vladimir Mayakovsky written in 1928–1929.

Research

Bed bug secretions can inhibit the growth of some bacteria and fungi; antibacterial components from the bed bug could be used against human pathogens, and be a source of pharmacologically active molecules as a resource for the discovery of new drugs.[78]

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Moth

Moths are a polyphyletic group of insects that includes all members of the order Lepidoptera that are not butterflies, with moths making up the vast majority of the order. There are thought to be approximately 160,000 species of moth,[1] many of which have yet to be described. Most species of moth are nocturnal, but there are also crepuscular and diurnal species.

Moths	
	
Emperor gum moth, *Opodiphthera eucalypti*	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Lepidoptera
(unranked):	Heterocera

Contents

Differences between butterflies and moths

While the butterflies form a monophyletic group, the moths, comprising the rest of the Lepidoptera, do not. Many attempts have been made to group the superfamilies of the Lepidoptera into natural groups, most of which fail because one of the two groups is not monophyletic: Microlepidoptera and Macrolepidoptera, Heterocera and Rhopalocera, Jugatae and Frenatae, Monotrysia and Ditrysia.[2]

Although the rules for distinguishing moths from butterflies are not well established, one very good guiding principle is that butterflies have thin antennae and (with the exception of the family Hedylidae) have small balls or clubs at the end of their antennae. Moth antennae are usually feathery with no ball on the end. The divisions are named by this principle: "club-antennae" (Rhopalocera) or "varied-antennae" (Heterocera).

Etymology

The modern English word "moth" comes from Old English "*moððe*" (cf. Northumbrian "*mohðe*") from Common Germanic (compare Old Norse "*motti*", Dutch "*mot*", and German "*Motte*" all meaning "moth"). Its origins are possibly related to the Old English "*maða*" meaning "maggot" or from the root of "midge" which until the 16th century was used mostly to indicate the larva, usually in reference to devouring clothes.

Caterpillar

Poplar hawk-moth caterpillar (*Laothoe populi*)

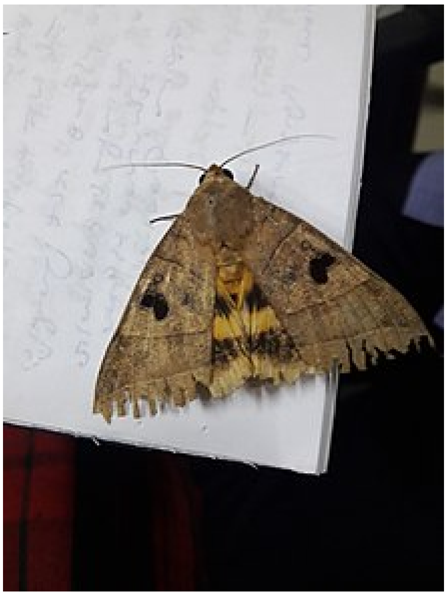
Moth larvae, or caterpillars, make cocoons from which they emerge as fully grown moths with wings. Some moth caterpillars dig holes in the ground, where they live until they are ready to turn into adult moths.[3]

History

Moth larva from India

Moths evolved long before butterflies, with fossils having been found that may be 190 million years old. Both types of Lepidoptera are thought to have evolved along with flowering plants, mainly because most modern species feed on flowering plants, both as adults and larvae. One of the earliest species thought to be a moth-ancestor is *Archaeolepis mane*, whose fossil fragments show scaled wings similar to caddisflies in their veining.[4]

Economics



Moth from Kerala, India

Significance to humans

Some moths, particularly their caterpillars, can be major agricultural pests in many parts of the world. Examples include corn borers and bollworms.[5] The caterpillar of the gypsy moth (*Lymantria dispar*) causes severe damage to forests in the northeastern United States, where it is an invasive species. In temperate climates, the codling moth causes extensive damage, especially to fruit farms. In tropical and subtropical climates, the diamondback moth (*Plutella xylostella*) is perhaps the most serious pest of brassicaceous crops. Also in sub-Saharan Africa, the African sugarcane borer is a major pest of sugarcane, maize, and sorghum.[6]

Several moths in the family Tineidae are commonly regarded as pests because their larvae eat fabric such as clothes and blankets made from natural proteinaceous fibers such as wool or silk.[7] They are less likely to eat mixed materials containing some artificial fibers. There are some reports that they may be repelled by the scent of wood from juniper and cedar, by lavender, or by other natural oils; however, many consider this unlikely to prevent infestation. Naphthalene (the chemical used in mothballs) is considered more effective, but there are concerns over its effects on human health.

Moth larvae may be killed by freezing the items which they infest for several days at a temperature below −8 °C (18 °F).[8]

Despite being notorious for eating clothing, most moth adults do not eat at all. Many, like the Luna, Polyphemus, Atlas, Promethea, cecropia, and other large moths do not have mouth parts. While there are many species of adult moths that do eat, there are many that will drink nectar.[7]

Some moths are farmed for their economic value. The most notable of these is the silkworm, the larva of the domesticated moth *Bombyx mori*. It is farmed for the silk with which it builds its cocoon. As of 2002, the silk industry produces more than 130 million kilograms of raw silk, worth about 250 million U.S. dollars, each year.[9][10][11]

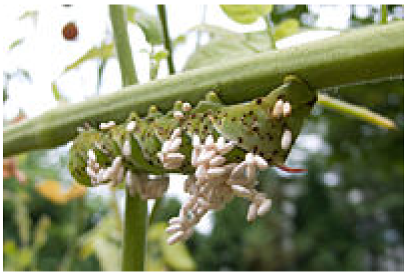
Not all silk is produced by *Bombyx mori*. There are several species of Saturniidae that also are farmed for their silk, such as the ailanthus moth (*Samia cynthia* group of species), the Chinese oak silkmoth (*Antheraea pernyi*), the Assam silkmoth (*Antheraea assamensis*), and the Japanese silk moth (*Antheraea yamamai*).

An adult male pine processionary moth (*Thaumetopoea pityocampa*). This species is a serious forest pest when in its larval state. Notice the bristle springing from the underside of the hindwing (frenulum) and running forward to be held in a small catch of the forewing, whose function is to link the wings together.

The larvae of many species are used as food, particularly in Africa, where they are an important source of nutrition. The mopane worm, the caterpillar of *Gonimbrasia belina*, from the family Saturniidae, is a significant food resource in southern Africa. Another saturniid used as food is the cavorting emperor (*Usta terpsichore*). In one country alone, Congo, more than 30 species of moth larvae are harvested. Some are sold not only in the local village markets, but are shipped by the ton from one country to another.[12]

Predators and parasites

Nocturnal insectivores often feed on moths; these include some bats, some species of owls and other species of birds. Moths also are eaten by some species of lizards, amphibians, cats, dogs, rodents, and some bears. Moth larvae are vulnerable to being parasitized by Ichneumonidae.



Tomato hornworm parasitized by braconid wasps

Baculoviruses are parasite double-stranded DNA insect viruses that are used mostly as biological control agents. They are members of the Baculoviridae, a family that is restricted to insects. Most baculovirus isolates have been obtained from insects, in particular from Lepidoptera.

There is evidence that ultrasound in the range emitted by bats causes flying moths to make evasive maneuvers because bats eat moths. Ultrasonic frequencies trigger a reflex action in the noctuid moth that causes it to drop a few inches in its flight to evade attack.[13] Tiger moths also emit clicks which can foil bats' echolocation.[14][15]

The fungus *Ophiocordyceps sinensis* infects the larvae of many different species of moths.[16]

Ecological importance

Some studies indicate that certain species of moths, such as those belonging to the families Erebidae and Sphingidae, may be the key pollinators for some flowering plants in the Himalayan ecosystem.[17][18]

Attraction to light

Moths frequently appear to circle artificial lights, although the reason for this behavior (positive phototaxis) remains unknown. One hypothesis is called celestial or transverse orientation. By maintaining a constant angular relationship to a bright celestial light, such as the moon, they can fly in a straight line. Celestial objects are so far away that, even after travelling great distances, the change in angle between the moth and the light source is negligible; further, the moon will always be in the upper part of the visual field, or on the horizon. When a moth encounters a much closer artificial light and uses it for navigation, the angle changes noticeably after only a short distance, in addition to being often below the horizon. The moth instinctively attempts to correct by turning toward the light, thereby causing airborne moths to come plummeting downward, and resulting in a spiral flight path that gets closer and closer to the light source.[19]

Studies have found that light pollution caused by increasing use of artificial lights has either led to a severe decline in moth population in some parts of the world[20][21][22] or has severely disrupted nocturnal pollination.[23][24]


Assorted moths in the University of Texas Insect Collection

Noteworthy moths

- Atlas moth (*Attacus atlas*), the largest moth in the world
- White witch moth (*Thysania agrippina*), the Lepidopteran with the longest wingspan
- Madagascan sunset moth (*Chrysiridia rhipheus*), considered to be one of the most impressive and beautiful Lepidoptera[25]
- Death's-head hawkmoth (*Acherontia* spp.), is associated with the supernatural and evil and has been featured in art and movies
- Peppered moth (*Biston betularia*), the subject of a well-known study in natural selection
- Luna moth (*Actias luna*)
- Grease moth (*Aglossa cuprina*), known to have fed on the rendered fat of humans[26]
- Emperor gum moth (*Opodiphthera eucalypti*)
- Polyphemus moth (*Antheraea polyphemus*)
- Bogong moth (*Agrotis infusa*), known to have been a food source for southeastern indigenous Australians
- Ornate moth (*Utetheisa ornatrix*), the subject of numerous behavioral studies regarding sexual selection

Moths of economic significance

- Gypsy moth (*Lymantria dispar*), an invasive species pest of hardwood trees in North America
- Winter moth (*Operophtera brumata*), an invasive species pest of hardwood trees, cranberry and blueberry in northeastern North America
- Corn earworm or cotton bollworm (*Helicoverpa zea*), a major agricultural pest
- Indianmeal moth (*Plodia interpunctella*), a major pest of grain and flour
- Codling moth (*Cydia pomonella*), a pest mostly of apple, pear and walnut trees
- Light brown apple moth (*Epiphyas postvittana*), a highly polyphagous pest
- Silkworm (*Bombyx mori*), for its silk
- Wax moths (*Galleria mellonella*, *Achroia grisella*), pests of bee hives
- *Duponchelia fovealis*, a new invasive pest of vegetables and ornamental plants in the United States

Gallery

Diagram of a plume moth from Robert Hooke's *Micrographia*

Leaf-shaped moth (*Pergesa acteus*)

Giant grey moth (*Agrius convolvuli*)

Oleander hawk-moth or army green moth (*Daphnis nerii*)

Six-spot burnet moths mating (*Zygaena filipendulae*)

Protective silk (or similar material) case (cocoon)

A caterpillar of death's-head hawkmoth

Mating pair of *Laothoe populi*, or poplar hawkmoths, showing two different color variants

White-lined sphinx moth in Colorado, United States

Closeup of a common clothes moth

Giant silk moth (*Adelowalkeria tristygma*)

Adult emperor moth (*Gonimbrasia belina*)

Sphingidae - Kerala

See also

- Baculovirus
- Butterfly
- Clothing moth
- Comparison of butterflies and moths
- Lepidoptera
- List of moths
- Lepidopterism
- Pollination

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Evolution of Moths and Butterflies (http://cdri.org/publications/nature-notes/evolution-ecology/evolution-of-moths-and-butterflies/) Archived (https://web.archive.org/web/20140106184057/http://cdri.org/publications/nature-notes/evolution-ecology/evolution-of-moths-and-butterflies/) 2014-01-06 at the Wayback Machine
Studying the evolution of butterflies and moths is challenging, since fossils are so rare. But the few Lepidopteran fossils that exist, captured in amber or compressed in fine-grained rocks, show great detail. The earliest Lepidopteran fossils appear in rocks that are about 190 million years old. These tiny fragments of scaled wings and bodies clearly indicate that moths evolved before butterflies.

Wikipedia

Ant

Ants are eusocial insects of the family **Formicidae** and, along with the related wasps and bees, belong to the order Hymenoptera. Ants evolved from wasp-like ancestors in the Cretaceous period, about 140 million years ago, and diversified after the rise of flowering plants. More than 12,500 of an estimated total of 22,000 species have been classified.[5][6] They are easily identified by their elbowed antennae and the distinctive node-like structure that forms their slender waists.

Ants form colonies that range in size from a few dozen predatory individuals living in small natural cavities to highly organised colonies that may occupy large territories and consist of millions of individuals. Larger colonies consist of various castes of sterile, wingless females, most of which are workers (ergates), as well as soldiers (dinergates) and other specialised groups.[7][8] Nearly all ant colonies also have some fertile males called "drones" (aner) and one or more fertile females called "queens" (gynes).[8] The colonies are described as superorganisms because the ants appear to operate as a unified entity, collectively working together to support the colony.[9][10]

Ants have colonised almost every landmass on Earth. The only places lacking indigenous ants are Antarctica and a few remote or inhospitable islands. Ants thrive in most ecosystems and may form 15–25% of the terrestrial animal biomass.[11] Their success in so many environments has been attributed to their social organisation and their ability to modify habitats, tap resources, and defend themselves. Their long co-evolution with other species has led to mimetic, commensal, parasitic, and mutualistic relationships.[12]

Ant societies have division of labour, communication between individuals, and an ability to solve complex problems.[13] These parallels with human societies have long been an inspiration and subject of study. Many human cultures make use of ants in cuisine, medication, and rituals. Some species are valued in their role as biological pest control agents.[14] Their ability to exploit resources may bring ants into conflict with humans, however, as they can damage crops and invade buildings. Some species, such as the red imported fire ant (*Solenopsis invicta*), are regarded as invasive species, establishing themselves in areas where they have been introduced accidentally.[15]

Ants

Temporal range: 140–0 Ma[1]

PreЄ Є O S D C P T J K PgN

Berriasian – Present

A group of fire ants.

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Superfamily:	Formicoidea
Family:	Formicidae Latreille, 1809

Type species

Formica rufa
Linnaeus, 1761

Subfamilies

Contents

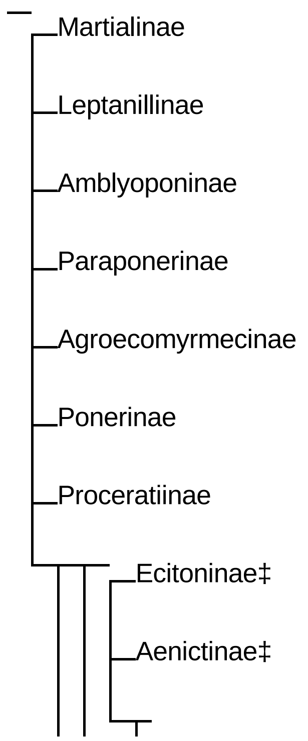
Etymology

The word *ant* and its chiefly dialectal form *emmet*[16] come from *ante*, *emete* of Middle English, which come from *ǣmette* of Old English, and these are all related to the dialectal Dutch *emt* and the Old High German *āmeiza*, from which comes the modern German *Ameise*. All of these words come from West Germanic **ǣmaitjōn*, and the original meaning of the word was "the biter" (from Proto-Germanic **ai-*, "off, away" + **mait-* "cut").[17][18] The family name Formicidae is derived from the Latin *formīca* ("ant")[19] from which the words in other Romance languages, such as the Portuguese *formiga*, Italian *formica*, Spanish *hormiga*, Romanian *furnică*, and French *fourmi* are derived. It has been hypothesised that a Proto-Indo-European word *morwi- was used, cf. Sanskrit vamrah, Latin formīca, Greek μύρμηξ *mýrmēx*, Old Church Slavonic *mravijі*, Old Irish *moirb*, Old Norse *maurr*, Dutch *mier*.[20]

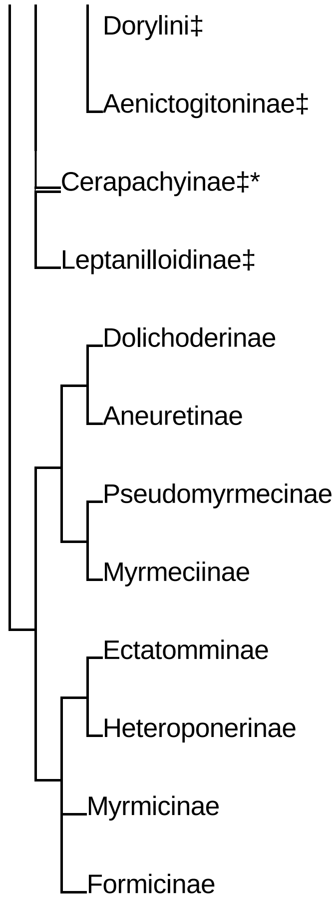
Taxonomy and evolution

- Agroecomyrmecinae
- Amblyoponinae (incl. "Apomyrminae")
- Aneuretinae
- †Brownimeciinae
- Dolichoderinae
- Dorylinae
- Ectatomminae
- †Formiciinae
- Formicinae
- Heteroponerinae
- Leptanillinae
- Martialinae
- Myrmeciinae (incl. "Nothomyrmeciinae")
- Myrmicinae
- Paraponerinae
- Ponerinae
- Proceratiinae
- Pseudomyrmecinae
- †Sphecomyrminae

Cladogram of subfamilies



The family Formicidae belongs to the order Hymenoptera, which also includes sawflies, bees, and wasps. Ants evolved from a lineage within the stinging wasps, and a 2013 study suggests that they are a sister group of the Apoidea.[21] In 1966, E. O. Wilson and his colleagues identified the fossil remains of an ant (*Sphecomyrma*) that lived in the Cretaceous period. The specimen, trapped in amber dating back to around 92 million years ago, has features found in some wasps, but not found in modern ants.[22] *Sphecomyrma* was possibly a ground forager, while *Haidomyrmex* and *Haidomyrmodes*, related genera in subfamily Sphecomyrminae, are reconstructed as active arboreal predators.[23] Older ants in the genus *Sphecomyrmodes* have been found in 99 million year-old amber from Myanmar.[24][25] A 2006 study suggested that ants arose tens of millions of years earlier than previously thought, up to 168 million years ago.[1] After the rise of flowering plants about 100 million years ago they diversified and assumed ecological dominance around 60 million years ago.[26][1][27][28] Some groups, such as the Leptanillinae and Martialinae, are suggested to have diversified from early primitive ants that were likely to have been predators underneath the surface of the soil.[3][29]

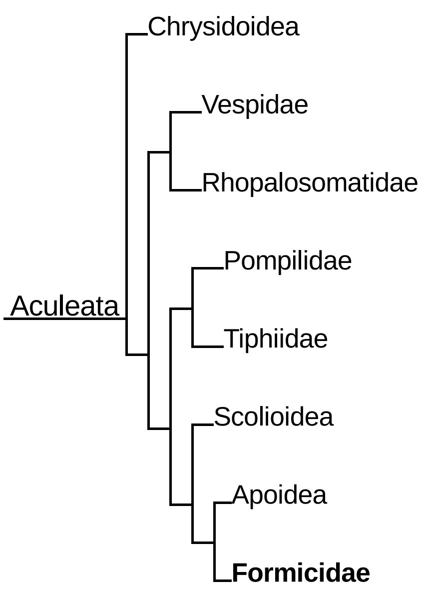


A phylogeny of the extant ant subfamilies.[2][3]

*Cerapachyinae is paraphyletic

‡ The previous dorylomorph subfamilies were synonymized under Dorylinae by Brady *et al.* in 2014[4]

During the Cretaceous period, a few species of primitive ants ranged widely on the Laurasian supercontinent (the Northern Hemisphere). They were scarce in comparison to the populations of other insects, representing only about 1% of the entire insect population. Ants became dominant after adaptive radiation at the beginning of the Paleogene period. By the Oligocene and Miocene, ants had come to represent 20–40% of all insects found in major fossil deposits. Of the species that lived in the Eocene epoch, around one in 10 genera survive to the present. Genera surviving today comprise 56% of the genera in Baltic amber fossils (early Oligocene), and 92% of the genera in Dominican amber fossils (apparently early Miocene).[26][30]



Phylogenetic position of the Formicidae.[21]

Play media

(video) Ants gathering food

Termites live in colonies and are sometimes called ‘white ants’, but termites are not ants. They are the sub-order Isoptera, and together with cockroaches they form the order Blattodea. Blattodeans are related to mantids, crickets, and other winged insects that do not undergo full metamorphosis. Like ants, termites are eusocial, with sterile workers, but they differ greatly in the genetics of reproduction. The similarity of their social structure to that of ants is attributed to convergent evolution.[31] Velvet ants look like large ants, but are wingless female wasps.[32][33]

Distribution and diversity

Ants fossilised in Baltic amber

Region	Number of species [34]
Neotropics	2,162
Nearctic	580
Europe	180
Africa	2,500
Asia	2,080
Melanesia	275
Australia	985
Polynesia	42

Ants are found on all continents except Antarctica, and only a few large islands, such as Greenland, Iceland, parts of Polynesia and the Hawaiian Islands lack native ant species.[35][36] Ants occupy a wide range of ecological niches and exploit many different food resources as direct or indirect herbivores, predators and scavengers. Most ant species are omnivorous generalists, but a few are specialist feeders. Their ecological dominance is demonstrated by their biomass: ants are estimated to contribute 15–20 % (on average and nearly 25% in the tropics) of terrestrial animal biomass, exceeding that of the vertebrates.[11]

Ants range in size from 0.75 to 52 millimetres (0.030–2.0 in),[37][38] the largest species being the fossil *Titanomyrma giganteum*, the queen of which was 6 centimetres (2.4 in) long with a wingspan of 15 centimetres (5.9 in).[39] Ants vary in colour; most ants are red or black, but a few species are green and some tropical species have a metallic lustre. More than 12,000 species are currently known (with upper estimates of the potential existence of about 22,000) (see the article List of ant genera), with the greatest diversity in the tropics. Taxonomic studies continue to resolve the classification and systematics of ants. Online databases of ant species, including AntBase (http://antbase.org/) and the Hymenoptera Name Server (https://hns.osu.edu/), help to keep track of the known and newly described species.[40] The relative ease with which ants may be sampled and studied in ecosystems has made them useful as indicator species in biodiversity studies.[41][42]

Morphology

Ants are distinct in their morphology from other insects in having elbowed antennae, metapleural glands, and a strong constriction of their second abdominal segment into a node-like petiole. The head, mesosoma, and metasoma are the three distinct body segments (formally tagmata). The petiole forms a narrow waist between their mesosoma (thorax plus the first abdominal segment, which is fused to it) and gaster (abdomen less the abdominal segments in the petiole). The petiole may be formed by one or two nodes (the second alone, or the second and third abdominal segments).[43]

Like other insects, ants have an exoskeleton, an external covering that provides a protective casing around the body and a point of attachment for muscles, in contrast to the internal skeletons of humans and other vertebrates. Insects do not have lungs; oxygen and other gases, such as carbon dioxide, pass through their exoskeleton via tiny valves called spiracles. Insects also lack closed blood vessels; instead, they have a long, thin, perforated tube along the top of the body (called the "dorsal aorta") that functions like a heart, and pumps haemolymph toward the head, thus driving the circulation of the internal fluids. The nervous system consists of a ventral nerve cord that runs the length of the body, with several ganglia and branches along the way reaching into the extremities of the appendages.[44]

Head

An ant's head contains many sensory organs. Like most insects, ants have compound eyes made from numerous tiny lenses attached together. Ant eyes are good for acute movement detection, but do not offer a high resolution image. They also have three small ocelli (simple eyes) on the top of the head that detect light levels and polarization.[45] Compared to vertebrates, most ants have poor-to-mediocre eyesight and a few subterranean species are completely blind. However, some ants, such as Australia's

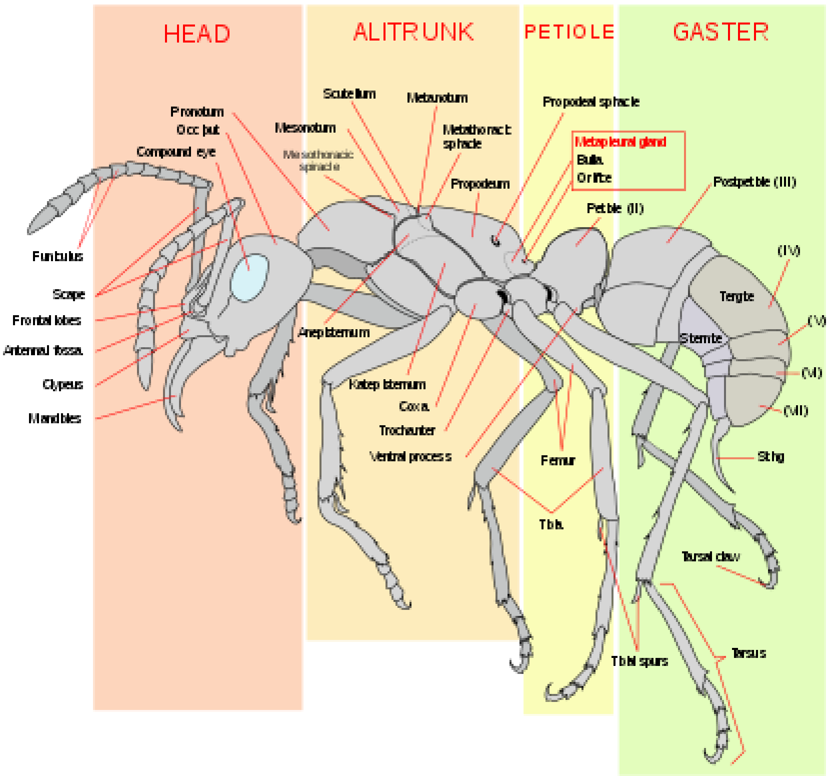


Diagram of a worker ant (*Pachycondyla verenae*)

bulldog ant, have excellent vision and are capable of discriminating the distance and size of objects moving nearly a metre away.[46]

Two antennae ("feelers") are attached to the head; these organs detect chemicals, air currents, and vibrations; they also are used to transmit and receive signals through touch. The head has two strong jaws, the mandibles, used to carry food, manipulate objects, construct nests, and for defence.[44] In some species, a small pocket (infrabuccal chamber) inside the mouth stores food, so it may be passed to other ants or their larvae.[47]

Mesosoma

Both the legs and wings of the ant are attached to the mesosoma ("thorax"). The legs terminate in a hooked claw which allows them to hook on and climb surfaces.[48] Only reproductive ants, queens, and males, have wings. Queens shed their wings after the nuptial flight, leaving visible stubs, a distinguishing feature of queens. In a few species, wingless queens (ergatoids) and males occur.[44]

Macro portrait of an ant

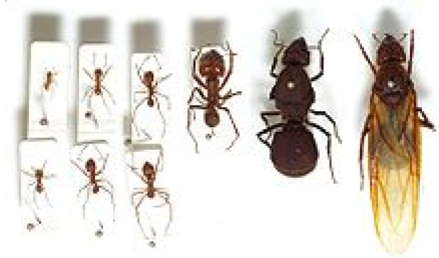
Bull ant showing the powerful mandibles and the relatively large compound eyes that provide excellent vision

Metasoma

The metasoma (the "abdomen") of the ant houses important internal organs, including those of the reproductive, respiratory (tracheae), and excretory systems. Workers of many species have their egg-laying structures modified into stings that are used for subduing prey and defending their nests.[44]

Polymorphism

In the colonies of a few ant species, there are physical castes—workers in distinct size-classes, called minor, median, and major ergates. Often, the larger ants have disproportionately larger heads, and correspondingly stronger mandibles. These are known as macrergates while smaller workers are known as micrergates.[8] Although formally known as dinergates, such individuals are sometimes called "soldier" ants because their stronger mandibles make them more effective in fighting, although they still are workers and their "duties" typically do not vary greatly from the minor or median workers. In a few species, the median workers are absent, creating a sharp divide between the minors and majors.[49] Weaver ants, for example, have a distinct bimodal size distribution.[50][51] Some other species show continuous variation in the size of workers. The smallest and largest workers in *Pheidologeton diversus* show nearly a 500-fold difference in their dry-weights.[52]



Seven leafcutter ant workers of various castes (left) and two queens (right)

Workers cannot mate; however, because of the haplodiploid sex-determination system in ants, workers of a number of species can lay unfertilised eggs that become fully fertile, haploid males. The role of workers may change with their age and in some species, such as honeypot ants, young workers are fed until their gasters are distended, and act as living food storage vessels. These food storage workers are called *repletes*.[53] For instance, these replete workers develop in the North American honeypot ant *Myrmecocystus mexicanus*. Usually the largest workers in the colony develop into repletes; and, if repletes are removed from the colony, other workers become repletes, demonstrating the flexibility of this particular polymorphism.[54] This polymorphism in morphology and behaviour of workers initially was thought to be determined by environmental factors such as nutrition and hormones that led to different developmental paths; however, genetic differences between worker castes have been noted in *Acromyrmex* sp.[55] These polymorphisms are caused by relatively small genetic changes; differences in a single gene of *Solenopsis invicta* can decide whether the colony will have single or multiple queens.[56] The Australian jack jumper ant (*Myrmecia pilosula*) has only a single pair of chromosomes (with the males having just one chromosome as they are haploid), the lowest number known for any animal, making it an interesting subject for studies in the genetics and developmental biology of social insects.[57][58]

Life cycle

Meat eater ant nest during swarming

The life of an ant starts from an egg. If the egg is fertilised, the progeny will be female diploid; if not, it will be male haploid. Ants develop by complete metamorphosis with the larva stages passing through a pupal stage before emerging as an adult. The larva is largely immobile and is fed and cared for by workers. Food is given to the larvae by trophallaxis, a process in which an ant regurgitates liquid food held in its crop. This is also how adults share food, stored in the "social stomach". Larvae, especially in the later stages, may also be provided solid food, such as trophic eggs, pieces of prey, and seeds brought by workers.

The larvae grow through a series of four or five moults and enter the pupal stage. The pupa has the appendages free and not fused to the body as in a butterfly pupa.[59] The differentiation into queens and workers (which are both female), and different castes of workers, is influenced in some species by the nutrition the larvae obtain. Genetic influences and the control of gene expression by the developmental environment are complex and the determination of caste continues to be a subject of research.[60] Winged male ants, called drones, emerge from pupae along with the usually winged breeding females. Some species, such as army ants, have wingless queens. Larvae and pupae need to be kept at fairly constant temperatures to ensure proper development, and so often, are moved around among the various brood chambers within the colony.[61]

A new ergate spends the first few days of its adult life caring for the queen and young. She then graduates to digging and other nest work, and later to defending the nest and foraging. These changes are sometimes fairly sudden, and define what are called temporal castes. An explanation for the sequence is suggested by the high casualties involved in foraging, making it an acceptable risk only for ants who are older and are likely to die soon of natural causes.[62][63]

Ant colonies can be long-lived. The queens can live for up to 30 years, and workers live from 1 to 3 years. Males, however, are more transitory, being quite short-lived and surviving for only a few weeks.[64] Ant queens are estimated to live 100 times as long as solitary insects of a similar size.[65]

Ants are active all year long in the tropics, but, in cooler regions, they survive the winter in a state of dormancy known as hibernation. The forms of inactivity are varied and some temperate species have larvae going into the inactive state (diapause), while in others, the adults alone pass the winter in a state of reduced activity.[66]

Reproduction

Alate male ant, *Prenolepis imparis*

A wide range of reproductive strategies have been noted in ant species. Females of many species are known to be capable of reproducing asexually through thelytokous parthenogenesis.[67] Secretions from the male accessory glands in some species can plug the female genital opening and prevent females from re-mating.[68] Most ant species have a system in which only the queen and breeding females have the ability to mate. Contrary to popular belief, some ant nests have multiple queens, while others may exist without queens. Workers with the ability to reproduce are called "gamergates" and colonies that lack queens are then called gamergate colonies; colonies with queens are said to be queen-right.[69]

Ants mating

Drones can also mate with existing queens by entering a foreign colony. When the drone is initially attacked by the workers, it releases a mating pheromone. If recognized as a mate, it will be carried to the queen to mate.[70] Males may also patrol the nest and fight others by grabbing them with their mandibles, piercing their exoskeleton and then marking them with a pheromone. The marked male is interpreted as an invader by worker ants and is killed.[71]

Fertilised meat-eater ant queen beginning to dig a new colony

Most ants are univoltine, producing a new generation each year.[72] During the species-specific breeding period, winged females and winged males, known to entomologists as alates, leave the colony in what is called a nuptial flight. The nuptial flight usually takes place in the late spring or early summer when the weather is hot and humid. Heat makes flying easier and freshly fallen rain makes the ground softer for mated queens to dig nests.[73] Males typically take flight before the females. Males then use visual cues to find a common mating ground, for example, a landmark such as a pine tree to which other males in the area converge. Males secrete a mating pheromone that females follow. Males will mount females in the air, but the actual mating process usually takes place on the ground. Females of some species mate with just one male but in others they may mate with as many as ten or more different males, storing the sperm in their spermathecae.[74]

Mated females then seek a suitable place to begin a colony. There, they break off their wings and begin to lay and care for eggs. The females can selectively fertilise future eggs with the sperm stored to produce diploid workers or lay unfertilized haploid eggs to produce drones. The first workers to hatch are known as nanitics,[75] and are weaker and smaller than later workers, but they begin to serve the colony immediately. They enlarge the nest, forage for food, and care for the other eggs. Species that have multiple queens may have a queen leaving the nest along with some workers to found a colony at a new site,[74] a process akin to swarming in honeybees.

Behaviour and ecology

Communication

Two *Camponotus sericeus* workers communicating through touch and pheromones

Ants communicate with each other using pheromones, sounds, and touch.[76] The use of pheromones as chemical signals is more developed in ants, such as the red harvester ant, than in other hymenopteran groups. Like other insects, ants perceive smells with their long, thin, and mobile antennae. The paired antennae provide information about the direction and intensity of scents. Since most ants live on the ground, they use the soil surface to leave pheromone trails that may be followed by other ants. In species that forage in groups, a forager that finds food marks a trail on the way back to the colony; this trail is followed by other ants, these ants then reinforce the trail when they head back with food to the colony. When the food source is exhausted, no new trails are marked by returning ants and the scent slowly dissipates. This behaviour helps ants deal with changes in their environment. For instance, when an established path to a food source is blocked by an obstacle, the foragers leave the path to explore new routes. If an ant is successful, it leaves a new trail marking the shortest route on its return. Successful trails are followed by more ants, reinforcing better routes and gradually identifying the best path.[77]

Ants use pheromones for more than just making trails. A crushed ant emits an alarm pheromone that sends nearby ants into an attack frenzy and attracts more ants from farther away. Several ant species even use "propaganda pheromones" to confuse enemy ants and make them fight among themselves.[78] Pheromones are produced by a wide range of structures including Dufour's glands, poison glands and glands on the hindgut, pygidium, rectum, sternum, and hind tibia.[65] Pheromones also are exchanged, mixed with food, and passed by trophallaxis, transferring information within the colony.[79] This allows other ants to detect what task group (e.g., foraging or nest maintenance) other colony members belong to.[80] In ant species with queen castes, when the dominant queen stops producing a specific pheromone, workers begin to raise new queens in the colony.[81]

Some ants produce sounds by stridulation, using the gaster segments and their mandibles. Sounds may be used to communicate with colony members or with other species.[82][83]

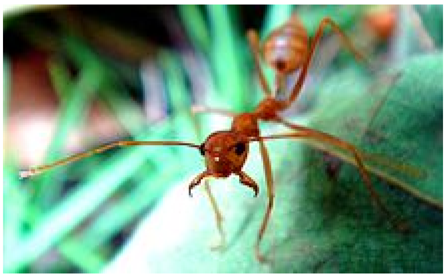
Defence

A *Plectroctena* sp. attacks another of its kind to protect its territory.

Ants attack and defend themselves by biting and, in many species, by stinging, often injecting or spraying chemicals, such as formic acid in the case of formicine ants, alkaloids and piperidines in fire ants, and a variety of protein components in other ants. Bullet ants (*Paraponera*), located in Central and South America, are considered to have the most painful sting of any insect, although it is usually not fatal to humans. This sting is given the highest rating on the Schmidt Sting Pain Index.

The sting of jack jumper ants can be fatal,[84] and an antivenom has been developed for it.[85]

Fire ants, *Solenopsis* spp., are unique in having a venom sac containing piperidine alkaloids.[86] Their stings are painful and can be dangerous to hypersensitive people.[87]


A weaver ant in fighting position, mandibles wide open

Trap-jaw ants of the genus *Odontomachus* are equipped with mandibles called trap-jaws, which snap shut faster than any other predatory appendages within the animal kingdom.[88] One study of *Odontomachus bauri* recorded peak speeds of between 126 and 230 km/h (78 and 143 mph), with the jaws closing within 130 microseconds on average. The ants were also observed to use their jaws as a catapult to eject intruders or fling themselves backward to escape a threat.[88] Before striking, the ant opens its mandibles extremely widely and locks them in this position by an internal mechanism. Energy is stored in a thick band of muscle and explosively released when triggered by the stimulation of sensory organs resembling hairs on the inside of the mandibles. The mandibles also permit slow and fine movements for other tasks. Trap-jaws also are seen in the following genera: *Anochetus*, *Orectognathus*, and *Strumigenys*,[88] plus some members of the Dacetini tribe,[89] which are viewed as examples of convergent evolution.

A Malaysian species of ant in the *Camponotus cylindricus* group has enlarged mandibular glands that extend into their gaster. If combat takes a turn for the worse, a worker may perform a final act of suicidal altruism by rupturing the membrane of its gaster, causing the content of its mandibular glands to burst from the anterior region of its head, spraying a poisonous, corrosive secretion containing acetophenones and other chemicals that immobilise small insect attackers. The worker subsequently dies.[90]

Suicidal defences by workers are also noted in a Brazilian ant, *Forelius pusillus*, where a small group of ants leaves the security of the nest after sealing the entrance from the outside each evening.[91]

In addition to defence against predators, ants need to protect their colonies from pathogens. Some worker ants maintain the hygiene of the colony and their activities include undertaking or *necrophory*, the disposal of dead nest-mates.[92] Oleic acid has been identified as the compound released from dead ants that triggers necrophoric behaviour in *Atta mexicana*[93] while workers of *Linepithema humile* react to the absence of characteristic chemicals (dolichodial and iridomyrmecin) present on the cuticle of their living nestmates to trigger similar behaviour.[94]


Ant mound holes prevent water from entering the nest during rain.

