Insects - Behavior, Development and Evolution

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Chapter 1

Insect

Insects **Temporal range: 396–0 Ma** **Early Devonian – Recent**	

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

Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Hexapoda
Class:	**Insecta** Linnaeus, 1758

Subclasses and classes

Monocondylia
Archaeognatha
Dicondylia
Pterygota

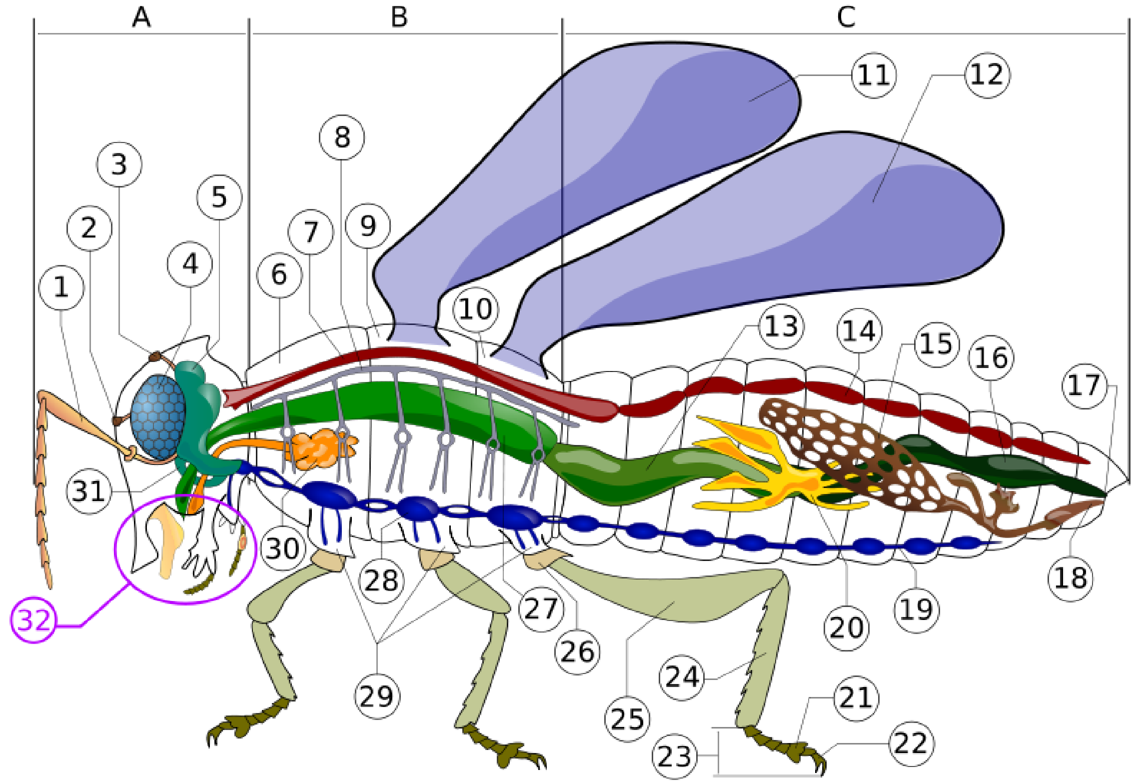
Insects are a class within the arthropods that have a chitinous exoskeleton, a three-part body (head, thorax, and abdomen), three pairs of jointed legs, compound eyes, and two antennae. They are among the most diverse group of animals on the planet and include more than a million described species and represent more than half of all known living organisms. The number of extant species is estimated at between six and ten million, and potentially represent over 90% of the differing metazoan life forms on Earth. Insects may be found in nearly all environments, although only a small number of species occur in the oceans, a habitat dominated by another arthropod group, the crustaceans.

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

Insects typically move about by walking, flying or occasionally swimming. Because 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. Insects are the only invertebrates to have evolved flight. Many insects spend at least part of their life underwater, with larval adaptations that include gills and some adult insects are aquatic and have adaptations for swimming. Some species, like water striders, are capable of walking on the surface of water. Insects are mostly solitary, but some insects, such as certain bees, ants, and termites are social and live in large, well-organized colonies. Some insects, like 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 distances of many kilometers. Other species communicate with sounds: crickets stridulate, or rub their wings together, to attract a mate and repel other males. Lampyridae in the beetle order Coleoptera communicate with light.

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 or fruits, a few bite humans and livestock, alive and dead, to feed on blood and some are capable of transmitting diseases to humans, pets and livestock. Many other insects are considered ecologically beneficial and a few provide direct economic benefit. Silkworms and bees have been domesticated by humans for the production of silk and honey, respectively.

External Morphology



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

General body plan

Insects have segmented bodies supported by an exoskeleton, a 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. The head supports a pair of sensory antennae, a pair of compound eyes, and, if present, one to three simple eyes (or ocelli) and three sets of variously modified appendages that form the mouthparts. The thorax has six segmented legs—one pair each for the prothorax, mesothorax and the metathorax segments making up the thorax—and, if present in the species, two or four wings. 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. There is considerable variation and many adaptations in the body parts of insects especially wings, legs, antenna, mouth-parts etc.

Exoskeleton

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 others in a sandwich pattern, while the exocuticle is rigid and hardened. The exocuticle is greatly reduced in many soft-bodied insects (e.g., caterpillars), especially during their larval stages.

Insects are the only invertebrates to have developed active flight capability, and this has played an important role in their success. These 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 more efficient and allows more muscle connections; crustaceans also use the same method, though all spiders use hydraulic pressure to extend their legs, a system inherited from their pre-arthropod ancestors. Unlike insects, though, most aquatic crustaceans are biomineralized with calcium carbonate extracted from the water.

Internal Morphology

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 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.

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. 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 sensations of pain. 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. Although nociception has been demonstrated in insects, there is not a consensus that insects feel pain consciously.

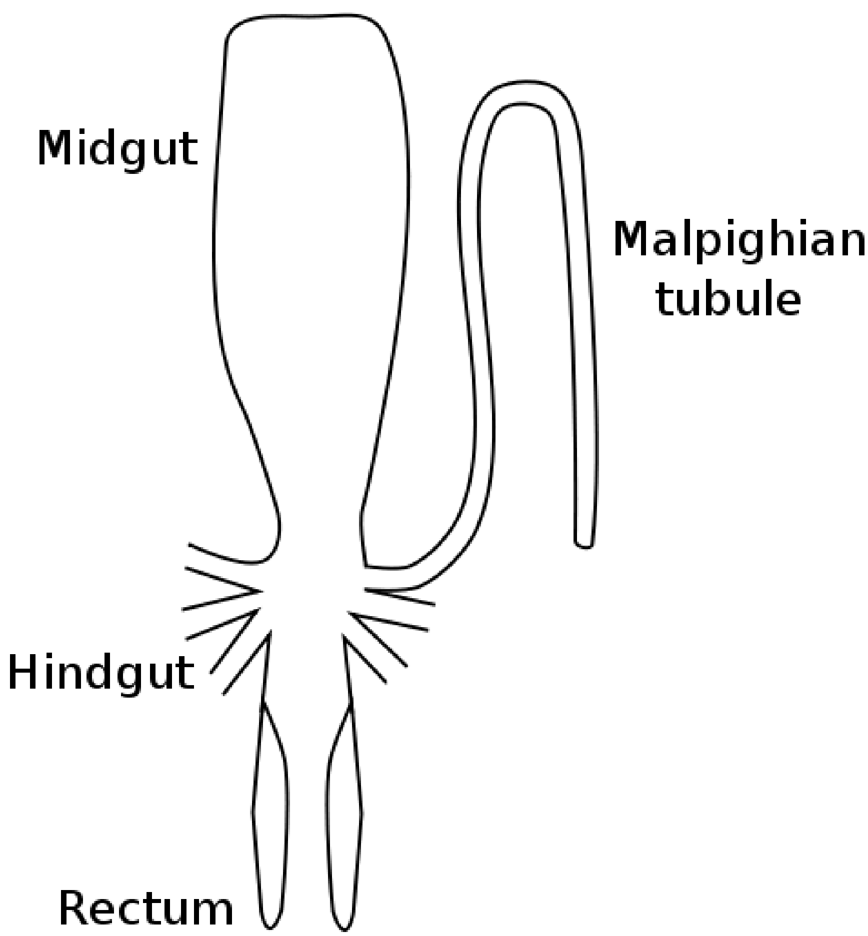
Digestive system

An insect uses its digestive system to extract nutrients and other substances from the food it consumes. 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.

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.

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. 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. The gut is where almost all of insects' digestion takes place. It can be divided into the foregut, midgut and hindgut.

Foregut



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

The first section of the alimentary canal is the foregut (element 27 in numbered diagram), or stomodaeum. The foregut is line 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. Here, digestion starts 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 on ward 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.

Bee defecating. Note the contraction of the anus which provides internal pressure.

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.

Hindgut

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. The uric acid is formed using hemolymph waste products diffused from the Malpighian tubules (element 20). It is then emptied directly into the alimentary canal, at the junction between the midgut and hindgut. The number of Malpighian tubules possessed by a given insect varies between species, ranging from only two tubules in some insects to over 100 tubules in others.

Respiration and circulation

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). Since oxygen is delivered directly, the circulatory system is not used to carry oxygen, and is therefore greatly reduced. The insect circulatory system has no veins or arteries, and instead consists of little more than a single, perforated dorsal tube which pulses peristaltically. Toward the thorax, the dorsal tube (element 14) divides into chambers and acts like the insect's heart. The opposite end of the dorsal tube is like the aorta of the insect circulating the hemolymph, arthropods' fluid analog of blood, inside the body cavity. Air is taken in through openings on the sides of the abdomen called spiracles.

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. 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. 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.

Reproduction and development

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

The majority of insects hatch from eggs. The fertilization and development takes place inside the egg, enclosed by a shell (chorion). 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. 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. Some insects, like parasitic wasps, show polyembryony, where a single fertilized egg divides into many and in some cases thousands of separate embryos.

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

Other developmental and reproductive variations include haplodiploidy, polymorphism, paedomorphosis or peramorphosis, sexual dimorphism, parthenogenesis and more rarely hermaphroditism. 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. Polymorphism is the 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 females have notably different appearances, such as the moth *Orgyia recens* as an exemplar 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. 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. 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. Still other insects have evolved mechanisms of diapause that allow eggs or pupae to survive these conditions.

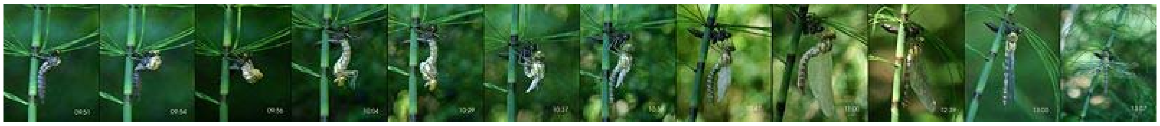
Metamorphosis

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

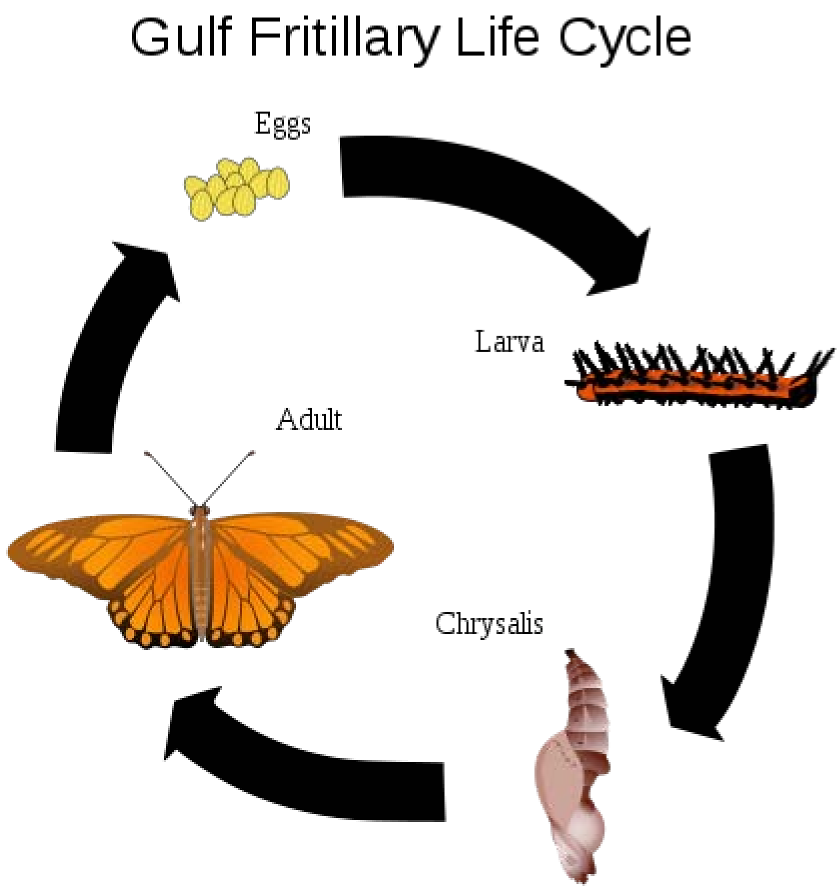
Insects that show hemimetabolism, or incomplete metamorphosis, change gradually by undergoing a series of molts. An insect molts when it outgrows its exoskeleton, which does not stretch and would otherwise restrict the insect's growth. The molting process begins as the insect's epidermis secretes a new epicuticle. 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. Other arthropods have a much different process and only molt; though must accommodate for the difference in exoskeleton structure and make up with other enzymes.

Immature insects that go through incomplete metamorphosis are called nymphs or in the case of dragonflies and damselflies as 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.



Like other insects that develop through incomplete metamorphosis, this Southern Hawker dragonfly molts its exoskeleton (shown above) several times during its pre-adult life.

Complete metamorphosis



Gulf Fritillary life cycle, an example of holometabolism.

Holometabolism, or complete metamorphosis, is where the insect changes all in four stages, an egg or embryo, a larva, a pupa, and the adult or imago. In these species, 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. Insects undergo considerable change in form during the pupal stage, and emerge as adults. Butterflies are a well known example of an insects that undergo complete metamorphosis, although most insects use this life cycle. Some insects have evolved this system to hypermetamorphosis.

Some of the oldest and most successful insect groups, such Endopterygota, use a system of complete metamorphosis. Strangely though, complete metamorphosis is unique to certain insect orders, like Diptera, Lepidoptera, and Hymenoptera, and no other arthropods undergo it, but incomplete metamorphosis.

Senses and communication

Many insects possess very sensitive and/or 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. 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 MHz., and some grasshoppers can hear up to 50 MHz. 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. 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, 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

Insects have compound eyes and two antennae.

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. 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. The colors of emitted light vary from dull blue (*Orfelia fultoni*, Mycetophilidae) to the familiar greens and the rare reds (*Phrixothrix tiemanni*, Phengodidae).

Most insects, except some species of cave dwelling crickets, are able to perceive light and dark. Many species have acute vision capable of detecting minute movements. The eyes 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.

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 and musculature. The African cicada *Brevisana brevis* has been measured at 106.7 decibels at a distance of 50 cm (20 in). Some insects, such as the hawk moths and Hedylid butterflies, can hear ultrasound and take evasive action when they sense that they have been detected by bats. 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. Some otherwise palatable moths have evolved to mimic these calls.

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. Most insects are also able to sense vibrations transmitted through surfaces. For example, an insect is caught in a spider web and struggles to escape. The vibrations it produces are sensed by the spider, who is alerted to its presence. Through these vibrations, the spider can tell where on the web the insect is located, as well as how big it is.

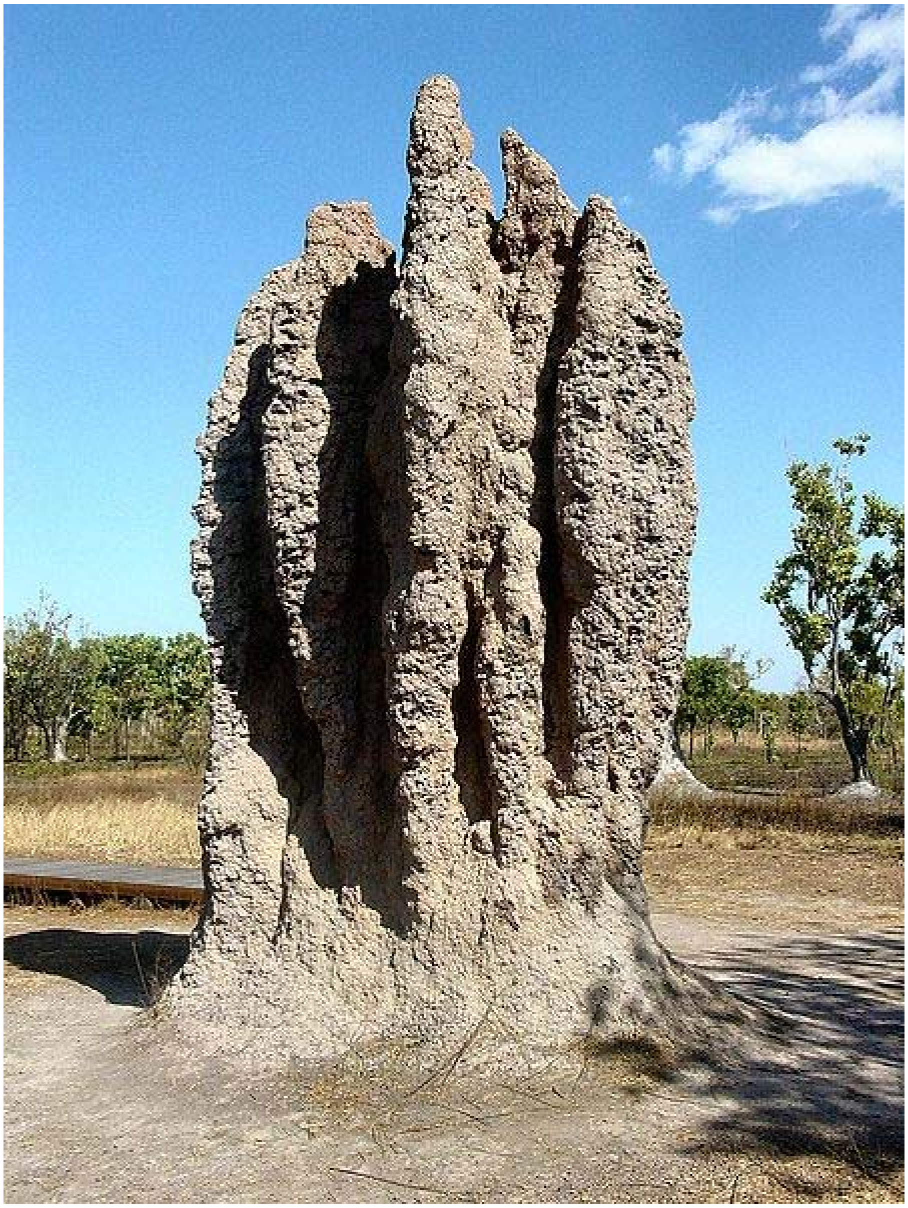
Communication using surface-borne vibrational signals is more widespread among insects because of size constraints in producing air-borne sounds. Insects cannot effectively produce low-frequency sounds, and high-frequency sounds tend to disperse more in a dense environment (such as foliage), so insects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

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*. 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. The Madagascar hissing cockroach has the ability to press air through its spiracles to make a hissing noise as a sign of aggression; 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.

Chemical communication

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. Allomonea 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.

Social behavior



A cathedral mound created by termites (Isoptera).

Social insects, such as termites, ants and many bees and wasps, are the most familiar species of eusocial animal. 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.

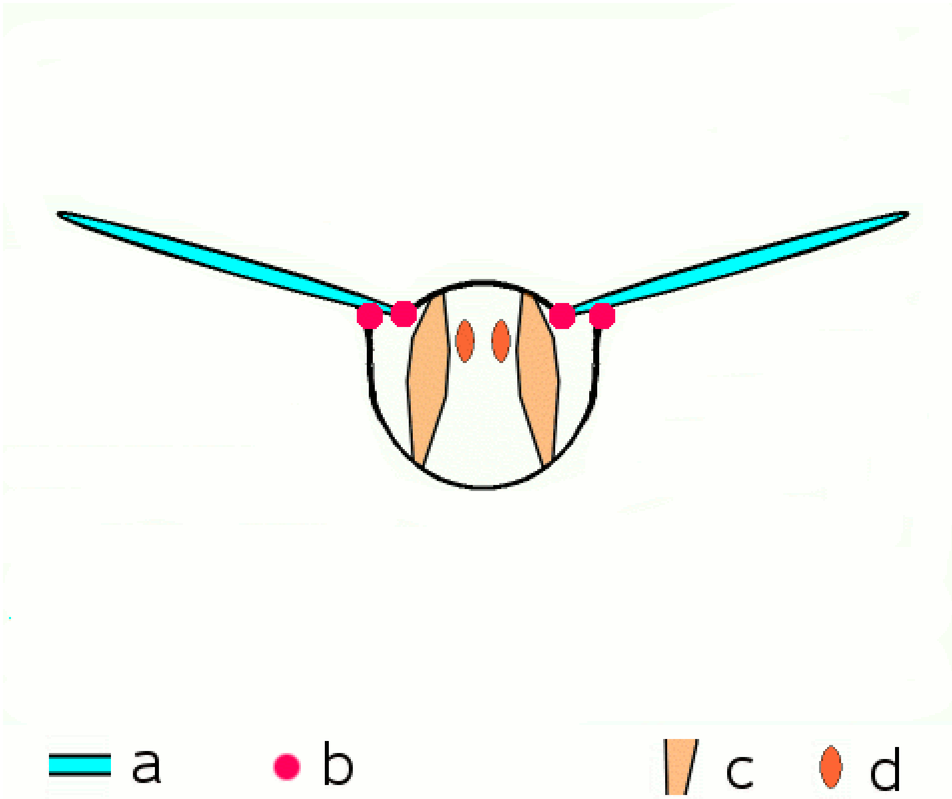
Only insects which live in nests or colonies demonstrate any true capacity for fine-scale spatial orientation or homing. This can allow an insect to return unerringly to a single hole a few millimeters in diameter among thousands of apparently identical holes clustered together, after a trip of up to 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. A few insects seasonally migrate large distances between different geographic regions (e.g., the overwintering areas of the Monarch butterfly).