Nests may be protected from physical threats such as flooding and overheating by elaborate nest architecture.[95][96] Workers of *Cataulacus muticus*, an arboreal species that lives in plant hollows, respond to flooding by drinking water inside the nest, and excreting it outside.[97] *Camponotus anderseni*, which nests in the cavities of wood in mangrove habitats, deals with submergence under water by switching to anaerobic respiration.[98]

Learning

Many animals can learn behaviours by imitation, but ants may be the only group apart from mammals where interactive teaching has been observed. A knowledgeable forager of *Temnothorax albipennis* will lead a naive nest-mate to newly discovered food by the process of tandem running. The follower obtains knowledge through its leading tutor. The leader is acutely sensitive to the progress of the follower and slows down when the follower lags and speeds up when the follower gets too close.[99]

Controlled experiments with colonies of *Cerapachys biroi* suggest that an individual may choose nest roles based on her previous experience. An entire generation of identical workers was divided into two groups whose outcome in food foraging was controlled. One group was continually rewarded with prey, while it was made certain that the other failed. As a result, members of the successful group intensified their foraging attempts while the unsuccessful group ventured out fewer and fewer times. A month later, the successful foragers continued in their role while the others had moved to specialise in brood care.[100]

Nest construction


Leaf nest of weaver ants, Pamalican, Philippines

Complex nests are built by many ant species, but other species are nomadic and do not build permanent structures. Ants may form subterranean nests or build them on trees. These nests may be found in the ground, under stones or logs, inside logs, hollow stems, or even acorns. The materials used for construction include soil and plant matter,[74] and ants carefully select their nest sites; *Temnothorax albipennis* will avoid sites with dead ants, as these may indicate the presence of pests or disease. They are quick to abandon established nests at the first sign of threats.[101]

The army ants of South America, such as the *Eciton burchellii* species, and the driver ants of Africa do not build permanent nests, but instead, alternate between nomadism and stages where the workers form a temporary nest (bivouac) from their own bodies, by holding each other together.[102]

Weaver ant (*Oecophylla* spp.) workers build nests in trees by attaching leaves together, first pulling them together with bridges of workers and then inducing their larvae to produce silk as they are moved along the leaf edges. Similar forms of nest construction are seen in some species of *Polyrhachis*.[103]

Formica polyctena, among other ant species, constructs nests that maintain a relatively constant interior temperature that aids in the development of larvae. The ants maintain the nest temperature by choosing the location, nest materials, controlling ventilation and maintaining the heat from solar radiation, worker activity and metabolism, and in some moist nests, microbial activity in the nest materials.[104]

Some ant species, such as those that use natural cavities, can be opportunistic and make use of the controlled micro-climate provided inside human dwellings and other artificial structures to house their colonies and nest structures.[105][106]

Ant bridge

Cultivation of food

Myrmecocystus, honeypot ants, store food to prevent colony famine

Most ants are generalist predators, scavengers, and indirect herbivores,[27] but a few have evolved specialised ways of obtaining nutrition. It is believed that many ant species that engage in indirect herbivory rely on specialized symbiosis with their gut microbes [107] to upgrade the nutritional value of the food they collect [108] and allow them to survive in nitrogen poor regions, such as rainforest canopies.[109] Leafcutter ants (*Atta* and *Acromyrmex*) feed exclusively on a fungus that grows only within their colonies. They continually collect leaves which are taken to the colony, cut into tiny pieces and placed in fungal gardens. Ergates specialise in related tasks according to their sizes. The largest ants cut stalks, smaller workers chew the leaves and the smallest tend the fungus. Leafcutter ants are sensitive enough to recognise the reaction of the fungus to different plant material, apparently detecting chemical signals from the fungus. If a particular type of leaf is found to be toxic to the fungus, the colony will no longer collect it. The ants feed on structures produced by the fungi called *gongylidia*. Symbiotic bacteria on the exterior surface of the ants produce antibiotics that kill bacteria introduced into the nest that may harm the fungi.[110]

Navigation

An ant trail

Foraging ants travel distances of up to 200 metres (700 ft) from their nest [111] and scent trails allow them to find their way back even in the dark. In hot and arid regions, day-foraging ants face death by desiccation, so the ability to find the shortest route back to the nest reduces that risk. Diurnal desert ants of the genus *Cataglyphis* such as the Sahara desert ant navigate by keeping track of direction as well as distance travelled. Distances travelled are measured using an internal pedometer that keeps count of the steps taken[112] and also by evaluating the movement of objects in their visual field (optical flow).[113] Directions are measured using the position of the sun.[114] They integrate this information to find the shortest route back to their nest.[115] Like all ants, they can also make use of visual landmarks when available[116] as well as olfactory and tactile cues to navigate.[117][118] Some species of ant are able to use the Earth's magnetic field for navigation.[119] The compound eyes of ants have specialised cells that detect polarised light from the Sun, which is used to determine direction.[120][121] These polarization detectors are sensitive in the ultraviolet region of the light spectrum.[122] In some army ant species, a group of foragers who become separated from the main column may sometimes turn back on themselves and form a circular ant mill. The workers may then run around continuously until they die of exhaustion.[123]

Locomotion

Play media

Ant in Slow Motion

The female worker ants do not have wings and reproductive females lose their wings after their mating flights in order to begin their colonies. Therefore, unlike their wasp ancestors, most ants travel by walking. Some species are capable of leaping. For example, Jerdon's jumping ant (*Harpegnathos saltator*) is able to jump by synchronising the action of its mid and hind pairs of legs.[124] There are several species of gliding ant including *Cephalotes atratus*; this may be a common trait among arboreal ants with small colonies. Ants with this ability are able to control their horizontal movement so as to catch tree trunks when they fall from atop the forest canopy.[125]

Other species of ants can form chains to bridge gaps over water, underground, or through spaces in vegetation. Some species also form floating rafts that help them survive floods.[126] These rafts may also have a role in allowing ants to colonise islands.[127] *Polyrhachis sokolova*, a species of ant found in Australian mangrove swamps, can swim and live in underwater nests. Since they lack gills, they go to trapped pockets of air in the submerged nests to breathe.[128]

Cooperation and competition

Not all ants have the same kind of societies. The Australian bulldog ants are among the biggest and most basal of ants. Like virtually all ants, they are eusocial, but their social behaviour is poorly developed compared to other species. Each individual hunts alone, using her large eyes instead of chemical senses to find prey.[129]


Meat-eater ants feeding on a cicada: social ants cooperate and collectively gather food

Some species (such as *Tetramorium caespitum*) attack and take over neighbouring ant colonies. Others are less expansionist, but just as aggressive; they invade colonies to steal eggs or larvae, which they either eat or raise as workers or slaves. Extreme specialists among these slave-raiding ants, such as the Amazon ants, are incapable of feeding themselves and need captured workers to survive.[130] Captured workers of enslaved *Temnothorax* species have evolved a counter strategy, destroying just the female pupae of the slave-making *Temnothorax americanus*, but sparing the males (who don't take part in slave-raiding as adults).[131]


A worker *Harpegnathos saltator* (a jumping ant) engaged in battle with a rival colony's queen

Ants identify kin and nestmates through their scent, which comes from hydrocarbon-laced secretions that coat their exoskeletons. If an ant is separated from its original colony, it will eventually lose the colony scent. Any ant that enters a colony without a matching scent will be attacked.[132] Also, the reason why two separate colonies of ants will attack each other even if they are of the same species is because the genes responsible for pheromone production are different between them. The Argentine ant, however, does not have this characteristic, due to lack of genetic diversity, and has become a global pest because of it.

Parasitic ant species enter the colonies of host ants and establish themselves as social parasites; species such as *Strumigenys xenos* are entirely parasitic and do not have workers, but instead, rely on the food gathered by their *Strumigenys perplexa* hosts.[133][134] This form of parasitism is seen across many ant genera, but the parasitic ant is usually a species that is closely related to its host. A variety of methods are employed to enter the nest of the host ant. A parasitic queen may enter the host nest before the first brood has hatched, establishing herself prior to development of a colony scent. Other species use pheromones to confuse the host ants or to trick them into carrying the parasitic queen into the nest. Some simply fight their way into the nest.[135]

A conflict between the sexes of a species is seen in some species of ants with these reproducers apparently competing to produce offspring that are as closely related to them as possible. The most extreme form involves the production of clonal offspring. An extreme of sexual conflict is seen in *Wasmannia auropunctata*, where the queens produce diploid daughters by thelytokous parthenogenesis and males produce clones by a process whereby a diploid egg loses its maternal contribution to produce haploid males who are clones of the father.[136]

Relationships with other organisms

Ants form symbiotic associations with a range of species, including other ant species, other insects, plants, and fungi. They also are preyed on by many animals and even certain fungi. Some arthropod species spend part of their lives within ant nests, either preying on ants, their larvae, and eggs, consuming the food stores of the ants, or avoiding predators. These inquilines may bear a close resemblance to ants. The nature of this ant mimicry (myrmecomorphy) varies, with some cases involving Batesian mimicry, where the mimic reduces the risk of predation. Others show Wasmannian mimicry, a form of mimicry seen only in inquilines.[137][138]

The spider *Myrmarachne plataleoides* (female shown) mimics weaver ants to avoid predators.

An ant collects honeydew from an aphid

Aphids and other hemipteran insects secrete a sweet liquid called honeydew, when they feed on plant sap. The sugars in honeydew are a high-energy food source, which many ant species collect.[139] In some cases, the aphids secrete the honeydew in response to ants tapping them with their antennae. The ants in turn keep predators away from the aphids and will move them from one feeding location to another. When migrating to a new area, many colonies will take the aphids with them, to ensure a continued supply of honeydew. Ants also tend mealybugs to harvest their honeydew. Mealybugs may become a serious pest of pineapples if ants are present to protect mealybugs from their natural enemies.[140]

Myrmecophilous (ant-loving) caterpillars of the butterfly family Lycaenidae (e.g., blues, coppers, or hairstreaks) are herded by the ants, led to feeding areas in the daytime, and brought inside the ants' nest at night. The caterpillars have a gland which secretes honeydew when the ants massage them. Some caterpillars produce vibrations and sounds that are perceived by the ants.[141] A similar adaptation can be seen in Grizzled skipper butterflies that emit vibrations by expanding their wings in order to communicate with ants, which are natural predators of these butterflies.[142] Other caterpillars have evolved from ant-loving to ant-eating: these myrmecophagous caterpillars secrete a pheromone that makes the ants act as if the caterpillar is one of their own larvae. The caterpillar is then taken into the ant nest where it feeds on the ant larvae.[143] A number of specialized bacterial have been found as endosymbionts in ant guts. Some of the dominant bacteria belong to the order Rhizobiales whose members are known for being nitrogen-fixing symbionts in legumes but the species found in ant lack the ability to fix nitrogen.[144][145] Fungus-growing ants that make up the tribe Attini, including leafcutter ants, cultivate certain species of fungus in the genera *Leucoagaricus* or *Leucocoprinus* of the family Agaricaceae. In this ant-fungus mutualism, both species depend on each other for survival. The ant *Allomerus decemarticulatus* has evolved a three-way association with the host plant, *Hirtella physophora* (Chrysobalanaceae), and a sticky fungus which is used to trap their insect prey.[146]

Lemon ants make devil's gardens by killing surrounding plants with their stings and leaving a pure patch of lemon ant trees, (*Duroia hirsuta*). This modification of the forest provides the ants with more nesting sites inside the stems of the *Duroia* trees.[147] Although some ants obtain nectar from flowers, pollination by ants is somewhat rare, one example being of the pollination of the orchid *Leporella fimbriata* which induces male *Myrmecia urens* to pseudocopulate with the flowers, transferring pollen in the process.[148] One theory that has been proposed for the rarity of pollination is that the secretions of the metapleural gland inactivate and reduce the viability of pollen.[149][150] Some plants have special nectar exuding structures, extrafloral nectaries, that provide food for ants, which in turn protect the plant from more damaging herbivorous insects.[151] Species such as the bullhorn acacia (*Acacia cornigera*) in Central America have

Ants may obtain nectar from flowers such as the dandelion but are only rarely known to pollinate flowers.

hollow thorns that house colonies of stinging ants (*Pseudomyrmex ferruginea*) who defend the tree against insects, browsing mammals, and epiphytic vines. Isotopic labelling studies suggest that plants also obtain nitrogen from the ants.[152] In return, the ants obtain food from protein- and lipid-rich Beltian bodies. In Fiji *Philidris nagasau* (Dolichoderinae) are known to selectively grow species of epiphytic *Squamellaria* (Rubiaceae) which produce large domatia inside which the ant colonies nest. The ants plant the seeds and the domatia of young seedling are immediately occupied and the ant faeces in them contribute to rapid growth.[153] Similar dispersal associations are found with other dolichoderines in the region as well.[154] Another example of this type of ectosymbiosis comes from the *Macaranga* tree, which has stems adapted to house colonies of *Crematogaster* ants.[155]

Many plant species have seeds that are adapted for dispersal by ants.[156] Seed dispersal by ants or myrmecochory is widespread, and new estimates suggest that nearly 9% of all plant species may have such ant associations.[157][156] Often, seed-dispersing ants perform directed dispersal, depositing the seeds in locations that increase the likelihood of seed survival to reproduction.[158] Some plants in arid, fire-prone systems are particularly dependent on ants for their survival and dispersal as the seeds are transported to safety below the ground.[159] Many ant-dispersed seeds have special external structures, elaiosomes, that are sought after by ants as food.[160]

A convergence, possibly a form of mimicry, is seen in the eggs of stick insects. They have an edible elaiosome-like structure and are taken into the ant nest where the young hatch.[161]


A meat ant tending a common leafhopper nymph

Most ants are predatory and some prey on and obtain food from other social insects including other ants. Some species specialise in preying on termites (*Megaponera* and *Termitopone*) while a few Cerapachyinae prey on other ants.[111] Some termites, including *Nasutitermes corniger*, form associations with certain ant species to keep away predatory ant species.[162] The tropical wasp *Mischocyttarus drewseni* coats the pedicel of its nest with an ant-repellent chemical.[163] It is suggested that many tropical wasps may build their nests in trees and cover them to protect themselves from ants. Other wasps, such as *A. multipicta*, defend against ants by blasting them off the nest with bursts of wing buzzing.[164] Stingless bees (*Trigona* and *Melipona*) use chemical defences against ants.[111]

Flies in the Old World genus *Bengalia* (Calliphoridae) prey on ants and are kleptoparasites, snatching prey or brood from the mandibles of adult ants.[165] Wingless and legless females of the Malaysian phorid fly (*Vestigipoda myrmolarvoidea*) live in the nests of ants of the genus *Aenictus* and are cared for by the ants.[165]

Fungi in the genera *Cordyceps* and *Ophiocordyceps* infect ants. Ants react to their infection by climbing up plants and sinking their mandibles into plant tissue. The fungus kills the ants, grows on their remains, and produces a fruiting body. It appears that the fungus alters the behaviour of the ant to help disperse its spores [166] in a microhabitat that best suits the fungus.[167] Strepsipteran parasites also manipulate their ant host to climb grass stems, to help the parasite find mates.[168]

A nematode (*Myrmeconema neotropicum*) that infects canopy ants (*Cephalotes atratus*) causes the black-coloured gasters of workers to turn red. The parasite also alters the behaviour of the ant, causing them to carry their gasters high. The conspicuous red gasters are mistaken by birds for ripe fruits, such as *Hyeronima alchorneoides*, and eaten. The droppings of the bird are collected by other ants and fed to their young, leading to further spread of the nematode.[169]

South American poison dart frogs in the genus *Dendrobates* feed mainly on ants, and the toxins in their skin may come from the ants.[170]

Army ants forage in a wide roving column, attacking any animals in that path that are unable to escape. In Central and South America, *Eciton burchellii* is the swarming ant most commonly attended by "ant-following" birds such as antbirds and woodcreepers.[171][172] This behaviour was once considered mutualistic, but later studies found the birds to be parasitic. Direct kleptoparasitism (birds stealing food from the ants' grasp) is rare and has been noted in Inca doves which pick seeds at nest entrances as they are being transported by species of *Pogonomyrmex*.[173] Birds that follow ants eat many prey insects and thus decrease the foraging success of ants.[174] Birds indulge in a peculiar behaviour called anting that, as yet, is not fully understood. Here birds rest on ant nests, or pick and drop ants onto their wings and feathers; this may be a means to remove ectoparasites from the birds.


Spiders sometimes feed on ants.

Anteaters, aardvarks, pangolins, echidnas and numbats have special adaptations for living on a diet of ants. These adaptations include long, sticky tongues to capture ants and strong claws to break into ant nests. Brown bears (*Ursus arctos*) have been found to feed on ants. About 12%, 16%, and 4% of their faecal volume in spring, summer, and autumn, respectively, is composed of ants.[175]

Relationship with humans


Weaver ants are used as a biological control for citrus cultivation in southern China.

Ants perform many ecological roles that are beneficial to humans, including the suppression of pest populations and aeration of the soil. The use of weaver ants in citrus cultivation in southern China is considered one of the oldest known applications of biological control.[14] On the other hand, ants may become nuisances when they invade buildings, or cause economic losses.

In some parts of the world (mainly Africa and South America), large ants, especially army ants, are used as surgical sutures. The wound is pressed together and ants are applied along it. The ant seizes the edges of the wound in its mandibles and locks in place. The body is then cut off and the head and mandibles remain in place to close the wound.[176][177][178] The large heads of the dinergates (soldiers) of the leafcutting ant *Atta cephalotes* are also used by native surgeons in closing wounds.[179]

Some ants have toxic venom and are of medical importance. The species include *Paraponera clavata* (tocandira) and *Dinoponera* spp. (false tocandiras) of South America [180] and the *Myrmecia* ants of Australia.[181]

In South Africa, ants are used to help harvest the seeds of rooibos (*Aspalathus linearis*), a plant used to make a herbal tea. The plant disperses its seeds widely, making manual collection difficult. Black ants collect and store these and other seeds in their nest, where humans can gather them *en masse*. Up to half a pound (200 g) of seeds may be collected from one ant-heap.[182][183]

Although most ants survive attempts by humans to eradicate them, a few are highly endangered. These tend to be island species that have evolved specialized traits and risk being displaced by introduced ant species. Examples include the critically endangered Sri Lankan relict ant (*Aneuretus simoni*) and *Adetomyrma venatrix* of Madagascar.[184]

It has been estimated by E.O. Wilson that the total number of individual ants alive in the world at any one time is between one and ten quadrillion (short scale) (i.e., between 10^{15} and 10^{16}). According to this estimate, the total biomass of all the ants in the world is approximately equal to the total biomass of the entire human race.[185] Also, according to this estimate, there are approximately 1 million ants for every human on Earth.[186]

As food

Roasted ants in Colombia

Ant larvae for sale in Isaan, Thailand

Ants and their larvae are eaten in different parts of the world. The eggs of two species of ants are used in Mexican *escamoles*. They are considered a form of insect caviar and can sell for as much as US$40 per pound ($90/kg) because they are seasonal and hard to find. In the Colombian department of Santander, *hormigas culonas* (roughly interpreted as "large-bottomed ants") *Atta laevigata* are toasted alive and eaten.[187]

In areas of India, and throughout Burma and Thailand, a paste of the green weaver ant (*Oecophylla smaragdina*) is served as a condiment with curry.[188] Weaver ant eggs and larvae, as well as the ants, may be used in a Thai salad, *yam* (Thai: ยำ), in a dish called *yam khai mot daeng* (Thai: ยำไข่มดแดง) or red ant egg salad, a dish that comes from the Issan or north-eastern region of Thailand. Saville-Kent, in the *Naturalist in Australia* wrote "Beauty, in the case of the green ant, is more than skin-deep. Their attractive, almost sweetmeat-like translucency possibly invited the first essays at their consumption by the human species". Mashed up in water, after the manner of lemon squash, "these ants form a pleasant acid drink which is held in high favor by the natives of North Queensland, and is even appreciated by many European palates".[189]

In his *First Summer in the Sierra*, John Muir notes that the Digger Indians of California ate the tickling, acid gasters of the large jet-black carpenter ants. The Mexican Indians eat the replete workers, or living honey-pots, of the honey ant (*Myrmecocystus*).[189]

As pests

The tiny pharaoh ant is a major pest in hospitals and office blocks; it can make nests between sheets of paper.

Some ant species are considered as pests, primarily those that occur in human habitations, where their presence is often problematic. For example, the presence of ants would be undesirable in sterile places such as hospitals or kitchens. Some species or genera commonly categorized as pests include the Argentine ant, pavement ant, yellow crazy ant, banded sugar ant, pharaoh ant, carpenter ants, odorous house ant, red imported fire ant, and European fire ant. Some ants will raid stored food, others may damage indoor structures, some can damage agricultural crops directly (or by aiding sucking pests), and some will sting or bite.[15] The adaptive nature of ant colonies make it nearly impossible to eliminate entire colonies and most pest management practices aim to control local populations and tend to be temporary solutions. Ant populations are managed by a combination of approaches that make use of chemical, biological and physical methods. Chemical methods include the use of insecticidal bait which is gathered by ants as food and brought back to the nest where the poison is inadvertently spread to other colony members through trophallaxis. Management is based on the species and techniques can vary according to the location and circumstance.[15]

In science and technology

Observed by humans since the dawn of history, the behaviour of ants has been documented and the subject of early writings and fables passed from one century to another. Those using scientific methods, myrmecologists, study ants in the laboratory and in their natural conditions. Their complex and variable social structures have made ants ideal model organisms. Ultraviolet vision was first discovered in ants by Sir John Lubbock in 1881.[190] Studies on ants have tested hypotheses in ecology and sociobiology, and have been particularly important in examining the predictions of theories of kin selection and evolutionarily stable strategies.[191] Ant colonies may be studied by rearing or temporarily maintaining them in *formicaria*, specially constructed glass framed enclosures.[192] Individuals may be tracked for study by marking them with dots of colours.[193]

Camponotus nearcticus workers travelling between two formicaria through connector tubing

The successful techniques used by ant colonies have been studied in computer science and robotics to produce distributed and fault-tolerant systems for solving problems, for example Ant colony optimization and Ant robotics. This area of biomimetics has led to studies of ant locomotion, search engines that make use of "foraging trails", fault-tolerant storage, and networking algorithms.[13]

As pets

From the late 1950s through the late 1970s, ant farms were popular educational children's toys in the United States. Some later commercial versions use transparent gel instead of soil, allowing greater visibility at the cost of stressing the ants with unnatural light.[194]

In culture

Aesop's ants: picture by Milo Winter, 1888–1956

Anthropomorphised ants have often been used in fables and children's stories to represent industriousness and cooperative effort. They also are mentioned in religious texts.[195][196] In the Book of Proverbs in the Bible, ants are held up as a good example for humans for their hard work and cooperation.[197] Aesop did the same in his fable The Ant and the Grasshopper. In the Quran, Sulayman is said to have heard and understood an ant warning other ants to return home to avoid being accidentally crushed by Sulayman and his marching army. [Quran 27:18 (http://www.perseus.tufts.edu/hopper/text?doc=Perseus%3Atext%3A2002.02.0006%3Asura%3D27%3Averse%3D18)][198] In parts of Africa, ants are considered to be the messengers of the deities. Some Native American mythology, such as the Hopi mythology, considers ants as the very first animals. Ant bites are often said to have curative properties. The sting of some species of *Pseudomyrmex* is claimed to give fever relief.[199] Ant bites are used in the initiation ceremonies of some Amazon Indian cultures as a test of endurance.[200][201]

Ant society has always fascinated humans and has been written about both humorously and seriously. Mark Twain wrote about ants in his 1880 book *A Tramp Abroad*.[202] Some modern authors have used the example of the ants to comment on the relationship between society and the individual. Examples are Robert Frost in his poem "Departmental" and T. H. White in his fantasy novel *The Once and Future King*. The plot in French entomologist and writer Bernard Werber's *Les Fourmis* science-fiction trilogy is divided between the worlds of ants and humans; ants and their behaviour is described using contemporary scientific knowledge. H.G. Wells wrote about intelligent ants destroying human settlements in Brazil and threatening human civilization in his 1905 science-fiction short story, *The Empire of the Ants.* In more recent times, animated cartoons and 3-D animated films featuring ants have been produced including *Antz*, *A Bug's Life*, *The Ant Bully*, *The Ant and the Aardvark*, *Ferdy the Ant* and *Atom Ant.* Renowned myrmecologist E. O. Wilson wrote a short story, "Trailhead" in 2010 for *The New Yorker* magazine, which describes the life and death of an ant-queen and the rise and fall of her colony, from an ants' point of view.[203] The French neuroanatomist, psychiatrist and eugenicist Auguste Forel believed that ant societies were models for human society. He published a five volume work from 1921 to 1923 that examined ant biology and society.[204]

In the early 1990s, the video game *SimAnt*, which simulated an ant colony, won the 1992 Codie award for "Best Simulation Program".[205]

Ants also are quite popular inspiration for many science-fiction insectoids, such as the Formics of *Ender's Game*, the Bugs of *Starship Troopers*, the giant ants in the films *Them!* and *Empire of the Ants*, Marvel Comics' super hero Ant-Man, and ants mutated into super-intelligence in *Phase IV*. In computer strategy games, ant-based species often benefit from increased production rates due to their single-minded focus, such as the Klackons in the *Master of Orion* series of games or the ChCht in *Deadlock II*. These characters are often credited with a hive mind, a common misconception about ant colonies.[206]

See also

- Ant robotics
- Ant venom
- Glossary of ant terms
- International Union for the Study of Social Insects
- *Myrmecological News* (journal)
- Task allocation and partitioning of social insects

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House dust mite

House dust mites (**HDM**, or simply **dust mites**) are mites found in association with dust in dwellings.[1]

House dust mites (*Dermatophagoides pteronyssinus*) aggregate

The main species are:

- *Dermatophagoides farinae* (American house dust mite)
- *Dermatophagoides microceras*
- *Dermatophagoides pteronyssinus* (European house dust mite)
- *Euroglyphus maynei* (Mayne's house dust mite)

Contents

Biology

Taxonomy

The dust mites are cosmopolitan members of the mite family Pyroglyphidae.

Characteristics

House dust mites, due to their very small size and translucent bodies, are barely visible to the unaided eye.[2] A typical house dust mite measures 0.2–0.3 mm (0.008–0.012 in) in length.[3] For accurate identification, one needs at least 10× magnification. The body of the house dust mite has a striated cuticle.

Diet


A scanning electron micrograph of a female dust mite

They feed on skin flakes from animals, including humans, and on some mold. *Dermatophagoides farinae* fungal food choices in 16 tested species commonly found in homes was observed *in vitro* to be *Alternaria alternata*, *Cladosporium sphaerospermum*, and *Wallemia sebi*, and they disliked *Penicillium chrysogenum*, *Aspergillus versicolor*, and *Stachybotrys chartarum*.[4]

Predators

The predators of dust mites are other allergenic mites (*Cheyletiella*), silverfish and pseudoscorpions.[5]

Reproduction

The average life cycle for a house dust mite is 65–100 days.[6] A mated female house dust mite can live up to 70 days, laying 60 to 100 eggs in the last five weeks of her life. In a 10-week life span, a house dust mite will produce approximately 2,000 fecal particles and an even larger number of partially digested enzyme-covered dust particles.

Distribution

Dust mites are found worldwide, but are found more commonly in humid regions.[7] The species *Blomia tropicalis* is typically found only in tropical or subtropical regions.[8] Detectable dust mite allergen was found in the beds of about 84% of surveyed United States homes.[9] In Europe, detectable Der p 1 or Der f 1 allergen was found in 68% of surveyed homes.[10]

Health issues

Allergies

The mite's gut contains potent digestive enzymes (notably Peptidase 1) that persist in their feces and are major inducers of allergic reactions such as wheezing. The mite's exoskeleton can also contribute to allergic reactions. Unlike scabies mites or skin follicle mites, house dust mites do not burrow under the skin and are not parasitic.[11]

Severe dust mite infestation in the home has been linked to atopic dermatitis and epidermal barrier damage has been documented.[12]

House dust mites are associated with allergic rhinitis and asthma,[13] as well as allergic conjunctivitis.[14] Efforts to remove these mites from the environment have not been found to be effective.[13] Immunotherapy may be useful in those affected.[13] Subcutaneous injections have better evidence than under the tongue dosing.[15] Topical steroids as nasal spray or inhalation may be used.[16]

Oral mite anaphylaxis

Dermatophagoides spp. can cause oral mite anaphylaxis (AKA pancake syndrome) when found in flour.[17][18]

Control techniques

House dust mites are present indoors wherever humans live. Positive tests for dust mite allergies are extremely common among people with asthma. Dust mites are microscopic arachnids whose primary food is dead human skin cells, but they do not live on living people. They and their feces and other allergens which they produce are major constituents of house dust, but because they are so heavy they are not suspended for long in the air. They are generally found on the floor and other surfaces until disturbed (by walking, for example). It could take somewhere between twenty minutes and two hours for dust mites to settle back down out of the air.

Dust mites are a nesting species that prefers a dark, warm, and humid climate. They flourish in mattresses, bedding, upholstered furniture, and carpets. Their feces include enzymes that are released upon contact with a moist surface, which can happen when a person inhales, and these enzymes can kill cells within the human body.[19] House dust mites did not become a problem until humans began to use textiles, such as western style blankets and clothing.[20]

Furniture

Furniture with wooden or leather surfaces reduce the dust mite population.[21]

Bed linen

Hot tumble drying a bed linen for 1 hour will kill 99% of mites therein.[22]

Weekly changing the bed linen reduces the risk of exposure to dust mites.[16]

Cotton covers not covered with complete mattress covers are very likely to become colonised by bacteria and molds; they must be cleaned periodically (at least every second to third month).[23]

Dust mite eggs are freeze tolerant (−70 °C for 30 minutes); hatching can normally be prevented by exposure of fabrics to:[24]

- Direct sunlight for 3 hours or
- Dry or wet heat of at least 60 °C (140 °F) for a minimum of 30 minutes.

Dust mites drown in water.[25]

Dust mite-proof encasements to mattress, pillow, and duvet, prevents chronic contact with allergens.[16][21]

Good properties of anti-mite fabrics have been identified as being:[26]

- Thread count greater than 246.
- Pore size of between 2 and 10 microns.
- Allergen impenetrability >99%.
- Dust leakage of less than 4%.
- Breathability between 2 and 6 cm^3/second/cm^2.

Indoor climate

Allergy patients are advised to keep the relative humidity below 50%, if possible. Very few mites can survive if the humidity is less than 45% (at 22 °C (72 °F)). However, they can survive if the humidity is high just for an hour and a half per day, for example due to cooking.[25]

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Earwig

Earwigs make up the insect order **Dermaptera**. With about 2,000 species[1] in 12 families, they are one of the smaller insect orders. Earwigs have characteristic cerci, a pair of forceps-like pincers on their abdomen, and membranous wings folded underneath short, rarely used forewings, hence the scientific order name, "skin wings". Some groups are tiny parasites on mammals and lack the typical pincers. Earwigs are found on all continents except Antarctica.

Earwigs are mostly nocturnal and often hide in small, moist crevices during the day, and are active at night, feeding on a wide variety of insects and plants. Damage to foliage, flowers, and various crops is commonly blamed on earwigs, especially the common earwig *Forficula auricularia.*

Earwigs have five molts in the year before they become adults. Many earwig species display maternal care, which is uncommon among insects. Female earwigs may care for their eggs, and even after they have hatched as nymphs will continue to watch over offspring until their second molt. As the nymphs molt, sexual dimorphism such as differences in pincer shapes begins to show.

Some earwig specimen fossils are in the extinct suborders Archidermaptera or Eodermaptera, the former dating to the Late Triassic and the latter to the Middle Jurassic. Many orders of insect have been theorized to be closely related to earwigs, though the icebugs of Notoptera are most likely.

Earwig

Temporal range: 208–0 Ma

PreЄ Є O S D C P T J K PgN

Late Triassic to Recent

Female common earwig, *Forficula auricularia*

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Infraclass:	Neoptera
Superorder:	Exopterygota
Order:	Dermaptera De Geer, 1773

Suborders

- †Archidermaptera
- †Eodermaptera
- Neodermaptera

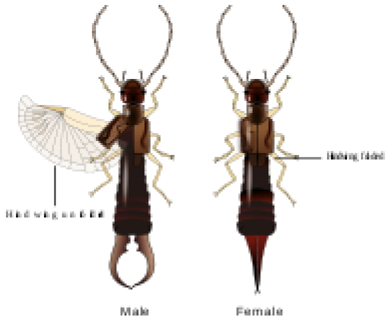
Synonyms

- Euplecoptera
- Euplexoptera
- Forficulida

Contents

Etymology

The scientific name for the order, "Dermaptera", is Greek in origin, stemming from the words *derma*, meaning skin, and *pteron* (plural *ptera*), wing. It was coined by Charles De Geer in 1773. The common term, *earwig*, is derived from the Old English *ēare*, which means "ear", and *wicga*, which means "insect", or literally, "beetle".[2] Entomologists suggest that the origin of the name is a reference to the appearance of the hindwings, which are unique and distinctive among insects, and resemble a human ear when unfolded.[3][4] The name is more popularly thought to be related to the old wives' tale that earwigs burrowed into the brains of humans through the ear and laid their eggs there.[5] Earwigs are not known to purposefully climb into ear canals, but there have been anecdotal reports of earwigs being found in the ear.[6]



Earwig diagram with wings extended and closed

Distribution

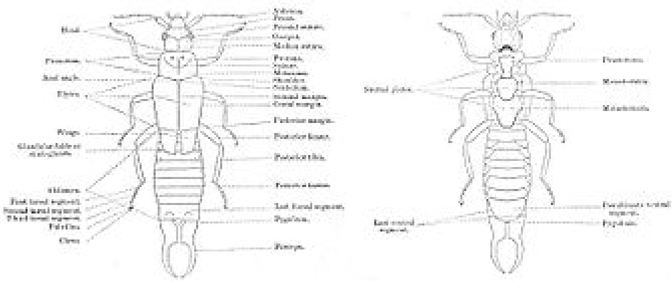
Earwigs are abundant and can be found throughout the Americas and Eurasia. The common earwig was introduced into North America in 1907 from Europe, but tends to be more common in the southern and southwestern parts of the United States.[7]:739 The only native species of earwig found in the north of the United States is the spine-tailed earwig (*Doru aculeatum*),[8]:144 found as far north as Canada, where it hides in the leaf axils of emerging plants in southern Ontario wetlands. However, other families can be found in North America, including Forficulidae (*Doru* and *Forficula* being found there), Spongiphoridae, Anisolabididae, and Labiduridae.[9]


An earwig from the Western Ghats

Few earwigs survive winter outdoors in cold climates. They can be found in tight crevices in woodland, fields and gardens.[7]:739[10] Out of about 1,800 species, about 25 occur in North America, 45 in Europe (including 7 in Great Britain), and 60 in Australia.[11]

Morphology

Most earwigs are flattened (which allows them to fit inside tight crevices, such as under bark) with an elongated body generally 7–50 millimetres (0.28–1.97 in) long.[11] The largest extant species is the Australian giant earwig (*Titanolabis colossea*) which is approximately 50 mm (2.0 in) long,[12]:10 while the possibly extinct Saint Helena earwig (*Labidura herculeana*) reached 78 mm (3.1 in).[13] Earwigs are characterized by the cerci, or the pair of forceps-like pincers on their abdomen; male earwigs generally have more curved pincers than females. These pincers are used to capture prey, defend themselves and fold their wings under the short tegmina.[14] The antennae are thread-like with at least 10 segments.[7]:738–739


Male earwig, external morphology. Click on image for a larger view

The forewings are short oblong leathery plates used to cover the hindwings like the elytra of a beetle, rather than to fly. Most species have short and leather-like forewings with very thin hindwings, though species in the former suborders Arixeniina and Hemimerina (epizoic species, sometimes considered as ectoparasites[15][16]) are wingless and blind with filiform segmented cerci (today these are both included merely as families in the suborder Neodermaptera).[11][17][18] The hindwing is a very thin membrane that expands like a fan, radiating from one point folded under the forewing. Even though most earwigs have wings and are capable of flight, they are rarely seen in flight. These wings are unique in venation and in the pattern of folding that requires the use of the cerci.[19]

Internal

The neuroendocrine system is typical of insects. There is a brain, a subesophageal ganglion, three thoracic ganglia, and six abdominal ganglia. Strong neuron connections connect the neurohemal corpora cardiaca to the brain and frontal ganglion, where the closely related median corpus allatum produces juvenile hormone III in close proximity to the neurohemal dorsal arota. The digestive system of earwigs is like all other insects, consisting of a fore-, mid-, and hindgut, but earwigs lack gastric caecae which are specialized for digestion in many species of insect. Long, slender (excretory) malpighian tubules can be found between the junction of the mid- and hind gut.[20]

The reproductive system of females consist of paired ovaries, lateral oviducts, spermatheca, and a genital chamber. The lateral ducts are where the eggs leave the body, while the spermatheca is where sperm is stored. Unlike other insects, the gonopore, or genital opening is behind the seventh abdominal segment. The ovaries are primitive in that they are polytrophic (the nurse cells and oocytes alternate along the length of the ovariole). In some species these long ovarioles branch off the lateral duct, while in others, short ovarioles appear around the duct.[20]

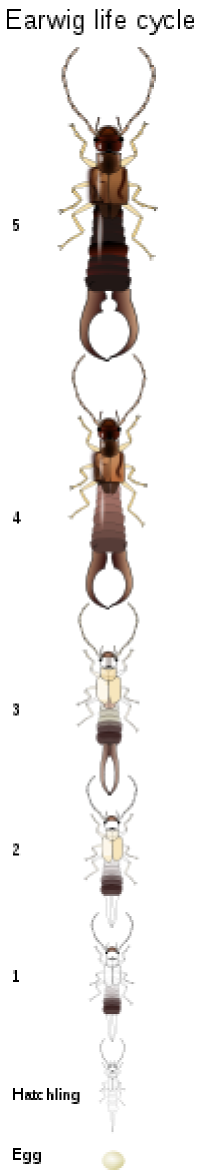
Life cycle and reproduction

Earwigs are hemimetabolous, meaning they undergo incomplete metamorphosis, developing through a series of 4 to 6 molts. The developmental stages between molts are called instars. Earwigs live for about a year from hatching. They start mating in the autumn, and can be found together in the autumn and winter. The male and female will live in a chamber in debris, crevices, or soil 2.5 centimetres (1 in) deep.[7]:739 After mating, the sperm may remain in the female for months before the eggs are fertilized. From midwinter to early spring, the male will leave, or be driven out by the female. Afterward the female will begin to lay 20 to 80 pearly white eggs in 2 days. Some earwigs, those parasitic in the suborders Arixeniina and Hemimerina, are viviparous (give birth to live young); they would be fed by a sort of placenta.[7]:739–740[17] When first laid, the eggs are white or cream-colored and oval-shaped, but right before hatching they become kidney-shaped and brown.[21] Each egg is approximately 1 mm (0.04 in) tall and 0.8 mm (0.03 in) wide.[18]

Earwigs are among the few non-social insect species that show maternal care. The mother will pay close attention to the needs of her eggs, such as warmth and protection, though studies have shown that the mother does not pay attention to the eggs as she collects them.[17] The mother has been shown to pick up wax balls by accident, but they would eventually be rejected as they do not have the proper scent. The mother will also faithfully defend the eggs from predators, not leaving them to eat unless the clutch goes bad.[7]:740 Another distinct maternal care unique to earwigs is that the mother continuously cleans the eggs to protect them from fungi. Studies have found that the urge to clean the eggs persists for days after they are removed; when the eggs were replaced after hatching, the mother continued to clean them for up to 3 months.[17]

Female earwig in her nest, with eggs

Female earwig in her nest with newly hatched young



The life cycle and development of a male earwig from egg to each instar

The eggs hatch in about 7 days. The mother may assist the nymphs in hatching. When the nymphs hatch, they eat the egg casing and continue to live with the mother. The nymphs look similar to their parents, only smaller, and will nest under their mother and she will continue to protect them until their second molt. The nymphs feed on food regurgitated by the mother,[22] and on their own molts. If the mother dies before the nymphs are ready to leave, the nymphs may eat her.[7]:740[23]

An earwig on a wall in Haldia, West Bengal, India.

An earwig on a wooden door in Haldia, West Bengal, India.

After five to six instars, the nymphs will molt into adults. The male's forceps will become curved, while the females' forceps remain straight. They will also develop their natural color, which can be anything from a light brown (as in the Tawny earwig) to a dark black (as in the Ringlegged earwig). In species of winged earwigs, the wings will start to develop at this time. The forewings of an earwig are sclerotized to serve as protection for the membranous hindwings.

Behavior

Most earwigs are nocturnal and inhabit small crevices, living in small amounts of debris, in various forms such as bark and fallen logs. Species have been found to be blind and living in caves, or cavernicolous, reported to be found on the island of Hawaii and in South Africa. Food typically consists of a wide array of living and dead plant and animal matter.[20] For protection from predators, the species *Doru taeniatum* of earwigs can squirt foul-smelling yellow liquid in the form of jets from scent glands on the dorsal side of the third and fourth abdominal segment. It aims the discharges by revolving the abdomen, a maneuver that enables it simultaneously to use its pincers in defense.[24]

Ecology

Earwigs are mostly scavengers, but some are omnivorous or predatory.[7]:739–740 The abdomen of the earwig is flexible and muscular. It is capable of maneuvering as well as opening and closing the forceps. The forceps are used for a variety of purposes. In some species, the forceps have been observed in use for holding prey, and in copulation. The forceps tend to be more curved in males than in females.[25]

A male of *Forficula auricularia* feeding on flowers.