Care of young

Most insects 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 of bees and various types of wasps.

Locomotion

Flight



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.

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. The pleuron is membrane on the sides of the thorax. 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. 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. 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.

Unlike birds, many small insects are swept along by the prevailing winds although many of the larger insects are known to make migrations. Aphids are known to be transported long distances by low-level jet streams. 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.

Walking

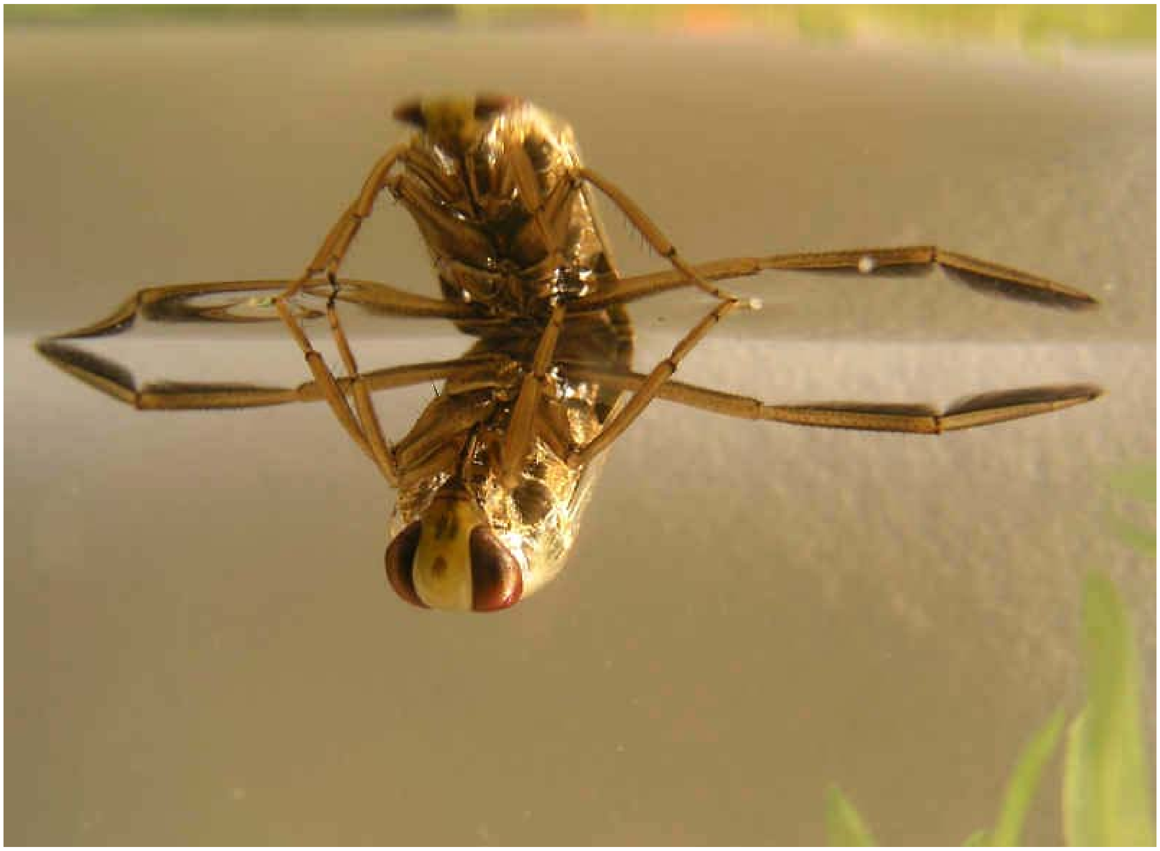
Many adult insects use six legs for walking and have adopted a tripedal gait. The tripedal gait allows for rapid walking while always having a stable stance and has been studied extensively in cockroaches. The legs are used in alternate triangles touching the ground. For the first step, the middle right 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. 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, or avoiding obstacles, four or more feet may be touching the ground. Insects can also adapt their gait to cope with the loss of one or more limbs.

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 the bugs 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.

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.

Swimming



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

A large number of insects live either parts 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.

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. 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. 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*).

Phylogeny and systemics

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

The evolutionary relationships of insects to other animal groups remain unclear. Although more traditionally grouped with millipedes and centipedes, evidence has emerged favoring closer evolutionary ties with crustaceans. In the Pancrustacea theory, insects, together with Remipedia and Malacostraca, make up a natural clade. 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 legs characteristic of adult insects.

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. 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.

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, there is no evidence that suggests that the insects were a particularly successful group of animals before they evolved to have wings.

Late Carboniferous and Early Permian insect orders include both extant groups and a number of Paleozoic species, 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.

The remarkably successful Hymenopterans 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.

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.

Insects were among the earliest terrestrial herbivores and acted as major selection agents on plants. 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. This successful evolutionary pattern has also been utilized 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 has usually given Hexapoda the rank of superclass, and identified four groups within it: insects (Ectognatha), springtails (Collembola), Protura and Diplura, the latter three being grouped together as 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 Hexapoda is polyphyletic (where the last common ancestor was not a member of the group), with the entognath classes having separate evolutionary histories from Insecta. 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 (Thysanura). Archaeognatha make up the Monocondylia based on the shape of their mandibles, while Thysanura and Pterygota are grouped together as Dicondylia. It is possible that the Thysanura themselves are not monophyletic, with the family Lepidotrichidae being a sister group to the Dicondylia (Pterygota and the remaining Thysanura).

Paleoptera and Neoptera are the winged orders of insects differentiated by the presence of hardened body parts called sclerites; also, in 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, Paraneoptera has turned out to be more closely related to 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. Phasmatodea and Embiidina have been suggested to form Eukinolabia. Mantodea, Blattodea and Isoptera are thought to form a monophyletic group termed Dictyoptera.

It is likely that Exopterygota is paraphyletic in regard to Endopterygota. Matters that have had a lot of 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. The Neuropterida are often lumped or split on the whims of the taxonomist. Fleas are now thought to be closely related to boreid mecopterans. Many questions remain to be answered when it comes to basal relationships amongst endopterygote orders, particularly 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.

Relationship to humans

Aedes aegypti, a parasite, and vector of dengue fever and yellow fever.

Many insects are considered pests by humans. Insects commonly regarded as pests include those that are parasitic (mosquitoes, 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 relying 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.

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.

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.

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. 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. 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.

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. The genome of *D. melanogaster* was sequenced in 2000, reflecting the organism's important role in biological research.

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

Insectivorous insects, or insects which feed on other insects, are beneficial to humans because 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 get significantly reduce pest aphid populations. While birds are perhaps more visible predators of insects, insects themselves account for the vast majority of insect consumption. Without predators to keep them in check, insects can undergo almost unstoppable population explosions.

Many insects, especially beetles, are scavengers that feed on dead animals and fallen trees and thereby recycle biological materials into forms found useful by other organisms. Insects are responsible for much of the process by which topsoil is created. The ancient Egyptian religion considered dung beetles sacred, and represented them as beetle-shaped amulets, or scarabs. Dung beetles have been used in countries including Australia as an agent of biological pest control to reduce the populations of pestilent flies and parasitic worms. The Australian Dung Beetle Project successfully introduced 23 species of dung beetle, including *Onthophagus gazella* and *Euoniticellus intermedius* from South Africa and Europe. This resulting in a 90% reduction in bush flies as well as improved soil fertility and quality.

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. Adult insects, such as crickets, and insect larvae of various kinds are also commonly used as fishing bait.

Entomophagy

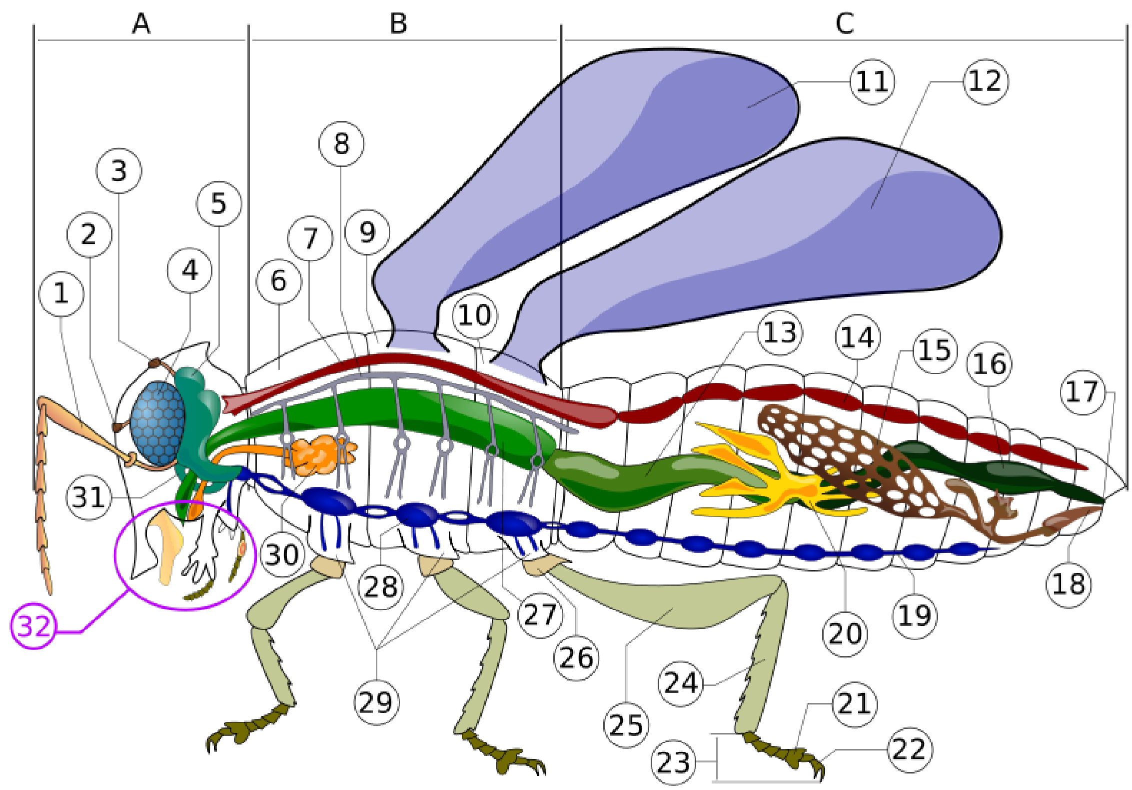
In some parts of the world, insects are used for human food, while being a taboo in other places. In some cultures, insects, especially deep-fried cicadas, are considered to be delicacies, while in other places they form part of the normal diet as they have a high protein content for their mass. In most first-world countries, however, entomophagy, or the consumption of insects, is taboo. There are proponents of developing this use to provide a major source of protein in human nutrition. Since it is impossible to entirely eliminate pest insects from the human food chain, insects are present in many foods, especially grains. Food safety laws in many countries do not prohibit insect parts in food, but rather limit the 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.

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 which signify the impossibility of immortality. Amongst 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 which holds much cultural significance including creation and zen-like patience in waiting.

Chapter 2

Insect Morphology



Insect morphology

Legend of body parts

Tagmata : 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

The **morphology** of **insects** enables the phenomenal success of this class of arthropods. The sheer quantity and diversity of its taxa are matched by a large variation of modifications in its body structure. The high rate of speciation, short generations and long lineage have caused insects to evolve in many ways resulting in very large variations in morphology. These modifications allow insects to occupy almost every ecological niche, utilise a staggering variety of food sources and possess diverse lifestyles. Insect body sizes range from 0.3 mm in the case of mymarid wasps which parasitise insect eggs to the 30 cms wingspan of the American owlet moth *Thysania agrippina* (family Noctuidae).

Insects are by far the most successful group in the Arthropoda. They differ in significant ways from the other classes of Hexapoda, such as Protura, Collembola and others) who are now considered by some authorities to be more basal than insects.

Due to paucity of paleontological record, morphology was the main source for inputs for constructing insect phylogeny but was invariably beset with conjecture and conditionality. A stable and reliable phylogeny of insects is slowly developing due to the advent of DNA genome analysis. This has reduced the importance of morphology in evolutionary studies. However morphology still plays a great part in understanding how insects adapt and cope with their myriad lifestyles on planet Earth.

Summary

Insects possess segmented bodies supported by an exoskeleton, a hard jointed 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. The head supports a pair of sensory antennae, a pair of compound eyes, if present, one to three simple eyes or (ocelli) and three sets of variously modified appendages that form the mouthparts. The thorax has six segmented legs (one pair each for the prothorax, mesothorax and the metathorax segments making up the thorax) and two or four wings (if present in the species). The abdomen (made up of eleven segments some of which may be reduced or fused) has most of the digestive, respiratory, excretory and reproductive internal structures. There is considerable variation and many adaptations in the body parts of insects especially wings, legs, antenna, mouth-parts etc.

External morphology

Exoskeleton

Their 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 another layer under it called the procuticle. This is chitinous and much thicker than the epicuticle and has two layers, the outer being the exocuticle while the inner is the endocuticle. The tough and flexible endocuticle is built from numerous layers of fibrous chitin and proteins, criss-crossing each others in a sandwich pattern, while the exocuticle is rigid and sclerotized. The exocuticle is greatly reduced in many soft-bodied insects, especially the larval stages (e.g., caterpillars). Chemically chitin is a long-chain polymer of a N-acetylglucosamine, a derivative of glucose. In its unmodified form, chitin is translucent, pliable, resilient and quite tough. In arthropods, however, it is often modified, becoming embedded in a hardened proteinaceous matrix, which forms much of the exoskeleton. In its pure form it is leathery, but when encrusted in calcium carbonate it becomes much harder. The difference between the unmodified and modified forms can be seen by comparing the body wall of a caterpillar (unmodified) to a beetle (modified).

From the embryonic stages itself, a layer of columnar or cuboidal epithelial cells give rise to the external cuticle and an internal basement membrane. The majority of insect material is held in the endocuticle. The cuticle provides muscular support and acts as a protective shield as the insect develops. However since it cannot grow the external sclerotised part of the cuticle is periodically shed in a process called "moulting". As the time for moulting approaches, most of the exocuticle material is reabsorbed. In moulting, first the old cuticle separates from the epidermis (apodysis). Enzymatic moulting fluid is released in between the old cuticle and epidermis which separates the exocuticle by digesting the endocuticle and sequestering its material for the new cuticle. When the new cuticle has formed sufficiently, the epicuticle and reduced exocuticle are shed in ecdysis.

There are four principal regions of an insect body segment: tergum or dorsal, sternum or ventral and the two pleura or lateral. Hardened plates in the exoskeleton are called sclerites. Sclerites that are subdivisions of the major regions are tergites, sternites and pleurites, for the respective regions tergum, sternum and pleuron.

Head

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. Out of all the insect orders, Orthoptera displays the most features found in other insects, including the sutures and sclerites. 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 degrees to become parallel to the primary axis of the body. In some species this region is modified and assumes a different name.

The ecdysial suture is made of the coronal, frontal, epicranial sutures plus the ecdysial and cleavage lines; which is varies among different species of insects. The ecdysial suture is longitudinally placed on the vertex and separates the epicranial halves of the head to the left and right sides. Depending in the insect, the suture may come in different shapes: like either a Y, U, or V. those diverging lines that make up the ecdysial suture are called the frontal sutures or fontogenal sutures. Not all species of insect have frontal sutures, but in those who do, it helps the individual emerge from the integument when molting. The frons is that part of the head that is ventrad, or towards the ventral and lower, of the vertex. the frons varies in size and is sometimes hard to identify, especially its borders in some species. However in most species, the frons is separated by the frontoclypeal or epistomal sutures; a transverse suture located under the antennae sockets.

The clypeus is a sclerite between the face and labrum, which is dorsally separated from the frons by the frontoclypeal suture in primitive insects. The clypeogenal suture laterally democrates the clypeus, with the clypeus ventrally separated from the labrum by the clypeolabral suture. The clypeus differs in shape and size, such as species of Lepidoptera with a large clypeus with elongated mouthparts. The cheek or gena forms the sclerotized area on each side of the head below the compound eyes extending to the gular suture. Like many of the the other parts making up the insect's head, the gena varies among species with its boundaries difficult to establish. For example, in dragonflies and damselflies (Odonata) is between the compound eyes, clypeus, and mouthparts. The postgena is the area immediately posteriad, or posterior or lower of the gena of pterygote insects and form the lateral and ventral parts of the occipital arch. The occipital arch is a narrow band forming the posterior edge of the head capsule arching dorsally over the foramen. The subgenal area is usually narrow, located above the mouthparts; this area also includes the hypostoma and pleurostoma.The vertex extends anteriorly above the bases of the antennae as a prominent, pointed, concave rostrum. The posterior wall of the head capsule is penetrated by a large aperture, the foramen. Through it pass the organ systems, such as nerve cord, esophagus, salivary ducts, and musculature, connecting the head with the thorax.

Of the posterior aspect of the head, included are the occiput, postgena, occipital formen, posterior tentorial pit, gula, postgenal bridge, the hypostomal suture and bridge, and the mandibles, labium, and maxilla. The occiputal suture is well founded in species of Orthoptera, but not so much in other orders. Where found, the occipital suture is arched, horseshoe-shaped groove on the back of the head, ending at the posterior of each mandible. The postoccipital suture is a landmark on the posterior surface of the head and is typically near the occipital foremen. In pterygotes, the postocciput forms the extreme posterior, often U-shaped which forms the rim of the head extending to the postoccipital suture. In pterygotes, such as those of Orthoptera, the occipital foramen and the mouth are not separated. The three types of occipital closures, or points under the occipital foramen that separate the two lower halves of the postgena: the hypostomal bridge, postgenal bridge, and the gula. The hypstosaml bridge is usually found in insects with hypognathous orientation. The postgenal bridge is found in the adult species of higher Diptera, and aculeate Hymenoptera, while the gula is found on some Coleoptera, Neuroptera,and Isoptera which typically display a prognathous orientated mouthparts.

Compound eyes and ocelli

In most insects there is one pair of large, prominent compound eyes composed of units called ommatidia (ommatidium, singular), of which there may be up to 30,000 ommatidia in a single compound eye. This type of eye gives less resolution than eyes found in vertebrates, but it gives acute perception of movement. There can also be an additional two or three ocelli, which help detect low light or small changes in light intensity. The image perceived is a combination of inputs from the numerous ommatidia, which are located on a convex surface, thus pointing in slightly different directions. Compared with simple eyes, compound eyes possess a very large view angle, and can detect fast movement and, in some cases, the polarization of light. Because the individual lenses are so small, the effects of diffraction impose a limit on the possible resolution that can be obtained (assuming that they do not function as phased arrays). This can only be countered by increasing lens size and number. To see with a resolution comparable to our simple eyes, humans would require compound eyes which would each reach the size of their head. Compound eyes fall into two groups: apposition eyes, which form multiple inverted images, and superposition eyes, which form a single erect image. Compound eyes grow at their margins by the addition of new ommatidia.

Antennae

The antennae function almost exclusively in sensory perception, some of the sensory uses of antennae include motion and orientation, odor, sound, humidity, and a variety of chemical cues. Antennae vary greatly among insects, but all follow a basic plan, of which include the first and second segments are termed the scape and pedicel, respectively. The remaining antennal segments or flagellomeres are jointly called the flagellum. There are many different types of antennae among different species, including setaceous, moniliform, serrate, pectinate, clavate, lamellate, geniculate, and plumose.

- **Aristate**: These forms of antennae are pouch-like with a lateral bristle.(e.g. Diptera)

- **Filiform**: These forms of antennae are common amongst many different genera, which have a simple thread-like shape.

- **Setaceous**: These forms of antennae have many joints. The antenna tapers gradually from the base to the tip (e.g. Thysanura, Blattodea, Ephemeroptera, Plecoptera and Trichoptera).

- **Moniliform**: These forms of antennae have round segments that make the antenna look like a string of beads (e.g. Coleoptera)

- **Serrate**: These forms of antennae have segments that are angled on one side giving the appearance of a saw edge (e.g. Coleoptera)

- **Pectinate**: These forms of antennae have segments that are longer on one side giving the appearance of a comb (e.g. Hemynoptera - Symphyta sp. and Coleoptera).