The common earwig is an omnivore, eating plants and ripe fruit as well as actively hunting arthropods. To a large extent, this species is also a scavenger, feeding on decaying plant and animal matter if given the chance. Observed prey include largely plant lice, but also large insects such as bluebottle flies and woolly aphids.[10] Plants that they feed on typically include clover, dahlias, zinnias, butterfly bush, hollyhock, lettuce, cauliflower, strawberry, blackberry, sunflowers, celery, peaches, plums, grapes, potatoes, roses, seedling beans and beets, and tender grass shoots and roots; they have also been known to eat corn silk, damaging the corn.[26]

Species of the suborders Arixeniina and Hemimerina are generally considered epizoic, or living on the outside of other animals, mainly mammals. In the Arixeniina, family Arixeniidae, species of the genus *Arixenia* are normally found deep in the skin folds and gular pouch of Malaysian hairless bulldog bats (*Cheiromeles torquatus*), apparently feeding on bats' body or glandular secretions. On the other hand, species in the genus *Xeniaria* (still of the suborder Arixeniina) are believed to feed on the guano and possibly the guanophilous arthropods in the bat's roost, where it has been found. Hemimerina includes *Araeomerus* found in the nest of Long-tailed pouch rats (*Beamys*), and *Hemimerus* which are found on Giant *Cricetomys* rats.[16][27]

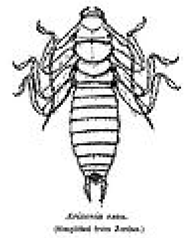
Earwigs are generally nocturnal, and typically hide in small, dark, and often moist areas in the daytime. They can usually be seen on household walls and ceilings. Interaction with earwigs at this time results in a defensive free-fall to the ground followed by a scramble to a nearby cleft or crevice.[25] During the summer they can be found around damp areas such as near sinks and in bathrooms. Earwigs tend to gather in shady cracks or openings or anywhere that they can remain concealed during daylight. Picnic tables, compost and waste bins, patios, lawn furniture, window frames, or anything with minute spaces (even artichoke blossoms) can potentially harbour them.[28]

Predators and parasites

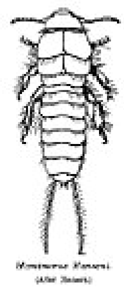
Earwigs are regularly preyed upon by birds, and like many other insect species they are prey for insectivorous mammals, amphibians, lizards, centipedes, assassin bugs, and spiders.[29] European naturalists have observed bats preying upon earwigs.[29] Their primary insect predators are parasitic species of Tachinidae, or tachinid flies, whose larvae are endoparasites. One species of tachinid fly, *Triarthria setipennis*, has been demonstrated to be successful as a biological control of earwigs for almost a century.[30][31] Another tachinid fly and parasite of earwigs, *Ocytata pallipes*, has shown promise as a biological control agent as well.[32] The common predatory wasp, the yellow jacket (*Vespula maculifrons*), preys upon earwigs when abundant.[33] A small species of roundworm, *Mermis nigrescens*, is known to occasionally parasitize earwigs that have consumed roundworm eggs with plant matter.[34] At least 26 species of parasitic fungus from the order Laboulbeniales have been found on earwigs.[35] The eggs and nymphs are also cannibalized by other earwigs.[36] A species of tyroglyphoid mite, *Histiostoma polypori* (Histiostomatidae, Astigmata), are observed on common earwigs, sometimes in great densities;[37] however, this mite feeds on earwig cadavers and not its live earwig transportation.[38] Hippolyte Lucas observed scarlet acarine mites on European earwigs.[39]

Evolution

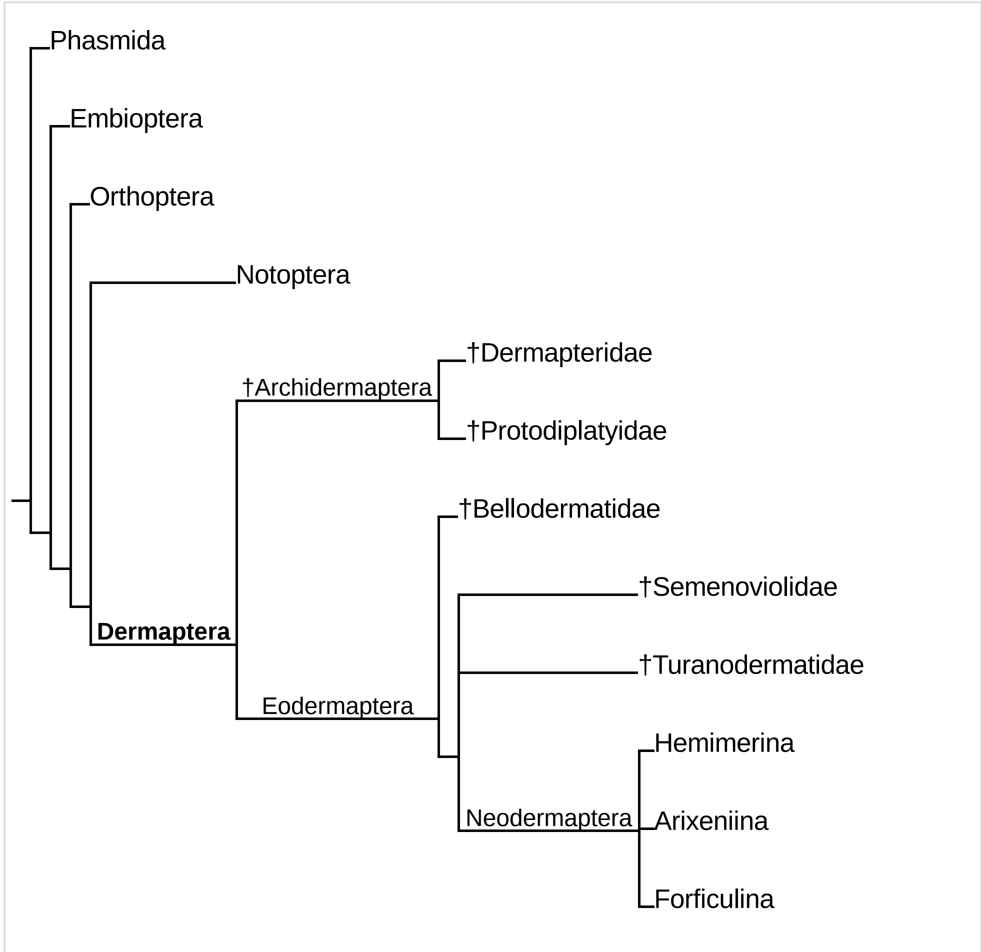
The fossil record of the Dermaptera starts in the Late Triassic to Early Jurassic period about 208 million years ago in England and Australia, and comprises about 70 specimens in the extinct suborder Archidermaptera. Some of the traits believed by neontologists to belong to modern earwigs are not found in the earliest fossils, but adults had five-segmented tarsi (the final segment of the leg), well developed ovipositors, veined tegmina (forewings) and long segmented cerci; in fact the pincers would not have been curled or used as they are now.[14] The theorized stem group of the Dermaptera are the Protelytroptera. These insects, which resemble modern Blattodea, or cockroaches owing to shell-like forewings and the large, unequal anal fan, are known from the Permian of North America, Europe and Australia. There are no fossils from the Triassic when the morphological changes from Protelytroptera to Dermaptera took place.[42] The most likely, and most closely resembling, related order of insects is Notoptera, theorized by Giles in 1963. However, other arguments have been made by other authors linking them to Phasmida, Embioptera, Plecoptera, and Dictyoptera.[11]



Arixenia esau from the extinct suborder Arixeniina



Hemimerus hanseni from the extinct suborder Hemimerina



Earwigs and their relatives[40][41]

Archidermaptera is believed to be sister to the remaining earwig groups, the extinct Eodermaptera and the living suborder Neodermaptera (= former suborders Forficulina, Hemimerina, and Arixeniina). The extinct suborders have tarsi with five segments (unlike the three found in Neodermaptera) as well as unsegmented cerci. No fossil Hemimeridae and Arixeniidae are known.[43] Species in Hemimeridae were at one time in their own order, Diploglassata, Dermodermaptera, or Hemimerina. Like most other epizoic species, there is no fossil record, but they are probably no older than late Tertiary.[14]

Some evidence of early evolutionary history is the structure of the antennal heart, a separate circulatory organ consisting of two ampullae, or vesicles,[44] that are attached to the frontal cuticle to the bases of the antennae.[45] These features have not been found in other insects. An independent organ exists for each antenna, consisting of an ampulla, attached to the frontal cuticle medial to the antenna base and forming a thin-walled sac with a valved ostium on its ventral side. They pump blood by elastic connective tissue, rather than muscle.[46]

Molecular studies suggest that this order is the sister to Plecoptera or to Ephemeroptera.[47]

Taxonomy

Distinguishing characteristics

The characteristics which distinguish the order Dermaptera from other insect orders are:[48]

- *General body shape*: Elongate; dorso-ventrally flattened.
- *Head*: Prognathous. Antennae are segmented. Biting-type mouthparts. Ocelli absent. Compound eyes in most species, reduced or absent in some taxa.
- *Appendages*: Two pairs of wings normally present. The forewings are modified into short smooth, veinless tegmina. Hindwings are membranous and semicircular with veins radiating outwards.
- *Abdomen*: Cerci are unsegmented and resemble forceps. The ovipositor in females is reduced or absent.

The overwhelming majority of earwig species are in Forficulina, grouped into nine families of 180 genera,[42] including *Forficula auricularia*, the common European Earwig. Species within Forficulina are free-living, have functional wings and are not parasites. The cerci are unsegmented and modified into large, forceps-like structures.

The first epizoic species of earwig was discovered by a London taxidermist on the body of a Malaysian hairless bulldog bat in 1909, then described by Karl Jordan. By the 1950s, the two suborders *Arixeniina* and *Hemimerina* had been added to Dermaptera.[16]

Arixeniina represents two genera, *Arixenia* and *Xeniaria,* with a total of five species in them. As with Hemimerina, they are blind and wingless, with filiform segmented cerci. Hemimerina are viviparous ectoparasites, preferring the fur of African rodents in either *Cricetomys* or *Beamys* genera.[43] Hemimerina also has two genera, *Hemimerus* and *Araeomerus*, with a total of 11 species.[43]

Phylogeny

Dermaptera is relatively small compared to the other orders of Insecta, with only about 2,000 species, 3 suborders and 15 families, including the extinct suborders Archidermaptera and Eodermaptera with their extinct families Protodiplatyidae, Dermapteridae, Semenoviolidae, and Turanodermatidae. The phylogeny of the Dermaptera is still debated. The extant Dermaptera appear to be monophyletic and there is support for the monophyly of the families Forficulidae, Chelisochidae, Labiduridae and Anisolabididae, however evidence has supported the conclusion that the former suborder Forficulina was paraphyletic through the exclusion of Hemimerina and Arixeniina which should instead be nested within the Forficulina.[42][49] Thus, these former suborders were eliminated in the most recent higher classification.

A female of the common earwig in a threat pose

Relationship with humans

Earwigs are fairly abundant and are found in many areas around the world. There is no evidence that they transmit diseases to humans or other animals. Their pincers are commonly believed to be dangerous, but in reality, even the curved pincers of males cause little or no harm to humans.[50] Earwigs have been rarely known[51] to crawl into the ears of humans, but they do not lay eggs inside the human body or human brain.[52][53]

There is a debate whether earwigs are harmful or beneficial to crops, as they eat both the foliage and the insects eating such foliage, such as aphids, though it would take a large population to do considerable damage. The common earwig eats a wide variety of plants, and also a wide variety of foliage, including the leaves and petals. They have been known to cause economic losses in fruit and vegetable crops. Some examples are the flowers, hops, red raspberries,[54] and corn crops in Germany, and in the south of France, earwigs have been observed feeding on peaches and apricots. The earwigs attacked mature plants and made cup-shaped bite marks 3–11 mm (0.12–0.43 in) in diameter.[55]

In literature and folklore

- Oscar Cook wrote the short story (appearing in *Switch On The Light*, April, 1931; *A Century Of Creepy Stories* 1934; *Pan Horror 2*, 1960) *Boomerang*, which was later adapted by Rod Serling for the Night Gallery tv-series episode, *The Caterpillar*.[56] It tells the tale of the use of an earwig as a murder instrument applied by a man obsessed with the wife of an associate.
- Robert Herrick in *Hesperides* describes a feast attended by Queen Titania through writing: "Beards of mice, a newt's stew'd thigh, A bloated Earwig and a fly".
- Thomas Hood discusses the myth of earwigs finding shelter in the human ear in the poem "Love Lane" by saying the following: " 'Tis vain to talk of hopes and fears, / And hope the least reply to wing, / From any maid that stops her ears / In dread of earwigs creeping in!"[57]
- In some parts of rural England the earwig is called "battle-twig", which is present in Alfred, Lord Tennyson's poem *The Spinster's Sweet-Arts*: " 'Twur as bad as battle-twig 'ere i' my oan blue chamber to me."[58]
- In some regions of Japan, earwigs are called "Chinpo-Basami" or "Chinpo-Kiri", which means "penis cutter". Kenta Takada, a Japanese cultural entomologist, has inferred that these names may be derived from the fact that earwigs were seen around old Japanese-style toilets.[59]
- In George's Marvellous Medicine, George's Grandma encourages him to eat unwashed celery with beetles and earwigs still on them. " A big fat earwig is very tasty,' Grandma said, licking her lips. 'But you've got to be very quick, my dear, when you put one of those in your mouth. It has a pair of sharp nippers on its back end and if it grabs your tongue with those, it never lets go. So you've got to bite the earwig first, chop chop, before it bites you."[60]

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Fly

True **flies** are insects of the order **Diptera**, the name being derived from the Greek δι- *di-* "two", and πτερόν *pteron* "wings". Insects of this order use only a single pair of wings to fly, the hindwings having evolved into advanced mechanosensory organs known as halteres, which act as high-speed sensors of rotational movement and allow dipterans to perform advanced aerobatics.[1] Diptera is a large order containing an estimated 1,000,000 species including horse-flies,[a] crane flies, hoverflies and others, although only about 125,000 species have been described.[4]

Flies have a mobile head, with a pair of large compound eyes, and mouthparts designed for piercing and sucking (mosquitoes, black flies and robber flies), or for lapping and sucking in the other groups. Their wing arrangement gives them great maneuverability in flight, and claws and pads on their feet enable them to cling to smooth surfaces. Flies undergo complete metamorphosis; the eggs are laid on the larval food-source and the larvae, which lack true limbs, develop in a protected environment, often inside their food source. The pupa is a tough capsule from which the adult emerges when ready to do so; flies mostly have short lives as adults.

Diptera is one of the major insect orders and of considerable ecological and human importance. Flies are important pollinators, second only to the bees and their Hymenopteran relatives. Flies may have been among the evolutionarily earliest pollinators responsible for early plant pollination. Fruit flies are used as model organisms in research, but less benignly, mosquitoes are vectors for malaria, dengue, West Nile fever, yellow fever, encephalitis, and other infectious diseases; and houseflies, commensal with humans all over the world, spread food-borne illnesses. Flies can be annoyances especially in some parts of the world where they can occur in large numbers, buzzing and settling on the skin or eyes to bite or seek fluids. Larger flies such as tsetse flies and screwworms cause significant economic harm to cattle. Blowfly larvae, known as gentles, and other dipteran larvae, known more generally as maggots, are used as fishing bait and as food for carnivorous animals. They are also used in medicine in debridement to clean wounds.

Fly

Temporal range: 245 –0 Ma

PreЄ Є O S D C P T J K PgN

Middle Triassic – Recent

Syrphus ribesii, showing characteristic dipteran features: large eyes, small antennae, sucking mouthparts, single pair of flying wings, hindwings reduced to clublike halteres

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Superorder:	Panorpida
(unranked):	Antliophora
Order:	Diptera Linnaeus, 1758

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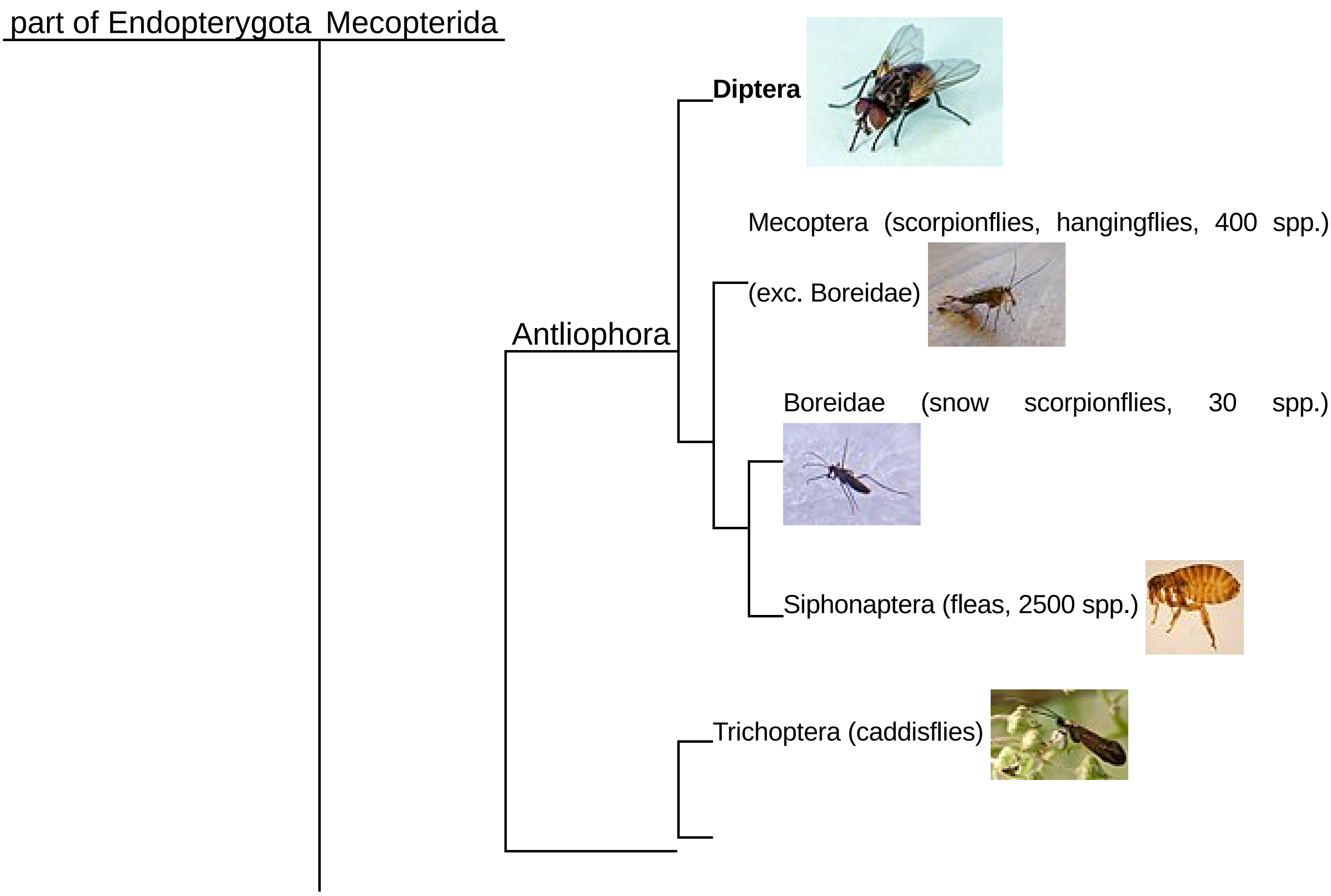
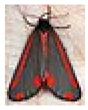
Taxonomy and phylogeny

Relationships to other insects

Dipterans are endopterygotes, insects that undergo radical metamorphosis. They belong to the Mecopterida, alongside the Mecoptera, Siphonaptera, Lepidoptera and Trichoptera.[5][6] The possession of a single pair of wings distinguishes most true flies from other insects with "fly" in their names. However, some true flies such as Hippoboscidae (louse flies) have become secondarily wingless.[7]

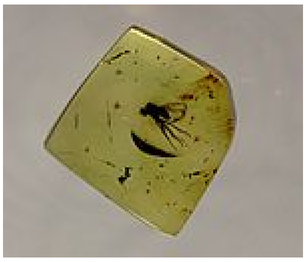
The cladogram represents the current consensus view.[8]



Lepidoptera (butterflies and moths) 

Hymenoptera (sawflies, wasps, ants, bees) 

Relationships between fly subgroups and families



Fossil brachyceran in Baltic amber. Lower Eocene, c. 50 million years ago

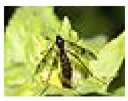
Fossil nematoceran in Dominican amber. Sandfly, *Lutzomyia adiketis* (Psychodidae), Early Miocene, c. 20 million years ago

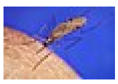
The first true dipterans known are from the Middle Triassic (around 240 million years ago), and they became widespread during the Middle and Late Triassic.[9] Modern flowering plants did not appear until the Cretaceous (around 140 million years ago), so the original dipterans must have had a different source of nutrition other than nectar. Based on the attraction of many modern fly groups to shiny droplets, it has been suggested that they may have fed on honeydew produced by sap-sucking bugs which were abundant at the time, and dipteran mouthparts are well-adapted to softening and lapping up the crusted residues.[10] The basal clades in the Diptera include the Deuterophlebiidae and the enigmatic Nymphomyiidae.[11] Three episodes of evolutionary radiation are thought to have occurred based on the fossil record. Many new species of lower Diptera developed in the Triassic, about 220 million years ago. Many lower Brachycera appeared in the Jurassic, some 180 million years ago. A third radiation took place among the Schizophora at the start of the Paleogene, 66 million years ago.[11]

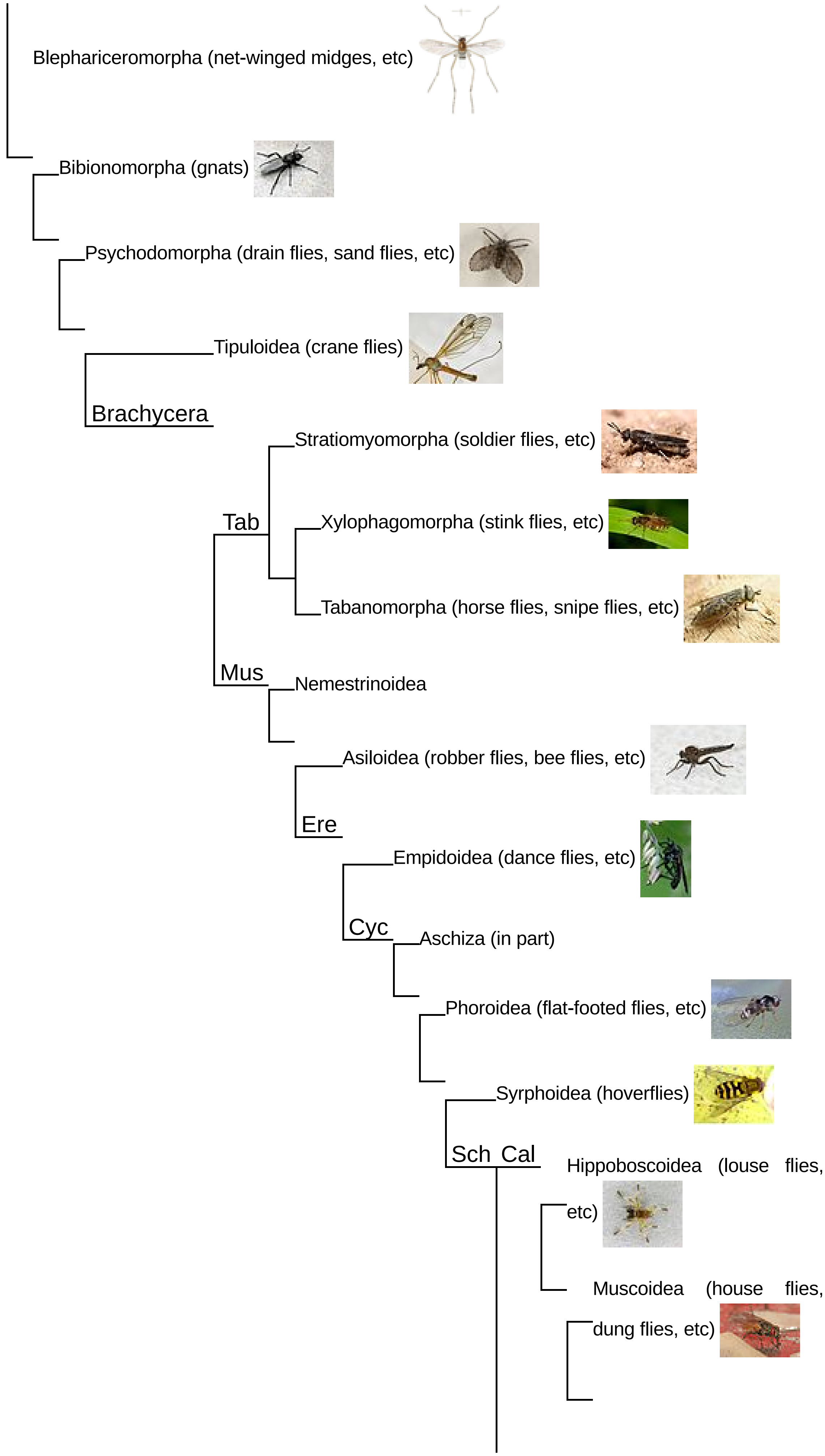
The phylogenetic position of Diptera has been controversial. The monophyly of holometabolous insects has long been accepted, with the main orders being established as Lepidoptera, Coleoptera, Hymenoptera and Diptera, and it is the relationships between these groups which has caused difficulties. Diptera is widely thought to be a member of Mecopterida, along with Lepidoptera (butterflies and moths), Trichoptera (caddisflies), Siphonaptera (fleas), Mecoptera (scorpionflies) and possibly Strepsiptera (twisted-wing flies). Diptera has been grouped with Siphonaptera and Mecoptera in the Antliophora, but this has not been confirmed by molecular studies.[12]

Diptera were traditionally broken down into two suborders, Nematocera and Brachycera, distinguished by the differences in antennae. The Nematocera are identified by their elongated bodies and many-segmented, often feathery antennae as represented by mosquitoes and crane flies. The Brachycera have rounder bodies and much shorter antennae.[13][14] Subsequent studies have identified the Nematocera as being non-monophyletic with modern phylogenies placing the Brachycera within grades of groups formerly placed in the Nematocera. The construction of a phylogenetic tree has been the subject of ongoing research. The following cladogram is based on the FLYTREE project.[11][15][16]

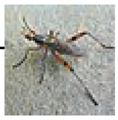
Nematocera

Ptychopteromorpha (phantom and primitive crane-flies) 

Culicomorpha (mosquitoes) 


Blephariceromorpha (net-winged midges, etc)
Bibionomorpha (gnats)
Psychodomorpha (drain flies, sand flies, etc)
Tipuloidea (crane flies)
Brachycera
Stratiomyomorpha (soldier flies, etc)
Tab
Xylophagomorpha (stink flies, etc)
Tabanomorpha (horse flies, snipe flies, etc)
Mus
Nemestrinoidea
Asiloidea (robber flies, bee flies, etc)
Ere
Empidoidea (dance flies, etc)
Cyc
Aschiza (in part)
Phoroidea (flat-footed flies, etc)
Syrphoidea (hoverflies)
Sch Cal
Hippoboscoidea (louse flies, etc)
Muscoidea (house flies, dung flies, etc)

Oestroidea (blow flies, flesh flies, etc) 

Acalyptratae (marsh flies, etc) 

Abbreviations used in the cladogram:

- Cal=Calyptratae
- Cyc=Cyclorrhapha
- Ere=Eremoneura
- Mus=Muscomorpha
- Sch=Schizophora
- Tab=Tabanomorpha

Diversity

Gauromydas heros is the largest fly in the world.

Flies are often abundant and are found in almost all terrestrial habitats in the world apart from Antarctica. They include many familiar insects such as house flies, blow flies, mosquitoes, gnats, black flies, midges and fruit flies. More than 150,000 have been formally described and the actual species diversity is much greater, with the flies from many parts of the world yet to be studied intensively.[17][18] The suborder Nematocera include generally small, slender insects with long antennae such as mosquitoes, gnats, midges and crane-flies, while the Brachycera includes broader, more robust flies with short antennae. Many nematoceran larvae are aquatic.[19] There are estimated to be a total of about 19,000 species of Diptera in Europe, 22,000 in the Nearctic region, 20,000 in the Afrotropical region, 23,000 in the Oriental region and 19,000 in the Australasian region.[20] While most species have restricted distributions, a few like the housefly (*Musca domestica*) are cosmopolitan.[21] *Gauromydas heros* (Asiloidea), with a length of up to 7 cm (2.8 in), is generally considered to be the largest fly in the world,[22] while the smallest is *Euryplatea nanaknihali*, which at 0.4 mm (0.016 in) is smaller than a grain of salt.[23]

Brachycera are ecologically very diverse, with many being predatory at the larval stage and some being parasitic. Animals parasitised include molluscs, woodlice, millipedes, insects, mammals,[20] and amphibians.[24] Flies are the second largest group of pollinators after the Hymenoptera (bees, wasps and relatives). In wet and colder environments flies are significantly more important as pollinators. Compared to bees, they need less food as they do not need to provision their young. Many flowers that bear low nectar and those that have evolved trap pollination depend on flies.[25] It is thought that some of the earliest pollinators of plants may have been flies.[26]

The greatest diversity of gall forming insects are found among the flies, principally in the family Cecidomyiidae (gall midges).[27] Many flies (most importantly in the family Agromyzidae) lay their eggs in the mesophyll tissue of leaves with larvae feeding between the surfaces forming blisters and mines.[28] Some families are mycophagous or fungus feeding. These include the cave dwelling Mycetophilidae (fungus gnats) whose larvae are the only diptera with bioluminescence. The Sciaridae are also fungus feeders. Some plants are pollinated by fungus feeding flies that visit fungus infected male flowers.[29]

The larvae of *Megaselia scalaris* (Phoridae) are almost omnivorous and consume such substances as paint and shoe polish.[30] The *Exorista mella (Walker)* fly are considered generalists and parasitoids of a variety of hosts[31]. The larvae of the shore flies (Ephydridae) and some Chironomidae survive in extreme environments including glaciers (*Diamesa* sp., Chironomidae[32]), hot springs, geysers, saline pools, sulphur pools, septic tanks and even crude oil (*Helaeomyia petrolei*[32]).[20] Adult hoverflies (Syrphidae) are well known for their mimicry and the larvae adopt diverse lifestyles including being inquiline scavengers inside the nests of social insects.[33] Some brachycerans are agricultural pests, some bite animals and humans and suck their blood, and some transmit diseases.[20]

Anatomy and morphology

Flies are adapted for aerial movement and typically have short and streamlined bodies. The first tagma of the fly, the head, bears the eyes, the antennae, and the mouthparts (the labrum, labium, mandible, and maxilla make up the mouthparts). The second tagma, the thorax, bears the wings and contains the flight muscles on the second segment, which is greatly enlarged; the first and third segments have been reduced to collar-like structures, and the third segment bears the halteres, which help to balance the insect during flight. The third tagma is the abdomen consisting of 11 segments, some of which may be fused, and with the 3 hindmost segments modified for reproduction.[34] Some Dipterans are mimics and can only be distinguished from their models by very careful inspection. An example of this is *Spilomyia longicornis*, which is a fly but mimics a vespid wasp.

Head of *a horse-fly* showing large compound eyes and stout piercing mouthparts

Flies have a mobile head with a pair of large compound eyes on the sides of the head, and in most species, three small ocelli on the top. The compound eyes may be close together or widely separated, and in some instances are divided into a dorsal region and a ventral region, perhaps to assist in swarming behaviour. The antennae are well-developed but variable, being thread-like, feathery or comb-like in the different families. The mouthparts are adapted for piercing and sucking, as in the black flies, mosquitoes and robber flies, and for lapping and sucking as in many other groups.[34] Female horse-flies use knife-like mandibles and maxillae to make a cross-shaped incision in the host's skin and then lap up the blood that flows. The gut includes large diverticulae, allowing the insect to store small quantities of liquid after a meal.[35]

For visual course control, flies' optic flow field is analyzed by a set of motion-sensitive neurons.[36] A subset of these neurons is thought to be involved in using the optic flow to estimate the parameters of self-motion, such as yaw, roll, and sideward translation.[37] Other neurons are thought to be involved in analyzing the content of the visual scene itself, such as separating figures from the ground using motion parallax.[38][39] The H1 neuron is responsible for detecting horizontal motion across the entire visual field of the fly, allowing the fly to generate and guide stabilizing motor corrections midflight with respect to yaw.[40] The ocelli are concerned in the detection of changes in light intensity, enabling the fly to react swiftly to the approach of an object.[41]

Like other insects, flies have chemoreceptors that detect smell and taste, and mechanoreceptors that respond to touch. The third segments of the antennae and the maxillary palps bear the main olfactory receptors, while the gustatory receptors are in the labium, pharynx, feet, wing margins and female genitalia,[42] enabling flies to taste their food by walking on it. The taste receptors in females at the tip of the abdomen receive information on the suitability of a site for ovipositing.[41] Flies that feed on blood have special sensory structures that can detect infrared emissions, and use them to home in on their hosts, and many blood-sucking flies can detect the raised concentration of carbon dioxide that occurs near large animals.[43] Some tachinid flies (Ormiinae) which are parasitoids of bush crickets, have sound receptors to help them locate their singing hosts.[44]

Diptera have one pair of fore wings on the mesothorax and a pair of halteres, or reduced hind wings, on the metathorax. A further adaptation for flight is the reduction in number of the neural ganglia, and concentration of nerve tissue in the thorax, a feature that is most extreme in the highly derived Muscomorpha infraorder.[35] Some species of flies are exceptional in that they are secondarily flightless. The only other order of insects bearing a single pair of true, functional wings, in addition to any form of halteres, are the Strepsiptera. In contrast to the flies, the Strepsiptera bear their halteres on the mesothorax and their flight wings on the metathorax.[45] Each of the fly's six legs has a typical insect structure of coxa, trochanter, femur, tibia and tarsus, with the tarsus in most instances being subdivided into five tarsomeres.[34] At the tip of the limb is a pair of claws, and between these are cushion-like structures known as pulvilli which provide adhesion.[46]

A cranefly, showing the hind wings reduced to drumstick-shaped halteres

The abdomen shows considerable variability among members of the order. It consists of eleven segments in primitive groups and ten segments in more derived groups, the tenth and eleventh segments having fused.[47] The last two or three segments are adapted for reproduction. Each segment is made up of a dorsal and a ventral sclerite, connected by an elastic membrane. In some females, the sclerites are rolled into a flexible, telescopic ovipositor.[34]

Flight

Flies are capable of great manoeuvrability during flight due to the presence of the halteres. These act as gyroscopic organs and are rapidly oscillated in time with the wings; they act as a balance and guidance system by providing rapid feedback to the wing-steering muscles, and flies deprived of their halteres are unable to fly. The wings and halteres move in synchrony but the amplitude of each wing beat is independent, allowing the fly to turn sideways.[48] The wings of the fly are attached to two kinds of muscles, those used to power it and another set used for fine control.[49]

Tabanid fly in flight

Flies tend to fly in a straight line then make a rapid change in direction before continuing on a different straight path. The directional changes are called saccades and typically involve an angle of 90°, being achieved in 50 milliseconds. They are initiated by visual stimuli as the fly observes an object, nerves then activate steering muscles in the thorax that cause a small change in wing stroke which generate sufficient torque to turn. Detecting this within four or five wingbeats, the halteres trigger a counter-turn and the fly heads off in a new direction.[50]

Flies have rapid reflexes that aid their escape from predators but their sustained flight speeds are low. Dolichopodid flies in the genus *Condylostylus* respond in less than 5 milliseconds to camera flashes by taking flight.[51] In the past, the deer bot fly, *Cephenemyia*, was claimed to be one of the fastest insects on the basis of an estimate made visually by Charles Townsend in 1927.[52] This claim, of speeds of 600 to 800 miles per hour, was regularly repeated until it was shown to be physically impossible as well as incorrect by Irving Langmuir. Langmuir suggested an estimated speed of 25 miles per hour.[53][54][55]

Although most flies live and fly close to the ground, a few are known to fly at heights and a few like *Oscinella* (Chloropidae) are known to be dispersed by winds at altitudes of up to 2000 ft and over long distances.[56] Some hover flies like *Metasyrphus corollae* have been known to undertake long flights in response to aphid population spurts.[57]

Males of fly species such as *Cuterebra*, many hover flies,[58] bee flies (Bombyliidae)[59] and fruit flies (Tephritidae)[60] maintain territories within which they engage in aerial pursuit to drive away intruding males and other species.[61] While these territories may be held by individual males, some species, such as *A. freeborni*,[62] form leks with many males aggregating in displays.[60] Some flies maintain an airspace and still others form dense swarms that maintain a stationary location with respect to landmarks. Many flies mate in flight while swarming.[63]

Life cycle and development

Diptera go through a complete metamorphosis with four distinct life stages – egg, larva, pupa and adult.

Mating anthomyiid flies

Larva

In many flies, the larval stage is long and adults may have a short life. Most dipteran larvae develop in protected environments; many are aquatic and others are found in moist places such as carrion, fruit, vegetable matter, fungi and, in the case of parasitic species, inside their hosts. They tend to have thin cuticles and become desiccated if exposed to the air. Apart from the Brachycera, most dipteran larvae have sclerotinised head capsules, which may be reduced to remnant mouth hooks; the Brachycera, however, have soft, gelatinized head capsules from which the sclerites are reduced or missing. Many of these larvae retract their heads into their thorax.[34][64]

Life cycle of stable fly *Stomoxys calcitrans*, showing eggs, 3 larval instars, pupa, and adult

Some other anatomical distinction exists between the larvae of the Nematocera and the Brachycera. Especially in the Brachycera, little demarcation is seen between the thorax and abdomen, though the demarcation may be visible in many Nematocera, such as mosquitoes; in the Brachycera, the head of the larva is not clearly distinguishable from the rest of the body, and few, if any, sclerites are present. Informally, such brachyceran larvae are called maggots,[65] but the term is not technical and often applied indifferently to fly larvae or insect larvae in general. The eyes and antennae of brachyceran larvae are reduced or absent, and the abdomen also lacks appendages such as cerci. This lack of features is an adaptation to food such as carrion, decaying detritus, or host tissues surrounding endoparasites.[35] Nematoceran larvae generally have well-developed eyes and antennae, while those of Brachyceran larvae are reduced or modified.[66]

Dipteran larvae have no jointed, "true legs",[64] but some dipteran larvae, such as species of Simuliidae, Tabanidae and Vermileonidae, have prolegs adapted to hold onto a substrate in flowing water, host tissues or prey.[67] The majority of dipterans are oviparous and lay batches of eggs, but some species are ovoviviparous, where the larvae starting development inside the eggs before they hatch or viviparous, the larvae hatching and maturing in the body of the mother before being externally deposited. These are found especially in groups that have larvae dependent on food sources that are short-lived or are accessible for brief periods.[68] This is widespread in some families such as the Sarcophagidae. In *Hylemya strigosa* (Anthomyiidae) the larva moults to the second instar before hatching, and in *Termitoxenia* (Phoridae) females have incubation pouches, and a full developed third instar larva is deposited by the adult and it almost immediately pupates with no freely feeding larval stage. The tsetse fly (as well as other Glossinidae, Hippoboscidae, Nycteribidae and Streblidae) exhibits adenotrophic viviparity; a single fertilised egg is retained in the oviduct and the developing larva feeds on glandular secretions. When fully grown, the female finds a spot with soft soil and the larva works its way out of the oviduct, buries itself and pupates. Some flies like *Lundstroemia parthenogenetica* (Chironomidae) reproduce by thelytokous parthenogenesis, and some gall midges have larvae that can produce eggs (paedogenesis).[69][70]

Pupa

The pupae take various forms. In some groups, particularly the Nematocera, the pupa is intermediate between the larval and adult form; these pupae are described as "obtect", having the future appendages visible as structures that adhere to the pupal body. The outer surface of the pupa may be leathery and bear spines, respiratory features or locomotory paddles. In other groups, described as "coarctate", the appendages are not visible. In these, the outer surface is a puparium, formed from the last larval skin, and the actual pupa is concealed within. When the adult insect is ready to emerge from this tough, desiccation-resistant capsule, it inflates a balloon-like structure on its head, and forces its way out.[34]

Adult

The adult stage is usually short, its function only to mate and lay eggs. The genitalia of male flies are rotated to a varying degree from the position found in other insects.[71] In some flies, this is a temporary rotation during mating, but in others, it is a permanent torsion of the organs that occurs during the pupal stage. This torsion may lead to the anus being below the genitals, or, in the case of 360° torsion, to the sperm duct being wrapped around the gut and the external organs being in their usual position. When flies mate, the male initially flies on top of the female, facing in the same direction, but then turns around to face in the opposite direction. This forces the male to lie on his back for his genitalia to remain engaged with those of the female, or the torsion of the male genitals allows the male to mate while remaining upright. This leads to flies having more reproduction abilities than most insects, and much quicker. Flies occur in large populations due to their ability to mate effectively and quickly during the mating season.[35]

Ecology

As ubiquitous insects, dipterans play an important role at various trophic levels both as consumers and as prey. In some groups the larvae complete their development without feeding, and in others the adults do not feed. The larvae can be herbivores, scavengers, decomposers, predators or parasites, with the consumption of decaying organic matter being one of the most prevalent feeding behaviours. The fruit or detritus is consumed along with the associated micro-organisms, a sieve-like filter in the pharynx being used to concentrate the particles, while flesh-eating larvae have mouth-hooks to help shred their food. The larvae of some groups feed on or in the living tissues of plants and fungi, and some of these are serious pests of agricultural crops. Some aquatic larvae consume the films of algae that form underwater on rocks and plants. Many of the parasitoid larvae grow inside and eventually kill other arthropods, while parasitic larvae may attack vertebrate hosts.[34]

Whereas many dipteran larvae are aquatic or live in enclosed terrestrial locations, the majority of adults live above ground and are capable of flight. Predominantly they feed on nectar or plant or animal exudates, such as honeydew, for which their lapping mouthparts are adapted. The flies that feed on vertebrate blood have sharp stylets that pierce the skin, the insects inserting anticoagulant saliva and absorbing the blood that flows; in this process, certain diseases can be transmitted. The bot flies (Oestridae) have evolved to parasitize mammals. Many species complete their life cycle inside the bodies of their hosts.[72] In many dipteran groups, swarming is a feature of adult life, with clouds of insects gathering in certain locations; these insects are mostly males, and the swarm may serve the purpose of making their location more visible to females.[34]

Anti-predator adaptations

Flies are eaten by other animals at all stages of their development. The eggs and larvae are parasitised by other insects and are eaten by many creatures, some of which specialise in feeding on flies but most of which consume them as part of a mixed diet. Birds, bats, frogs, lizards, dragonflies and spiders are among the predators of flies.[73] Many flies have evolved mimetic resemblances that aid their protection. Batesian mimicry is widespread with many hoverflies resembling bees and wasps,[74][75] ants[76] and some species of tephritid fruit fly resembling spiders.[77] Some species of hoverfly are myrmecophilous, their young live and grow within the nests of ants. They are protected from the ants by imitating chemical odours given by ant colony members.[78] Bombyliid bee flies such as *Bombylius major* are short-bodied, round, furry, and distinctly bee-like as they visit flowers for nectar, and are likely also Batesian mimics of bees.[79]

In contrast, *Drosophila subobscura*, a species of fly in the genus *Drosophila*, lacks a category of hemocytes that are present in other studied species of *Drosophila*, leading to an inability to defend against parasitic attacks, a form of innate immunodeficiency.[80]

The large bee-fly, *Bombylius major*, is a Batesian mimic of bees.

In culture

Symbolism

Petrus Christus's 1446 painting *Portrait of a Carthusian* has a fly painted on a trompe l'oeil frame.

Flies play a variety of symbolic roles in different cultures. These include both positive and negative roles in religion. In the traditional Navajo religion, Big Fly is an important spirit being.[81][82][83] In Christian demonology, Beelzebub is a demonic fly, the "Lord of the Flies", and a god of the Philistines.[84][85][86]

Flies have appeared in literature since ancient Sumer.[87] In a Sumerian poem, a fly helps the goddess Inanna when her husband Dumuzid is being chased by *galla* demons.[87] In the Mesopotamian versions of the flood myth, the dead corpses floating on the waters are compared to flies.[87] Later, the gods are said to swarm "like flies" around the hero Utnapishtim's offering.[87] Flies appear on Old Babylonian seals as symbols of Nergal, the god of death.[87] Fly-shaped lapis lazuli beads were often worn in ancient Mesopotamia, along with other kinds of fly-jewellery.[87]

In *Prometheus Bound*, which is attributed to the Athenian tragic playwright Aeschylus, a gadfly sent by Zeus's wife Hera pursues and torments his mistress Io, who has been transformed into a cow and is watched constantly by the hundred eyes of the herdsman Argus:[88][89] "Io: Ah! Hah! Again the prick, the stab of gadfly-sting! O earth, earth, hide, the hollow shape—Argus—that evil thing—the hundred-eyed."[89] William Shakespeare, inspired by Aeschylus, has Tom o'Bedlam in *King Lear*, "Whom the foul fiend hath led through fire and through flame, through ford and whirlpool, o'er bog and quagmire", driven mad by the constant pursuit.[89] In *Antony and Cleopatra*, Shakespeare similarly likens Cleopatra's hasty departure from the Actium battlefield to that of a cow chased by a gadfly.[90] More recently, in 1962 the biologist Vincent Dethier wrote *To Know a Fly*, introducing the general reader to the behaviour and physiology of the fly.[91]

Flies appear in popular culture in concepts such as fly-on-the-wall documentary-making in film and television production. The metaphoric name suggests that events are seen candidly, as a fly might see them.[92] Flies have inspired the design of miniature flying robots.[93] Steven Spielberg's 1993 film *Jurassic Park* relied on the idea that DNA could be preserved in the stomach contents of a blood-sucking fly fossilised in amber, though the mechanism has been discounted by scientists.[94]

Economic importance

Dipterans are an important group of insects and have a considerable impact on the environment. Some leaf-miner flies (Agromyzidae), fruit flies (Tephritidae and Drosophilidae) and gall midges (Cecidomyiidae) are pests of agricultural crops; others such as tsetse flies, screwworm and botflies (Oestridae) attack livestock, causing wounds, spreading disease, and creating significant economic harm. See article: Parasitic flies of domestic animals. A few can even cause myiasis in humans. Still others such as mosquitoes (Culicidae), blackflies (Simuliidae) and drain flies (Psychodidae) impact human health, acting as vectors of major tropical diseases. Among these, *Anopheles* mosquitoes transmit malaria, filariasis, and arboviruses; *Aedes aegypti* mosquitoes carry dengue fever and the Zika virus; blackflies carry river blindness; sand flies carry leishmaniasis. Other dipterans are a nuisance to humans, especially when present in large numbers; these include houseflies, which contaminate food and spread food-borne illnesses; the biting midges and sandflies (Ceratopogonidae) and the houseflies and stable flies (Muscidae).[34] In tropical regions, eye flies (Chloropidae) which visit the eye in search of fluids can be a nuisance in some seasons.[95]

An *Anopheles stephensi* mosquito drinking human blood. The species carries malaria.

Many dipterans serve roles that are useful to humans. Houseflies, blowflies and fungus gnats (Mycetophilidae) are scavengers and aid in decomposition. Robber flies (Asilidae), tachinids (Tachinidae) and dagger flies and balloon flies (Empididae) are predators and parasitoids of other insects, helping to control a variety of pests. Many dipterans such as bee flies (Bombyliidae) and hoverflies (Syrphidae) are pollinators of crop plants.[34]

Uses

Diptera in research: *Drosophila melanogaster* fruit fly larvae being bred in tubes in a genetics laboratory

Drosophila melanogaster, a fruit fly, has long been used as a model organism in research because of the ease with which it can be bred and reared in the laboratory, its small genome, and the fact that many of its genes have counterparts in higher eukaryotes. A large number of genetic studies have been undertaken based on this species; these have had a profound impact on the study of gene expression, gene regulatory mechanisms and mutation. Other studies have investigated physiology, microbial pathogenesis and development among other research topics.[96] The studies on dipteran relationships by Willi Hennig helped in the development of cladistics, techniques that he applied to morphological characters but now adapted for use with molecular sequences in phylogenetics.[97]

Maggots found on corpses are useful to forensic entomologists. Maggot species can be identified by their anatomical features and by matching their DNA. Maggots of different species of flies visit corpses and carcases at fairly well-defined times after the death of the victim, and so do their predators, such as beetles in the family Histeridae. Thus, the presence or absence of particular species provides evidence for the time since death, and sometimes other details such as the place of death, when species are confined to particular habitats such as woodland.[98]

Blowflies feeding on the fresh corpse of a porcupine, *Hystrix africaeaustralis*

Maggots used as animal feed at London Zoo

Some species of maggots such as blowfly larvae (gentles) and bluebottle larvae (casters) are bred commercially; they are sold as bait in angling, and as food for carnivorous animals (kept as pets, in zoos, or for research) such as some mammals,[99] fishes, reptiles, and birds. It has been suggested that fly larvae could be used at a large scale as food for farmed chickens, pigs, and fish. However, consumers are opposed to the inclusion of insects in their food, and the use of insects in animal feed remains illegal in areas such as the European Union.[100][101]

Fly larvae can be used as a biomedical tool for wound care and treatment. Maggot debridement therapy (MDT) is the use of blow fly larvae to remove the dead tissue from wounds, most commonly being amputations. Historically, this has been used for centuries, both intentional and unintentional, on battlefields and in early hospital settings.[102] Removing the dead tissue promotes cell growth and healthy wound healing. The larvae also have biochemical properties such as antibacterial activity found in their secretions as they feed.[103] These medicinal maggots are a safe and effective treatment for chronic wounds.[104]

Casu marzu is a traditional Sardinian sheep milk cheese that contains larvae of the cheese fly, *Piophila casei*.

The Sardinian cheese casu marzu is exposed to flies known as cheese skippers such as *Piophila casei*, members of the family Piophilidae.[105] The digestive activities of the fly larvae soften the cheese and modify the aroma as part of the process of maturation. At one time European Union authorities banned sale of the cheese and it was becoming hard to find,[106] but the ban has been lifted on the grounds that the cheese is a traditional local product made by traditional methods.[107]

Notes

a. Some authors draw a distinction in writing the common names of insects. True flies are in their view best written as two words, such as crane fly, robber fly, bee fly, moth fly, and fruit fly. In contrast, common names of non-dipteran insects that have "fly" in their names are written as one word, e.g. butterfly, stonefly, dragonfly, scorpionfly, sawfly, caddisfly, whitefly.[2] In practice, however, this is a comparatively new convention; especially in older books, names like "saw fly" and "caddis fly", or hyphenated forms such as house-fly and dragon-fly are widely used.[3] In any case, non-entomologists cannot, in general, be expected to tell dipterans, "true flies", from other insects, so it would be unrealistic to expect rigour in the use of common names. Also, exceptions to this rule occur, such as the hoverfly, which is a true fly, and the Spanish fly, a type of blister beetle.

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WIKIPEDIA

Storage pest

A **storage pest** is an insect or other animal that damages or destroys stored food or other stored valuable organic matter.[1] Insects are a large proportion of storage pests with each type of crop having specific insects that gravitate towards them such as the genus *Tribolium* that consists of insects such as *Tribolium castaneum* (red flour beetle) or *Tribolium confusum* (confused flour beetle) which damage flour crops primarily.[2][3]

Contents

Insects

Many insects act as storage pests in crops including grain crops, and destroy approximately 25-33% of crops worldwide, each year.[3] Crops can be completely destroyed or even partially damaged affecting the quality of the crop and the ability to germinate new ones, by decreasing the protein content and removing the seeds from the grains.

Types of Insect Pests

There are two types of grain insect pests, primary and secondary pests.

Lesser grain borer (*Rhyzopertha dominica*).

Primary Pests

Primary grain pests attack the whole grain. The eggs are laid outside the grain, before the larvae mature inside the grain and then chew their way out. Some of these pets include the Lesser grain borer, Granary weevil and Rice weevil.[3]

Lesser grain borer (*Rhyzopertha dominica*)

The lesser grain borer has a dark coloured cylindrical structure with the head concealed.[4] When lesser grain borer eggs are laid, they are laid outside the grain, however mature inside the shell of the seed which can take up to 6 weeks if the temperature is cooler, with the adult borers not living for longer than two months. This species is known to damage stored wheat, corn and cereal crops with the seeds become hollowed out husks. Products with small infestations should be discarded however the grains can be treated with smaller amounts of spray. However, large infestations require more control, including complete fumigation.

Rice weevil (*Sitophilus oryzae*)

Rice weevil (*Sitophilus oryzae*).

The adult rice weevil has an orange-black exoskeleton and lays up to 450 eggs in pores of the damaged grains with each hatched egg further damaging the grain from the inside. Similarly to the lesser grain borer, maturation also happens inside the grain with the matured adult rice weevil eating through the husk of the grain to get out. The life cycle is similar to that of the lesser grain borer in summer months (approximately one month) and adult weevils live up to 8 months after the experience their life cycle.[3]

Secondary Pests

Rust-red flour beetle (*Tribolium castaneum*).

Secondary grain insects feed on broken grain and any powder products left as a result of the broken grain. These pests include the genus *Tribolium*, beetle species and moth species.

Rust-red flour beetle (*Tribolium castaneum*)

The Rust-red flour beetle is a red-brown beetle with an exoskeleton that darkens in colour as the beetle increases in age, with the maximum adult age being a year. Unlike primary pests, Rust-red flour beetles can produce up to 1000 eggs and lay them inside the damaged grain with parts of the larvae able to use the damaged grains and cereal as their food source.[3]

Warehouse moth (*Ephestia spp*)

Warehouse moth (*Ephestia spp*).

The Warehouse moth is a grey moth that remains on the surface of the grain with the female moth laying up to 200 eggs, however their life span is only 2 weeks long with a 4 week life cycle. Similarly to other secondary pests, the Warehouse moth eggs use the surface of the grain, although when the larvae hatch they leave a stream of silk that encapsulates the surface of the grain which can then be used as a cocoon for mature larvae.[3]

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Rhyzopertha

Rhyzopertha is a monotypic genus of beetles in the family Bostrichidae, the false powderpost beetles. The sole species, ***Rhyzopertha dominica***, is known commonly as the **lesser grain borer**, **American wheat weevil**, **Australian wheat weevil**, and **stored grain borer**.[3] It is a beetle commonly found within store bought products and pest of stored cereal grains located worldwide.[4] It is also a major pest of peanuts. The first documentation of wheat infestation by *R. dominica* was observed in Australia.[4] *R. dominica* are usually reddish brown to dark brown in coloration, vary in sizes, elongated and cylindrical when viewing through a cross-section.[4]

Rhyzopertha	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Bostrichidae
Genus:	***Rhyzopertha*** Stephens, 1830
Species:	***R. dominica***
Binomial name	
Rhyzopertha dominica (Fabricius, 1792)	
Synonyms[1][2]	

- *Synodendron dominicum* Fabricius, 1792
- *Synodendron pusillum* Fabricius, 1798
- *Sinodendron dominicum* Fabricius, 1801
- *Sinodendron pusillum* Fabricius, 1801
- *Rhyzopertha pusilla* Stephens, 1830
- *Rhizopertha pusilla* Bach, 1852

Contents

Identification

The average *R. dominica* are 2.1 - 3.0 mm in length.[1] Their body displays a reddish brown coloration with 11 antennae segments and a 3-segmented antennal club.[1] The pronotum is located near the base of the body with no depressions.[1] In addition, the basal part of the pronotum has a wrinkled appearance.[1] Distinct tubercles on the *R. dominica* are found on the anterior margin, but appear to be slightly apart at the median.[1] Moreover, it has clear elytral strioles that are angularly rounded at the apex, and short, yellowish, bent setae.[1] Externally there are no major recognizable differences between male and female adults of *R. dominica*.[1]

Distribution and Diversity

The geographical origin of *R. dominica* is still uncertain, however the scientific community has agreed that the Indian subcontinent is its most probable native home, as the region is inhabited by other bostrichid species.[4] Currently, *R. dominica* has a worldwide distribution, especially in warmer temperate climates zones, between latitude 40° North and South from the equator.[4] It is predominantly found in forested and grain storage environments.[4] As such, human interaction has aided in the widespread of *R. dominica* through the commercial transportation of grain.[4] A testament to their inhabitation of grain is the acquisition of the name "Australian Wheat Weevil", symbolizing their predominant infestation of wheat in Australia.[4]

- *Rhizopertha dominica* Lesne, 1896
- *Dinoderus pusillus* Horn, 1878
- *Ptinus piceus* Marsham, 1802
- *Ptinus fissicornis* Marsham, 1802
- *Apate rufa* Hope, 1845
- *Apate pusilla* Fairmaire, 1850
- *Apate frumentaria* Nördlinger, 1855
- *Bostrichus moderatus* Walker, 1859
- *Rhizopertha rufa* Waterhouse, 1888

Taxonomy

R. dominica is from the family Bostrichidae, commonly referred to as auger or powderpost beetles.[4] Currently the family consists of 550 bostrichid species, of which 77 of them are found in North America.[4] Bostrichids can be distinguished from other beetles due to their rasp-like pronotum, 5-segmented tarsi and straight antennae with 3-3 segments.[4] The genus Rhyzopertha is monotypic, consisting of only *R. dominica*. Further classification of this genus places it within the subfamily Dinordeinae.[4]

Diet

There are various substrates that make up the resources and diet for the *R. dominica*.[4] This includes grains, such as rice, wheat, sorghum, oat, pearl, millet, malt barley from the family Poaceae, and chickpeas, peanuts and beans from the family Leguminosae.[4] Although most insect prefers foods such as trees and dried fruit, *R. dominica* seems to be preadapted for feeding on dry grains.[4] It feeds on the whole grain in both larval and adult stages.[4]

Courtship Behaviour and Reproduction

R. dominica follows a 4-stage life cycle: egg, larval, pupal, and adult.[4] The mating behaviour in the *R. dominica* follows within 24 hour after the individual hatches from the egg.[4] The females do not display any courtship behavior such as initiation of mating or attempt to attract male beetles.[4] In some instances, the males will attempt to mate with other males, whereas this type of interaction is absent in females.[4] Female attraction to the male occurs upon physical contact, whereby the close proximity allows for the olfactory senses to detect the male produced pheromones.[4] The pheromones are also responsible for the attraction between male beetles.[4] Stimulation from the pheromones is characterized (in both male-to-male and male-to-female interaction) by an excited and rapid walking motion; the head, thorax, and antennae are extended forward and up, in the direction of the pheromone source.[4] When they are around a pheromone source, the beetles walk around with their antennae extended and they actively palpate the abdominal area.[4] The males will initiate a palp mediated mating response and mount the beetle if it were a female.[4] This occurs after he touches his maxillary palp to the tips of her elytra.[4] While mounting the female, the male moves to the posterior dorsal surface.[4] The male walks forward and taps lightly on top of the female's elytra and thorax with his palpi.[4] Contact with the vagina is made when the last sternite of the male beetle is lowered and the aedeagus protrudes to the vagina.[4] Once the male is firmly mounted, copulation has been achieved.[4] Copulation lasts for 2 hours and can occur multiple times in *R. dominica*, as females require more than one mating to fertilize effectively all the eggs produced during her lifetime.[4] Externally there are no major recognizable differences between male and female adults of *R. dominica*.[4] A reported minor difference is the last ventral abdominal sternite of the female, seen as pale yellow as compared to the uniformly brown males.[4]

Infestation

Maximum reproductive success is achieved on dry grains, such as wheat, explaining the infestation issue it causes from residual insect populations in grain storages and immigration from outside.[4] These products, which are stored in bulk, are understood to be human created ecosystems with a stable microclimate suited to fit the pest's needs.[5] These ecosystems allow females to deposit their eggs loosely within the grain mass and allows the first larva to enter the kernel.[6][7] The larva after undergoing 4 larval instar development, will emerge from the kernel as an adult.[8] The duration of development takes up to 35 days, with optimal conditions of 28 °C and 50% humidity.[7] Once it reaches adulthood, they have difficulty moving on flat and smooth surfaces, due to reduced friction, and as a result are unable to access food.[9] Therefore, the grain mass is the most suitable for them due to their diet of grain based products, which can facilitate the appearance of more fungi and pests.[10] At the adult life stage, *R. dominica* flies to the surface of the grain mass and slowly works its way downward through the grain mass as far at 12m, further than other grain beetles.[4] Together with the deep movement into the grain mass and the cryptic feeding on the kernels, it can becomes difficult to detect initial *R. dominica* infestation.[4] Overtime, because of *R. dominica* infestation, a sweetish odor is left within the infested grain as a result of the aggregation pheromones produced by males.[4] A large amount of frass is also produced from adult feeding activities, containing ovoid granules of undigested endosperm mixed with a finer flour, larvae exuvae, feces, fragments of immature insects, and various by products affecting the overall quality of the grain.[4] Adult and larval stages of *R. dominica* feed on the germ and endosperm. This degree of feeding can vary with the age of the beetles, with the highest amount of feeding done by young adult beetles.[4]

Natural Enemies

Various predaceous organisms are capable of coexisting with *R. dominica*, such as mites, bugs, and parasitoids that are also found infesting stored grain.[4] Two hemipterans, found in the family Anthocoridae, four mites from the families Acarophenacidae, Pediculoidae, and Cheyletidae have all found to attack *R. dominica* within the storage, including five parasitoids from the families Bethylidae and Pteromalidae.[4] All of these predators attacked the eggs or larval stage rather than the adult or pupal stage.[4] Mortality of *R. dominica* can also occur because of nematodes, fungi, protozoans and bacteria, acting as predators, while harming the larval and adult stages.[4]

Flight

The flight capacity of *R. dominica* has not been researched thoroughly, however, *R. dominica* is capable of flight.[4] This, aside from human intervention, permits their widespread spatial distribution between isolated resources.[4] They boast an impressive flying capacity as it has been observed to fly over 5 km from an infested location. Moreover, winds and wind drift can substantially assist in dispersal.[4] The attraction to pheromones can additionally aid them to fly upwind to the pheromone sources, possibly stimulated by pheromone molecules, without which dispersal is reduced.[4]

Control

Physical

Commercial and agricultural methods are being implemented to manage infestation and pest control of *R. dominica*.[4] Approaches includes minimizing pest migration and build-up within grain storage areas, through thorough cleaning of the equipment before harvest, sealing storage, spraying bins and units, and cleaning up any grain spills.[4] Close monitoring of the temperature in storage areas is a crucial step of managing, as it can influence the insect population.[4] Harvested wheat temperatures ranging from 27 °C to 34 °C degrees is optimal for insect reproduction and growth.[4] *R. dominica* are more vulnerable to the cold than other grain pests.[4] Temperatures below 15 °C are unfavourable for *R. dominica* to maintain their bodily activities.[4] To compensate, they become dormant, but this greatly increases their susceptibility to death at temperatures of

2 °C or lower.[4] Thus, aeration or grain drying, where grain is mechanically ventilated, can also be used to manage infestation through the maintenance of low temperatures in storage areas.[4] Unfortunately, *R. dominica* cannot be completely controlled solely with aeration. Although it is recommended for quality of grains, feasible and effective in reducing insect growth rate, damage from fungi and moisture.[4]

Biological

Predation by natural enemies of *R. dominica*, arthropod species, are insufficient methods of biological control due to their low numbers as compared to fecundity of *R. dominica*.[4] Moreover, the natural predators and parasitoids can fall prey themselves to other types of organisms, which is quite disadvantageous.[4] This in tandem with their deep burrowing feature, which allows them to successfully escape predation and risk, allows for effective *R. dominica* proliferation.[4]

Chemical

Insecticide grain protectants worldwide are also ineffective for *R. dominica* management. Many of these protectants are either not effective or the pest has grown resistance to them.[4] The protectant include organophosphorus insecticides such as chlorpyrifos methyl, fenitrothion, pirimiphos methyl and malathion.[4] When infestations become severe, fumigation is a suggested form of control.[4] The fumigant phosphine is key to controlling *R. dominica* since it targets all insect life stages, is easy to utilize, effective, feasible, and is a residue-free tactic.[4] Unfortunately, due to active dispersal, *R. dominica* has distributed resistance genes to certain fumigants and insecticides.[11] Other alternatives such as the use of ozone as a fumigant is also being tested on immature stages, larvae or pupae, which are more prone to being effected as compared to adults.[12] Aside from the evolution of resistance, the internal feeding technique of *R. dominica* confers protection from potential insecticides by creating safe spaces and shelter within the grain mass.[13] Further studies suggest that fumigants are not the only method of detecting and pest management implemented in the grain industry.[4] Research shows that soft x-ray methods are also being used to identify potential infested wheat kernels.[14] Despite, all efforts to manage *R. dominica*, they remain a detrimental pest in the production of wheat, rice and pasta[14]

Gallery

Rhyzopertha dominica (Lesser Grain Borer)

The lesser grain borer, "Rhyzopertha dominica", on wheat

Rhyzopertha dominica (Lesser grain borer)

Rhyzopertha dominica from USA

External links

- Home stored product entomology

- Bugguide.net page on the lesser grain borer: https://bugguide.net/node/view/242035
- *Rhyzopertha* (http://www.faunaeur.org/full_results.php?id=101036) Fauna Europaea.

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Wikipedia

Rice weevil

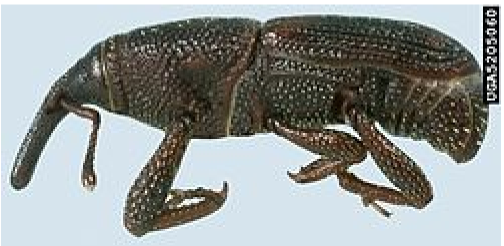
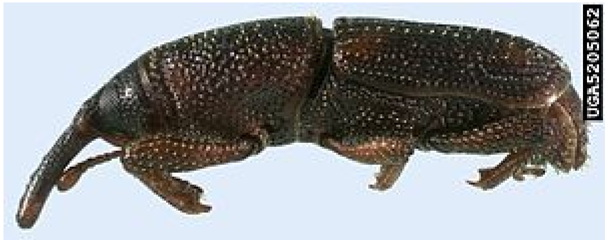
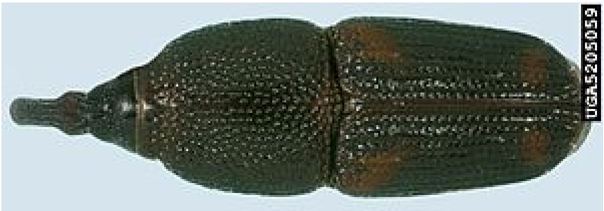
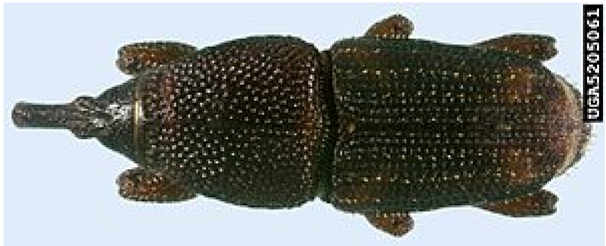
The **rice weevil** (*Sitophilus oryzae*) is a stored product pest which attacks several crops, including wheat, rice, and maize.

Rice weevil	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Curculionidae
Subfamily:	Dryophthorinae
Genus:	*Sitophilus*
Species:	***S. oryzae***
Binomial name	
Sitophilus oryzae (Linnaeus, 1763) [1]	

Contents

Description

The adults are around 2 mm long with a long snout. The body color appears to be brown/black, but on close examination, four orange/red spots are arranged in a cross on the wing covers. It is easily confused with the similar looking maize weevil, but there are several distinguishing features:[2]

Rice weevil (*S. oryzae*)	Maize weevil (*S. zeamais*) family :
	
	
Longitudinally elliptical punctures on pronotal dorsum	Circular punctures on pronotal dorsum
Pronotal punctures are separated by a flat, median, longitudinal puncture-free zone	Pronotal punctures have no median puncture-free area and are nearly equally spaced apart
Less than 20 pronotal punctures along the approximate midline, running from neck to scutellum	More than 20 pronotal punctures along the approximate midline, running from neck to scutellum
Scutellar elevations relatively closer together compare to their longitudinal length	Scutellar elevations relatively farther apart compared to their longitudinal length
Scutellar elevations extend longitudinally approximately more than halfway down the scutellum	Scutellar elevations extend longitudinally approximately halfway down the scutellum
Proepimera meets behind the fore coxae and along the posterior edge, has a distinct curved notch	Proepimera meets behind the fore coxae and has a barely discernible notch along the posterior edge at the site of the meeting point
Aedeagus (in males) is smooth and shiny on the dorsal surface	Aedeagus has two dorsal, longitudinal grooves

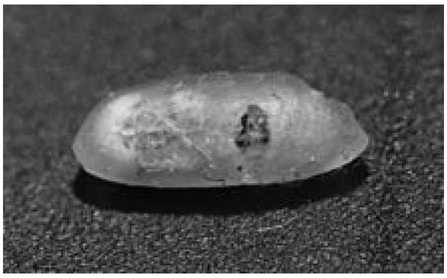
Biology

Adult rice weevils are able to fly,[3] and can live for up to two years. Females lay 2-6 eggs per day and up to 300 over their lifetime. The female uses strong mandibles to chew a hole into a grain kernel after which she deposits a single egg within the hole, sealing it with secretions from her ovipositor. The larva develops within the grain, hollowing it out while feeding. It then pupates within the grain kernel and emerges 2–4 days after eclosion.

Male *S. orzyae* produce an aggregation pheromone called sitophilure ((4S,5R)-5-Hydroxy-4-methylheptan-3-one) to which males and females are drawn. A synthetic version is available which attracts rice weevils, maize weevils and grain weevils. Females produce a pheromone which attracts only males.

Control

Control of weevils involves locating and removing all potentially infested food sources. Rice weevils in all stages of development can be killed by freezing infested food below 0 °F (-18 °C) for a period of three days, or heating to 60 °C (140 °F) for a period of 15 minutes.[4]



An adult emerges from inside a grain of rice

See also

- Granary weevil (*Sitophilus granarius*)
- Maize weevil (*Sitophilus zeamais*)

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WIKIPEDIA

Khapra beetle

The **biscuit beetle** (*Trogoderma granarium*), also called **cabinet beetle**,[1] which originated in South Asia, is one of the world's most destructive pests of grain products and seeds.[2] It is considered one of the 100 worst invasive species in the world.[3] Infestations are difficult to control because of the insect's ability to survive without food for long periods, its preference for dry conditions and low-moisture food, and its resistance to many insecticides.[3] There is a federal quarantine restricting the importation of rice into the U.S. from countries with known infestations of the beetle.[4] Khapra beetle infestation can spoil otherwise valuable trade goods and threaten significant economic losses if introduced to a new area. Handling or consuming contaminated grain and seed products can lead to health issues such as skin irritation and gastrointestinal distress.[5]

Khapra beetle	
	
Adult Khapra beetle	
	
Larvae of *Trogoderma granarium*	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Dermestidae
Genus:	*Trogoderma*
Species:	***T. granarium***
Binomial name	
Trogoderma granarium Everts, 1898	

Contents

Description

Adult beetles are brownish and reddish 1.6–3 mm long. Immature larvae are up to 5 millimeters long and are covered in dense, reddish-brown hair. The larval stage can last four to six weeks, but can be extended up to seven years.[5] Males are dark brown or black, and females are slightly larger with lighter colors.[5] The lifespan of adult Khapra beetle is usually between five and ten days.[5] The beetle prefers hot, dry conditions and can be found in areas where grain and other potential food is stored, such as pantries, malt houses, grain and fodder processing plants, and stores of used grain sacks or crates. The species is native to India, with a native range extending from Burma to Western Africa.[6] The Khapra beetle is a synanthrope, predominantly living in close association with humans. Information regarding the beetle's behavior in non-human environments is limited.[7]

The eggs of the khapra beetle are cylindrical with one end more rounded and the other more pointed, about 0.7 mm long and 0.25 mm broad, weighing about 0.02 mg.[8][5] The pointy end has a number of spine-like projections.[8] The eggs are initially a milky white but over several hours turn a pale yellowish color.[8]

The Khapra beetle's physiology is significantly impacted by its diet. Borzoi et al. found that rye provides the most optimal environment for breeding and development of individuals.[9] Conversely, walnut and rice diets reduced female fertility and adult weight of the individuals, while increasing the duration of the larval stage.[9]

As an Invasive Species

The Khapra beetle has become established in many Mediterranean, Middle Eastern, Asian and African countries.[6] It has also been discovered in North America. United States customs agents have discovered it in isolated infestations on the East and West coast of the United States, but until this point have been successful in containing and eradicating the pest.[5] US customs agents intercepted the beetle 100 times in 2011, "compared to three to six per year in 2005 and 2006, and averaging about 15 per year from 2007 to 2009".[10] In 2017, the beetle was recorded for the first time in Sri Lanka. The beetle was found in the packaging of one consignment of tea from Sri Lanka, which was transported to Russia. The Sri Lanka Tea Board expressed that the specimen may have remained in the shipping container following the use of the same container for a previous transport of grain, not of Sri Lankan origin.[11][12]

The type of product in which the beetle is transported can contribute to its ability to take hold in a new environment. Whole barley flour and cracked wheat kernels were found to support significantly more larvae and adult beetles than other grain products, whereas polished pearl barley, maize, and whole oats supported lower populations.[13]

The Khapra beetle does not present any direct ecological threats to an environment as an invasive species. Indirect effects of its introduction are of greatest concern from a human perspective. Reduced grain seed viability and loss of stored grain seeds can threaten large-scale agriculture and international trade, hence the significant focus by multiple countries on limiting its expansion.

Control Methods

Fumigation with methyl bromide is the most effective treatment.[14] Powdered neem has been used to control the beetle in wheat stores in India.[15] Neem powder repels many insects due to its strong odor, but generally does not kill insects. However, it is still useful in protecting crops from infestations.

Research into natural pest management methods has found that extracts from Datura metel leaves present significant contact toxicity and multi-generational effects to Khapra beetles.[16] Higher concentrations of extract led to higher mortality among the initial generation and subsequent offspring.[16] Prolonged exposure to extreme cold and heat have demonstrated marginal impact, but most larvae were found to have survived extremes well beyond the threshold needed to kill adult beetles.[17]

Policy & Regulation

The United States Department of Agriculture’s Animal and Plant Health Inspection Service has established restrictions on grain and cereal imports from regions known for Khapra beetle infestation since July 2011. These import regulations concern the import of rice, chickpeas, safflower seeds, and soybeans from regions determined to be infested with the Khapra beetle.[18] Any of these products shipped from regions in question must first be subject to a phytosanitary treatment, and a certificate stating the shipment has been inspected and found clean must be included with the product.[19] Many North African, Middle East, and South Asian countries, such as Afghanistan, Iran, Egypt, Syria, Morocco, Sri Lanka, and India are subject to these regulations.[20] An amendment to the Khapra beetle import regulations was passed in December 2014, adding Kuwait, Oman, Qatar, the United Arab Emirates, South Sudan, and Palestinian Authority to the list of regulated nations.[21]

Australia maintains Khapra beetle import restrictions on all types of seeds, nuts, spices, dried fruits and vegetables, and any unprocessed agricultural products.[22] Any imports of these products require a phytosanitary certificate stating the product is inspected and cleaned.[22] Countries of origin in question for this policy include much of Africa, the Middle East, and South Asia.[22]

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External links

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- Khapra beetle at Pestproducts.com (http://www.pestproducts.com/khapra-beetles.htm)
- PestTracker Invasive Insect: Khapra beetle (http://pest.ceris.purdue.edu/pest.php?code=INATANA) at Center for Environmental and Regulatory Information Systems
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- Hungry Pests Campaign (https://www.aphis.usda.gov/aphis/resources/pests-diseases/hungry-pests/the-threat/khapra-beetle/khapra-beetle), USDA APHIS (Animal and Plant Health Inspection Service)
- Species Profile - Khapra Beetle (*Trogoderma granarium*) (https://www.invasivespeciesinfo.gov/profile/khapra-beetle), National Invasive Species Information Center, United States National Agricultural Library.

Ephestia elutella

Caterpillars

Cacao moth	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Lepidoptera
Family:	Pyralidae
Tribe:	Phycitini
Genus:	*Ephestia*
Species:	***E. elutella***
Binomial name	
Ephestia elutella (Hübner, 1796)	
Synonyms	
Numerous, see text	

Ephestia elutella, the **cacao moth**, **tobacco moth** or **warehouse moth**, is a small moth of the family Pyralidae. It is probably native to Europe, but has been transported widely, even to Australia. A subspecies is *E. e. pterogrisella*.

The wingspan is 14–20 mm. This moth flies throughout the warmer months, e.g. from the end of April to October in Belgium and the Netherlands.

The caterpillars are often considered a pest, as they feed on dry plant produce, such as cocoa beans and tobacco, as well as cereals and dried fruit and nuts. Less usual foods include[1] dried-out meat and animal carcasses, specimens in insect collections, and dry wood.

This species has been known under a number of junior synonyms:[2]

- *Ephestia amarella* Dyar, 1904
- *Ephestia icosiella* Ragonot, 1888
- *Ephestia infumatella* Ragonot, 1887
- *Ephestia roxburghi* (*lapsus*)
- *Ephestia roxburghii* Gregson, 1873
- *Ephestia roxburgii* (*lapsus*)
- *Ephestia uniformata* Dufrane, 1942 (variety)
- *Homoeosoma affusella* Ragonot, 1888
- *Hyphantidium sericarium* Scott, 1859
- *Phycis angusta* (Haworth, 1811)
- *Phycis elutea* Haworth, 1811; (unjustified emendation)
- *Phycis rufa* Haworth, 1811
- *Phycis semirufa* Haworth, 1811
- *Tinea elutella* Hübner, 1796

Footnotes

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External links

- Lepidoptera of Belgium (http://webh01.ua.ac.be/vve/Checklists/Lepidoptera/Pyralidae/Eelutella.htm)
- Cacao moth on UKMoths (https://ukmoths.org.uk/show.php?id=3328)

WIKIPEDIA

Maize weevil

The **maize weevil** (*Sitophilus zeamais*), known in the United States as the **greater rice weevil,**[1][2] is a species of beetle in the family Curculionidae. It can be found in numerous tropical areas around the world, and in the United States, and is a major pest of maize.[3] This species attacks both standing crops and stored cereal products, including wheat, rice, sorghum,[4][5][6] oats, barley, rye, buckwheat,[6] peas, and cottonseed. The maize weevil also infests other types of stored, processed cereal products such as pasta, cassava,[5] and various coarse, milled grains. It has even been known to attack fruit while in storage, such as apples.[7]

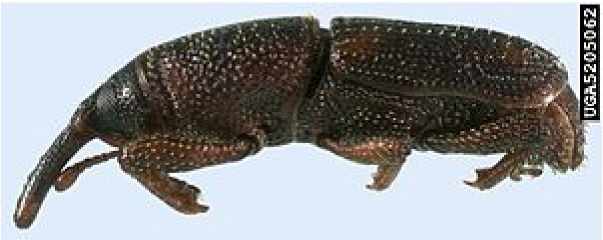
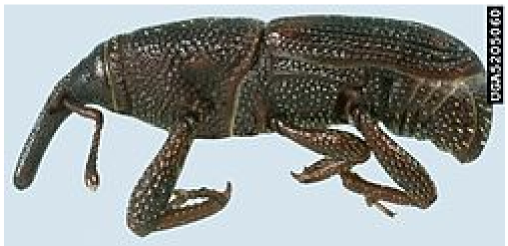
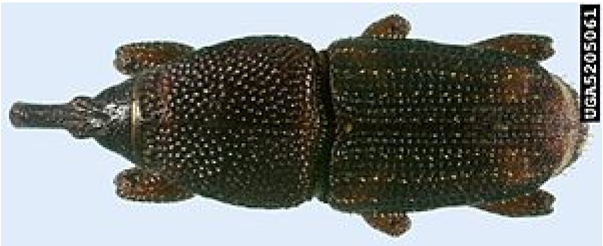
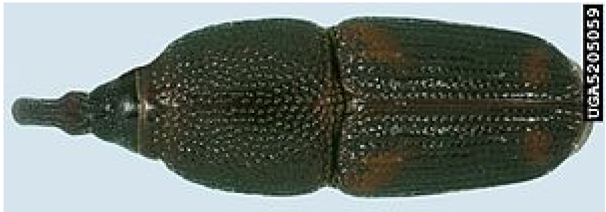
Maize weevil	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Curculionidae
Subfamily:	Dryophthorinae
Genus:	*Sitophilus*
Species:	***S. zeamais***
Binomial name	
Sitophilus zeamais (Motschulsky), 1855	

Contents

Description

A close relative of the rice weevil,[6] the maize weevil has a length of 2.5 mm to 4 mm.[1][2] This small, brown weevil has four reddish-brown spots on the wing covers (elytra). It has a long, thin snout, and elbowed antennae.[6] *Sitophilus zeamais* appears similar to the rice weevil (*Sitophilus oryzae*), but has more clearly marked spots on the wing covers, and is somewhat larger.[2] It is able to fly.[6]

Although the maize weevil and rice weevil do look alike, and are easily confused with one another, there are several distinguishing features:[7]

Maize weevil (*S. zeamais*)	**Rice weevil (*S. oryzae*)**
	
	
Circular punctures on pronotal dorsum	Longitudinally elliptical punctures on pronotal dorsum
Pronotal punctures have no median puncture-free area and are nearly equally spaced apart	Pronotal punctures are separated by a flat, median, longitudinal puncture-free zone
More than 20 pronotal punctures along the approximate midline, running from neck to scutellum	Less than 20 pronotal punctures along the approximate midline, running from neck to scutellum
Scutellar elevations relatively farther apart compared to their longitudinal length	Scutellar elevations relatively closer together compare to their longitudinal length
Scutellar elevations extend longitudinally approximately halfway down the scutellum	Scutellar elevations extend longitudinally approximately more than halfway down the scutellum
Proepimera meets behind the forecasting coxae and has a barely discernible notch along the posterior edge at the site of the meeting point	Proepimera meets behind the fore coxae and along the posterior edge, has a distinct curved notch
Aedeagus has two dorsal, longitudinal grooves	Aedeagus (in males) is smooth and shiny on the dorsal surface

Distribution

S. zeamais occurs throughout warm, humid regions around the world, especially in locations where maize is grown,[2] including: Polynesia, Argentina, Brazil, Burma, Cambodia, Greece, Japan, Morocco, Spain, Syria, Turkey, United States, USSR, Sub Saharan Africa and Yugoslavia. It is also widely distributed throughout agricultural areas of northern Australia.[7] This species has also been recorded in Canada, in the provinces of Ontario and Quebec,[6] and has been intercepted at ports, but is not well established there. It has, however, been present for several years in Montreal, where grain from the U.S. is stored.[8]

Life cycle

The complete development time for the life cycle of this species averages 36 days.[7] The female chews through the surface of the grain, creating a hole. She then deposits a small oval white egg, and covers the hole as the ovipositor is removed, with a waxy secretion that creates a plug.[6] The plug quickly hardens, and leaves a small raised area on the seed surface. This provides the only visible evidence that the kernel is infested.[7] Only one egg is laid inside each grain. When the egg hatches into a white, legless grub, it will remain inside and begin feeding on the grain. The larvae will pupate while inside, then chew a circular exit hole,[1] and emerge as an adult beetle. A single female may lay 300 to 400 eggs during her lifetime. Adults can live for 5 to 8 months.[2] Breeding conditions require temperatures between 15 and 34 °C and40% relative humidity.