- **Clavate**: These forms of antennae have segments that become wider towards the tip of the antenna. This may be gradual along its length, or a sudden increase (Capitate) and therefore mainly affecting the last few joints and giving the appearance of a club (e.g. Lepidoptera and Coleoptera)

- **Lamellate**: These forms of antennae have segments that towards the end are flattened and plate-like. This gives the appearance of a fan towards the end of the antennae. (e.g. Coleoptera - Scarabaeidae sp.)

- **Geniculate**: In these forms of antennae, there is an abrupt bend or elbow part of the way along the antenna (e.g. Hymenoptera - Formicidae sp. and Coleoptera).

- **Plumose**: These forms of antennae have segments which each have a number of fine thread-like branches. This gives the appearance of a feather (e.g. Diptera)

Mouthparts

The insect mouthparts consist of the maxilla, libium, and in some species the mandibles. The labrum is a simple fused sclerite, often called the upper lip and moves longitudinally which is hinged to the clypeus. The mandibles (jaws) are a highly sclerotized pair of structures that move at right angles to the body; used for biting, chewing and severing food. The maxillae are paired structures that can also move at right angles to the body and possess segmented palps. The labium (lower lip) is the fused structure that moves longitudinally and possesses a pair of segmented palps.

The mouthparts, along with the rest of the head, can be articulated in at least three different positions: prognathous, opisthognathous and hypognathous. In species with prognathous articulation, the head is positioned vertically aligned with the body, such as species of Formicidae; while in a hypognathous type, the head is aligned horizontally adjacent to the body. In a opisthognathous head, it was positioned diagonally, such as species of Blattodea and some Coleopterans. The mouthparts very greatly among insects of different orders but there are two main functional groups: mandibulate and haustellate. Haustellate mouthparts are those used for sucking liquids and can be further classified, by the presence of stylets, which include: piercing-sucking, sponging, and siphoning. The stylets are needle-like projections used to penetrate plant and animal tissue. The stylets and the feeding tube form the modified mandibles, maxilla, and hypopharynx.

- **Mandibulate**: These forms of mouthparts are among the most common in insects, which are used for biting and grinding solid foods.

- **Piercing-sucking**: These forms of mouthparts have stylets, and are used to penetrate solid tissue and then suck up liquid food.

- **Sponging**: These forms of mouthparts are used to sponge and suck liquids and lack stylets (e.g. most Diptera).

- **Siphoning**: These forms of mouthparts lack stylets and are used to suck liquids, which are commonly found among species of Lepidoptera.

Thorax

Wings

Most phylogenetically advanced insects have two pairs of wings located on the second and third thoracic segments. Insects are the only invertebrates to have developed flight capability, and this has played an important part in their success. Insect flight is not very well understood, relying heavily on turbulent aerodynamic effects. The primitive insect groups use muscles that act directly on the wing structure. The more advanced groups making up the Neoptera have foldable wings and their muscles act on the thorax wall and power the wings indirectly. These muscles are able to contract multiple times for each single nerve impulse, allowing the wings to beat faster than would ordinarily be possible.

Legs

Internal Morphology

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 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.

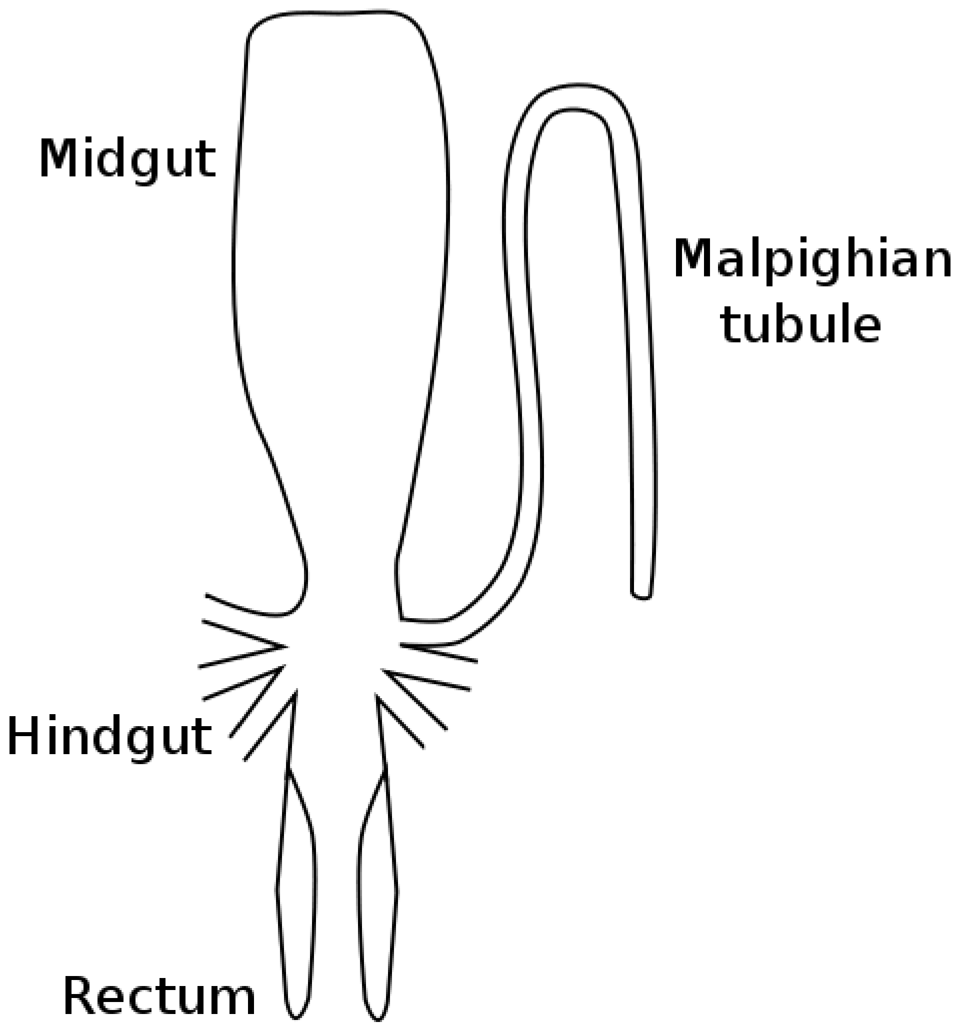
The thoracic segments have one ganglion on each side, which are connected into a pair, one pair per segment. This arrangement is also seen in the abdomen but only in the first eight segments. Many species of insects have reduced numbers of ganglia due to fusion or reduction. Some cockroaches have just 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 sensations of pain. 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. Although nociception has been demonstrated in insects, there is not a consensus that insects feel pain consciously.

Digestive system

An insect uses its digestive system to extract nutrients and other substances from the food it consumes. 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. 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 in one direction: 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. The gut is where almost all of insects' digestion takes place. It can be divided into the foregut, midgut and hindgut.

Foregut



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

The first section of the alimentary canal is the foregut (element 27 in numbered diagram), or stomodaeum. The foregut is line 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. Here, digestion starts 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 on ward 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.

Bee defecating. Note the contraction of the anus which provides internal pressure.

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.

Hindgut

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. The uric acid is formed using hemolymph waste products diffused from the Malpighian tubules (element 20). It is then emptied directly into the alimentary canal, at the junction between the midgut and hindgut. The number of Malpighian tubules possessed by a given insect varies between species, ranging from only two tubules in some insects to over 100 tubules in others.

Respiratory systems

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). Since oxygen is delivered directly, the circulatory system is not used to carry oxygen, and is therefore greatly reduced. The insect circulatory system has no veins or arteries, and instead consists of little more than a single, perforated dorsal tube which pulses peristaltically. Toward the thorax, the dorsal tube (element 14) divides into chambers and acts like the insect's heart. The opposite end of the dorsal tube is like the aorta of the insect circulating the hemolymph, arthropods' fluid analog of blood, inside the body cavity. Air is taken in through openings on the sides of the abdomen called spiracles.

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. 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. 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.

Circulatory system

Endocrine system

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. 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.

Microscopic composition

Internal of different taxa

Blattodea

Cockroaches are most common in tropical and subtropical climates. Some species are in close association with human dwellings and widely found around garbage or in the kitchen. Cockroaches are generally omnivorous with the exception of the wood-eating species such as *Cryptocercus*; these roaches are incapable of digesting cellulose themselves, but have symbiotic relationships with various protozoans and bacteria that digest the cellulose, allowing them to extract the nutrients. The similarity of these symbionts in the genus *Cryptocercus* to those in termites are such that it has been suggested that they are more closely related to termites than to other cockroaches, and current research strongly supports this hypothesis of relationships. 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, and which recent genetic studies indicates are very primitive cockroaches.

Cockroaches, like all insects, breathe through a system of tubes called *tracheae*. The tracheae of insects are attached to the spiracles, excluding the head. Thus cockroaches, like all insects, are not dependent on the mouth and windpipe to breathe. The valves open when the CO_2 level in the insect rises to a high level; then the CO_2 diffuses out of the tracheae to the outside and fresh O_2 diffuses in. Unlike in vertebrates that depend on blood for transporting O_2 and CO_2, the tracheal system brings the air directly to cells, the tracheal tubes branching continually like a tree until their finest divisions, tracheoles, are associated with each cell, allowing gaseous oxygen to dissolve in the cytoplasm lying across the fine cuticle lining of the tracheole. CO_2 diffuses out of the cell into the tracheole. While cockroaches do not have lungs and thus do not actively breathe in the vertebrate lung manner, in some very large species the body musculature may contract rhythmically to forcibly move air out and in the spiracles; this may be considered a form of breathing.

Coleoptera

The digestive system of beetles is primarily based on plants which they for the most part feed upon, with mostly the anterior midgut performing digestion. Although, in predatory species (e.g., Carabidae) most digestion occurs in the crop by means of midgut enzymes. In Elateridae species, the predatory larvae defecate enzymes on their prey, with digestion being extraorally. The alimentary canal basically comprises of a short narrow pharynx, a widened expansion, the crop and a poorly developed gizzard. After there is a midgut, that varies in dimensions between species, with a large amount of cecum, with a hingut, with varying lengths. There are typically four to six Malpighian tubules.

The nervous system in beetles contains all the types found in insects, varying between different species. With three thoracic and seven or eight abdominal ganglia can be distinguished to that in which all the thoracic and abdominal ganglia are fused to form a composite structure. Oxygen is obtained via a tracheal system. Air enters a series of tubes along the body through openings called spiracles, and is then taken into increasingly finer fibers. Pumping movements of the body force the air through the system. Beetles have hemolymph instead of blood like other insect species, the open circulatory system of the beetle is driven by a tube-like heart attached to the top inside of the thorax. Some species of diving beetles (**Dytiscidae**) carry a bubble of air with them whenever they dive beneath the water surface. This bubble may be held under the elytra or it may be trapped against the body using specialized hairs. The bubble usually covers one or more spiracles so the insect can breathe air from the bubble while submerged. An air bubble provides an insect with only a short-term supply of oxygen, but thanks to its unique physical properties, oxygen will diffuse into the bubble and displacing the nitrogen, called passive diffusion, however the volume of the bubble eventually diminishes and the beetle will have to return to the surface.