When the adults emerge, the females move to a high surface and release sex pheromones. Males are then attracted to this pheromone.[7]

Host range

The maize weevil commonly attacks standing crops, in particular, maize before harvest, and is also commonly associated with rice. It infests raw or processed cereals such as wheat, oats, barley, sorghum, rye and buckwheat. It can breed in crops with a moisture content of a much wider range than *S. oryzae*, and has been found in fruit, such as apples during storage. Although the maize weevil cannot readily breed in finely processed grains, it can easily breed in products such as macaroni and noodles, and milled cereals that have been exposed to excessive moisture.[7]

Damage and detection

Early detection of infestation is difficult. As *S. zeamais* larvae feed on the interior of individual grains, often leaving only the hulls, a flour-like grain dust, mixed with frass is evident. Infested grains contain holes through which adults have emerged. A possible indication of infestation is grain, when placed in water, floating to the surface.[7] Ragged holes in individual grains, similar to damage caused by the rice weevil and granary weevil, may indicate infestation.[6] In large stores of grain, an increase in temperature may be detected. The most obvious sign of infestation is the emergence of adults. One study recorded, 5 weeks after infestation, the emergence of 100 adults per kg per day.[1]

Maize damaged by maize weevil larvae

See also

- Granary weevil, also known as the wheat weevil (*S. granarius*)
- Rice weevil (*S. oryzae*)
- Home stored product entomology
- Invasive species
- List of common household pests
- Pest control

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External links

- Images (http://www.invasive.org/search/action.cfm?q=Sitophilus%20zeamais)
- USDA study on temperature management of the maize weevil (http://ddr.nal.usda.gov/bitstream/10113/13133/1/IND20551576.pdf)
- USDA study on contest behaviour of maize weevil larvae when competing within seeds (http://www.ars.usda.gov/sp2userfiles/place/54300530/pdf/1081_AnBe_79.281.pdf)
- African Journal of Biotechnology: Laboratory evaluation of four medicinal plants as protectants against the maize weevil (http://ajol.info/index.php/ajb/article/viewFile/55935/44391)

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Migratory locust

The **migratory locust** (*Locusta migratoria*) is the most widespread locust species, and the only species in the genus *Locusta*. It occurs throughout Africa, Asia, Australia and New Zealand. It used to be common in Europe but has now become rare there. Because of the vast geographic area it occupies, which comprises many different ecological zones, numerous subspecies have been described. However, not all experts agree on the validity of some of these subspecies.

Many other species of grasshopper with gregarious and possibly migratory behaviour are referred to as 'locusts' in the vernacular, including the widely distributed desert locust.

At 6.5 Gbp,[1] the migratory locust possesses the largest known insect genome.[2]

Migratory locust

Female migratory locust

Conservation status

Least Concern (IUCN 3.1)

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Orthoptera
Suborder:	Caelifera
Family:	Acrididae
Subfamily:	Oedipodinae
Genus:	*Locusta* Linnaeus, 1758
Species:	***L. migratoria***

Binomial name

Locusta migratoria
(Linnaeus, 1758)

Synonyms

- *Acridium migratorium*
- *Acridium plorans*

Contents

Polyphenism

The migratory locust is polyphenic. It transitions between two main phenotypes in response to population density; the solitary phase and the gregarious phase. As the density of the population increases the locust transforms progressively from the solitary phase towards the gregarious phase with intermediate phases:

> Solitaire = solitary phase → transiens congregans (intermediate form) → gregarious phase → transiens dissocians (intermediate form) → solitaire = solitary phase.

Pigmentation and size of the migratory locust vary according to its phase (gregarious or solitary form) and its age. Gregarious larvae have a yellow to orange covering with black spots; solitary larvae are green or brown. The gregarious adult is brownish with yellow, the latter colour becoming more intense and extensive on maturation. The solitary adult is brown with varying extent of green colour depending on the colour of the vegetation. Gregarious adults vary in size between 40 and 60 mm according to the sex; they are smaller than the solitary adults.

- *Pachytylus australis* (Saussure, 1884)
- *Pachytylus migratorius* (Linnaeus, 1758)
- *Pachytylus migratorioides* (Fairmaire & L.J. Reiche, 1849)

Relationship with humans

Economic impact

Adult female (top), adult male (bottom left), fifth instar nymph (bottom right)

Locusts are highly mobile, and usually fly with the wind at a speed of about 15 to 20 kilometres per hour (9.3 to 12.4 mph). Swarms can travel 5 to 130 km or more in a day. Locust swarms can vary from less than one square kilometre to several hundred square kilometres with 40 to 80 million individuals per square kilometre. An adult locust can consume its own weight (several grams) in fresh food per day. For every million locusts, one ton of food is eaten.

In Africa, the last serious widespread plague of *L. m. migratorioides* occurred from 1928 to 1942. Since then, environmental transformations have made the development of swarms from the African migratory locust unlikely. Nevertheless, potential outbreaks are constantly monitored as plagues can be devastating. The Malagasy migratory locust (*L. m. capito*) still regularly swarms (roughly twice every ten years). The desert locust, which is very similar to the African migratory locust, remains a major threat too.

Locust survey and control are primarily the responsibility of the Ministry of Agriculture in locust-affected countries and are operations undertaken by national locust units. The Food and Agriculture Organization (FAO) of the United Nations provides information on the general locust situation to all interested countries and gives warnings and forecasts to those countries in danger of invasion.

As food / edibility

The migratory locust is an edible insect.[3][4] In Europe, the migratory locust is officially approved for the use in food in Switzerland (since May 2017).[5]

Subspecies of *Locusta migratoria*

L. migratoria is found over a vast geographic area, and its range covers many different ecological zones. Because of this, numerous subspecies have been described; however, not all experts agree on the validity of some of these subspecies.[6]

- *L. m. burmana* Ramme, 1951
- *L. m. capito* Saussure, 1884 (Malagasy migratory locust: Madagascar)
- *L. m. cinerascens* Fabricius, 1781 (Italy, Spain)
- *L. m. manilensis* (Meyen, 1835) 1 (eastern Asia)
- *L. m. migratoria* (Linnaeus, 1758) (Eurasian migratory locust: West and Central Asia, eastern Europe)
- *L. m. migratorioides* (Fairmaire & L.J. Reiche, 1849) (African migratory locust: Africa and Atlantic islands)

- *L. m. tibetensis* Chen, Yonglin, 1963
- *L. m. danica* (Linnaeus, 1767) = *L. m. migratoria* (Linnaeus, 1758)
- *L. m. gallica* Remaudičre, 1947 = *L. m. migratoria* (Linnaeus, 1758)
- *L. m. solitaria* Carthy, 1955 = *L. m. migratoria* (Linnaeus, 1758)

L. m. migratorioides female (solitary)

Other species called 'locusts'

Other species of Orthoptera that display gregarious and migratory behaviour are called 'locusts'.

- American locust, *Schistocerca americana*
- Australian plague locust, *Chortoicetes terminifera*
- Bombay locust, *Nomadacris succincta*
- Brown locust, *Locustana pardalina*
- Desert locust, *Schistocerca gregaria*
- Egyptian locust, *Anacridium aegyptium*
- Italian locust, *Calliptamus italicus*
- Moroccan locust, *Dociostaurus maroccanus*
- Red locust, *Nomadacris septemfasciata*
- Rocky Mountain locust, *Melanoplus spretus* – extinct
- Sahelian tree locusts, *Anacridium melanorhodon*
- Spur-throated locust, *Austracris guttulosa* (note: "spur-throated grasshoppers/locusts" may also refer to spp. in other genera)
- Sudan plague locust, *Aiolopus simulatrix*

The Senegalese grasshopper (*Oedaleus senegalensis*) also often displays locust-like behaviour in the Sahel region.

L. m. migratorioides male (solitary)

Photos

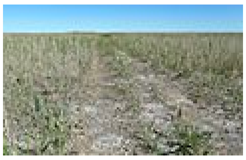
First instar nymph (gregarious)

Second and fourth instar nymphs (gregarious)

Third instar nymphs (gregarious)

Fourth instar nymph (gregarious)

Part of a hopper band in Kazakhstan



Hopper band in Kazakhstan

See also

- 2004 locust outbreak
- 2013 Madagascar locust infestation
- Australian Plague Locust Commission (APLC)

Footnotes

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Colorado potato beetle

The **Colorado potato beetle** (*Leptinotarsa decemlineata*), also known as the **Colorado beetle**, the **ten-striped spearman**, the **ten-lined potato beetle** or the **potato bug**, is a major pest of potato crops. It is approximately 10 millimetres (0.39 in) long, with a bright yellow/orange body and five bold brown stripes along the length of each of its elytra. Native to America, it spread rapidly in potato crops across America and then Europe from 1859 onwards.

Colorado potato beetle

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Chrysomelidae
Genus:	*Leptinotarsa*
Species:	***L. decemlineata***

Binomial name

Leptinotarsa decemlineata
Say, 1824[1]

Synonyms[2]

- *Doryphora decemlineata* Say, 1824
- *Stilodes decemlineata*

Contents

Taxonomy

The Colorado potato beetle was first observed in 1811 by Thomas Nuttall and was formally described in 1824 by the American entomologist Thomas Say.[3] The beetles were collected in the Rocky Mountains where they were feeding on the buffalo bur, *Solanum rostratum*.[4] The genus *Leptinotarsa* is assigned to the chrysolmelid beetle tribe *Doryphorini* (located in subfamily Chrysomelinae), which it shares with five other *genera*: *Doryphora*, *Calligrapha*, *Labidomera*, *Proseicela*, and *Zygogramma*.[5]

Description

Adult beetles average 6–11 millimetres (0.24–0.43 in) in length and 3 millimetres (0.12 in) in width. The beetles are orange-yellow in colour with ten characteristic black stripes on the elytra. The species name *decemlineata*, meaning 'ten-lined', derives from this feature.[4][6] Adult beetles may, however, be visually confused with *L. juncta*, the false potato beetle, which is not an agricultural pest. *L. juncta* also has alternating black and white strips on its back, but one of the white strips in the center of each wing cover is missing and replaced by a light brown strip.[7]

Leptinotarsa decemlineata adult specimen

The orange-pink larvae have a large, nine segmented, abdomen and black head, prominent spiracles and may measure up to 15 millimetres (0.59 in) in length in their final instar stage. The beetle larva has four instar stages. The head remains black throughout these stages, but the pronotum changes colour from black in first- and second-instar larvae to having an orange-brown edge in its third-instar. In fourth-instar larvae, about half the pronotum is coloured light brown.[4][8] This tribe is characterised within the subfamily by round to oval shaped convex bodies which are usually brightly coloured, simple claws which separate at the base, open cavities behind the procoxae, and a variable apicial segment of the maxillary palp.[9][6]

Distribution

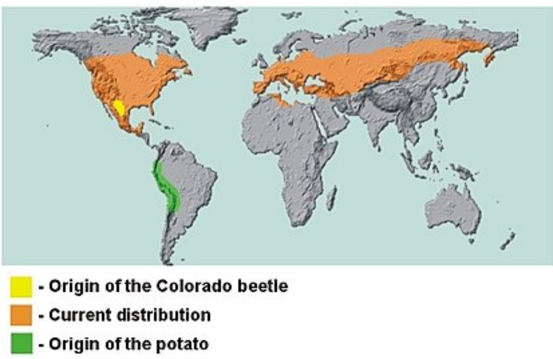
The beetle is native to North America, and is present in every state and province except Alaska, California, Hawaii, and Nevada.[4] It now has a wide distribution across Europe and Asia,[10] totalling over 16 million km^2.[11]

Its first association with the potato plant (*Solanum tuberosum*) was not made until about 1859 when it began destroying potato crops in the region of Omaha, Nebraska. Its spread eastward was rapid, at an average distance of 140 km per year.[12] By 1874 it had reached the Atlantic Coast.[4] From 1871, the American entomologist Charles Valentine Riley warned Europeans about the potential for an accidental infestation caused by the transportation of the beetle from America.[12] From 1875, several western European countries, including Germany, Belgium, France and Switzerland, banned imports of American potatoes to avoid infestation by *L. decemlineata*.[13]

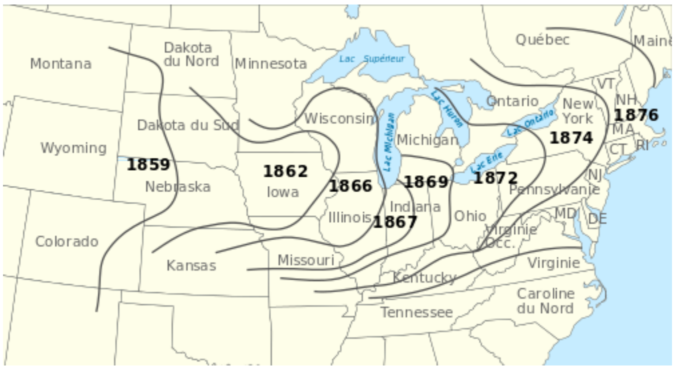
These controls proved ineffective as the beetle soon reached Europe. In 1877, *L. decemlineata* reached the United Kingdom and was first recorded from Liverpool docks, but it did not become established. There have been many further outbreaks: the species has been eradicated in the UK at least 163 times. The last major outbreak was in 1976. It remains as a notifiable quarantine pest in the United Kingdom and is monitored by DEFRA to prevent it from becoming established.[14] A cost-benefit analysis from 1981 suggested that the cost of the measures used to exclude *L. decemlineata* from the UK was less than the likely costs of control if it became established.[15]

Elsewhere in Europe, the beetle became established near USA military bases in Bordeaux during or immediately following World War I and had proceeded to spread by the beginning of World War II to Belgium, the Netherlands and Spain. The population increased dramatically during and immediately following World War II and spread eastward, and the beetle is now found over much of the continent. After World War II, in the Soviet occupation zone of Germany, almost half of all potato fields were infested by the beetle by 1950. In East Germany they were known as *Amikäfer* ('Yankee beetles') following a governmental claim that the beetles were dropped by American planes. In the EU it remains a regulated (quarantine) pest for the UK, Republic of Ireland, Balearic Islands, Cyprus, Malta and southern parts of Sweden and Finland. It is not established in any of these Member States, but occasional infestations can occur when, for example, wind blows adults from Russia to Finland.[16][17]

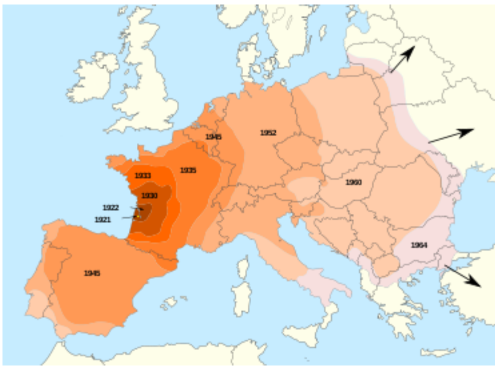
The beetle has the potential to spread to temperate areas of East Asia, India, South America, Africa, New Zealand, and Australia.[18]



Native range of the potato and native and current range of the Colorado beetle.



Expansion of the Colorado potato beetle's range in North America, 1859–1876.



Expansion of the Colorado potato beetle's range in Europe, 1921–1964.

Lifecycle

Colorado potato beetle females are very prolific and are capable of laying over 500 eggs in a 4- to 5-week period.[19] The eggs are yellow to orange, and are about 1 mm (0.039 in) long. They are usually deposited in batches of about 30 on the underside of host leaves. Development of all life stages depends on temperature. After 4–15 days, the eggs hatch into reddish-brown larvae with humped backs and two rows of dark brown spots on either side. They feed on the leaves of their host plant. Larvae progress through four distinct growth stages (instars). First instars measure approximately 1.50 mm (0.059 in) long, and the last (fourth) instars measure 8 mm (0.31 in) in length. The first through third instars each last about 2–3 days duration; the fourth lasts 4–7 days. Upon reaching full size, each fourth instar spends several days as a nonfeeding prepupa, which can be recognized by its inactivity and lighter coloration. The prepupae drop to the soil and burrow to a depth of several inches, then pupate.[4] In 5 to 10 days, the adult beetle emerges to feed and mate. This beetle can thus go from egg to adult in as little as 21 days.[19] Depending on temperature, light conditions, and host quality, the adults may enter diapause and delay emergence until spring. They then return to their host plants to mate and feed; overwintering adults may begin mating within 24 hours of spring emergence.[20] In some locations, three or more generations may occur each growing season.[4]

Eggs laid on the underside of a leaf

First-instar larva after hatching

Early (3rd) instar stage of larvae

Late (4th) instar stage of larva, before pupation

Pupa

Adult beetle after emergence

Mating adult beetles

Behavior and ecology

Diet

L. decemlineata has a strong association with plants in the family Solanaceae, particularly those of the genus *Solanum*. It is directly associated with *Solanum cornutum* (buffalo-bur), *Solanum nigrum* (black nightshade), *Solanum melongena* (eggplant or aubergine), *Solanum dulcamara* (bittersweet nightshade), *Solanum luteum* (hairy nightshade), *Solanum tuberosum* (potato), and *Solanum elaeagnifolium* (silverleaf nightshade). They are also associated with other plants in this family, namely the species *Solanum lycopersicum* (tomato) and the genus *Capsicum* (pepper).[21]

Predators

Coleomegilla maculata preying upon Colorado beetle eggs

At least 13 insect genera, three spider families, one phalangid (Opiliones), and one mite have been recorded as either generalist or specialized predators of the varying stages of *L. decemlineata*. These include the ground beetle *Lebia grandis*, the Coccinellid beetles *Coleomegilla maculata* and *Hippodamia convergens*, the shield bugs *Perillus bioculatus* and *Podisus maculiventris*, as well as various species of the lacewing genus *Chrysopa*, the wasp genus *Polistes*, and the damsel bug genus *Nabis*.[22]

The predatory ground beetle *L. grandis* is a predator of both the eggs and larvae of *L. decemlineata*, and its larvae are parasitoids of the pupae. An adult *L. grandis* may consume up to 23 eggs or 3.3 larvae in a single day.[23]

In a laboratory experiment, *Podisus maculiventris* was used as a predatory threat to female *L. decemlineata* specimens, resulting in the production of unviable trophic eggs alongside viable ones; this response to a predator ensured that additional food was available for newly hatched offspring in order to increase their survival rate. The same experiment also demonstrated the cannibalism of unhatched eggs by newly hatched *L. decemlineata* larvae as an anti-predator response.[24]

Examples of parasitoids, predators, and pathogens of different life stages of *Leptinotarsa decemlineata* [1]

Type	Species	Order	Predates	Location	Reference
Parasitoid	*Chrysomelobia labidomerae*	Acari	Adults	USA, Mexico	[25]
	Edovum puttleri	Hymenoptera	Eggs	USA, Mexico, Colombia	[26]
	Anaphes flavipes	Hymenoptera	Eggs	USA	
	Myiopharus aberrans	Diptera	Eggs	USA	
	Myiopharus doryphorae	Diptera	Larvae	USA, Canada	
	Meigenia mutabilis	Diptera	Larvae	Russia	
	Megaselia rufipes	Diptera	Adults	Germany	
	Heterorhabditis bacteriophora	Nematoda	Adults	Cosmopolitan	[27]
	Heterorhabditis heliothidis	Nematoda	Adults	Cosmopolitan	
Predator	*Lebia grandis*	Coleoptera	Eggs, Larvae, Adults	USA	
	Hippodamia convergens	Coleoptera	Eggs, Larvae	USA, Mexico	
	Euthyrhynchus floridanus	Hemiptera	Larvae	USA	[28]
	Oplomus dichrous	Hemiptera	Eggs, Larvae	USA, Mexico	[29]
	Perillus bioculatus	Hemiptera	Eggs, Larvae, Adults	USA, Mexico, Canada	[30]
	Podisus maculiventris	Hemiptera	Larvae	USA	[31]
	Pselliopus cinctus	Hemiptera	Larvae	USA	
	Sinea diadema	Hemiptera	Larvae	USA	
	Stiretrus anchorago	Hemiptera	Larvae	USA, Mexico	
Pathogen	*Bacillus thuringiensis* subsp. *tenebrionis*	Bacteria	Larvae	USA, Canada, Europe	
	Photorhabdus luminescens	Bacteria	Adults, Larvae	Cosmopolitan	[32]
	Spiroplasma	Bacteria	Adults, Larvae	North America, Europe	[33]
	Beauveria bassiana	Hypocreales	Adults, Larvae	USA	[34]

As an agricultural pest

Potato crop pest

In about 1840, *L. decemlineata* adopted the cultivated potato into its host range and it rapidly became a most destructive pest of potato crops. They are today considered to be the most important insect defoliator of potatoes.[18] They may also cause considerable damage to tomato and eggplant crops with both adults and larvae feeding on the plant's foliage. Larvae may defoliate potato plants resulting in yield losses of up to 100% if the damage occurs prior to tuber formation.[35] Larvae may consume 40 cm^2 of potato leaves during the entire larval stage, but adults are capable of consuming 10 cm^2 of foliage per day.[36]

The economic cost of insecticide resistance is significant, but published data on the subject is minimal.[37] In 1994, total costs of the insecticide and crop losses in the US state of Michigan were $13.3 million, representing 13.7% of the total value of the crop. The estimate of the cost implication of insecticides and crop losses per hectare is $138–368. Long-term increased cost to the Michigan potato industry caused by insecticide resistance in Colorado potato beetle was estimated at $0.9 to $1.4 million each year.[38]

Play media

Dutch newsreel from 1947

Insecticidal management

The large scale use of insecticides in agricultural crops effectively controlled the pest until it became resistant to DDT in 1952 and dieldrin in 1958.[39] Insecticides remain the main method of pest control on commercial farms. However, many chemicals are often unsuccessful when used against this pest because of the beetle's ability to rapidly develop insecticide resistance. Different populations in different geographic regions have, between them, developed resistance to all major classes of insecticide,[40][41] although not every population is resistant to every chemical.[40] The species as a whole has evolved resistance to 56 different chemical insecticides.[42] The mechanisms used include improved metabolism of the chemicals, reduced sensitivity of target sites, less penetration and greater excretion of the pesticides, as well as some changes in the behavior of the beetles.[40]

Examples of insecticides available for the control of Colorado potato beetle on different crops in Kentucky, USA.[19]

Insecticide class	Common examples	Potato	Eggplant	Tomato	Notes
Organophosphates	phosmet	X			on US Emergency Planning List of Extremely Hazardous Substances
	disulfoton	X		X	Usage restricted by US government; manufacturer Bayer exited US market 2009
Carbamates	carbaryl	X	X	X	Widely used in US
	carbofuran	X			One of the most toxic carbamates
Chlorinated hydrocarbons	methoxychlor	X		X	Banned in EU 2002, in USA 2003
(Cycloldienes)	endosulfan	X	X	X	Acutely toxic, bioaccumulates, endocrine disruptor. Global ban 2012 with exemptions until 2017
Insect growth regulator	azadirachtin	X	X	X	
Spinosin	spinosad		X	X	
Avermectin	abamectin	X		X	

Non-pesticidal management

Bacterial insecticides can be effective if application is targeted towards the vulnerable early-instar larvae. Two strains of the bacterium *Bacillus thuringiensis* produce toxins which kill the larvae.[35] Other forms of pest control, through non-pesticidal management are available. Feeding can be inhibited by applying antifeedants, such as fungicides or products derived from Neem

(*Azadirachta indica*), but these may have negative effects on the plants as well.[35] The steam distillate of fresh leaves and flowers of tansy (*Tanacetum vulgare*) contains high levels of camphor and umbellulone and these chemicals are strongly repellent to *L. decemlineata*.[43]

East German Young Pioneers collecting beetles during the war against the potato beetle

Beauveria bassiana (Hyphomycetes) is a pathogenic fungus that infects a wide range of insect species, including the Colorado potato beetle.[44] It has shown to be particularly effective as a biological pesticide for *L. decemlineata* when used in combination with the bacterium *Bacillus thuringiensis*.[45]

Crop rotation is, however, the most important cultural control of *L. decemlineata*.[18] Rotation may delay the infestation of potatoes and can reduce the build-up of early season beetle populations because the adults emerging from diapause can only disperse to new food sources by walking.[35] One 1984 study showed that rotating potatoes with non-host plants reduced the density of early season adults by 95.8%.[46]

Other cultural controls may be used in combination with crop rotation: Mulching the potato crop with straw early in the growing season may reduce the beetle's ability to locate potato fields, and the mulch creates an environment that favours beetle's predators; Plastic-lined trenches have been used as pitfall traps to catch the beetles as they move toward a field of potatoes in the spring, exploiting their inability to fly immediately after emergence; Flamethrowers may also be used to kill the beetles when they are visible at the top of the plant's foliage.[47]

Relationship with humans

Cold War villain

During the Cold War it was claimed by some countries in the Warsaw Pact that the beetles had been introduced by the CIA in an attempt to reduce food security by destroying the agriculture of the Soviet Union.[48] A widespread campaign was launched against the beetles; posters were put up and school children were mobilized to gather the pests and drown them in benzene or spirit.[48]

Philately

L. decemlineata is an iconic species and has been used as an image on stamps because of its association with the recent history of both North America and Europe. For example, in 1956, Romania issued a set of four stamps calling attention to the campaign against insect pests[50] and it was featured on a 1967 stamp issued in Austria.[51] The beetle also appeared on stamps issued in Benin, Tanzania, the United Arab Emirates, and Mozambique.[52]

Statue of the Colorado potato beetle in Hédervár, Hungary. It marks the discovery of the beetle at the site in 1947 during the rapid spread of the pest in Europe throughout the 20th century.[49]

In popular culture

During the 2014 pro-Russian unrest in Ukraine, the word *kolorady*, from the Ukrainian and Russian term for Colorado beetle, (Ukrainian: жук колорадський, Russian: колорадский жук) gained popularity among Ukrainians as a derogatory term to describe pro-Russian separatists in the

Donetsk and Luhansk Oblasts (provinces) of Eastern Ukraine. The nickname reflects the similarity of black and orange stripes on so-called St. George's ribbons worn by many of the separatists.[53]

Notes

1. ^ For a more comprehensive list of natural predators, pathogens and parasitoids, see here (http://www.cabi.org/isc/datasheet/30380).

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Boll weevil

The **boll weevil** (*Anthonomus grandis*) is a beetle which feeds on cotton buds and flowers. Thought to be native to Central Mexico,[1] it migrated into the United States from Mexico in the late 19th century and had infested all U.S. cotton-growing areas by the 1920s, devastating the industry and the people working in the American South. During the late 20th century, it became a serious pest in South America as well. Since 1978, the Boll Weevil Eradication Program in the U.S. allowed full-scale cultivation to resume in many regions.

Boll weevil	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Curculionidae
Subfamily:	Curculioninae
Tribe:	Anthonomini
Genus:	*Anthonomus*
Species:	***A. grandis***
Binomial name	
Anthonomus grandis Boheman, 1843	

Contents

Description

The adult insect has a long snout, is grayish color, and is usually less than 6 mm long.

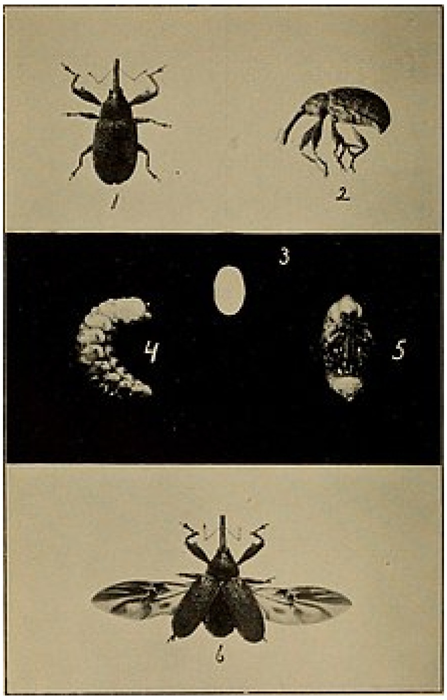
Lifecycle

Adult weevils overwinter in well-drained areas in or near cotton fields, and farms after diapause. They emerge and enter cotton fields from early spring through midsummer, with peak emergence in late spring, and feed on immature cotton bolls.

The boll weevil lays its eggs inside buds and ripening bolls (fruits) of the cotton plants. The female can lay up to 200 eggs over a 10- to 12-day period. The oviposition leaves wounds on the exterior of the flower bud. The eggs hatch in 3 to 5 days within the cotton squares (larger buds before flowering), feed for 8 to 10 days, and finally pupate. The pupal stage lasts another 5 to 7 days. The lifecycle from egg to adult spans about three weeks during the summer. Under optimal conditions, 8 to 10 generations per season may occur.

Boll weevils begin to die at temperatures at or below −5 °C (23 °F). Research at the University of Missouri indicates they cannot survive more than an hour at −15 °C (5 °F). The insulation offered by leaf litter, crop residues, and snow may enable the beetle to survive when air temperatures drop to these levels.

Other limitations on boll weevil populations include extreme heat and drought. Its natural predators include fire ants, insects, spiders, birds, and a parasitic wasp, *Catolaccus grandis*. The insects sometimes emerge from diapause before cotton buds are available.



1) Back view of adult; 2) side view of adult; 3) egg; 4) side view of larva; 5) ventral view of pupa; 6) adult, with wings spread

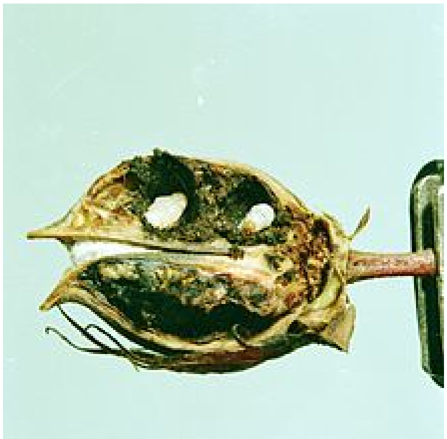
Infestation

The insect crossed the Rio Grande near Brownsville, Texas, to enter the United States from Mexico in 1892[2] and reached southeastern Alabama in 1909. By the mid-1920s, it had entered all cotton-growing regions in the U.S., travelling 40 to 160 miles per year. It remains the most destructive cotton pest in North America. Since the boll weevil entered the United States, it has cost U.S. cotton producers about $13 billion, and in recent times about $300 million per year.[2]

The boll weevil contributed to the economic woes of Southern farmers during the 1920s, a situation exacerbated by the Great Depression in the 1930s.

The boll weevil appeared in Venezuela in 1949 and in Colombia in 1950.[3] The Amazon Rainforest was thought to present a barrier to its further spread, but it was detected in Brazil in 1983, and an estimated 90% of the cotton farms in Brazil are now infested. During the 1990s, the weevil spread to Paraguay and Argentina. The International Cotton Advisory Committee has proposed a control program similar to that used in the U.S.[3]

Control


Cotton boll with weevil larvae.

During early years of the weevil's presence, growers sought relatively warm soils and early-ripening cultivars. Following World War II, the development of new pesticides such as DDT enabled U.S. farmers again to grow cotton as an economic crop. DDT was initially extremely effective, but U.S. weevil populations developed resistance by the mid-1950s.[4] Methyl parathion, malathion, and pyrethroids were subsequently used, but environmental and resistance concerns arose as they had with DDT, and control strategies changed.[4]

While many control methods have been investigated since the boll weevil entered the United States, insecticides have always remained the main control methods. In the 1980s, entomologists at Texas A&M University pointed to the spread of another invasive pest, the red imported fire ant, as a factor in the weevils' population decline in some areas.[5]

Other avenues of control that have been explored include weevil-resistant strains of cotton,[6] the parasitic wasp *Catolaccus grandis*,[7] the fungus *Beauveria bassiana*,[8] and the Chilo iridescent virus. Genetically engineered Bt cotton is not protected from the boll weevil.[9]

Although it was possible to control the boll weevil, to do so was costly in terms of insecticide costs. The goal of many cotton entomologists was to eventually eradicate the pest from U.S. cotton. In 1978, a large-scale test was begun in eastern North Carolina and in Southampton County, Virginia, to determine the feasibility of eradication. Based on the success of this test, area-wide programs were begun in the 1980s to eradicate the insect from whole regions. These are based on cooperative effort by all growers together with the assistance of the Animal and Plant Health Inspection Service of the United States Department of Agriculture (USDA).

The program has been successful in eradicating boll weevils from all cotton-growing states with the exception of Texas, and most of this state is free of boll weevils. Problems along the southern border with Mexico have delayed eradication in the extreme southern portions of this state. Follow-up programs are in place in all cotton-growing states to prevent the reintroduction of the pest. These monitoring programs rely on pheromone-baited traps for detection. The boll weevil eradication program, although slow and costly, has paid off for cotton growers in reduced pesticide costs. This program and the screwworm program of the 1950s are among the biggest and most successful insect control programs in history.[10]

Adult on a cotton boll

"Beat the boll weevil..." (U.S. Food Administration, Educational div., Advertising section, 1918-1919)

Eradication map (USDA, 2006)

Impact

The Library of Congress American Memory Project contains a number of oral history materials on the boll weevil's impact.[11]

A 2009 study found "that as the weevil traversed the American South [in the period 1892-1932], it seriously disrupted local economies, significantly reduced the value of land (at this time still the most important asset in the American South), and triggered substantial intraregional population movements."[12] A 2018 National Bureau of Economic Research paper found that the boll weevil spread between 1892 to 1922 had a beneficial impact on educational outcomes, as children were less likely to work on cultivating cotton.[13]

The boll weevil plaque in Enterprise, Alabama

The boll weevil infestation has been credited with bringing about economic diversification in the Southern US, including the expansion of peanut cropping. The citizens of Enterprise, Alabama, erected the Boll Weevil Monument in 1919, perceiving that their economy had been overly dependent on cotton, and that mixed farming and manufacturing were better alternatives.

The boll weevil is the mascot for the University of Arkansas at Monticello and is listed on several "silliest" or "weirdest" mascots of all time.[14][15] It was also the mascot of a short-lived minor league baseball team, the Temple Boll Weevils, which were alternatively called the "Cotton Bugs."

"Boll Weevil" is a traditional blues song which reached #2 on the Billboard chart in 1961.

In the original 1980s *Transformers* cartoon series, Decepticon character Bombshell's alternative form is loosely based on the boll weevil.

See also

- *Lixus concavus*, the rhubarb curculio weevil
- Female sperm storage

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Japanese beetle

The **Japanese beetle** (*Popillia japonica*) is a species of scarab beetle. The adult measures 15 mm (0.6 in) in length and 10 mm (0.4 in) in width, has iridescent copper-colored elytra and a green thorax and head. It is not very destructive in Japan, where it is controlled by natural predators, but in North America, it is a noted pest of about 300 species of plants including rose bushes, grapes, hops, canna, crape myrtles, birch trees, linden trees, and others.

The adult beetles damage plants by skeletonizing the foliage, that is, consuming only the leaf material between the veins, and may also feed on fruit on the plants if present, while the subterranean larvae feed on the roots of grasses.

Japanese beetle

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Scarabaeidae
Genus:	*Popillia*
Species:	***P. japonica***

Binomial name

Popillia japonica

Newman, 1841

Contents

Description

Adult *P. japonica* measure 15 mm (0.6 in) in length and 10 mm (0.4 in) in width, with iridescent copper-colored elytra and green thorax and head. A row of white tufts (spots) of hair project from under the wing covers on each side of the body.[1]

Distribution

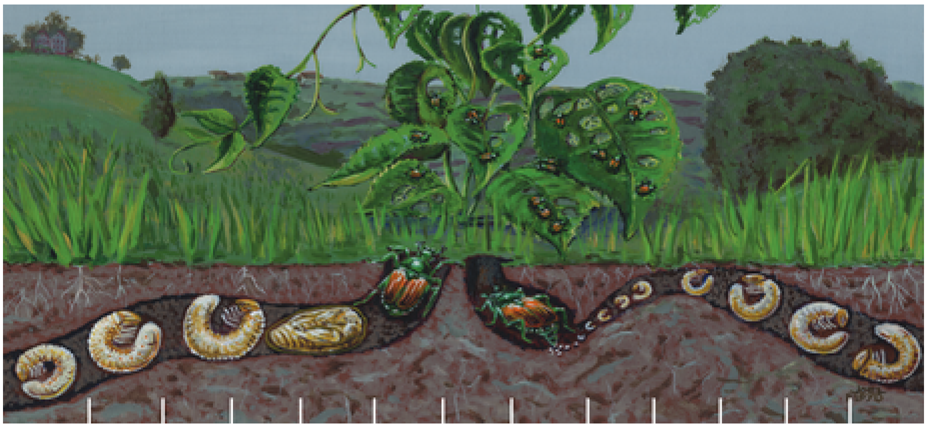
P. japonica is native to Japan, but is an invasive species in North America.

The first written evidence of the insect appearing within the United States was in 1916 in a nursery near Riverton, New Jersey.[2] The beetle larvae are thought to have entered the United States in a shipment of iris bulbs prior to 1912, when inspections of commodities entering the country began. As of 2015, only nine western US states were considered free of Japanese beetles.[3] Beetles have been detected in airports on the west coast of the United States since the 1940s.

The first Japanese beetle found in Canada was in a tourist's car at Yarmouth, arriving in Nova Scotia by ferry from Maine in 1939. During the same year, three additional adults were captured at Yarmouth and three at Lacolle in southern Quebec.[4]

Japanese beetles have been found in the islands of the Azores since the 1970s.[5] In 2014, the first population in mainland Europe was discovered near Milan in Italy.[6][7] In 2017 the pest was detected in Switzerland, most likely having spread over the border from Italy. Swiss authorities are attempting to eradicate the pest.[8]

Lifecycle



Lifecycle of the Japanese beetle. Larvae feed on roots underground, while adults feed on leaves and stems.

Ova are laid individually, or in small clusters near the soil surface.[9] Within approximately two weeks, the ova hatch, the larvae feeding on fine roots and other organic material. As the larvae mature, they become c-shaped grubs which consume progressively coarser roots and may do economic damage to pasture and turf at this time.

Larvae hibernate in small cells in the soil, emerging in the spring when soil temperatures rise again.[9] Within 4–6 weeks of breaking hibernation, the larvae will pupate. Most of the beetle's life is spent as a larva, with only 30–45 days spent as an imago. Adults feed on leaf material above ground, using pheromones to attract other beetles and overwhelm plants, skeletonizing leaves from the top of the plant downward. The aggregation of beetles will alternate daily between mating, feeding, and ovipositing. An adult female may lay as many as 40–60 ova in her lifetime.[9]

A typical cluster of Japanese beetle eggs

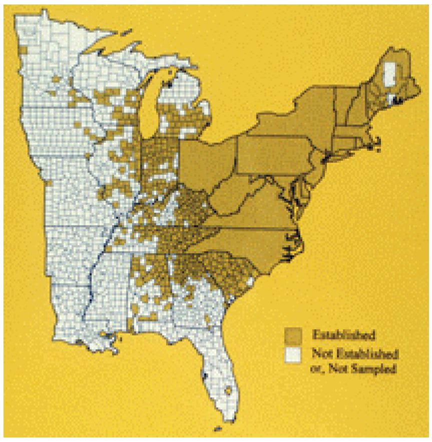
Throughout the majority of the Japanese beetle's range, its lifecycle takes one full year, however in the extreme northern parts of its range, as well as high altitude zones as found in its native Japan, development may take two years.[10]

Control

Owing to its destructive nature, traps have been invented specifically to target Japanese beetles. These comprise a pair of crossed walls with a bag or plastic container underneath, and are baited with floral scent, pheromone, or both. However, studies conducted at the University of Kentucky and Eastern Illinois University suggest beetles attracted to traps frequently do not end up in the traps, but alight on plants in the vicinity, thus causing more damage along the flight path of the beetles and near the trap than may have occurred if the trap were not present.[11][12]

A Japanese beetle pupa shortly after moulting

During the larval stage, the Japanese beetle lives in lawns and other grasslands, where it eats the roots of grasses. During that stage, it is susceptible to a fatal disease called milky spore disease, caused by a bacterium called milky spore, *Paenibacillus* (formerly *Bacillus*) *popilliae.* The USDA developed this biological control and it is commercially available in powder form for application to lawn areas. Standard applications (low density across a broad area) take from one to five years to establish maximal protection against larval survival (depending on climate), expanding through the soil through repeated rounds of infection.



Map showing the parts of the US infested by Japanese beetles, as of November 2006: They were present in many more sites as of July 2012.

On field crops such as squash, floating row covers can be used to exclude the beetles, but this may necessitate hand pollination of flowers. Kaolin sprays can also be used as barriers.

Research performed by many US extension service branches has shown pheromone traps attract more beetles than they catch.[13][14] Traps are most effective when spread out over an entire community, and downwind and at the borders (i.e., as far away as possible, particularly upwind), of managed property containing plants being protected. Natural repellents include catnip, chives, garlic, and tansy,[15] as well as the remains of dead beetles, but these methods have limited effectiveness.[16] Additionally, when present in small numbers, the beetles may be manually controlled using a soap-water spray mixture, shaking a plant in the morning hours and disposing of the fallen beetles,[14] or simply picking them off attractions such as rose flowers, since the presence of beetles attracts more beetles to that plant.[16]


Egg of biocontrol, tachinid fly *Istocheta aldrichi*, introduced from Japan

Several insect predators and parasitoids have been introduced to the United States for biocontrol. Two of them, *Istocheta aldrichi* and *Tiphia vernalis*, are well established with significant rates of parasitism.

Hostplants

While the larvae of Japanese beetles feed on the roots of many genera of grasses, the adults consume the leaves of a much wider range of hosts, including these common crops:[4] bean, strawberry, tomato, pepper, grape, hop, rose, cherry, plum, pear, peach, raspberry, blackberry, corn, pea, okra, and blueberry.

List of adult beetle hostplant genera

- *Abelmoschus*
- *Acer* (maple)
- *Aesculus* (horse chestnut)
- *Alcea*
- *Aronia*
- *Asimina* (pawpaw)
- *Asparagus*
- *Aster*
- *Buddleja*
- *Calluna*
- *Caladium*
- *Canna*
- *Cannabis sativa*
- *Chaenomeles*
- *Castanea* (sweet chestnut)
- *Cirsium* (thistle)
- *Cosmos*
- *Dahlia*
- *Daucus* (carrot)
- *Dendranthema*
- *Digitalis*
- *Dolichos*
- *Echinacea* (coneflower)
- *Hemerocallis*
- *Heuchera*
- *Hibiscus*
- *Humulus* (hop)
- *Hydrangea*
- *Ilex* (holly)
- *Impatiens*

- *Ipomoea* (morning glory)
- *Iris*
- *Juglans* (walnut)
- *Lagerstroemia*
- *Liatris*
- *Ligustrum* (privet)
- *Malus* (apple, crabapple)
- *Malva* (mallow)
- *Mentha* (mint)
- *Myrica*
- *Ocimum* (basil)
- *Oenothera* (evening primrose)
- *Parthenocissus*
- *Phaseolus*
- *Phlox*
- *Physocarpus*
- *Pistacia*
- *Platanus* (plane)
- *Polygonum* (Japanese knotweed)
- *Populus* (poplar)
- *Prunus* (plum, peach)
- *Quercus* (oak)
- *Ribes* (gooseberry, currants, etc.)
- *Rheum*
- *Rhododendron*
- *Rosa* (rose)
- *Rubus* (raspberry, blackberry, etc.)
- *Salix* (willows)
- *Sambucus* (elder)
- *Sassafras*
- *Solanum* (nightshades, including potato, tomato, eggplant)
- *Spinacia* (spinach)
- *Syringa* (lilac)
- *Thuja* (arborvitae)
- *Tilia* (basswood, linden, UK: lime)
- *Toxicodendron* (poison oak, poison ivy, sumac)
- *Ulmus* (elm)
- *Vaccinium* (blueberry)
- *Viburnum*
- *Vitis* (grape)
- *Weigelia*
- *Wisteria*
- *Zea*
- *Zinnia*

Gallery

Japanese beetle larva (grub)

Japanese beetle pupa

Japanese beetle adult

Adult Japanese beetles feeding on peach tree

Mating, Ottawa, Ontario, Canada

Feeding, Ottawa

Japanese beetle feeding on calla lily, Ottawa, Ontario, Canada

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External links

- Japanese beetle (http://entomology.ifas.ufl.edu/creatures/orn/beetles/japanese_beetle.htm) on the UF/IFAS Featured Creatures Web site
- Japanese Beetle (http://www.inspection.gc.ca/english/plaveg/pestrava/popjap/popjape.shtml), Canadian Food Inspection Agency
- Organic methods of Japanese Beetle Control (http://www.bluehorizonfarm.com/organic-gardening/japanese-beetles.html)
- Species Profile - Japanese Beetle (*Popillia japonica*) (https://www.invasivespeciesinfo.gov/profile/japanese-beetle), National Invasive Species Information Center, United States National Agricultural Library.

Aphid

Aphids are small sap-sucking insects and members of the superfamily **Aphidoidea**. Common names include **greenfly** and **blackfly**,[a] although individuals within a species can vary widely in colour. The group includes the fluffy white woolly aphids. A typical life cycle involves flightless females giving living birth to female nymphs without the involvement of males. Maturing rapidly, females breed profusely so that the number of these insects multiplies quickly. Winged females may develop later in the season, allowing the insects to colonise new plants. In temperate regions, a phase of sexual reproduction occurs in the autumn, with the insects often overwintering as eggs.

The life cycle of some species involves an alternation between two species of host plants, for example between an annual crop and a woody plant. Some species feed on only one type of plant, while others are generalists, colonising many plant groups. About 5,000 species of aphid have been described, all included in the family Aphididae. Around 400 of these are found on food and fibre crops, and many are serious pests of agriculture and forestry, as well as an annoyance for gardeners. So-called dairying ants have a mutualistic relationship with aphids, tending them for their honeydew, and protecting them from predators.

Aphids are among the most destructive insect pests on cultivated plants in temperate regions. In addition to weakening the plant by sucking sap, they act as vectors for plant viruses and disfigure ornamental plants with deposits of honeydew and the subsequent growth of sooty moulds. Because of their ability to rapidly increase in numbers by asexual reproduction, they are a highly successful group of organisms from an ecological standpoint.[1]

Control of aphids is not easy. Insecticides do not always produce reliable results, given resistance to several classes of insecticide and the fact that aphids often feed on the undersides of leaves. On a garden scale, water jets and soap sprays are quite effective. Natural enemies include predatory ladybugs, hoverfly larvae, parasitic wasps, aphid midge larvae, crab spiders, lacewing larvae, and entomopathogenic fungi. An integrated pest management strategy using biological pest control can work, but is difficult to achieve except in enclosed environments such as glasshouses.

Aphids

Temporal range: Permian–present

PreЄ Є O S D C P T J K PgN

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hemiptera
Suborder:	Sternorrhyncha
Infraorder:	Aphidomorpha
Superfamily:	Aphidoidea Geoffroy, 1762

Families

- Aphididae Latreille, 1802
- †Bajsaphididae Homan, Zyla & Wegierek, 2015
- †Canadaphididae Richards, 1966
- †Cretamyzidae Heie, 1992
- †Drepanochaitophoridae Zhang & Hong, 1999
- †Oviparosiphidae Shaposhnikov, 1979
- †Parvaverrucosidae Poinar & Brown, 2006

Contents

- †Sinaphididae Zhang, Zhang, Hou & Ma, 1989
- *incertae sedis*
  - †*Palaeoforda tajmyrensis* Kononova, 1977
  - †*Penaphis* Lin, 1980
  - †*Plioaphis subhercynica* Heie, 1968
  - †*Sbenaphis* Scudder, 1890
  - †*Sunaphis* Hong & Wang, 1990
  - †*Xilutiancallis* Wang, 1991
  - †*Yueaphis* Wang, 1993

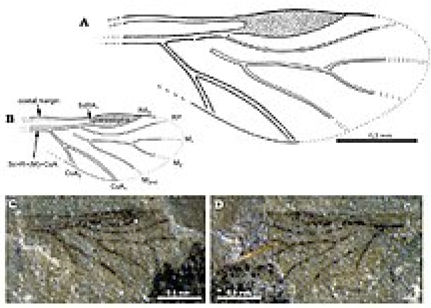
Distribution

Aphids are distributed worldwide, but are most common in temperate zones. In contrast to many taxa, aphid species diversity is much lower in the tropics than in the temperate zones.[2] They can migrate great distances, mainly through passive dispersal by winds. Winged aphids may also rise up in the day as high as 600 m where they are transported by strong winds.[3][4] For example, the currant-lettuce aphid, *Nasonovia ribisnigri*, is believed to have spread from New Zealand to Tasmania around 2004 through easterly winds.[5] Aphids have also been spread by human transportation of infested plant materials, making some species nearly cosmopolitan in their distribution.[6]

Evolution

Fossil history

Aphids, and the closely related adelgids and phylloxerans, probably evolved from a common ancestor some 280 million years ago, in the Early Permian period.[8] They probably fed on plants like Cordaitales or Cycadophyta. With their soft bodies, aphids do not fossilize well, and the oldest known fossil is of the species *Triassoaphis cubitus* from the Triassic.[9] They do however sometimes get stuck in plant exudates which solidify into amber. In 1967, when Professor Ole Heie wrote his monograph *Studies on Fossil Aphids*, about sixty species have been described from the Triassic, Jurassic, Cretaceous and mostly the Tertiary periods, with Baltic amber contributing another forty species.[10] The total number of species was small, but increased considerably with the appearance of the angiosperms 160 million years ago, as this allowed aphids to specialise, the speciation of aphids going hand-in-hand with the diversification of flowering plants. The earliest aphids were probably polyphagous, with monophagy developing later.[11] It has been hypothesized that the ancestors of the Adelgidae lived on conifers while those of the Aphididae fed on the sap of Podocarpaceae or Araucariaceae that survived extinctions in the late Cretaceous. Organs like the cornicles did not appear until the Cretaceous period.[8][12] One study alternatively suggests that ancestral aphids may have lived on angiosperm bark and that feeding on leaves may be a derived trait. The Lachninae have long mouth parts that are suitable for living on bark and it has been suggested that the mid-Cretaceous ancestor fed on the bark of angiosperm trees, switching to leaves of conifer hosts in the late Cretaceous.[13] The Phylloxeridae may well be the oldest family still extant, but their fossil record is limited to the Lower Miocene *Palaeophylloxera*.[14]



Forewing of the early Middle Triassic (early Anisian) aphid *Vosegus triassicus*[7]

Taxonomy

An aphid fossilised in Baltic amber (Eocene)

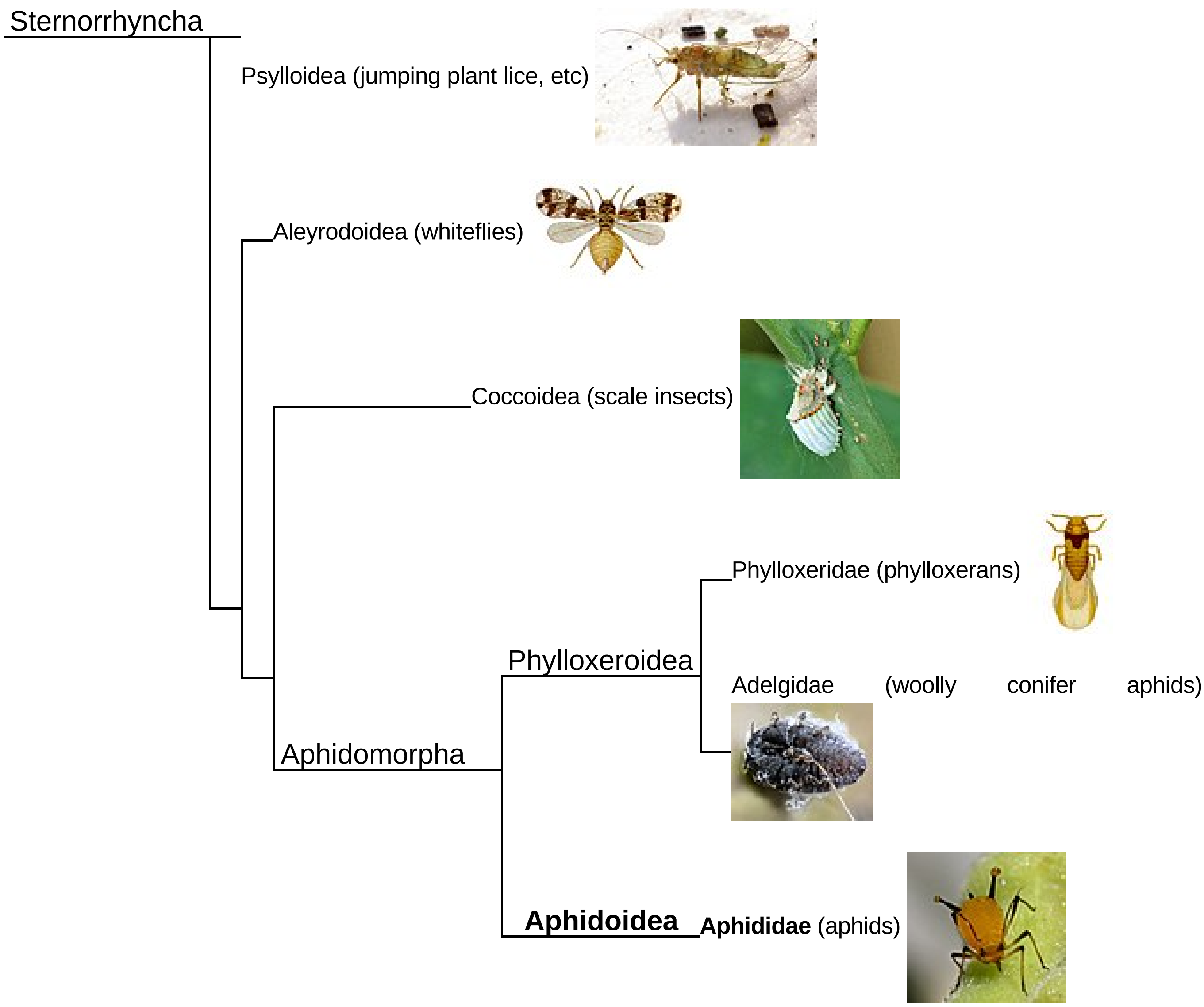
Late 20th-century reclassification within the Hemiptera reduced the old taxon "Homoptera" to two suborders: Sternorrhyncha (aphids, whiteflies, scales, psyllids, etc.) and Auchenorrhyncha (cicadas, leafhoppers, treehoppers, planthoppers, etc.) with the suborder Heteroptera containing a large group of insects known as the true bugs. The infraorder Aphidomorpha within the Sternorrhyncha varies with circumscription with several fossil groups being especially difficult to place but includes the Adelgoidea, the Aphidoidea and the Phylloxeroidea.[15] Some authors use a single superfamily Aphidoidea within which the Phylloxeridae and Adelgidae are also included while others have Aphidoidea with a sister superfamily Phylloxeroidea within which the Adelgidae and Phylloxeridae are placed.[16] Early 21st-century reclassifications substantially rearranged the families within Aphidoidea: some old families were reduced to subfamily rank (*e.g.*, Eriosomatidae), and many old subfamilies were elevated to family rank. The most recent authoritative classifications have three superfamilies Adelgoidea, Phylloxeroidea and Aphidoidea. The Aphidoidea includes a single large family Aphididae that includes all the ~5000[2] extant species.[17]

Phylogeny

External

Aphids, adelgids, and phylloxerids are very closely related, and are all within the suborder Sternorrhyncha, the plant-sucking bugs. They are either placed in the insect superfamily Aphidoidea[18] or into the superfamily Phylloxeroidea which contains the family Adelgidae and the family Phylloxeridae.[11] Like aphids, phylloxera feed on the roots, leaves, and shoots of grape plants, but unlike aphids, do not produce honeydew or cornicle secretions.[19] Phylloxera (*Daktulosphaira vitifoliae*) are insects which caused the Great French Wine Blight that devastated European viticulture in the 19th century. Similarly, adelgids or woolly conifer aphids, also feed on plant phloem and are sometimes described as aphids, but are more properly classified as aphid-like insects, because they have no cauda or cornicles.[20]

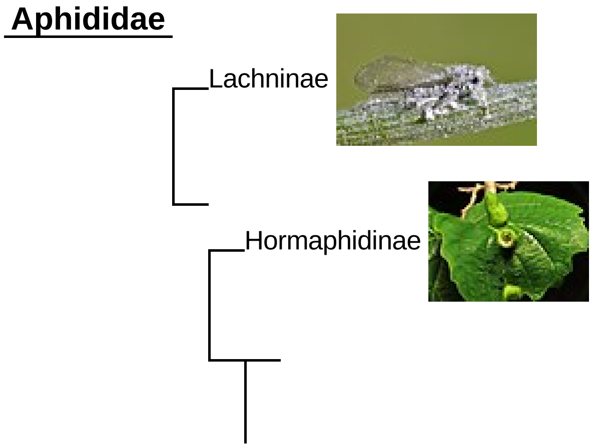
The treatment of the groups especially with respect to fossil groups varies greatly due to difficulties in resolving relationships. Most modern treatments include the three superfamilies, the Adelogidea, the Aphidoidea and the Phylloxeroidea within the infraorder Aphidomorpha along with several fossil groups[21] but other treatments have the Aphidomorpha containing the Aphidoidea with the families Aphididae, Phylloxeridae and Adelgidae; or the Aphidomorpha with two superfamilies, Aphidoidea and Phylloxeroidea, the latter containing the Phylloxeridae and the Adelgidae. The phylogenetic tree of the Sternorrhyncha is inferred from analysis of small subunit (18S) ribosomal RNA.[22]

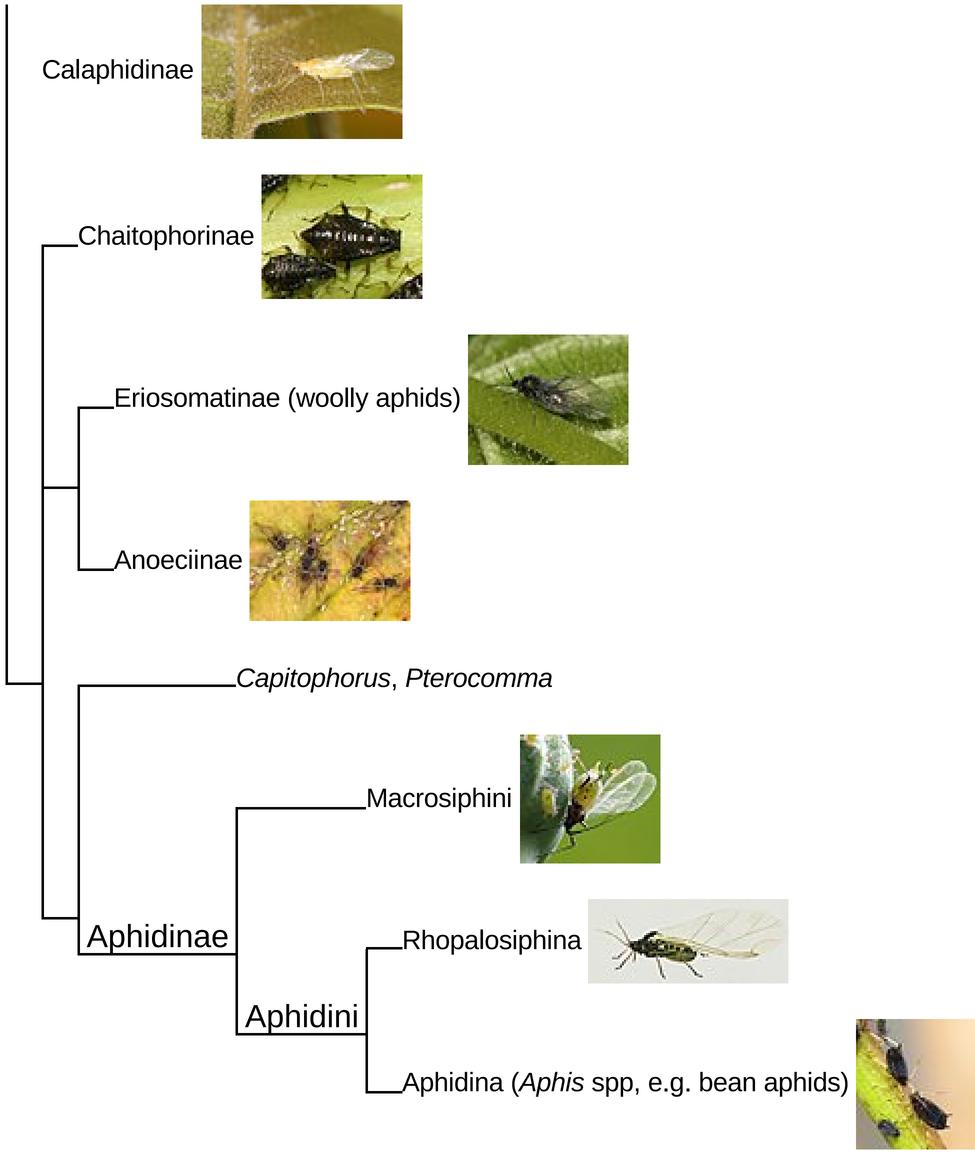


Internal

The phylogenetic tree, based on Papasotiropoulos 2013 and Kim 2011, with additions from Ortiz-Rivas and Martinez-Torres 2009, shows the internal phylogeny of the Aphididae.[23][24][25]

It has been suggested that the phylogeny of the aphid groups might be revealed by examining the phylogeny of their bacterial endosymbionts, especially the obligate endosymbiont *Buchnera*. The results depend on the assumption that the symbionts are strictly transmitted vertically through the generations. This assumption is well supported by the evidence, and several phylogenetic relationships have been suggested on the basis of endosymbiont studies.[26][27][28]





Anatomy

Front view of wheat aphid, *Schizaphis graminum*, showing the piercing-sucking mouthparts

Most aphids have soft bodies, which may be green, black, brown, pink, or almost colorless. Aphids have antennae with two short, broad basal segments and up to four slender terminal segments. They have a pair of compound eyes, with an ocular tubercle behind and above each eye, made up of three lenses (called triommatidia).[11] They feed on sap using sucking mouthparts called stylets, enclosed in a sheath called a rostrum, which is formed from modifications of the mandible and maxilla of the insect mouthparts.[29]

They have long, thin legs with two-jointed, two-clawed tarsi. The majority of aphids are wingless, but winged forms are produced at certain times of year in many species. Most aphids have a pair of cornicles (siphunculi), abdominal tubes on the dorsal surface of their fifth abdominal segment, through which they exude droplets of a quick-hardening defensive fluid[29] containing triacylglycerols, called cornicle wax. Other defensive compounds can also be produced by some species.[20] Aphids have a tail-like protrusion called a cauda above their rectal apertures.[11][30]

When host plant quality becomes poor or conditions become crowded, some aphid species produce winged offspring (alates) that can disperse to other food sources. The mouthparts or eyes can be small or missing in some species and forms.[20]

Diet

Many aphid species are monophagous (that is, they feed on only one plant species). Others, like the green peach aphid feed on hundreds of plant species across many families. About 10% of species feed on different plants at different times of year.[31]

A new host plant is chosen by a winged adult by using visual cues, followed by olfaction using the antennae; if the plant smells right, the next action is probing the surface upon landing. The stylus is inserted and saliva secreted, the sap is sampled, the xylem may be tasted and finally the phloem is tested. Aphid saliva may inhibit phloem-sealing mechanisms and has pectinases that ease penetration.[32] Non-host plants can be rejected at any stage of the probe, but the transfer of viruses occurs early in the investigation process, at the time of the introduction of the saliva, so non-host plants can become infected.[31]

Aphids usually feed passively on sap of phloem vessels in plants, as do many of other hemipterans such as scale insects and cicadas. Once a phloem vessel is punctured, the sap, which is under pressure, is forced into the aphid's food canal. Occasionally, aphids also ingest xylem sap, which is a more dilute diet than phloem sap as the concentrations of sugars and amino acids are 1% of those in the phloem.[33][34] Xylem sap is under negative hydrostatic pressure and requires active sucking, suggesting an important role in aphid physiology.[35] As xylem sap ingestion has been observed following a dehydration period, aphids are thought to consume xylem sap to replenish their water balance; the consumption of the dilute sap of xylem permitting aphids to rehydrate.[36] However, recent data showed aphids consume more xylem sap than expected and they notably do so when they are not dehydrated and when their fecundity decreases. This suggests aphids, and potentially, all the phloem-sap feeding species of the order Hemiptera, consume xylem sap for reasons other than replenishing water balance.[37] Although aphids passively take in phloem sap, which is under pressure, they can also draw fluid at negative or atmospheric pressure using the cibarial-pharyngeal pump mechanism present in their head.[38]

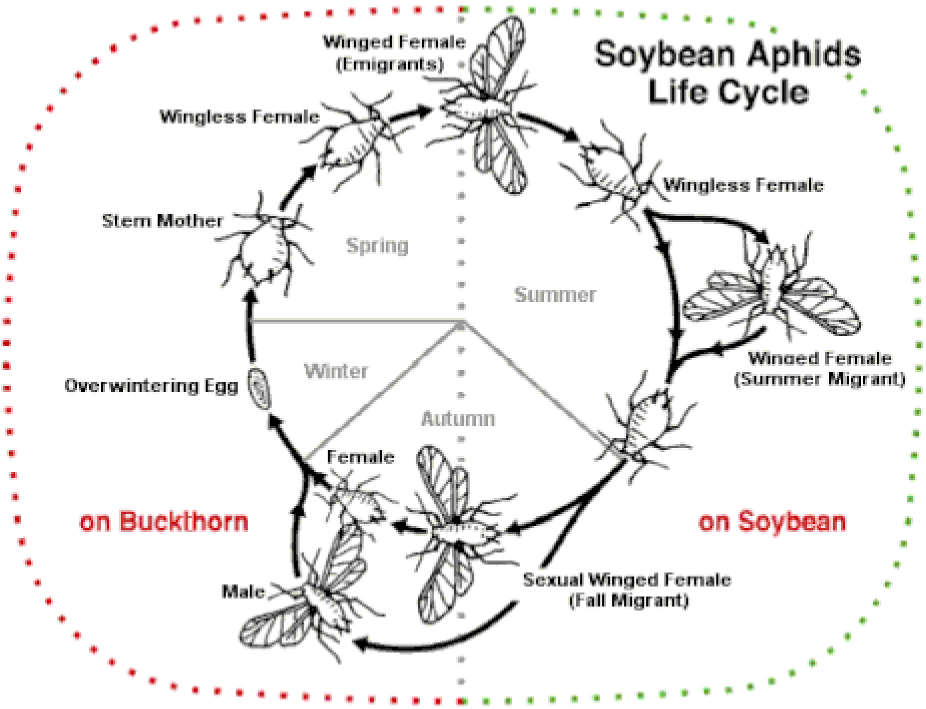
Xylem sap consumption may be related to osmoregulation.[37] High osmotic pressure in the stomach, caused by high sucrose concentration, can lead to water transfer from the hemolymph to the stomach, thus resulting in hyperosmotic stress and eventually to the death of the insect. Aphids avoid this fate by osmoregulating through several processes. Sucrose concentration is directly reduced by assimilating sucrose toward metabolism and by synthesizing oligosaccharides from several sucrose molecules, thus reducing the solute concentration and consequently the osmotic pressure.[39][40] Oligosaccharides are then excreted through honeydew, explaining its high sugar concentrations, which can then be used by other animals such as ants. Furthermore, water is transferred from the hindgut, where osmotic pressure has already been reduced, to the stomach to dilute stomach content.[41] Eventually, aphids consume xylem sap to dilute the stomach osmotic pressure.[37] All these processes function synergetically, and enable aphids to feed on high-sucrose-concentration plant sap, as well as to adapt to varying sucrose concentrations.[37]

Plant sap is an unbalanced diet for aphids, as it lacks essential amino acids, which aphids, like all animals, cannot synthesise, and possesses a high osmotic pressure due to its high sucrose concentration.[34][42] Essential amino acids are provided to aphids by bacterial endosymbionts, harboured in special cells, bacteriocytes.[43] These symbionts recycle glutamate, a metabolic waste of their host, into essential amino acids.[44][45]

Carotenoids and photoheterotrophy

Some species of aphids have acquired the ability to synthesise red carotenoids by horizontal gene transfer from fungi.[46] They are the only animals other than two-spotted spider mites with this capability.[47] Using their carotenoids, aphids may well be able to absorb solar energy and convert it to a form that their cells can use, ATP. This is the only known example of photoheterotrophy in animals. The carotene pigments in aphids form a layer close to the surface of the cuticle, ideally placed to absorb sunlight. The excited carotenoids seem to reduce NAD to NADH which is oxidized in the mitochondria for energy.[48]

Reproduction



Soybean aphid alternates between hosts and between asexual and sexual reproduction.[49]

The simplest reproductive strategy is for an aphid to have a single host all year round. On this it may alternate between sexual and asexual generations (holocyclic) or alternatively, all young may be produced by parthenogenesis, eggs never being laid (anholocyclic). Some species can have both holocyclic and anholocyclic populations under different circumstances but no known aphid species reproduce solely by sexual means.[50] The alternation of sexual and asexual generations may have evolved repeatedly.[51]

However, aphid reproduction is often more complex than this and involves migration between different host plants. In about 10% of species, there is an alternation between woody (primary hosts) on which the aphids overwinter and herbaceous (secondary) host plants, where they reproduce abundantly in the summer.[20][50] A few species can produce a soldier caste, other species show extensive polyphenism under different environmental conditions and some can control the sex ratio of their offspring depending on external factors.[52]

When a typical sophisticated reproductive strategy is used, only females are present in the population at the beginning of the seasonal cycle (although a few species of aphids have been found to have both male and female sexes at this time). The overwintering eggs that hatch in the spring result in females, called fundatrices (stem mothers). Reproduction typically does not involve males (parthenogenesis) and results in live birth (viviparity).[53] The live young are produced by pseudoplacental viviparity, which is the development of eggs, deficient in yolk, the embryos fed by a tissue acting as a placenta. The young emerge from the mother soon after hatching.[54]

Eggs are parthenogenetically produced without meiosis[55][53] and the offspring are clonal to their mother, so they are all female (thelytoky).[11][54] The embryos develop within the mothers' ovarioles, which then give birth to live (already hatched) first-instar female nymphs. As the eggs begin to develop immediately after ovulation, an adult female can house developing female nymphs which already have parthenogenetically developing embryos inside them. This telescoping of generations enables aphids to increase in number with great rapidity. The offspring resemble their parent in every way except size. Thus, a female's diet can affect the body size and birth rate of more than two generations (daughters and granddaughters).[11][56][57]

This process repeats itself throughout the summer, producing multiple generations that typically live 20 to 40 days. For example, some species of cabbage aphids (like *Brevicoryne brassicae*) can produce up to 41 generations of females in a season. Thus, one female hatched in spring can theoretically produce billions of descendants, were they all to survive.[58]

Aphid giving birth to live young: populations are often entirely female.

In autumn, aphids reproduce sexually and lay eggs. Environmental factors such as change in photoperiod and temperature, or perhaps a lower food quantity or quality, causes females to parthenogenetically produce sexual females and males.[55] The males are genetically identical to their mothers except that, with the aphids' X0 sex-determination system, they have one fewer sex chromosome.[55] These sexual aphids may lack wings or even mouthparts.[20] Sexual females and males mate, and females lay eggs that develop outside the mother. The eggs survive the winter and hatch into winged (alate) or wingless females the following spring. This occurs in, for example, the life cycle of the rose aphid (*Macrosiphum rosae*), which may be considered typical of the family. However, in warm environments, such as in the tropics or in a greenhouse, aphids may go on reproducing asexually for many years.[29]

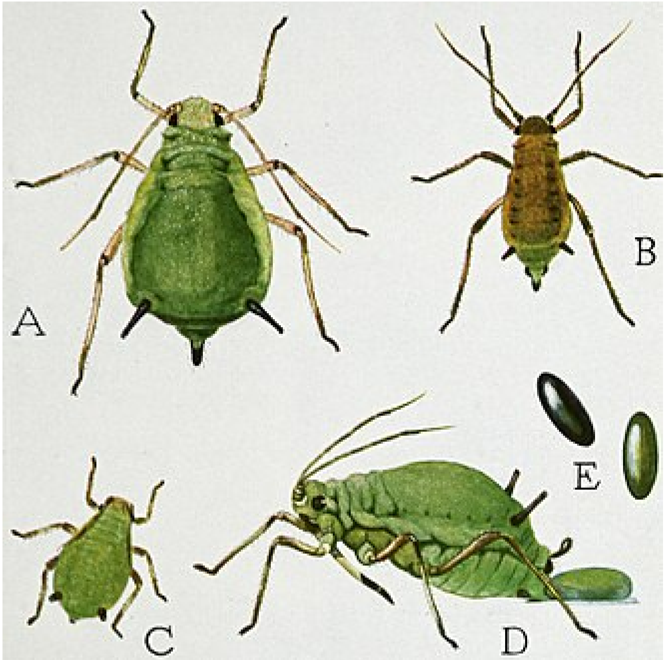
Aphids reproducing asexually by parthenogenesis can have genetically identical winged and non-winged female progeny. Control is complex; some aphids alternate during their life-cycles between genetic control (polymorphism) and environmental control (polyphenism) of production of winged or wingless forms.[59] Winged progeny tend to be produced more abundantly under unfavorable or stressful conditions. Some species produce winged progeny in response to low food quality or quantity. e.g. when a host plant is starting to senesce.[60] The winged females migrate to start new colonies on a new host plant. For example, the apple aphid (*Aphis pomi*), after producing many generations of wingless females gives rise to winged forms that fly to other branches or trees of its typical food plant.[61] Aphids that are attacked by ladybugs, lacewings, parasitoid wasps, or other predators can change the dynamics of their progeny production. When aphids are attacked by these predators, alarm pheromones, in particular beta-farnesene, are released from the cornicles. These alarm pheromones cause several behavioral modifications that, depending on the aphid species, can include walking away and dropping off the host plant. Additionally, alarm pheromone perception can induce the aphids to produce winged progeny that can leave the host plant in search of a safer feeding site.[62] Viral infections, which can be extremely harmful to aphids, can also lead to the production of winged offspring.[63] For example, *Densovirus* infection has a negative impact on rosy apple aphid (*Dysaphis plantaginea (https://influentialpoints.com/Gallery/Dysaphis_plantaginea_Rosy_apple_aphid.htm)*) reproduction, but contributes to the development of aphids with wings, which can transmit the virus more easily to new host plans.[64] Additionally, symbiotic bacteria that live inside of the aphids can also alter aphid reproductive strategies based on the exposure to environmental stressors.[65]

In the autumn, host-alternating (heteroecious) aphid species produce a special winged generation that flies to different host plants for the sexual part of the life cycle. Flightless female and male sexual forms are produced and lay eggs .[66] Some species such as *Aphis fabae* (blackfly of beans), *Metopolophium dirhodum* (rose-grain aphid), *Myzus persicae* (peach-potato aphid), and *Rhopalosiphum padi* (bird cherry-oat aphid) and *Aphis glycines* (soybean aphid)[49] are serious pests. They overwinter on tree or bush primary hosts; in summer, they migrate to their secondary host on a herbaceous plant, often a crop, then the gynoparae return to the tree in autumn. Another example is the soybean aphid (*Aphis glycines*). As fall approaches, the soybean plants begin to senesce from the bottom upwards. The aphids are forced upwards and start to produce winged forms, first females and later males, which fly off to the primary host, buckthorn. Here they mate and overwinter as eggs.[49]

Ecology

Ant mutualism

Some species of ants farm aphids, protecting them on the plants where they are feeding, and consuming the honeydew the aphids release from the terminations of their alimentary canals. This is a mutualistic relationship, with these dairying ants milking the aphids by stroking them with their antennae.[b][67] Although mutualistic, the feeding behaviour of aphids is altered by ant attendance. Aphids attended by ants tend to increase the production of honeydew in smaller drops with a greater concentration of amino acids.[68]



The life stages of the green apple aphid (*Aphis pomi*). Drawing by Robert Evans Snodgrass, 1930

Some farming ant species gather and store the aphid eggs in their nests over the winter. In the spring, the ants carry the newly hatched aphids back to the plants. Some species of dairying ants (such as the European yellow meadow ant, *Lasius flavus*)[69] manage large herds of aphids that feed on roots of plants in the ant colony. Queens leaving to start a new colony take an aphid egg to found a new herd of underground aphids in the new colony. These farming ants protect the aphids by fighting off aphid predators.[67]


Ants tending aphids


An ant guards its aphids

An interesting variation in ant–aphid relationships involves lycaenid butterflies and *Myrmica* ants. For example, *Niphanda fusca* butterflies lay eggs on plants where ants tend herds of aphids. The eggs hatch as caterpillars which feed on the aphids. The ants do not defend the aphids from the caterpillars, since the caterpillars produce a pheromone which deceives the ants into treating them like ants, and carrying the caterpillars into their nest. Once there, the ants feed the caterpillars, which in return produce honeydew for the ants. When the caterpillars reach full size, they crawl to the colony entrance and form cocoons. After two weeks, the adult butterflies emerge and take flight. At this point, the ants attack the butterflies, but the butterflies have a sticky wool-like substance on their wings that disables the ants' jaws, allowing the butterflies to fly away without being harmed.[70] Some bees in coniferous forests collect aphid honeydew to make forest honey.[29]


Ant extracting honeydew from an aphid

Another ant-mimicking gall aphid, *Paracletus cimiciformis* (Eriosomatinae), has evolved a complex double strategy involving two morphs of the same clone and *Tetramorium* ants. Aphids of the round morph cause the ants to farm them, as with many other aphids. The flat morph aphids are aggressive mimics with a "wolf in sheep's clothing" strategy: they have hydrocarbons in their cuticle that mimic those of the ants, and the ants carry them into the brood chamber of the ants' nest and raise them like ant larvae. Once there, the flat morph aphids behave as predators, drinking the body fluids of ant larvae.[71]

Bacterial endosymbiosis

Endosymbiosis with micro-organisms is common in insects, with more than 10% of insect species relying on intracellular bacteria for their development and survival.[72] Aphids harbour a vertically transmitted (from parent to its offspring) obligate symbiosis with *Buchnera aphidicola*, the primary symbiont, inside specialised cells, the bacteriocytes.[73] Five of the bacteria genes have been transferred to the aphid nucleus.[74] The original contamination occurred in a common ancestor 280 to 160 million years ago and enabled aphids to exploit a new ecological niche, feeding on phloem-sap of vascular plants. *B. aphidicola* provides its host with essential amino acids, which are present in low concentrations in plant sap. The stable intracellular conditions, as well as the bottleneck effect experienced during the transmission of a few bacteria from the mother to each nymph, increase the probability of transmission of mutations and gene deletions.[75][76] As a result, the size of the *B. aphidicola* genome is greatly reduced, compared to its putative ancestor.[77] Despite the apparent loss of transcription factors in the reduced genome, gene expression is highly regulated, as shown by the ten-fold variation in expression levels between different genes under normal conditions.[78] *Buchnera aphidicola* gene transcription, although not well understood, is thought to be regulated by a small number of global transcriptional regulators and/or through nutrient supplies from the aphid host.[79]