Different glands specialize for different pheromones produced for finding mates. Pheromones from species of Rutelinea are produced from epithelial cells lining the inner surface of the apical abdominal segments or amino acid based pheromones of Melolonthinae 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. For means of finding a mate also, fireflies (Lampyridae) utilized modified fat body cells woth transparent surfaces backed with reflective uric acid crystals to biosynthetically produce light, or bioluminescence. The light produce is highly efficient, as it is produced by oxidation of luciferin by the enzymes luciferase in the presence of ATP (adenosine triphospate) and oxygen, producing oxyluciferin, carbon dioxide, and light.

A notable number of species have developed special glands that produce chemicals for deterring predators. The Ground beetle's (of Carabidae) defensive glands, located at the posterior, produce a variety of hydrocarbons, aldehydes, phenols, quinones, esters, and acids released from an opening at the end of the abdomen. While african carabid beetles (e.g., *Anthia* and *Thermophilium*) employ the same chemicals as ants: formic acid. While Bombardier beetles have well developed, like other carabid beetles, pygidial glands that empty from the lateral edges of the intersegment membranes between the seventh and eighth abdominal segments. The gland is made of two containing chambers. The first holds hydroquinones and hydrogen peroxide, with the second holding just hydrogen peroxide plus catalases. These chemicals mix and result in an explosive ejection, forming temperatures of around 100 C, with the brake down of hydroquinone to H_2 + O_2 + quinone, with the O_2 propelling the excretion.

Tympanal organs or hearing organs, which is a membrane (tympanum) stretched across a frame backed by an air sac and associated sensory neurons, are described in two families. Several species of the genus *Cicindela* (**Cicindelidae**) have ears on the dorsal surface of the first abdominal segment beneath the wing; two tribes tribes in the family Dynastinae (**Scarabaeidae**) have ears just beneath the pronotal shield or neck membrane. The ears of both families are to ultrasonic frequencies, with strong evidence that they function to detect the presence of bats via there ultrasonic echolocation. Even though beetles constitute a large order and live in a variety of niches, examples of hearing is surprisingly lacking in species, though it is likely that most are just undiscovered.

Dermaptera

The neuroendocrine system consist of what typical insect would. There is a Brain, a subesophageal ganglion, three thoratic ganglia, and six abdominal ganglia; a ganglion being a mass of neurons. Strong neuron connects connect the neurohemal corpora cardiaca to the brain and frontal ganglion, where the closely related median corpus allatum produces Jeuvenile 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, albeit, earwigs lack gastric caecae which specialize in many species of insects for digestion. Long, slender (extratory) malpighian tubules can be found between the juntion of the mid- and hind gut.

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; or 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.

Diptera

The genitalia of female flies are rotated to a varying degree from the position found in other insects. 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 located below the genitals, or, in the case of 360° torsion, to the sperm duct being wrapped around the gut, despite 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 round to face in the opposite direction. This forces the male to lie on its back in order for its 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 at a much quicker rate. Flies come in great populations due ir ability to mate effectively and in a short period of time especially during the mating season.

The female lays her eggs as close to the food source as possible, and development is very rapid, allowing the larva to consume as much food **as** possible in a short period of time before transforming into the adult. The eggs hatch immediately after being laid, or the flies are ovoviviparous, with the larva hatching inside the mother. Larval flies, or maggots, have no true legs, and little demarcation between the thorax and abdomen; in the more derived species, the head is not clearly distinguishable from the rest of the body. Maggots are limbless, or else have small prolegs. The eyes and antennae are reduced or absent, and the abdomen also lacks appendages such as cerci. This lack of features is an adaptation to a food-rich environment, such as within rotting organic matter, or as an endoparasite. The pupae take various forms, and in some cases develop inside a silk cocoon. After emerging from the pupa, the adult fly rarely lives more than a few days, and serves mainly to reproduce and to disperse in search of new food sources.

Lepidoptera

In reproductive system of butterflies and moths, the male genitalia are complex and unclear. In females there are three types of genitalia based on the relating taxa: monotrysian, exoporian, and dytresian. In the monotrysian type there is an opening on the fused segments of the sterna 9 and 10, which act as insemination and oviposition. In the exoporian type (in Hepaloidae and Mnesarchaeoidea) there are two separate places for insemination and oviposition, both occurring on the same sterna as the monotrysian type, 9/10. In most species the genitalia are flanked by two soft lobes, although they may be specialized and sclerotized in some species for ovipositing in area such as crevices and inside plant tissue. Hormones and the glands that produce them run the development of butterflies and moths as they go through their life cycle, called the endocrine system. The first insect hormone PTTH (Prothoracicotropic hormone) operates the species life cycle and diapause. This hormone is produced by corpora allata and corpora cardiaca, where it is also stored. Some glands are specialized to perform certain task such as producing silk or producing saliva in the palpi. While the corpora cardiaca produce PTTH, the corpora allata also produces jeuvanile hormones, and the prothorocic glands produce moulting hormones.

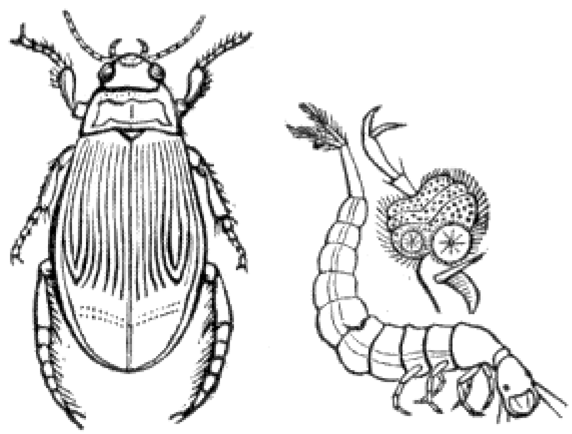
In the digestive system, the anterior region of the foregut has been modified to form a pharyngial sucking pump as they need it for the food they eat, which are for the most part liquids. An esophagus follows and leads to the posterior of the pharynx and in some species forms a form of crop. The midgut is short and straight, with the hindgut being longer and coiled. Ancestors of lepidopteran species, stemming from Hymenoptera, had midgut ceca, although this is lost in current butterflies and moths. Instead, all the digestive enzymes other then initial digestion, are immobilized at the surface of the midgut cells. In larvae, long-necked and stalked goblet cells are found in the anterior and posterior midgut regions, respectively. In insects, the goblet cells excrete positive potassium ions, which are absorbed from leaves ingested by the larvae. Most butterflies and moths display the usual digestive cycle, however species that have a different diet require adaptations to meet these new demands.

In the circulatory system, hemolymph, or insect blood, is used to circulate heat in a form of thermoregulation, where muscles contraction produces heat which is transferred to the rest of the body when conditions are unfavorable. In lepidopteran species, hemolymph is circulated through the veins in the wings by some form of pulsating organ, either by the heart or by the intake of air into the trachea. Air is taken in through spiracles along the sides of the abdomen and thorax supplying the trachea with oxygen as it goes through the lepidopteran's respiratory system. There are three different tracheae supplying oxygen diffusing oxygen throughout the species body: The dorsal, ventral, and visceral. The dorsal tracheae supply oxygen to the dorsal musculature and vessels, while the ventral tracheae supply the ventral musculature and nerve cord, and the visceral tracheae supply the guts, fat bodies, and gonads.

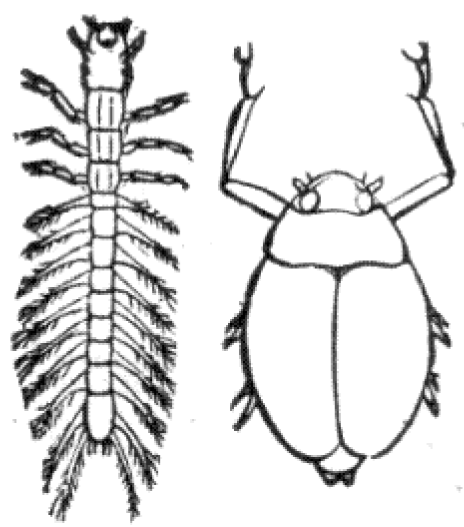
Chapter 3

Aquatic Insects and Insect Migration

Aquatic insects



A water beetle



A whirligig beetle

Aquatic insects live some portion of their life cycle in the water. They feed in the same ways as other insects. Some *diving* insects, such as predatory diving beetles, can hunt for food underwater where land-living insects cannot compete.

Breathing

One problem that aquatic insects must overcome is how to get oxygen while they are under water. All animals require a source of oxygen to live. Insects draw air into their bodies through spiracles, holes found along the sides of the abdomen. These spiracles are connected to tracheal tubes where oxygen can be absorbed. All aquatic insects have become adapted to their environment with the specialization of these structures.

Aquatic adaptations

1. Simple diffusion over a relatively thin integument
2. Breathing from a plastron or physical gill
3. Extraction of oxygen from water using a plastron or physical gill
4. Storage of oxygen in hemoglobin molecules in hemolymph
5. Taking oxygen from surface via breathing tubes (siphons)

Some insects have densely packed hairs (setae) around the spiracles that allow air to remain near, while keeping water away from, the body. They may even carry a bubble of air down from the surface. Others have a plastron that can be various combinations of hairs, scales, and undulations projecting from the cuticle, which hold a thin layer of air along the outer surface of the body. The trachea open through spiracles into this air film, allowing access to oxygen. The larvae and nymphs of mayflies, dragonflies and stoneflies still retain the air tubes they need for adult stage but when in larval stage they are equipped with gills that strain out oxygen in the water.

One mechanism used by some aquatic insects is one or more pockets of air called physical gills or sometimes 'gas gills'. When the insect dives into the water, it carries a layer of air over parts of its surface. The insect absorbs oxygen from this air as it would above the surface. Diffusion from the surrounding water replenishes the oxygen in the pocket of air. The large proportion of nitrogen in the air dissolves in water slowly and maintains the gas gill volume supporting oxygen diffusion. Insects need to periodically replenish their supply of air, not just oxygen.

Other aquatic insects can remain under water for long periods due to high concentrations of hemoglobin in their hemolymph circulating freely within the their body. Hemoglobin bonds strongly to oxygen molecules.

Orders with aquatic or semi-aquatic species

- Collembola - springtails (which are not technically insects, but are closely related)
- Ephemeroptera - mayflies
- Odonata - dragonflies and damselflies

- Plecoptera - stoneflies
- Hemiptera - true bugs
- Megaloptera - alderflies, fishflies, and dobsonflies
- Neuroptera - lacewings
- Coleoptera - beetles
- Hymenoptera - ants (e.g. *Polyrhachis sokolova*) and wasps
- Diptera - flies
- Mecoptera - scorponflies
- Lepidoptera - moths
- Trichoptera - caddisflies

Insect migration

Monarch butterfly cluster in Santa Cruz, California, where they have migrated to overwinter.

Insect migration is the seasonal movement of insects, particularly those by species of dragonflies, beetles, butterflies and moths. The distance can vary from species to species, but in most cases these movements involve large numbers of individuals. In some cases the individuals that migrate in one direction may not return and the next generation may instead migrate in the opposite direction. This is a significant difference from bird migration. The most famous insect migration is that of the Monarch butterfly which migrates from southern Canada to wintering sites in central Mexico where they spend the winter. In the late winter/early spring, the adult monarchs leave the Transvolcanic mountain range in Mexico for points North. Mating occurs and the females begin seeking out milkweed to lay their eggs, usually first in northern Mexico and southern Texas. The caterpillars hatch and develop into adults that move north, where more offspring can go as far as Central Canada until next migratory cycle.

Definition

All insects move to some extent. The range of movement can vary from within a few centimeters for some sucking insects and wingless aphids to thousands of kilometres in the case of other insects such as locusts, butterflies and dragonflies. The definition of migration is therefore particularly difficult in the context of insects. A behaviour oriented definition proposed is

Migratory behaviour is persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends upon some temporary inhibition of station-keeping responses but promotes their eventual disinhibition and recurrence.
—Kennedy, 1985

This definition disqualifies movements made in the search of resources and which are terminated upon finding of the resource. Migration on the other hand involves longer distance movement and these movements are not affected by the availability of the resource items.

General patterns

Migrating butterflies fly within a boundary layer, with a specific upper limit above the ground. The air speeds in this region are typically lower than the flight speed of the insect. These 'boundary-layer' migrants include the larger day-flying insects, and their low-altitude flight is obviously easier to observe than that of most high-altitude windborne migrants.

Many migratory species tend to have polymorphic forms, a migratory one and a resident phase. The migratory phases are marked by their well developed and long wings. Such polymorphism is well known in aphids and grasshoppers. In the migratory locusts, there are distinct long and short-winged forms.

Migration being energetically costly has been studied in the context of life-history strategies. It has been suggested that adaptations for migration would be more valuable for insects that live in habitats where resource availability changes seasonally. Others have suggested that species living in isolated islands of suitable habitats are more likely to evolve migratory strategies. The role of migration in gene flow has also been studied in many species.

Orientation

Migration is usually marked by well defined destinations which need navigation and orientation. A flying insect needs to make corrections for crosswinds. It has been demonstrated that many migrating insects sense windspeed and direction and make suitable corrections. Day-flying insects primarily make use of the sun for orientation, however this requires that they compensate for the movement of the sun. Endogenous time-compensation mechanisms have been proposed and tested by releasing migrating butterflies that have been captured and kept in darkness to shift their internal clocks and observing changes in the directions chosen by them. Some species appear to make corrections while it has not been demonstrated in others.

Most insects are capable of sensing polarized light and they are able to use the polarization of the sky when the sun is occluded by clouds. The orientation mechanisms of nocturnal moths and other insects that migrate have not been well studied, however magnetic cues have been suggested in short distance fliers.

Recent studies suggest that migratory butterflies may be sensitive to the Earth's magnetic field on the basis of the presence of magnetite particles. In an experiment on the monarch butterfly, it was shown that a magnet changed the direction of initial flight of migrating monarch butterflies. However this result was not a strong demonstration since the directions of the experimental butterflies and the controls did not differ significantly in the direction of flight.

Lepidoptera

Migration in the butterflies and moths are particularly well known. The Bogong moth is a native insect of Australia that is known to migrate to cooler climates. The Madagascan sunset moth (*Chrysiridia rhipheus*) has migrations of up to thousands of individuals occur between the eastern and western ranges of their host plant, because they become depleted or unsuitable for consumption. In southern India, mass migrations of many species are noted prior to the monsoons. As many as 250 species of butterflies in India are migratory. These include members of the Pieridae and Nymphalidae.

Chapter 4

Insect Flight

A Tau Emerald (*Hemicordulia tau*) dragonfly in flight

Insects are the only group of invertebrates known to have evolved flight. Insects possess some remarkable flight characteristics and abilities, still far superior to attempts by humans to replicate their capabilities. Even our understanding of the aerodynamics of flexible, flapping wings and how insects fly is imperfect. One application of this research is in the engineering of extremely small micro air vehicles with low Reynolds numbers.

Evolution and adaptation

Hoverfly in flight (*Xanthogramma pedissequum*)

Sometime in the Carboniferous Period, some 350 million years ago, when there were only two major land masses, insects began flying. How and why insect wings developed, however, is not well understood, largely due to the scarcity of appropriate fossils from the period of their development in the Lower Carboniferous. Three main theories on the origins of **insect flight** are that wings developed from paranotal lobes, extensions of the thoracic terga; that they are modifications of movable abdominal gills as found on aquatic naiads of mayflies; or that they developed from thoracic protrusions used as radiators.

Paranotal hypothesis

The paranotal hypothesis suggests that the insect's wings developed from paranotal lobes, a preadaptation found in insect fossils that is believed to have assisted stabilization while hopping or falling.

In favor of this hypothesis is the tendency of most insects, when startled while climbing on branches, to escape by dropping to the ground. Such lobes would have served as parachutes and enable the insect to land more softly.

The theory suggests that these lobes gradually grew larger and in a later stage developed a joint with the thorax. Even later would appear the muscles to move these crude wings. This model implies a progressive increase in the effectiveness of the wings, starting with parachuting, then gliding and finally active flight.

Still, lack of substantial fossil evidence of the development of the wing joints and muscles poses a major difficulty to the theory, as does the seemingly spontaneous development of articulation and venation, and it has been largely rejected by experts in the field.

Epicoxal hypothesis

Some entomologists have suggested that a possible origin for insect wings might have been the movable abdominal gills found in many aquatic insects, such as on naiads of mayflies. According to this theory these tracheal gills, which started their way as exits of the respiratory system and over time were modified into locomotive purposes, eventually developed into wings. The tracheal gills are equipped with little winglets that perpetually vibrate and have their own tiny straight muscles.

Endite-exite hypothesis

The hypothesis with perhaps the strongest evidence is that which stems from the adaptation of endites and exites, appendages on the respective inner and outer aspects of the primitive arthropod limb. This was advanced by Trueman based on a study by Goldschmidt in 1945 on *Drosophila melanogaster*, in which a *pod* variation displayed a mutation transforming normal wings to what was interpreted as a triple-jointed leg arrangement with some additional appendages but lacking the tarsus, where the wing's costal surface normally would be. This mutation was reinterpreted as strong evidence for a dorsal exite and endite fusion, rather than a leg, with the appendages fitting in much better with this hypothesis. The innervation, articulation and musculature required for the evolution of wings are already present in podomeres.

Other hypotheses

Suggestions have been made that wings may have evolved initially for sailing on the surface of water as seen in some stoneflies. An alternative idea is that it drives from directed aerial gliding descent—a preflight phenomena found in some apterygote, a wingless sister taxa to the winged insects.

The earliest fliers were similar to dragonflies with two sets of wings, direct flight muscles, and no ability to fold their wings over their abdomens. Most insects today, which evolved from those first fliers, have simplified to either one pair of wings or two pairs functioning as a single pair and using a system of indirect flight muscles.

Natural selection has played an enormous role in refining the wings, control and sensory systems, and anything else that affects aerodynamics or kinematics. One noteworthy trait is wing twist. Most insect wings are twisted, as are helicopter blades, with a higher angle of attack at the base. The twist generally is between 10 and 20 degrees. In addition to this twist, the wing surfaces are not necessarily flat or featureless; most larger insects have wing membranes distorted and angled between the veins in such a way that the cross-section of the wings approximates an airfoil. Thus, the wing's basic shape already is capable of generating a small amount of lift at zero angle of attack. Most insects control their wings by adjusting tilt, stiffness, and flapping frequency of the wings with tiny muscles in the thorax (below). Some insects evolved other wing features that are not advantageous for flight, but play a role in something else, such as mating or protection.

Some insects, occupying the biological niches that they do, need to be incredibly maneuverable. They must find their food in tight spaces and be capable of escaping larger predators - or they may themselves be predators, and need to capture prey. Their maneuverability, from an aerodynamic viewpoint, is provided by high lift and thrust forces. Typical insect fliers can attain lift forces up to three times their weight and horizontal thrust forces up to five times their weight. There are two substantially different insect flight mechanisms, and each has its own advantages and disadvantages - just because odonates have a more primitive flight mechanism does not mean they are less able fliers; they are, in certain ways, more agile than anything that has evolved afterward.

Direct flight mechanism

Unlike most other insects, the wing muscles of mayflies and odonates (the two living orders traditionally classified as "Paleoptera") insert directly at the wing bases, which are hinged so that a small movement of the wing base downward, lifts the wing itself upward, very much like rowing through the air. In mayflies, the hind wings are reduced, sometimes absent, and play little role in their flight, which is not particularly agile or graceful. In contrast, even though dragonflies cannot hover in still air with this primitive mechanism (although, with careful use of wind currents, they can remain nearly stationary), damselflies can, and in both groups, the fore and hind wings are similar in shape and size, and operated independently, which gives a degree of fine control and mobility in terms of the abruptness with which they can change direction and speed, not seen in other flying insects. This is not surprising, given that odonates are all aerial predators, and they have always hunted other airborne insects - evolutionary pressures have led to more advanced flight ability.