Some aphid colonies also harbour secondary or facultative (optional extra) bacterial symbionts. These are vertically transmitted, and sometimes also horizontally (from one lineage to another and possibly from one species to another).[80][81] So far, the role of only some of the secondary symbionts has been described; *Regiella insecticola* plays a role in defining the host-plant range,[82][83] *Hamiltonella defensa* provides resistance to parasitoids but only when it is in turn infected by the bacteriophage APSE,[84][85] and *Serratia symbiotica* prevents the deleterious effects of heat.[86]

Predators

Aphids are eaten by many bird and insect predators. In a study on a farm in North Carolina, six species of passerine bird consumed nearly a million aphids per day between them, the top predators being the American goldfinch, with aphids forming 83% of its diet, and the vesper sparrow.[87] Insects that attack aphids include the adults and larvae of predatory ladybirds, hoverfly larvae, parasitic wasps, aphid midge larvae, "aphid lions" (the larvae of green lacewings), and arachnids such as crab spiders. Among ladybirds, *Myzia oblongoguttata* is a dietary specialist which only feeds on conifer aphids, whereas *Adalia bipunctata* and *Coccinella septempunctata* are generalists, feeding on large numbers of species. The eggs are laid in batches, each female laying several hundred. Female hoverflies lay several thousand eggs. The adults feed on pollen and nectar but the larvae feed voraciously on aphids; *Eupeodes corollae* adjusts the number of eggs laid to the size of the aphid colony.[88]

Aphids are often infected by bacteria, viruses, and fungi. They are affected by the weather, such as precipitation,[89] temperature[90] and wind.[91] Fungi that attack aphids include *Neozygites fresenii*, *Entomophthora*, *Beauveria bassiana*, *Metarhizium anisopliae*, and entomopathogenic fungi such as *Lecanicillium lecanii*. Aphids brush against the microscopic spores. These stick to the aphid, germinate, and penetrate the aphid's skin. The fungus grows in the aphid's hemolymph. After about three days, the aphid dies and the fungus releases more spores into the air. Infected aphids are covered with a woolly mass that progressively grows thicker until the aphid is obscured. Often, the visible fungus is not the one that killed the aphid, but a secondary infection.[89]

Aphids can be easily killed by unfavourable weather, such as late spring freezes.[92] Excessive heat kills the symbiotic bacteria that some aphids depend on, which makes the aphids infertile.[93] Rain prevents winged aphids from dispersing, and knocks aphids off plants and thus kills them from the impact or by starvation,[89][94][95] but cannot be relied on for aphid control.[96]

Predators eating aphids


Ladybird larva


Hoverfly larva


The ladybird beetle *Propylea quatuordecimpunctata*

Anti-predator defences


Aphid secreting defensive fluid from the cornicles

Most aphids have little protection from predators. Some species interact with plant tissues forming a gall, an abnormal swelling of plant tissue. Aphids can live inside the gall, which provides protection from predators and the elements. A number of galling aphid species are known to produce specialised "soldier" forms, sterile nymphs with defensive features which defend the gall from invasion.[29][97][98] For example, Alexander's horned aphids are a type of soldier aphid that has a hard exoskeleton and pincer-like mouthparts.[70]:144 A woolly aphid, *Colophina clematis*, has first instar "soldier" larvae that protect the aphid colony, killing larvae of ladybirds, hoverflies and the flower bug *Anthocoris nemoralis* by climbing on them and inserting their stylets.[99]

Although aphids cannot fly for most of their life cycle, they can escape predators and accidental ingestion by herbivores by dropping off the plant onto the ground.[100] Others species use the soil as a permanent protection, feeding on the vascular systems of roots and remaining underground all their lives. They are often attended by ants, for the honeydew they produce, and are carried from plant to plant by the ants through their tunnels.[87]

Some species of aphid, known as "woolly aphids" (Eriosomatinae), excrete a "fluffy wax coating" for protection.[29] The cabbage aphid, *Brevicoryne brassicae*, sequesters secondary metabolites from its host, stores them and releases chemicals that produce a violent chemical reaction and strong mustard oil smell to repel predators.[101] Peptides produced by aphids, Thaumatins, are thought to provide them with resistance to some fungi.[102]

It was common at one time to suggest that the cornicles were the source of the honeydew, and this was even included in the *Shorter Oxford English Dictionary*[103] and the 2008 edition of the *World Book Encyclopedia*.[104] In fact, honeydew secretions are produced from the anus of the aphid,[105] while cornicles mostly produce defensive chemicals such as waxes. There also is evidence of cornicle wax attracting aphid predators in some cases.[106]

Some clones of *Aphis craccivora* are sufficiently toxic to the invasive and dominant predatory ladybird *Harmonia axyridis* to suppress it locally, favouring other ladybird species; the toxicity is in this case narrowly specific to the dominant predator species.[107]

Parasitoids

Aphids are abundant and widespread, and serve as hosts to a large number of parasitoids, many of them being very small (c. 0.1 inches (2.5 mm) long) parasitoid wasps.[108] One species, *Aphis ruborum*, for example, is host to at least 12 species of parasitoid wasps.[109] Parasitoids have been investigated intensively as biological control agents, and many are used commercially for this purpose.[110]

Plant-aphid interactions

Aphids on plant host

Plants mount local and systemic defences against aphid attack. Young leaves in some plants contain chemicals which discourage attack while the older leaves have lost this resistance, while in other plant species, resistance is acquired by older tissues and the young shoots are vulnerable. Volatile products from interplanted onions have been shown to prevent aphid attack on adjacent potato plants by encouraging the production of terpenoids, a benefit exploited in the traditional practice of companion planting, while plants neighbouring infested plants showed increased root growth at the expense of the extension of aerial parts.[31] The wild potato, *Solanum berthaultii*, produces an aphid alarm pheromone, (E)-β-farnesene, as an allomone, a pheromone to ward off attack; it effectively repels the aphid *Myzus persicae* at a range of up to 3 millimetres.[111] *S. berthaultii* and other wild potato species have a further anti-aphid defence in the form of glandular hairs which, when broken by aphids, discharge a sticky liquid that can immobilise some 30% of the aphids infesting a plant.[112]

Plants exhibiting aphid damage can have a variety of symptoms, such as decreased growth rates, mottled leaves, yellowing, stunted growth, curled leaves, browning, wilting, low yields and death. The removal of sap creates a lack of vigour in the plant, and aphid saliva is toxic to plants. Aphids frequently transmit plant viruses to their hosts, such as to potatoes, cereals, sugarbeets, and citrus plants.[29] The green peach aphid, *Myzus persicae*, is a vector for more than 110 plant viruses. Cotton aphids (*Aphis gossypii*) often infect sugarcane, papaya and peanuts with viruses.[20] In plants which produce the phytoestrogen coumestrol, such as alfalfa, damage by aphids is linked with higher concentrations of coumestrol.[113]

Aphid with honeydew, from the anus not the cornicles

The coating of plants with honeydew can contribute to the spread of fungi which can damage plants.[114][115] Honeydew produced by aphids has been observed to reduce the effectiveness of fungicides as well.[116]

A hypothesis that insect feeding may improve plant fitness was floated in the mid-1970s by Owen and Wiegert. It was felt that the excess honeydew would nourish soil micro-organisms, including nitrogen fixers. In a nitrogen poor environment, this could provide an advantage to an infested plant over an uninfested plant. However, this does not appear to be supported by the observational evidence.[117]

Sociality

Some aphids show some of the traits of eusociality, joining insects such as ants, bees and termites. However, there are differences between these sexual social insects and the clonal aphids, which are all descended from a single female parthenogenetically and share an identical genome. About fifty species of aphid, scattered among the closely related, host-alternating families Pemphigidae and Hormaphididae, have some type of defensive morph. These are gall-creating species, with the colony living and feeding inside a gall that they form in the host's tissues. Among the clonal population of these aphids there may be a number of distinct morphs and this lays the foundation for a possible specialisation of function, in this case, a defensive caste. The soldier morphs are mostly first and second instars with the third instar being involved in *Eriosoma moriokense* and only in *Smythurodes betae* are adult soldiers known. The hind legs of soldiers are clawed, heavily sclerotised and the stylets are robust making it possible to rupture and crush small predators.[118] The larval soldiers are altruistic individuals, unable to advance to breeding adults but acting permanently in the interests of the colony. Another requirement for the development of sociality is provided by the gall, a colonial home to be defended by the soldiers.[119]

The soldiers of gall forming aphids also carry out the job of cleaning the gall. The honeydew secreted by the aphids is coated in a powdery wax to form "liquid marbles"[120] that the soldiers roll out of the gall through small orifices.[98] Aphids that form closed galls use the plant's vascular system for their plumbing: the inner surfaces of the galls are highly absorbent and wastes are absorbed and carried away by the plant.[98]

Interactions with humans

Pest status

About 5000 species of aphid have been described and of these, some 450 species have colonised food and fibre crops. As direct feeders on plant sap, they damage crops and reduce yields, but they have a greater impact by being vectors of plant viruses. The transmission of these viruses depends on the movements of aphids between different parts of a plant, between nearby plants and further afield. In this respect, the probing behaviour of an aphid tasting a host is more damaging than lengthy aphid feeding and reproduction by stay-put individuals. The movement of aphids influences the timing of virus epidemics.[121]

Aphids, especially during large outbreaks, have been known to trigger allergic inhalant reactions in sensitive humans.[122]

Dispersal can be by walking or flight, appetitive dispersal or by migration. Winged aphids are weak fliers, lose their wings after a few days and only fly by day. Dispersal by flight is affected by impact, air currents, gravity, precipitation and other factors, or dispersal may be accidental, caused by movement of plant materials, animals, farm machinery, vehicles or aircraft.[121]

Control


Parasitoid braconid wasp ovipositing in black bean aphid

Insecticide control of aphids is difficult, as they breed rapidly, so even small areas missed may enable the population to recover promptly. Aphids may occupy the undersides of leaves where spray misses them, while systemic insecticides do not move satisfactorily into flower petals. Finally, some aphid species are resistant to common insecticide classes including carbamates, organophosphates, and pyrethroids.[123]

For small backyard infestations, spraying plants thoroughly with a strong water jet every few days may be sufficient protection. An insecticidal soap solution can be an effective household remedy to control aphids, but it only kills aphids on contact and has no residual effect. Soap spray may damage plants, especially at higher concentrations or at temperatures above 32 °C (90 °F); some plant species are sensitive to soap sprays.[110][124][125]

Integrated pest management of various species of aphids can be achieved using biological insecticides based on fungi such as *Lecanicillium lecanii*, *Beauveria bassiana* or *Isaria fumosorosea*.[126] Fungi are the main pathogens of aphids; Entomophthorales can quickly cut aphid numbers in nature.[127]

Aphids may also be controlled by the release of natural enemies, in particular lady beetles and parasitoid wasps. However, since adult lady beetles tend to fly away within 48 hours after release, without laying eggs, repeated applications of large numbers of lady beetles are needed to be effective. For example, one large, heavily infested rose bush may take two applications of 1500 beetles each.[110][128]

The ability to produce allomones such as farnesene to repel and disperse aphids and to attract their predators has been experimentally transferred to transgenic *Arabidopsis thaliana* plants using an Eβf synthase gene in the hope that the approach could protect transgenic crops.[129] Eβ farnesene has however found to be ineffective in crop situations although stabler synthetic forms help improve the effectiveness of control using fungal spores and insecticides through increased uptake caused by movements of aphids.[130]

Green peach aphid, *Myzus persicae*, killed by the fungus *Pandora neoaphidis* (Entomophthorales)

In human culture

Aphids are familiar to farmers and gardeners, mainly as pests. Peter Marren and Richard Mabey record that Gilbert White described an invading "army" of black aphids that arrived in his village of Selborne in August 1774 in "great clouds", covering every plant, while in the unusually hot summer of 1783, White found that honeydew was so abundant as to "deface and destroy the beauties of my garden", though he thought the aphids were consuming rather than producing it.[131]

Infestation of the Chinese sumac (*Rhus chinensis*) by Chinese sumac aphids (*Schlechtendalia chinensis*) can create "Chinese galls" which are valued as a commercial product. As "Galla Chinensis", they are used in traditional Chinese medicine to treat coughs, diarrhoea, night sweats, dysentery and to stop intestinal and uterine bleeding. Chinese galls are also an important source of tannins.[29]

See also

- Aeroplankton
- Economic entomology
- Pineapple gall

Notes

a. The term "black fly" is also used for the Simuliidae, among them the vector of river blindness.

b. Dairying ants also milk mealybugs and other insects.

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Caterpillar

Caterpillars /ˈkætərˌpɪlər/ are the larval stage of members of the order Lepidoptera (the insect order comprising butterflies and moths).

Caterpillar of *Papilio machaon*

As with most common names, the application of the word is arbitrary, since the larvae of sawflies commonly are called caterpillars as well.[1][2] Both lepidopteran and symphytan larvae have eruciform body shapes.

Caterpillars of most species are herbivorous (folivorous), but not all; some (about 1%) are insectivorous, even cannibalistic. Some feed on other animal products; for example, clothes moths feed on wool, and horn moths feed on the hooves and horns of dead ungulates.

A monarch butterfly (*Danaus plexippus*) caterpillar feeding on an unopened seed pod of swamp milkweed

Caterpillars are typically voracious feeders and many of them are among the most serious of agricultural pests. In fact many moth species are best known in their caterpillar stages because of the damage they cause to fruits and other agricultural produce, whereas the moths are obscure and do no direct harm. Conversely, various species of caterpillar are valued as sources of silk, as human or animal food, or for biological control of pest plants.

Contents

Etymology

The origins of the word "caterpillar" date from the early 16th century. They derive from Middle English *catirpel*, *catirpeller*, probably an alteration of Old North French *catepelose*: *cate*, cat (from Latin *cattus*) + *pelose*, hairy (from Latin *pilōsus*).[3]

The inchworm, or looper caterpillars from the family Geometridae are so named because of the way they move, appearing to measure the earth (the word *geometrid* means *earth-measurer* in Greek);[4] the primary reason for this unusual locomotion is the elimination of nearly all the prolegs except the clasper on the terminal segment.

A geometrid caterpillar or inchworm

Description

Caterpillars have soft bodies that can grow rapidly between moults. Their size varies between species and instars (moults) from as small as 1 mm up to 14 cm.[5] Some larvae of the order Hymenoptera (ants, bees and wasps) can appear like the caterpillars of the Lepidoptera. Such larvae are mainly seen in the sawfly suborder. However while these larvae superficially resemble caterpillars, they can be distinguished by the presence of prolegs on every abdominal segment, an absence of crochets or hooks on the prolegs (these are present on lepidopteran caterpillars), one pair of prominent ocelli on the head capsule, and an absence of the upside-down Y-shaped suture on the front of the head.[6]

Crochets on a caterpillar's prolegs

Lepidopteran caterpillars can be differentiated from sawfly larvae by:

- the numbers of pairs of pro-legs; sawfly larvae have 6 or more pairs while caterpillars have a maximum of 5 pairs.
- the number of stemmata (simple eyes); the sawfly larvae have only two,[7] while caterpillars usually have six.
- the presence of crochets on the prolegs; these are absent in the sawflies.
- sawfly larvae have an invariably smooth head capsule with no cleavage lines, while lepidopterous caterpillars bear an inverted "Y" or "V" (adfrontal suture).

Larvae of *Craesus septentrionalis*, a sawfly showing 6 pairs of pro-legs.

Fossils

In 2019, a geometrid moth caterpillar dating back to the Eocene epoch, approximately 44 million years ago, was found preserved in Baltic amber. It was described under *Eogeometer vadens*.[8][9][10] Previously, another fossil dating back approximately 125 million years was found in Lebanese amber.[11][12]

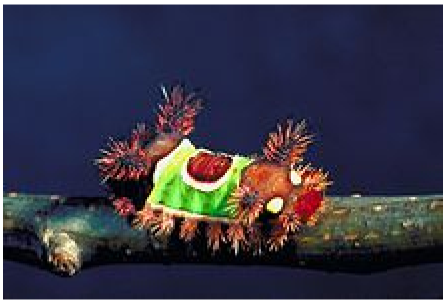
Eogeometer vadens, the earliest known geometrid moth caterpillar found in Baltic amber[8][9][10]

Defenses

Many animals feed on caterpillars as they are rich in protein. As a result, caterpillars have evolved various means of defense.

Caterpillars have evolved defenses against physical conditions such as cold, hot or dry environmental conditions. Some Arctic species like *Gynaephora groenlandica* have special basking and aggregation behaviours[13] apart from physiological adaptations to remain in a dormant state.[14]

Appearance


The saddleback caterpillar has urticating hair and aposematic colouring.

The appearance of a caterpillar can often repel a predator: its markings and certain body parts can make it seem poisonous, or bigger in size and thus threatening, or non-edible. Some types of caterpillars are indeed poisonous or distasteful and their bright coloring is aposematic. Others may mimic dangerous caterpillars or other animals while not being dangerous themselves. Many caterpillars are cryptically colored and resemble the plants on which they feed. An example of caterpillars that use camouflage for defence is the species *Nemoria arizonaria*. If the caterpillars hatch in the spring and feed on oak catkins they appear green. If they hatch in the summer they appear dark colored, like oak twigs. The differential development is linked to the tannin content in the diet.[15] Caterpillars may even have spines or growths that resemble plant parts such as thorns. Some look like objects in the environment such as bird droppings. Some Geometridae cover themselves in plant parts, while bagworms construct and live in a bag covered in sand, pebbles or plant material.


Costa Rican hairy caterpillar. The spiny bristles are a self-defense mechanism

Chemical defenses

More aggressive self-defense measures are taken by some caterpillars. These measures include having spiny bristles or long fine hair-like setae with detachable tips that will irritate by lodging in the skin or mucous membranes.[6] However some birds (such as cuckoos) will swallow even the hairiest of caterpillars. Other caterpillars acquire toxins from their host plants that render them unpalatable to most of their predators. For instance, ornate moth caterpillars utilize pyrrolizidine alkaloids that they obtain from their food plants to deter predators.[16] The most aggressive caterpillar defenses are bristles associated with venom glands. These bristles are called urticating hairs. A venom which is among the most potent defensive chemicals in any animal is produced by the South American silk moth genus *Lonomia*. Its venom is an anticoagulant powerful enough to cause a human to hemorrhage to death (See Lonomiasis).[17] This chemical is being investigated for potential medical applications. Most urticating hairs range in effect from mild irritation to dermatitis. Example: Brown-tail moth.


Giant swallowtail caterpillar everting its osmeterium in defense

Plants contain toxins which protect them from herbivores, but some caterpillars have evolved countermeasures which enable them to eat the leaves of such toxic plants. In addition to being unaffected by the poison, the caterpillars sequester it in their body, making them highly toxic to predators. The chemicals are also carried on into the adult stages. These toxic species, such as the cinnabar moth (*Tyria jacobaeae*) and monarch (*Danaus plexippus*) caterpillars, usually advertise themselves with the danger colors of red, yellow and black, often in bright stripes (see aposematism). Any predator that attempts to eat a caterpillar with an aggressive defense mechanism will learn and avoid future attempts.

Some caterpillars regurgitate acidic digestive juices at attacking enemies. Many papilionid larvae produce bad smells from extrudable glands called osmeteria.

Defensive behaviors

Many caterpillars display feeding behaviors which allow the caterpillar to remain hidden from potential predators. Many feed in protected environments, such as enclosed inside silk galleries, rolled leaves or by mining between the leaf surfaces.


Caterpillars linked together into a "train"

Some caterpillars, like early instars of the tomato hornworm and tobacco hornworm, have long "whip-like" organs attached to the ends of their body. The caterpillar wiggles these organs to frighten away flies and predatory wasps.[18] Some caterpillars can evade predators by using a silk line and dropping off from branches when disturbed. Many species thrash about violently when disturbed to scare away potential predators. One species (*Amorpha juglandis*) even makes high pitched whistles that can scare away birds.[19]

Social behaviors and relationships with other insects

Some caterpillars obtain protection by associating themselves with ants. The Lycaenid butterflies are particularly well known for this. They communicate with their ant protectors by vibrations as well as chemical means and typically provide food rewards.[20]

Some caterpillars are gregarious; large aggregations are believed to help in reducing the levels of parasitization and predation.[21] Clusters amplify the signal of aposematic coloration, and individuals may participate in group regurgitation or displays. Pine processionary (*Thaumetopoea pityocampa*) caterpillars often link into a long train to move through trees and over the ground. The head of the lead caterpillar is visible, but the other heads can appear hidden.[22] Forest tent caterpillars cluster during periods of cold weather.

Predators

Caterpillars suffer predation from many animals. The European pied flycatcher is one species that preys upon caterpillars. The flycatcher typically finds caterpillars among oak foliage. Paper wasps, including those in the genus *Polistes* and *Polybia* catch caterpillars to feed their young and themselves.

Behavior

Caterpillars have been called "eating machines", and eat leaves voraciously. Most species shed their skin four or five times as their bodies grow, and they eventually enter a pupal stage before becoming adults.[23] Caterpillars grow very quickly; for instance, a tobacco hornworm will increase its weight ten-thousandfold in less than twenty days. An adaptation that enables them to eat so much is a mechanism in a specialized midgut that quickly transports ions to the lumen (midgut cavity), to keep the potassium level higher in the midgut cavity than in the hemolymph.[24]


A pasture day moth caterpillar feeding on capeweed

Most caterpillars are solely herbivorous. Many are restricted to feeding on one species of plant, while others are polyphagous. Some, including the clothes moth, feed on detritus. Some are predatory, and may prey on other species of caterpillars (e.g. Hawaiian *Eupithecia*). Others feed on eggs of other insects, aphids, scale insects, or ant larvae. A few are parasitic on cicadas or leaf hoppers (Epipyropidae).[25] Some Hawaiian caterpillars (*Hyposmocoma molluscivora*) use silk traps to capture snails.[26]

A gypsy moth caterpillar

Many caterpillars are nocturnal. For example, the "cutworms" (of the family Noctuidae) hide at the base of plants during the day and only feed at night.[27] Others, such as gypsy moth (Lymantria dispar) larvae, change their activity patterns depending on density and larval stage, with more diurnal feeding in early instars and high densities.[28]

Economic effects

Hypsipyla grandela damages mahogany in Brazil

Caterpillars cause much damage, mainly by eating leaves. The propensity for damage is enhanced by monocultural farming practices, especially where the caterpillar is specifically adapted to the host plant under cultivation. The cotton bollworm causes enormous losses. Other species eat food crops. Caterpillars have been the target of pest control through the use of pesticides, biological control and agronomic practices. Many species have become resistant to pesticides. Bacterial toxins such as those from *Bacillus thuringiensis* which are evolved to affect the gut of Lepidoptera have been used in sprays of bacterial spores, toxin extracts and also by incorporating genes to produce them within the host plants. These approaches are defeated over time by the evolution of resistance mechanisms in the insects.[29]

Plants evolve mechanisms of resistance to being eaten by caterpillars, including the evolution of chemical toxins and physical barriers such as hairs. Incorporating host plant resistance (HPR) through plant breeding is another approach used in reducing the impact of caterpillars on crop plants.[30]

Some caterpillars are used in industry. The silk industry is based on the silkworm caterpillar.

Human health

Buck moth caterpillar sting on a shin twenty-four hours after occurrence in south Louisiana. The reddish mark covers an area about 20 mm at its widest point by about 70 mm in length.

Caterpillar hair can be a cause of human health problems. Caterpillar hairs sometimes have venoms in them and species from approximately 12 families of moths or butterflies worldwide can inflict serious human injuries ranging from urticarial dermatitis and atopic asthma to osteochondritis, consumption coagulopathy, renal failure, and intracerebral hemorrhage.[31] Skin rashes are the most common, but there have been fatalities.[32] *Lonomia* is a frequent cause of envenomation in Brazil, with 354 cases reported between 1989 and 2005. Lethality ranging up to 20% with death caused most often by intracranial hemorrhage.[33]

Caterpillar hair has also been known to cause kerato-conjunctivitis. The sharp barbs on the end of caterpillar hairs can get lodged in soft tissues and mucous membranes such as the eyes. Once they enter such tissues, they can be difficult to extract, often exacerbating the problem as they migrate across the membrane.[34]

This becomes a particular problem in an indoor setting. The hair easily enter buildings through ventilation systems and accumulate in indoor environments because of their small size, which makes it difficult for them to be vented out. This accumulation increases the risk of human contact in indoor environments.[35]

Caterpillars are a food source in some cultures. For example, in South Africa mopane worms are eaten by the bushmen, and in China silkworms are considered a delicacy.

In popular culture

William Blake's illustration of a caterpillar overlooking a child from his illustrated book *For Children The Gates of Paradise*.[36]

In the Old Testament of the Bible caterpillars are feared as pest that devour crops. They are part of the "pestilence, blasting, mildew, locus" because of their association with the locust, thus they are one of the plagues of Egypt. Jeremiah names them as one of the inhabitants of Babylon. The English word caterpillar derives from the old French *catepelose* (hairy cat) but merged with the *piller* (pillager). Caterpillars became a symbol for social dependents. Shakespeare's Bolingbroke described King Richard's friends as "The caterpillars of the commonwealth, Which I have sworn to weed and pluck away". In 1790 William Blake referenced this popular image in The Marriage of Heaven and Hell when he attacked priests: "as the caterpillar chooses the fairest leaves to lay her eggs on, so the priest lay his curse on the fairest joys".[37]

The role of caterpillars in the life stages of butterflies was badly understood. In 1679 Maria Sibylla Merian published the first volume of *The Caterpillars' Marvelous Transformation and Strange Floral Food*, which contained 50 illustrations and a description of insects, moths, butterflies and their larvae.[38] An earlier popular publication on moths and butterflies, and their caterpillars, by Jan Goedart had not included eggs in the life stages of European moths and butterflies, because he had believed that caterpillars were generated from water. When Merian published her study of caterpillars it was still widely believed that insects were spontaneously generated. Merian's illustrations supported the findings of Francesco Redi, Marcello Malpighi and Jan Swammerdam.[39]

A 1907 illustrations by Arthur Rackham of the Caterpillar talking to Alice in Alice's Adventures in Wonderland

Butterflies were regarded as symbol for the human soul since ancient time, and also in the Christian tradition.[40] Goedart thus located his empirical observations on the transformation of caterpillars into butterflies in the Christian tradition. As such he argued that the metamorphosis from caterpillar into butterfly was a symbol, and even proof, of Christ's resurrection. He argued "that from dead caterpillars emerge living animals; so it is equally true and miraculous, that our dead and rotten corpses will rise from the grave."[41] Swammerdam, who in 1669 had demonstrated that inside a caterpillar the rudiments of the future butterfly's limbs and wings could be discerned, attacked the mystical and religious notion that the caterpillar died and the butterfly subsequently resurrected.[42] As a militant Cartesian, Swammerdam attacked Goedart as ridiculous, and when publishing his findings he proclaimed "here we witness the digression of those who have tried to prove Resurrection of the Dead from these obviously natural and comprehensible changes within the creature itself."[43]

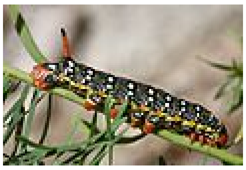
Since then the metamorphoses of the caterpillar into a butterfly has in Western societies been associated with countless human transformations in folktales and literature. There is no process in the physical life of human beings that resembles this metamorphoses, and the symbol of the caterpillar tends to depict a psychic transformation of a human. As such the caterpillar has in the Christian tradition become a metaphor for being "born again".[44]

Famously, in Lewis Carroll's Alice's Adventures in Wonderland a caterpillar asks Alice "Who are you?". When Alice comments on the caterpillar's inevitable transformation into a butterfly, the caterpillar champions the position that in spite of changes it is still possible to know something, and that Alice is the same Alice at the beginning and end of a considerable interval.[45] When the Caterpillar asks Alice to clarify a point, the child replies "I'm afraid I can't put it more clearly... for I can't but understand it myself, to begin with, and being so many different sizes in a day is very confusing". Here Carroll satirizes René Descartes, the founder of Cartesian philosophy, and his theory on innate ideas. Descartes argued that we are distracted by urgent bodily stimuli that swamp the human mind in childhood. Descartes also theorised that inherited preconceived opinions obstruct the human perception of the truth.[46]

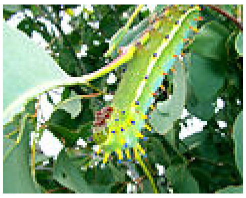
More recent symbolic references to caterpillars in popular media include the *Mad Men* season 3 episode "The Fog", in which Betty Draper has a drug-induced dream, while in labor, that she captures a caterpillar and holds it firmly in her hand.[47] In *The Sopranos* season 5 episode "The Test Dream", Tony Soprano dreams that Ralph Cifaretto has a caterpillar on his bald head that changes into a butterfly.

Gallery

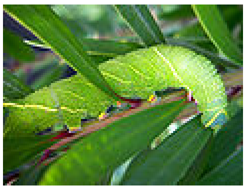
Click left or right for a slide show.



Caterpillar of the spurge hawk-moth, near Binn, Valais, Switzerland at c. 2 km altitude.



Caterpillar of the emperor gum moth.

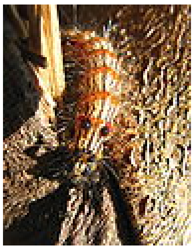


A poplar hawk-moth caterpillar (a common species of caterpillar in the UK).

Ant tending a lycaenid caterpillar.

Life cycle of the red-humped caterpillar (*Schizura concinna*).

Forest tent caterpillar (Malacosoma disstria)



Camouflage: apparently with eight eyes, only two of them are real. Photo in a eucalyptus tree, São Paulo, Brazil

Caterpillar of the Polyphemus moth (*Antheraea polyphemus*), Virginia, United States

Caterpillars on an apple tree in Victoria, British Columbia, Canada

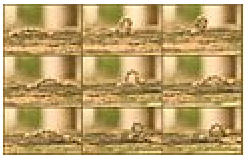
Caterpillar on a leaf

Caterpillar of Belize

Dryas iulia

Caterpillar of great orange tip resembling the common green vine snake (*Ahaetulla nasuta*)

Prepupa of cabbage looper in its cocoon



Locomotion of a small Geometrid caterpillar.

See also

- Edible caterpillars
- Larval food plants of Lepidoptera
- Lepidopterism - caterpillar dermatitis
- List of pests and diseases of roses
- Sericulture

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Grasshopper

Grasshoppers are a group of insects belonging to the suborder Caelifera. They are among what is probably the most ancient living group of chewing herbivorous insects, dating back to the early Triassic around 250 million years ago.

Grasshoppers are typically ground-dwelling insects with powerful hind legs which allow them to escape from threats by leaping vigorously. As hemimetabolous insects, they do not undergo complete metamorphosis; they hatch from an egg into a nymph or "hopper" which undergoes five moults, becoming more similar to the adult insect at each developmental stage. At high population densities and under certain environmental conditions, some grasshopper species can change color and behavior and form swarms. Under these circumstances, they are known as locusts.

Grasshoppers are plant-eaters, with a few species at times becoming serious pests of cereals, vegetables and pasture, especially when they swarm in their millions as locusts and destroy crops over wide areas. They protect themselves from predators by camouflage; when detected, many species attempt to startle the predator with a brilliantly-coloured wing-flash while jumping and (if adult) launching themselves into the air, usually flying for only a short distance. Other species such as the rainbow grasshopper have warning coloration which deters predators. Grasshoppers are affected by parasites and various diseases, and many predatory creatures feed on both nymphs and adults. The eggs are subject to attack by parasitoids and predators.

Grasshoppers have had a long relationship with humans. Swarms of locusts can have devastating effects and cause famine, and even in smaller numbers, the insects can be serious pests. They are used as food in countries such as Mexico and Indonesia. They feature in art, symbolism and literature.

Grasshopper

Temporal range: 252 Ma–Recent

American grasshopper (*Schistocerca americana*)

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Orthoptera
Suborder:	Caelifera
Infraorder:	Acrididea
Informal group:	Acridomorpha Dirsh, 1966

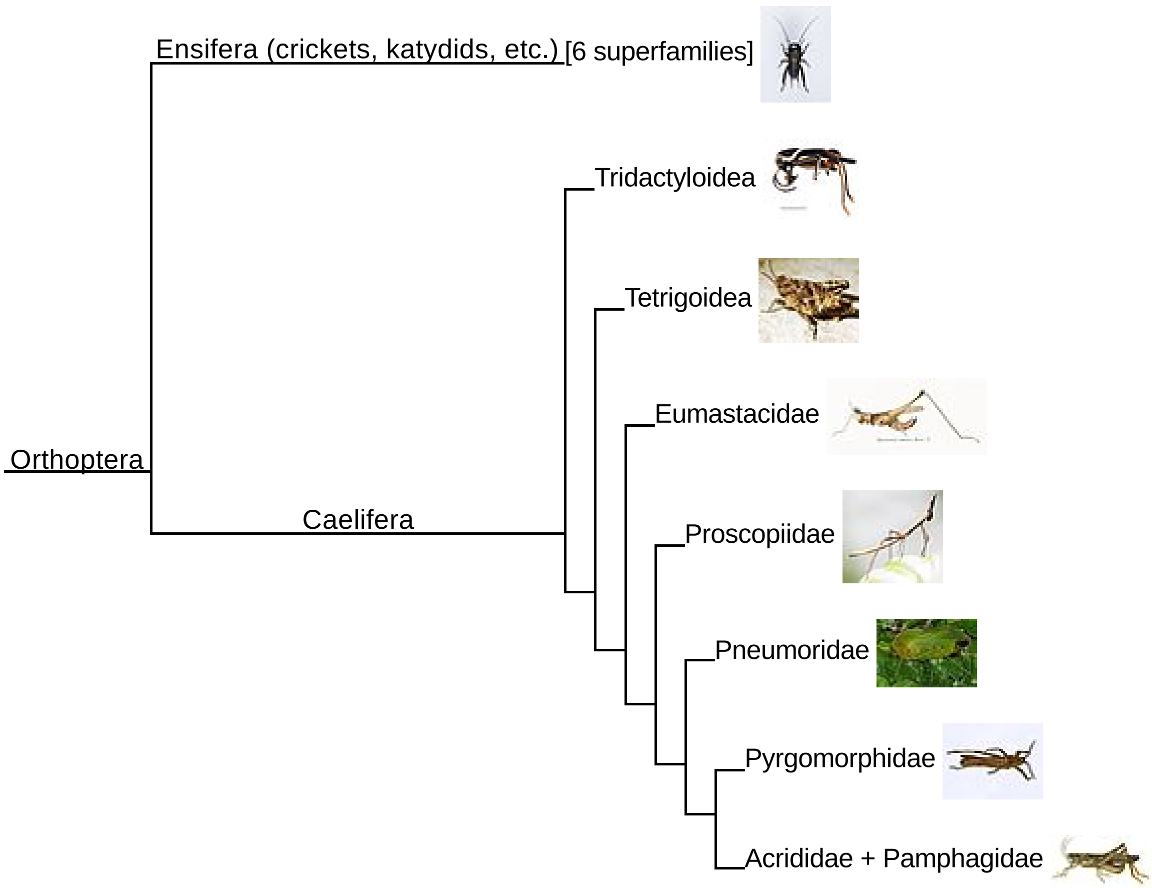
Superfamilies

- Acridoidea
- Eumastacoidea
- Pneumoroidea
- Proscopioidea
- Pyrgomorphoidea
- Tanaoceroidea
- Trigonopterygoidea

Contents

Phylogeny

Grasshoppers belong to the suborder Caelifera. Although, "grasshopper" is sometimes used as a common name for the suborder in general,[1][2][3] some sources restrict it to the more "advanced" groups.[4] They may be placed in the infraorder Acrididea[5] and have been referred-to as "short-horned grasshoppers" in older texts[6] to distinguish them from the also-obsolete term "long-horned grasshoppers" (now bush-crickets or katydids) with their much longer antennae. The phylogeny of the Caelifera, based on mitochondrial ribosomal RNA of thirty-two taxa in six out of seven superfamilies, is shown as a cladogram. The Ensifera (crickets, *etc.*), Caelifera and all the superfamilies of grasshoppers except Pamphagoidea appear to be monophyletic.[7][8]



In evolutionary terms, the split between the Caelifera and the Ensifera is no more recent than the Permo-Triassic boundary;[9] the earliest insects that are certainly Caeliferans are in the extinct families Locustopseidae and Locustavidae from the early Triassic, roughly 250 million years ago. The group diversified during the Triassic and have remained important plant-eaters from that time to now. The first modern families such as the Eumastacidae, Tetrigidae and Tridactylidae appeared in the Cretaceous, though some insects that might belong to the last two of these groups are found in the early Jurassic.[10][11] Morphological classification is difficult because many taxa have converged towards a common habitat type; recent taxonomists have concentrated on the internal genitalia, especially those of the male. This information is not available from fossil specimens, and the palaentological taxonomy is founded principally on the venation of the hindwings.[12]

Fossil grasshoppers at the Royal Ontario Museum

The Caelifera includes some 2,400 valid genera and about 11,000 known species. Many undescribed species probably exist, especially in tropical wet forests. The Caelifera have a predominantly tropical distribution with fewer species known from temperate zones, but most of the superfamilies have representatives worldwide. They are almost exclusively herbivorous and are probably the oldest living group of chewing herbivorous insects.[12]

The most diverse superfamily is the Acridoidea, with around 8,000 species. The two main families in this are the Acrididae (grasshoppers and locusts) with a worldwide distribution, and the Romaleidae (lubber grasshoppers), found chiefly in the New World. The Ommexechidae and Tristiridae are South American, and the Lentulidae, Lithidiidae and Pamphagidae are mainly African. The Pauliniids are nocturnal and can swim or skate on water, and the Lentulids are wingless.[10] Pneumoridae are native to Africa, particularly southern Africa, and are distinguished by the inflated abdomens of the males.[13]

Characteristics

Grasshoppers have the typical insect body plan of head, thorax and abdomen. The head is held vertically at an angle to the body, with the mouth at the bottom. The head bears a large pair of compound eyes which give all-round vision, three simple eyes which can detect light and dark, and a pair of thread-like antennae that are sensitive to touch and smell. The downward-directed mouthparts are modified for chewing and there are two sensory palps in front of the jaws.[14]

The thorax and abdomen are segmented and have a rigid cuticle made up of overlapping plates composed of chitin. The three fused thoracic segments bear three pairs of legs and two pairs of wings. The forewings, known as tegmina, are narrow and leathery while the hindwings are large and membranous, the veins providing strength. The legs are terminated by claws for gripping. The hind leg is particularly powerful; the femur is robust and has several ridges where different surfaces join and the inner ridges bear stridulatory pegs in some species. The posterior edge of the tibia bears a double row of spines and there are a pair of articulated spurs near its lower end. The interior of the thorax houses the muscles that control the wings and legs.[14]

The abdomen has eleven segments, the first of which is fused to the thorax and contains the tympanal organ and hearing system. Segments two to eight are ring-shaped and joined by flexible membranes. Segments nine to eleven are reduced in size; segment nine bears a pair of cerci and segments ten and eleven house the reproductive organs. Female grasshoppers are normally larger than males, with short ovipositors.[14] The name of the suborder "Caelifera" comes from the Latin and means *chisel-bearing*, referring to the shape of the ovipositor.[15]

Those species that make easily heard noises usually do so by rubbing a row of pegs on the hind legs against the edges of the forewings (stridulation). These sounds are produced mainly by males to attract females, though in some species the females also stridulate.[16]

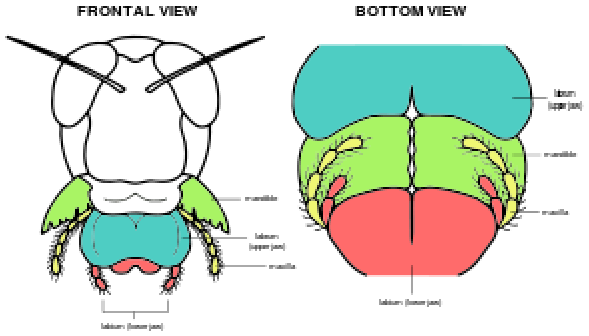
Grasshoppers may be confused with crickets, but they differ in many aspects; these include the number of segments in their antennae and the structure of the ovipositor, as well as the location of the tympanal organ and the methods by which sound is produced.[17] Ensiferans have antennae that can be much longer than the body and have at least 20–24 segments, while caeliferans have fewer segments in their shorter, stouter antennae.[16]

Ensifera, like this great green bush-cricket *Tettigonia viridissima*, somewhat resemble grasshoppers but have over 20 segments in their antennae and different ovipositors.

Biology

Diet and digestion

Most grasshoppers are polyphagous, eating vegetation from multiple plant sources,[18] but some are omnivorous and also eat animal tissue and animal faeces. In general their preference is for grasses, including many cereals grown as crops.[19] The digestive system is typical of insects, with Malpighian tubules discharging into the midgut. Carbohydrates are digested mainly in the crop, while proteins are digested in the ceca of the midgut. Saliva is abundant but largely free of enzymes, helping to move food and Malpighian secretions along the gut. Some grasshoppers possess cellulase, which by softening plant cell walls makes plant cell contents accessible to other digestive enzymes.[20]



Structure of mouthparts

Sensory organs

Grasshoppers have a typical insect nervous system, and have an extensive set of external sense organs. On the side of the head are a pair of large compound eyes which give a broad field of vision and can detect movement, shape, colour and distance. There are also three simple eyes (ocelli) on the forehead which can detect light intensity, a pair of antennae containing olfactory (smell) and touch receptors, and mouthparts containing gustatory (taste) receptors.[21] At the front end of the abdomen there is a pair of tympanal organs for sound reception. There are numerous fine hairs (setae) covering the whole body that act as mechanoreceptors (touch and wind sensors), and these are most dense on the antennae, the palps (part of the mouth), and on the cerci at the tip of the abdomen.[22] There are special receptors (campaniform sensillae) embedded in the cuticle of the legs that sense pressure and cuticle distortion.[23] There are internal "chordotonal" sense organs specialized to detect position and movement about the joints of the exoskeleton. The receptors convey information to the central nervous system through sensory neurons, and most of these have their cell bodies located in the periphery near the receptor site itself.[22]

Frontal view of Egyptian locust (*Anacridium aegyptium*) showing the compound eyes, tiny ocelli and numerous setae

Circulation and respiration

Like other insects, grasshoppers have an open circulatory system and their body cavities are filled with haemolymph. A heart-like structure in the upper part of the abdomen pumps the fluid to the head from where it percolates past the tissues and organs on its way back to the abdomen. This system circulates nutrients throughout the body and carries metabolic wastes to be excreted into the gut. Other functions of the haemolymph include wound healing, heat transfer and the provision of hydrostatic pressure, but the circulatory system is not involved in gaseous exchange.[24] Respiration is performed using tracheae, air-filled tubes, which open at the surfaces of the thorax and abdomen through pairs of valved spiracles. Larger insects may need to actively ventilate their bodies by opening some spiracles while others remain closed, using abdominal muscles to expand and contract the body and pump air through the system.[25]

Jumping

A large grasshopper, such as a locust, can jump about a metre (twenty body lengths) without using its wings; the acceleration peaks at about 20 g.[26] Grasshoppers jump by extending their large back legs and pushing against the substrate (the ground, a twig, a blade of grass or whatever else they are standing on); the reaction force propels them into the air.[27] They jump for several reasons; to escape from a predator, to launch themselves into flight, or simply to move from place to place. For the escape jump in particular there is strong selective pressure to maximize take-off velocity, since this determines the range. This means that the legs must thrust against the ground with both high force and a high velocity of movement. A fundamental property of muscle is that it cannot contract with high force and high velocity at the same time. Grasshoppers overcome this by using a catapult mechanism to amplify the mechanical power produced by their muscles.[28]

The jump is a three-stage process.[29] First, the grasshopper fully flexes the lower part of the leg (tibia) against the upper part (femur) by activating the flexor tibiae muscle (the back legs of the grasshopper in the top photograph are in this preparatory position). Second, there is a period of co-contraction in which force builds up in the large, pennate extensor tibiae muscle, but the tibia is kept flexed by the simultaneous contraction of the flexor tibiae muscle. The extensor muscle is much stronger than the flexor muscle, but the latter is aided by specialisations in the joint that give it a large effective mechanical advantage over the former when the tibia is fully flexed.[30] Co-contraction can last for up to half a second, and during this period the extensor muscle shortens and stores elastic strain energy by distorting stiff cuticular structures in the leg.[31] The extensor muscle contraction is quite slow (almost isometric), which allows it to develop high force (up to 14 N in the desert locust), but because it is slow only low power is needed. The third stage of the jump is the trigger relaxation of the flexor muscle, which releases the tibia from the flexed position. The subsequent rapid tibial extension is driven mainly by the relaxation of the elastic structures, rather than by further shortening of the extensor muscle. In this way the stiff cuticle acts like the elastic of a catapult, or the bow of a bow-and-arrow. Energy is put into the store at low power by slow but strong muscle contraction, and retrieved from the store at high power by rapid relaxation of the mechanical elastic structures.[32][33]

Stridulation

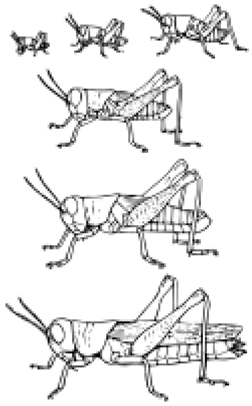
Male grasshoppers spend much of the day stridulating, singing more actively under optimal conditions and being more subdued when conditions are adverse; females also stridulate, but their efforts are insignificant when compared to the males. Late-stage male nymphs can sometimes be seen making stridulatory movements, although they lack the equipment to make sounds, demonstrating the importance of this behavioural trait. The songs are a means of communication; the male stridulation seems to express reproductive maturity, the desire for social cohesion and individual well-being. Social cohesion becomes necessary among grasshoppers because of their ability to jump or fly large distances, and the song can serve to limit dispersal and guide others to favourable habitat. The generalised song can vary in phraseology and intensity, and is modified in the presence of a rival male, and changes again to a courtship song when a female is nearby.[34] In male grasshoppers of the family Pneumoridae, the enlarged abdomen amplifies stridulation.[13]

Life cycle

In most grasshopper species, conflicts between males over females rarely escalate beyond ritualistic displays. Some exceptions include the chameleon grasshopper (*Kosciuscola tristis*), where males may fight on top of ovipositing females; engaging in leg grappling, biting, kicking and mounting.[35]

Romalea microptera grasshoppers: female (larger) is laying eggs, with male in attendance.

The newly emerged female grasshopper has a preoviposition period of a week or two while she increases in weight and her eggs mature. After mating, the female of most species digs a hole with her ovipositor and lays a batch of eggs in a pod in the ground near food plants, generally in the summer. After laying the eggs, she covers the hole with soil and litter.[14] Some, like the semi-aquatic *Cornops aquaticum*, deposit the pod directly into plant tissue.[36] The eggs in the pod are glued together with a froth in some species. After a few weeks of development, the eggs of most species in temperate climates go into diapause, and pass the winter in this state. Diapause is broken by a sufficiently low ground temperature, with development resuming as soon as the ground warms above a certain threshold temperature. The embryos in a pod generally all hatch out within a few minutes of each other. They soon shed their membranes and their exoskeletons harden. These first instar nymphs can then jump away from predators.[37]



Six stages (instars) of development, from newly hatched nymph to fully winged adult

Grasshoppers undergo incomplete metamorphosis: they repeatedly moult, each instar becoming larger and more like an adult, with the wing-buds increasing in size at each stage. The number of instars varies between species but is often six. After the final moult, the wings are inflated and become fully functional. The migratory grasshopper, *Melanoplus sanguinipes*, spends about 25 to 30 days as a nymph, depending on sex and temperature, and lives for about 51 days as an adult.[37]

Swarming

Millions of plague locusts on the move in Australia

Locusts are the swarming phase of certain species of short-horned grasshoppers in the family Acrididae. Swarming behaviour is a response to overcrowding. Increased tactile stimulation of the hind legs causes an increase in levels of serotonin.[38] This causes the grasshopper to change colour, feed more and breed faster. The transformation of a solitary individual into a swarming one is induced by several contacts per minute over a short period.[39]

Following this transformation, under suitable conditions dense nomadic bands of flightless nymphs known as "hoppers" can occur, producing pheromones which attract the insects to each other. With several generations in a year, the locust population can build up from localised groups into vast accumulations of flying insects known as plagues, devouring all the vegetation they encounter. The largest recorded locust swarm was one formed by the now-extinct Rocky Mountain locust in 1875; the swarm was 1,800 miles (2,900 km) long and 110 miles (180 km) wide,[40] and one estimate puts the number of locusts involved at 3.5 trillion.[41] An adult desert locust can eat about 2 g (0.1 oz) of plant material each day, so the billions of insects in a large swarm can be very destructive, stripping all the foliage from plants in an affected area and consuming stems, flowers, fruits, seeds and bark.[42]

Predators, parasites and pathogens

Grasshoppers have a wide range of predators at different stages of their lives; eggs are eaten by bee-flies, ground beetles and blister beetles; hoppers and adults are taken by other insects such as ants, robber flies and sphecid wasps, by spiders, and by many birds and small mammals including dogs and cats.[43]

Cottontop tamarin monkey eating a grasshopper

The eggs and nymphs are under attack by parasitoids including blow flies, flesh flies, and tachinid flies. External parasites of adults and nymphs include mites.[43] Female grasshoppers parasitised by mites produce fewer eggs and thus have fewer offspring than unaffected individuals.[44]

Grasshopper with parasitic mites

The grasshopper nematode (*Mermis nigrescens*) is a long slender worm that infects grasshoppers, living in the insect's hemocoel. Adult worms lay eggs on plants and the host becomes infected when the foliage is eaten.[45] *Spinochordodes tellinii* and *Paragordius tricuspidatus* are parasitic worms that infect grasshoppers and alter the behaviour of their hosts. When the worms are sufficiently developed, the grasshopper is persuaded to leap into a nearby body of water where it drowns, thus enabling the parasite to continue with the next stage of its life cycle, which takes place in water.[46][47]

Locusts killed by the naturally occurring fungus *Metarhizium*, an environmentally friendly means of biological control. CSIRO, 2005[48]

Grasshoppers are affected by diseases caused by bacteria, viruses, fungi and protozoa. The bacteria *Serratia marcescens* and *Pseudomonas aeruginosa* have both been implicated in causing disease in grasshoppers, as has the entomopathogenic fungus *Beauveria bassiana*. This widespread fungus has been used to control various pest insects around the world, but although it infects grasshoppers, the infection is not usually lethal because basking in the sun has the result of raising the insect's temperature above a threshold tolerated by the fungus.[49] The fungal pathogen *Entomophaga grylli* is able to influence the behaviour of its grasshopper host, causing it to climb to the top of a plant and cling to the stem as it dies. This ensures wide dispersal of the fungal spores liberated from the corpse.[50]

The fungal pathogen *Metarhizium acridum* is found in Africa, Australia and Brazil where it has caused epizootics in grasshoppers. It is being investigated for possible use as a microbial insecticide for locust control.[49] The microsporidian fungus *Nosema locustae*, once considered to be a protozoan, can be lethal to grasshoppers. It has to be consumed by mouth and is the basis for a bait-based commercial microbial pesticide. Various other microsporidians and protozoans are found in the gut.[49]

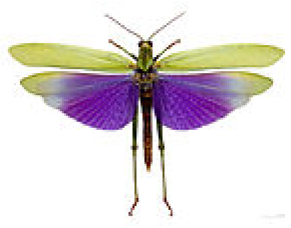
Anti-predator defences

Grasshoppers exemplify a range of anti-predator adaptations, enabling them to avoid detection, to escape if detected, and in some cases to avoid being eaten if captured. Grasshoppers are often camouflaged to avoid detection by predators that hunt by sight; some species can change their coloration to suit their surroundings.[51]

Several species such as the hooded leaf grasshopper *Phyllochoreia ramakrishnai* (Eumastacoidea) are detailed mimics of leaves. Stick grasshoppers (Proscopiidae) mimic wooden sticks in form and coloration.[52] Grasshoppers often have deimatic patterns on their wings, giving a sudden flash of bright colours that may startle predators long enough to give time to escape in a combination of jump and flight.[53]

Some species are genuinely aposematic, having both bright warning coloration and sufficient toxicity to dissuade predators. *Dictyophorus productus* (Pyrgomorphidae) is a "heavy, bloated, sluggish insect" that makes no attempt to hide; it has a bright red abdomen. A *Cercopithecus* monkey that ate other grasshoppers refused to eat the species.[54] Another species, the rainbow or painted grasshopper of Arizona, *Dactylotum bicolor* (Acridoidea), has been shown by experiment with a natural predator, the little striped whiptail lizard, to be aposematic.[55]

Gaudy grasshopper, *Atractomorpha lata*, evades predators with camouflage.



Lubber grasshopper, *Titanacris albipes*, has deimatically coloured wings, used to startle predators.

Leaf grasshopper, *Phyllochoreia ramakrishnai*, mimics a green leaf.

Painted grasshopper, *Dactylotum bicolor*, deters predators with warning coloration.

Spotted grasshopper, *Aularches miliaris*, defends itself with toxic foam and warning colours.[56]

Relationship with humans

In art and media

Grasshoppers are occasionally depicted in artworks, such as the Dutch Golden Age painter Balthasar van der Ast's still life oil painting, *Flowers in a Vase with Shells and Insects*, c. 1630, now in the National Gallery, London, though the insect may be a bush-cricket.[57]

Detail of grasshopper on table in Rachel Ruysch's painting *Flowers in a Vase*, c. 1685. National Gallery, London

Another orthopteran is found in Rachel Ruysch's still life *Flowers in a Vase*, c. 1685. The seemingly static scene is animated by a "grasshopper on the table that looks about ready to spring", according to the gallery curator Betsy Wieseman, with other invertebrates including a spider, an ant, and two caterpillars.[58][59]

Grasshoppers are also featured in cinema. The 1957 film *Beginning of the End* portrayed giant grasshoppers attacking Chicago.[60] In the 1998 Disney/Pixar animated film *A Bug's Life*, the heroes are Flik and the ant colony, and Hopper and his henchmen are the grasshoppers.[61]

Symbolism

Sir Thomas Gresham's gilded grasshopper symbol, Lombard Street, London, 1563

Grasshoppers are sometimes used as symbols.[62] During the Greek Archaic Era, the grasshopper was the symbol of the *polis* of Athens,[63] possibly because they were among the most common insects on the dry plains of Attica.[63] Native Athenians for a while wore golden grasshopper brooches to symbolise that they were of pure Athenian lineage with no foreign ancestors.[63] Another symbolic use of the grasshopper is Sir Thomas Gresham's gilded grasshopper in Lombard Street, London, dating from 1563;[a] the building was for a while the headquarters of the Guardian Royal Exchange, but the company declined to use the symbol for fear of confusion with the locust.[64]

When grasshoppers appear in dreams, these have been interpreted as symbols of "Freedom, independence, spiritual enlightenment, inability to settle down or commit to decision". Locusts are taken literally to mean devastation of crops in the case of farmers; figuratively as "wicked men and women" for non-farmers; and "Extravagance, misfortune, & ephemeral happiness" by "gypsies".[65]

As food

In some countries, grasshoppers are used as food.[66] In southern Mexico, grasshoppers, known as *chapulines*, are eaten in a variety of dishes, such as in tortillas with chilli sauce.[67] Grasshoppers are served on skewers in some Chinese food markets, like the Donghuamen Night Market.[68] Fried grasshoppers (*walang goreng*) are eaten in the Gunung Kidul Regency, Yogyakarta, Java in Indonesia.[69] In America, the Ohlone burned grassland to herd grasshoppers into pits where they could be collected as food.[70]

Fried grasshoppers from Gunung Kidul, Yogyakarta, Indonesia

It is recorded in the Bible that John the Baptist ate locusts and wild honey (Greek: ἀκρίδες καὶ μέλι ἄγριον, *akrídes kaì méli ágrion*) while living in the wilderness.[71] However, because of a tradition of depicting him as an ascetic, attempts have been made to explain that the *locusts* were in fact a suitably ascetic vegetarian food such as carob beans, notwithstanding the fact that the word *ἀκρίδες* means plainly *grasshoppers*.[72][73]

As pests

Crop pest: grasshopper eating a maize leaf

Grasshoppers eat large quantities of foliage both as adults and during their development, and can be serious pests of arid land and prairies. Pasture, grain, forage, vegetable and other crops can be affected. Grasshoppers often bask in the sun, and thrive in warm sunny conditions, so drought stimulates an increase in grasshopper populations. A single season of drought is not normally sufficient to stimulate a major population increase, but several successive dry seasons can do so, especially if the intervening winters are mild so that large numbers of nymphs survive. Although sunny weather stimulates growth, there needs to be an adequate food supply for the increasing grasshopper population. This means that although precipitation is needed to stimulate plant growth, prolonged periods of cloudy weather will slow nymphal development.[74]

Grasshoppers can best be prevented from becoming pests by manipulating their environment. Shade provided by trees will discourage them and they may be prevented from moving onto developing crops by removing coarse vegetation from fallow land and field margins and discouraging thick growth beside ditches and on roadside verges. With increasing numbers of grasshoppers, predator numbers may increase, but this seldom happens rapidly enough to have much effect on populations. Biological control is being investigated, and spores of the protozoan parasite *Nosema locustae* can be used mixed with bait to control grasshoppers, being more effective with immature insects.[75] On a small scale, neem products can be effective as a feeding deterrent and as a disruptor of nymphal development. Insecticides can be used, but adult grasshoppers are difficult to kill, and as they move into fields from surrounding rank growth, crops may soon become reinfested.[74]

Some grasshopper species, like the Chinese rice grasshopper, are a pest in rice paddies. Ploughing exposes the eggs on the surface of the field, to be destroyed by sunshine or eaten by natural enemies. Some eggs may be buried too deeply in the soil for hatching to take place.[76]

Locust plagues can have devastating effects on human populations, causing famines and population upheavals. They are mentioned in both the Koran and the Bible and have also been held responsible for cholera epidemics, resulting from the corpses of locusts drowned in the Mediterranean Sea and decomposing on beaches.[42] The FAO and other organisations monitor locust activity around the world. Timely application of pesticides can prevent nomadic bands of hoppers from forming before dense swarms of adults can build up.[77] Besides conventional control using contact insecticides,[77] biological pest control using the entomopathogenic fungus *Metarhizium acridum*, which specifically infects grasshoppers, has been used with some success.[78]

In literature

Egyptian hieroglyphs "snḥm"

The Egyptian word for locust or grasshopper was written *snḥm* in the consonantal hieroglyphic writing system. The pharaoh Ramesses II compared the armies of the Hittites to locusts: "They covered the mountains and valleys and were like locusts in their multitude."[79]

One of Aesop's Fables, later retold by La Fontaine, is the tale of *The Ant and the Grasshopper*. The ant works hard all summer, while the grasshopper plays. In winter, the ant is ready but the grasshopper starves. Somerset Maugham's short story "The Ant and the Grasshopper" explores the fable's symbolism via complex framing.[80] Other human weaknesses besides improvidence have become identified with the grasshopper's behaviour.[65] So an unfaithful woman (hopping from man to man) is "a grasshopper" in "Poprygunya", an 1892 short story by Anton Chekhov,[81] and in Jerry Paris's 1969 film *The Grasshopper*.[82][83]

In mechanical engineering

The name "Grasshopper" was given to the Aeronca L-3 and Piper L-4 light aircraft, both used for reconnaissance and other support duties in World War II. The name is said to have originated when Major General Innis P. Swift saw a Piper making a rough landing and remarked that it looked like a "damned grasshopper" for its bouncing progress.[83][84][85]

A grasshopper beam engine, 1847

Grasshopper beam engines were beam engines pivoted at one end, the long horizontal arm resembling the hind leg of a grasshopper. The type was patented by William Freemantle in 1803.[86][87][88]

Notes

a. The symbol is a wordplay on the name Gresham and "grass".[62]

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Manduca quinquemaculata

Manduca quinquemaculata, the **five-spotted hawkmoth**, is a brown and gray hawk moth of the family Sphingidae. The caterpillar, often referred to as the **tomato hornworm**, can be a major pest in gardens; they get their name from a dark projection on their posterior end and their use of tomatoes as host plants. Tomato hornworms are closely related to (and sometimes confused with) the tobacco hornworm *Manduca sexta*. This confusion arises because caterpillars of both species have similar morphologies and feed on the foliage of various plants from the family Solanaceae, so either species can be found on tobacco or tomato leaves. Because of this, the plant on which the caterpillar is found does not indicate its species.

Manduca quinquemaculata	
	
Male - dorsal view	
	
Male - ventral view	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Lepidoptera
Family:	Sphingidae
Genus:	*Manduca*
Species:	***M. quinquemaculata***
Binomial name	
Manduca quinquemaculata (Haworth, 1803)[1]	
Synonyms	

- *Sphinx 5-maculatus* Haworth, 1803
- *Phlegethontius quinquemaculatus*
- *Protoparce quinquemaculatus*

Contents

Range

M. quinquemaculata is found across North America and Australia. The tobacco hornworm, a close relative of the tomato hornworm, tends to dominate the south while tomato hornworms are more prevalent in the northern United States.[2]

Food plants

Larva

Tomato hornworms are known to eat various plants from the family Solanaceae, commonly feeding on tomato, eggplant, pepper, tobacco, moonflowers and potato. Females prefer to oviposit on young leaves near the stem of host plants, and early instar caterpillars can often be found here during the day.[3] In the evening or early morning when sunlight is less direct, the caterpillars will feed on more distal leaves.[4]

- *Phlegethontius celeus* Hübner, 1821
- *Protoparce quinquemaculatus wirti* Schaus, 1927

Adult

Adult diet

Adults feed on nectar from flowering plants including *Datura meteloides,*[5] *Oenothera caespitosa,* and *Mirabilis multiflora.* Most of the food plants they target have large, fragrant white flowers.[6]

Interactions with host plants

Hawkmoths, including *M. quinquemaculata,* are the primary pollinators of *D. meteloides.* The length of the moth's proboscis (around 10 cm), which is an elongated, tubular mouthpart used for sucking and feeding, is well-suited for retrieving nectar from the flowers. Aside from being a host plant for *M. quinquemaculata, D. meteloides* has also been used by humans for its opioid effects. *D. meteloides* contains tropane alkaloids, which are present throughout the plant including in the flowers.[5] These alkaloids have an intoxicating effects on the moth, which displays erratic flight patterns as well as uncoordinated, and often unsuccessful, landing attempts after consuming the nectar. Despite the impairment the nectar causes, the moths have been observed returning to the flowers and consuming more nectar. It has been hypothesized that the "spiked" nectar offers the moths reward beyond just nutrients.[5]

Both *Mirabilis multiflora* and *Oenothera caespitosa* are also dependent on hawkmoths for pollination. *M. quinquemaculata* has been found to feed from *Oenothera caespitosa* first and only later to visit *Mirabilis multiflora,* indicating a preference for the former.[6]

Life cycle

Oviposition

Females lay eggs singly on the surface of host plant leaves in late spring. Larvae hatch after approximately one week.[7] The female decides where to lay eggs based on an assessment of the risk of predation her offspring will face. On the tobacco plant *Nicotiana attenuata,* young leaves close to a plant's stem are more protected from predators and larvae that grow there gain more mass than larvae grown elsewhere on the plant; females prefer to oviposit, or lay their eggs, on these leaves.[3] Eggs are large and range in color from pale green to off-white.[4]

Larva

M. quinquemaculata larvae are large green caterpillars reaching a length of up to 10 cm when fully grown.[7] The caterpillars have a dark, pointed projection on their rear end that earns them the name "hornworm".[7] Although the tomato hornworm, *M. quinquemaculata,* can be confused with the tobacco hornworm, *M. sexta,* the larvae of these species can be distinguished by their lateral markings: tomato hornworms have eight V-shaped white markings with no borders and dark blue or black horns, while tobacco hornworms have seven white diagonal lines with a black border and red horns.[8]

Caterpillars hatch in late spring to early summer. They develop through five instars to reach maturity.[3][7] In warmer climates where the first generation emerges earlier in the year, two generations of caterpillars can coexist in a single summer.[4] Once fully grown, caterpillars fall from their host plants to pupate.[7]

Pupa

Caterpillars pupate in early fall, which means they enter a stage of their life cycle where they become a pupa and undergo transformation into a moth.[7] After pupation, *M. quinquemaculata* overwinter in the soil near their host plants, with adults emerging the following summer.[9][4]

Adults

Adults are large, with a wingspan of up to 13 cm.[7] The wings of the moth are brown and gray with large mottled front wings and smaller hindwings with light and dark zig-zag patterned bands. The abdomens are brown and white with a row of five yellow spots down each side, giving them the name "five-spotted hawkmoth."[10][4] The moths of *M. quinquemaculata* and *M. sexta* can be distinguished by the number of spots on their abdomens.[8]

Shortly after adults emerge from the soil, they mate and females lay their eggs on host plants, renewing the life cycle.[7]

Tomato hornworm larva

closely related tobacco hornworm - note the red horn and lack of V-shaped white markings

Female - dorsal view

Female - ventral view

Relationship with *M. sexta*

M. quinquemaculata and *M. sexta* are both large hawkmoths of the genus *Manduca.* The two species have similar appearances in both larvae and adults and share common food sources, including tobacco.[4][11] Past research, observing that the two species are similar, referred to the two as sister species. However, a recent phylogenetic analysis from Kawahara et al. (2013) found that the two species, though closely related, are not sister species. The authors tracked the ancestral origin of both species to Central America, where the two species diverged from one another.[12]

Pest control

Because the larvae are pests of crop plants such as tomatoes and tobacco, biological control agents and traps have been used to control their populations. Gardeners whose tomato plants are predated by the tomato hornworm pick the caterpillars off of their plants.[4] Some gardeners plant marigolds, which repel the species, near their tomato plants to reduce predation.[13]

Parasites

The parasitoid wasp *Trichogramma* attacks *M. quinquemaculata* eggs. The larvae of the wasp develop in the egg, preventing the development of the caterpillar larvae. *Trichogramma* is a natural enemy of the *M. quinquemaculata* and has also been used as a biological control agent by humans.[14]

Braconidae wasp

A second parasitoid wasp, *Cotesia congregata* of the family Braconidae, also kills *M. quinquemaculata*. Adult females lay their eggs inside the skin of the hornworm caterpillar. After hatching, the wasp larvae use the organs and tissues of the caterpillar as food sources before burrowing out of the skin and pupating on the back and sides of the caterpillar. Once the wasps have emerged from their cocoons, the weakened caterpillar dies. Like the parasitoid wasp mentioned above, these wasps have also been suggested as a means of biological control of the tomato hornworm.[15][16]

closely related tobacco hornworm parasitized by braconid wasp

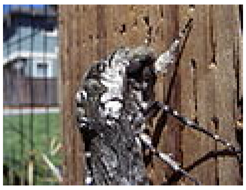
Traps

Adult *M. quinquemaculata* are most active in flight after dark.[10] Early studies found that the moths are attracted to blacklight, which is used as a lure in some traps. Although the traps can be used for research and the moths can be released after capture, traps like these have been suggested as a means of population control. However, one study found that the reduction in population was not strong enough to significantly impact population size.[17]

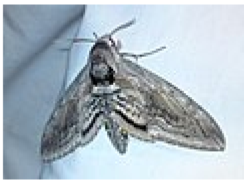
Images

Tomato hornworm larva

M. quinquemaculata diversity



Head detail



Live *M. quinquemaculata*

Tomato worm illuminated with UV on tomato plant

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Integrated pest management


An IPM boll weevil trap in a cotton field (Manning, South Carolina).

Integrated pest management (IPM), also known as **integrated pest control (IPC)** is a broad-based approach that integrates practices for economic control of pests. IPM aims to suppress pest populations below the economic injury level (EIL). The UN's Food and Agriculture Organization defines IPM as "the careful consideration of all available pest control techniques and subsequent integration of appropriate measures that discourage the development of pest populations and keep pesticides and other interventions to levels that are economically justified and reduce or minimize risks to human health and the environment. IPM emphasizes the growth of a healthy crop with the least possible disruption to agro-ecosystems and encourages natural pest control mechanisms."[1] Entomologists and ecologists have urged the adoption of IPM pest control since the 1970s.[2] IPM allows for safer pest control.

The introduction and spread of invasive species can also be managed with IPM by reducing risks while maximizing benefits and reducing costs.[3][4][5]

Contents

History

Shortly after World War II, when synthetic insecticides became widely available, entomologists in California developed the concept of "supervised insect control".[6] Around the same time, entomologists in the US Cotton Belt were advocating a similar approach. Under this scheme, insect control was "supervised" by qualified entomologists and insecticide applications were based on conclusions reached from periodic monitoring of pest and natural-enemy populations. This was viewed as an alternative to calendar-based programs. Supervised control was based on knowledge of the ecology and analysis of projected trends in pest and natural-enemy populations.

Supervised control formed much of the conceptual basis for the "integrated control" that University of California entomologists articulated in the 1950s. Integrated control sought to identify the best mix of chemical and biological controls for a given insect pest. Chemical insecticides were to be used in the manner least disruptive to biological control. The term "integrated" was thus synonymous with "compatible." Chemical controls were to be applied only after regular monitoring indicated that a pest population had reached a level (the economic threshold) that required treatment to prevent the population from reaching a level (the economic injury level) at which economic losses would exceed the cost of the control measures.

IPM extended the concept of integrated control to all classes of pests and was expanded to include all tactics. Controls such as pesticides were to be applied as in integrated control, but these now had to be compatible with tactics for all classes of pests. Other tactics, such as host-plant resistance and cultural manipulations, became part of the IPM framework. IPM combined entomologists, plant pathologists, nematologists and weed scientists.

In the United States, IPM was formulated into national policy in February 1972 when President Richard Nixon directed federal agencies to take steps to advance the application of IPM in all relevant sectors. In 1979, President Jimmy Carter established an interagency IPM Coordinating Committee to ensure development and implementation of IPM practices.[7]

Perry Adkisson and Ray F. Smith received the 1997 World Food Prize for encouraging the use of IPM.[8]

Applications

IPM is used in agriculture, horticulture, forestry, human habitations, preventive conservation and general pest control, including structural pest management, turf pest management and ornamental pest management.

Principles

An American IPM system is designed around six basic components:[9]

- **Acceptable pest levels**—The emphasis is on *control*, not *eradication*. IPM holds that wiping out an entire pest population is often impossible, and the attempt can be expensive and unsafe. IPM programmes first work to establish acceptable pest levels, called action thresholds, and apply controls if those thresholds are crossed. These thresholds are pest and site specific, meaning that it may be acceptable at one site to have a weed such as white clover, but not at another site. Allowing a pest population to survive at a reasonable threshold reduces selection pressure. This lowers the rate at which a pest develops resistance to a control, because if almost all pests are killed then those that have resistance will provide the genetic basis of the future population. Retaining a significant number of unresistant specimens dilutes the prevalence of any resistant genes that appear. Similarly, the repeated use of a single class of controls will create pest populations that are more resistant to that class, whereas alternating among classes helps prevent this.
- **Preventive cultural practices**—Selecting varieties best for local growing conditions and maintaining healthy crops is the first line of defense. Plant quarantine and 'cultural techniques' such as crop sanitation are next, e.g., removal of diseased plants, and cleaning pruning shears to prevent spread of infections. Beneficial fungi and bacteria are added to the potting media of horticultural crops vulnerable to root diseases, greatly reducing the need for fungicides.
- **Monitoring**—Regular observation is critically important. Observation is broken into inspection and identification.[10] Visual inspection, insect and spore traps, and other methods are used to monitor pest levels. Record-keeping is essential, as is a thorough knowledge of target pest behavior and reproductive cycles. Since insects are cold-blooded, their physical development is dependent on area temperatures. Many insects have had their development cycles modeled in terms of degree-days. The degree days of an environment determines the optimal time for a specific insect outbreak. Plant pathogens follow similar patterns of response to weather and season.
- **Mechanical controls**—Should a pest reach an unacceptable level, mechanical methods are the first options. They include simple hand-picking, barriers, traps, vacuuming and tillage to disrupt breeding.
- **Biological controls**—Natural biological processes and materials can provide control, with acceptable environmental impact, and often at lower cost. The main approach is to promote beneficial insects that eat or parasitize target pests. Biological insecticides, derived from naturally occurring microorganisms (*e.g.*—*Bt*, entomopathogenic fungi and entomopathogenic nematodes), also fall in this category. Further 'biology-based' or 'ecological' techniques are under evaluation.
- **Responsible use**—Synthetic pesticides are used as required and often only at specific times in a pest's life cycle. Many newer pesticides are derived from plants or naturally occurring substances (*e.g.*—nicotine, pyrethrum and insect juvenile hormone analogues), but the toxophore or active component may be altered to provide increased biological activity or stability. Applications of pesticides must reach their intended targets.

Matching the application technique to the crop, the pest, and the pesticide is critical. The use of low-volume spray equipment reduces overall pesticide use and labor cost.

An IPM regime can be simple or sophisticated. Historically, the main focus of IPM programmes was on agricultural insect pests.[11] Although originally developed for agricultural pest management, IPM programmes are now developed to encompass diseases, weeds and other pests that interfere with management objectives for sites such as residential and commercial structures, lawn and turf areas, and home and community gardens.

Process

IPM is the selection and use of pest control actions that will ensure favourable economic condition, ecological and social consequences[12] and is applicable to most agricultural, public health and amenity pest management situations. The IPM process starts with monitoring, which includes inspection and identification, followed by the establishment of economic injury levels. The economic injury levels set the economic threshold level. That is the point when pest damage (and the benefits of treating the pest) exceed the cost of treatment.[13] This can also be an action threshold level for determining an unacceptable level that is not tied to economic injury. Action thresholds are more common in structural pest management and economic injury levels in classic agricultural pest management. An example of an action threshold is one fly in a hospital operating room is not acceptable, but one fly in a pet kennel would be acceptable. Once a threshold has been crossed by the pest population action steps need to be taken to reduce and control the pest. Integrated pest management employs a variety of actions including cultural controls such as physical barriers, biological controls such as adding and conserving natural predators and enemies of the pest, and finally chemical controls or pesticides. Reliance on knowledge, experience, observation and integration of multiple techniques makes IPM appropriate for organic farming (excluding synthetic pesticides). These may or may not include materials listed on the Organic Materials Review Institute (OMRI)[14] Although the pesticides and particularly insecticides used in organic farming and organic gardening are generally safer than synthetic pesticides, they are not always more safe or environmentally friendly than synthetic pesticides and can cause harm.[15] For conventional farms IPM can reduce human and environmental exposure to hazardous chemicals, and potentially lower overall costs.

Risk assessment usually includes four issues: 1) characterization of biological control agents, 2) health risks, 3) environmental risks and 4) efficacy.[16]

Mistaken identification of a pest may result in ineffective actions. E.g., plant damage due to over-watering could be mistaken for fungal infection, since many fungal and viral infections arise under moist conditions.

Monitoring begins immediately, before the pest's activity becomes significant. Monitoring of agricultural pests includes tracking soil/planting media fertility and water quality. Overall plant health and resistance to pests is greatly influenced by pH, alkalinity, of dissolved mineral and oxygen reduction potential. Many diseases are waterborne, spread directly by irrigation water and indirectly by splashing.

Once the pest is known, knowledge of its lifecycle provides the optimal intervention points.[17] For example, weeds reproducing from last year's seed can be prevented with mulches and pre-emergent herbicide.

Pest-tolerant crops such as soybeans may not warrant interventions unless the pests are numerous or rapidly increasing. Intervention is warranted if the expected cost of damage by the pest is more than the cost of control. Health hazards may require intervention that is not warranted by economic considerations.

Specific sites may also have varying requirements. E.g., white clover may be acceptable on the sides of a tee box on a golf course, but unacceptable in the fairway where it could confuse the field of play.[18]

Possible interventions include mechanical/physical, cultural, biological and chemical. Mechanical/physical controls include picking pests off plants, or using netting or other material to exclude pests such as birds from grapes or rodents from structures. Cultural controls include keeping an area free of conducive conditions by removing waste or diseased plants, flooding, sanding, and the use of disease-resistant crop varieties.[12] Biological controls are numerous. They include: conservation of natural predators or augmentation of natural predators, sterile insect technique (SIT).[19]

Augmentation, inoculative release and inundative release are different methods of biological control that affect the target pest in different ways. Augmentative control includes the periodic introduction of predators.[20][21][22][23][24] With inundative release, predators are collected, mass-reared and periodically released in large numbers into the pest area.[25][26][27] This is used for an immediate reduction in host populations, generally for annual crops, but is not suitable for long run use.[28] With inoculative release a limited number of beneficial organisms are introduced at the start of the growing season. This strategy offers long term control as the organism's progeny affect pest populations throughout the season and is common in orchards.[28][29] With seasonal inoculative release the beneficials are collected, mass-reared and released seasonally to maintain the beneficial population. This is commonly used in greenhouses.[29] In America and other western countries, inundative releases are predominant, while Asia and the eastern Europe more commonly use inoculation and occasional introductions.[28]

The sterile insect technique (SIT) is an area-wide IPM program that introduces sterile male pests into the pest population to trick females into (unsuccessful) breeding encounters, providing a form of birth control and reducing reproduction rates.[19] The biological controls mentioned above only appropriate in extreme cases, because in the introduction of new species, or supplementation of naturally occurring species can have detrimental ecosystem effects. Biological controls can be used to stop invasive species or pests, but they can become an introduction path for new pests.[30]

Chemical controls include horticultural oils or the application of insecticides and herbicides. A green pest management IPM program uses pesticides derived from plants, such as botanicals, or other naturally occurring materials.

Pesticides can be classified by their modes of action. Rotating among materials with different modes of action minimizes pest resistance.[12]

Evaluation is the process of assessing whether the intervention was effective, whether it produced unacceptable side effects, whether to continue, revise or abandon the program.[31]

Southeast Asia

The Green Revolution of the 1960s and '70s introduced sturdier plants that could support the heavier grain loads resulting from intensive fertilizer use. Pesticide imports by 11 Southeast Asian countries grew nearly sevenfold in value between 1990 and 2010, according to FAO statistics, with disastrous results. Rice farmers become accustomed to spraying soon after planting, triggered by signs of the leaf folder moth, which appears early in the growing season. It causes only superficial damage and doesn't reduce yields. In 1986, Indonesia banned 57 pesticides and completely stopped subsidizing their use. Progress was reversed in the 2000s, when growing production capacity, particularly in China, reduced prices. Rice production in Asia more than doubled. But it left farmers believing more is better—whether it's seed, fertilizer, or pesticides.[32]

The brown planthopper, *Nilaparvata lugens*, the farmers' main target, has become increasingly resistant. Since 2008, outbreaks have devastated rice harvests throughout Asia, but not in the Mekong Delta. Reduced spraying allowed natural predators to neutralize planthoppers in Vietnam. In 2010 and 2011, massive planthopper outbreaks hit 400,000 hectares of Thai rice fields, causing losses of about $64 million. The Thai government is now pushing the "no spray in the first 40 days" approach.[32]

By contrast early spraying kills frogs, spiders, wasps and dragonflies that prey on the later-arriving and dangerous planthopper and produced resistant strains. Planthoppers now require pesticide doses 500 times greater than originally. Overuse indiscriminately kills beneficial insects and decimates bird and amphibian populations. Pesticides are suspected of harming human health and became a common means for rural Asians to commit suicide.[32]

In 2001, scientists challenged 950 Vietnamese farmers to try IPM. In one plot, each farmer grew rice using their usual amounts of seed and fertilizer, applying pesticide as they chose. In a nearby plot, less seed and fertilizer were used and no pesticides were applied for 40 days after planting. Yields from the experimental plots was as good or better and costs were lower, generating 8% to 10% more net income. The experiment led to the "three reductions, three gains" campaign, claiming that cutting the use of seed, fertilizer and pesticide would boost yield, quality and income. Posters, leaflets, TV commercials and a 2004 radio soap opera that featured a rice farmer who gradually accepted the changes. It didn't hurt that a 2006 planthopper outbreak hit farmers using insecticides harder than those who didn't. Mekong Delta farmers cut insecticide spraying from five times per crop cycle to zero to one.

The Plant Protection Center and the International Rice Research Institute (IRRI) have been encouraging farmers to grow flowers, okra and beans on rice paddy banks, instead of stripping vegetation, as was typical. The plants attract bees and a tiny wasp that eats planthopper eggs, while the vegetables diversify farm incomes.[32]

Agriculture companies offer bundles of pesticides with seeds and fertilizer, with incentives for volume purchases. A proposed law in Vietnam requires licensing pesticide dealers and government approval of advertisements to prevent exaggerated claims. Insecticides that target other pests, such as *Scirpophaga incertulas* (stem borer), the larvae of moth species that feed on rice plants allegedly yield gains of 21% with proper use.[32]

See also

- Agroecology
- Agronomy
- Biodynamic agriculture
- Endangered arthropod
- Forest integrated pest management
- International Organization for Biological Control
- Pesticide application
- Professional Landcare Network (PLANET)
- Push-pull technology
- Soil contamination
- Sustainable agriculture

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