Indirect flight mechanism

Rare buzz pollination of parsley by a honeybee

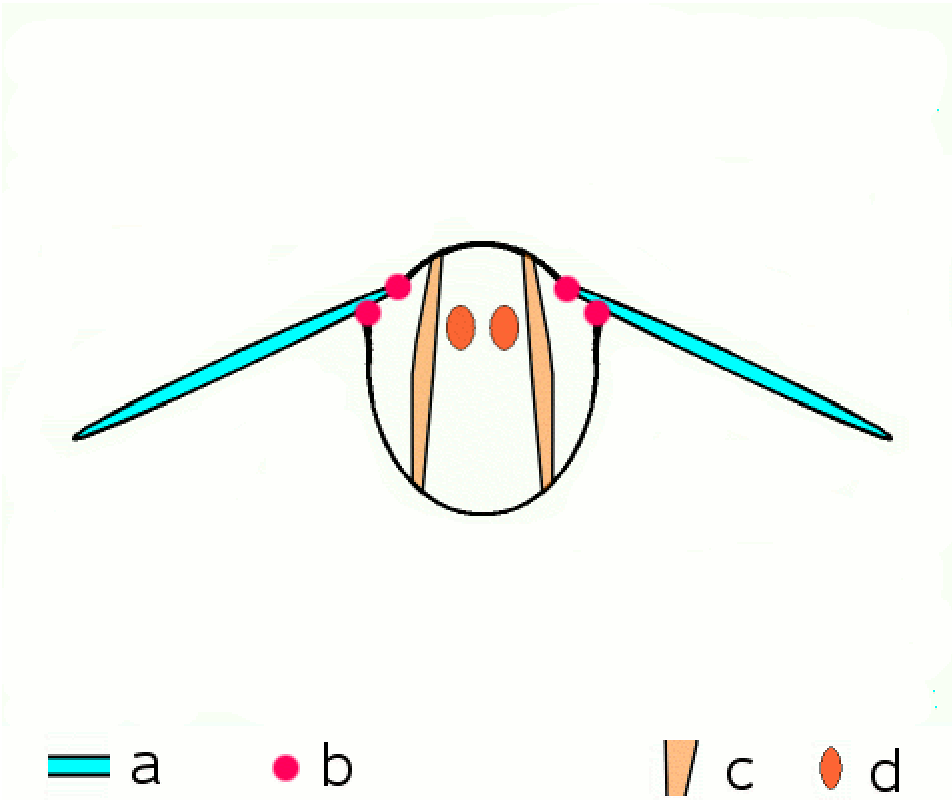
Other than the two orders with direct flight muscles, all other living winged insects fly using a different mechanism, involving indirect flight muscles. This mechanism evolved once, and is the defining feature (synapomorphy) for the infraclass Neoptera; it corresponds, probably not coincidentally, with the appearance of a wing-folding mechanism, which allows Neopteran insects to fold the wings back over the abdomen when at rest (though this ability has been lost secondarily in some groups, such as all butterflies).

In the higher groups with two functional pairs of wings, both pairs are linked together mechanically in various ways, and function as a single wing, although this is not true in the more primitive groups. What all Neoptera share, however, is the way the muscles in the thorax work: these muscles, rather than attaching to the wings, attach to the thorax and deform it; since the wings are extensions of the thoracic exoskeleton, the deformations of the thorax cause the wings to move as well. A set of **dorsal longitudinal muscles** compress the thorax from front to back, causing the dorsal surface of the thorax (notum) to bow upward, making the wings flip down. A set of **tergosternal muscles** pull the notum downward again, causing the wings to flip upward.

In a few groups, the downstroke is accomplished solely through the elastic recoil of the thorax when the tergosternal muscles are relaxed. Several small sclerites at the wing base have other, separate, muscles attached and these are used for fine control of the wing base in such a way as to allow various adjustments in the tilt and amplitude of the wing beats.

One of the final refinements that has appeared in some of the higher Neoptera (Coleoptera, Diptera, and Hymenoptera) is a type of muscular or neural control system whereby a single nerve impulse causes a muscle fiber to contract multiple times; this allows the frequency of wing beats to exceed the rate at which the nervous system can send impulses. This specialized form of muscle is termed **asynchronous flight muscle**. The overall effect is that many higher Neoptera can hover, fly backward, and perform other feats involving a degree of fine control that insects with direct flight muscles cannot achieve.

Basic aerodynamics



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

There are two basic aerodynamic models of insect flight. Most insects use a method that creates a spiralling leading edge vortex. These flapping wings move through two basic half-strokes. The downstroke starts up and back and is plunged downward and forward. Then the wing is quickly flipped over, supination, so that the leading edge is pointed backward. The upstroke then pushes the wing upward and backward. Then the wing is flipped again, pronation, and another downstroke can occur. The frequency range in insects with synchronous flight muscles typically is 5 to 200 hertz (Hz). In those with asynchronous flight muscles, wing beat frequency may exceed 1000 Hz. When the insect is hovering, the two strokes take the same amount of time. A slower downstroke, however, provides thrust.

Identification of major forces is critical to understanding insect flight. The first attempts to understand flapping wings assumed a quasi-steady state. This means that the air flow over the wing at any given time was assumed to be the same as how the flow would be over a non-flapping, steady-state wing at the same angle of attack. By dividing the flapping wing into a large number of motionless positions and then analysing each position, it would be possible to create a timeline of the instantaneous forces on the wing at every moment. The calculated lift was found to be too small by a factor of three, so researchers realised that there must be unsteady phenomena providing aerodynamic forces. There were several developing analytical models attempting to approximate flow close to a flapping wing. Some researchers predicted force peaks at supination. With a dynamically scaled model of a fruit fly, these predicted forces later were confirmed. Others argued that the force peaks during supination and pronation are caused by an unknown rotational effect that fundamentally is different from the translational phenomena. There is some disagreement with this argument. Through computational fluid dynamics, some researchers argue that there is no rotational effect. They claim that the high forces are caused by an interaction with the wake shed by the previous stroke.

Similar to the rotational effect mentioned above, the phenomena associated with flapping wings are not completely understood or agreed upon. Because every model is an approximation, different models leave out effects that are presumed to be negligible. For example, the *Wagner effect* says that circulation rises slowly to its steady-state due to viscosity when an inclined wing is accelerated from rest. This phenomenon would explain a lift value that is less than what is predicted. Typically, the case has been to find sources for the added lift. It has been argued that this effect is negligible for flow with a Reynolds number that is typical of insect flight. The Wagner effect was ignored, consciously, in at least one recent model.

One of the most important phenomena that occurs during insect flight is leading edge suction. This force is significant to the calculation of efficiency. The concept of leading edge suction first was put forth to describe vortex lift on sharp-edged delta wings. At high angles of attack, the flow separates over the leading edge, but reattaches before reaching the trailing edge. Within this bubble of separated flow is a vortex. Because the angle of attack is so high, a lot of momentum is transferred downward into the flow. These two features create a large amount of lift force as well as some additional drag. The important feature, however, is the lift. Because the flow has separated, yet it still provides large amounts of lift, this phenomenon is called *stall delay*. This effect was observed in flapping insect flight and it was proven to be capable of providing enough lift to account for the deficiency in the quasi-steady-state models. This effect is used by canoeists in a sculling draw stroke.

All of the effects on a flapping wing may be reduced to three major sources of aerodynamic phenomena: the leading edge vortex, the steady-state aerodynamic forces on the wing, and the wing's contact with its wake from previous strokes.

The size of flying insects ranges from about 20 micrograms to about 3 grams. As insect body mass increases, wing area increases and wing beat frequency decreases. For larger insects, the Reynolds number (Re) may be as high as 10000. For smaller insects, it may be as low as 10. This means that viscous effects are much more important to the smaller insects, although the flow is still laminar, even in the largest fliers.

Another interesting feature of insect flight is the body tilt. As flight speed increases, the insect body tends to tilt nose-down and become more horizontal. This reduces the frontal area and therefore, the body drag. Since drag also increases as forward velocity increases, the insect is making its flight more efficient as this efficiency becomes more necessary. Additionally, by changing the geometric angle of attack on the downstroke, the insect is able to keep its flight at an optimal efficiency through as many manoeuvres as possible.

The development of general thrust is relatively small compared with lift forces. Lift forces may be more than three times the insect's weight, while thrust at even the highest speeds may be as low as 20% of the weight. This force is developed primarily through the less powerful upstroke of the flapping motion.

The second method of flight, fling and clap, functions differently. In this process, the wings clap together above the insect's body and then fling apart. As they fling open, the air gets sucked in and creates a vortex over each wing. This bound vortex then moves across the wing and, in the clap, acts as the starting vortex for the other wing. By this effect, circulation and thus, lift are increased to the extent of being higher, in most cases, than the typical leading edge vortex effect. One of the reasons this method is not employed by more insects is the expected damage and wear to the wings caused by the repeated clapping. It is prevalent, however, among insects that are very small and experience low Reynolds numbers.

Wing coupling

"Oiketicus" spp. (Family Psychidae). The frenulum can be seen at the top of the rear wing, which hooks onto the retinaculum so that the wings travel together during flight. Magnification: 10x

Some four-winged insect orders, such as the Lepidoptera, have developed a wide variety of morphological wing-coupling mechanisms in the imago which render these taxa as "functionally dipterous". All, but the most basal forms, exhibit this wing-coupling. .

The mechanisms are of three different types - jugal, frenulo-retinacular and amplexiform.

The more primitive groups have an enlarged lobe-like area near the basal posterior margin, i.e. at the base of the forewing, called *jugum*, that folds under the hindwing in flight.

Other groups have a frenulum on the hindwing that hooks under a retinaculum on the forewing.

In the butterflies (except the male of one species of hesperiid) and in the Bombycoidea (except the Sphingidae), there is no arrangement of frenulum and retinaculum to couple the wings. Instead, an enlarged humeral area of the hindwing is broadly overlapped by the forewing. Despite the absence of a specific mechanical connection, the wings overlap and operate in phase. The power stroke of the forewing pushes down the hindwing in unison. This type of coupling is a variation of frenate type but where the frenulum and retinaculum are completely lost.

Biochemistry

The biochemistry of insect flight has been a focus of considerable study. While many insects use carbohydrates and lipids as the energy source for flight, many beetles and flies prefer to use the amino acid, proline, as their energy source. Some species also use a combination of sources and moths such as *Manduca sexta* prefer to use carbohydrates for pre-flight warm-up.

Chapter 5

Pupa

Pupa of the Cockchafer (*Melolontha melolontha*)

A **pupa** (Latin *pupa* for doll, pl: *pupae* or *pupas*) is the life stage of some insects undergoing transformation. The pupal stage is found only in holometabolous insects, those that undergo a complete metamorphosis, going through four life stages; embryo, larva, pupa and imago.

The pupae of different groups of insects have different names such as chrysalis in the Lepidoptera and tumbler in mosquitoes. Pupae may further be enclosed in other structures such as cocoons, nests or shells.

Some pupae remain inside the exoskeleton of the final larval instar and receive the name of puparium (plural, puparia); the flies of the families Stratiomyidae, Syrphidae and others have puparia.

Position in life cycle

In the life of an insect the pupal stage follows the larval stage and precedes adulthood (*imago*). It is during the time of pupation that the adult structures of the insect are formed while the larval structures are broken down. Pupae are inactive, and usually sessile (not able to move about). They have a hard protective coating and often use camouflage to evade potential predators.

Duration

Pupation may last weeks, months or even years. For example it is 2 weeks in monarch butterflies. The pupa may enter dormancy or *diapause* until the appropriate season for the adult insect. In temperate climate pupae usually stay dormant during winter, in the tropics pupae usually do so during the dry season. Anise Swallowtails sometimes emerge after years as a chrysalis.

Emergence

Eclosion of *Papilio dardanus*

Insects emerge (**eclose**) from pupae by splitting the pupal case, and the whole process of pupation is controlled by the insect's hormones. Most butterflies emerge in the morning. In mosquitoes the emergence is in the evening or night. In fleas the process is triggered by vibrations that indicate the possible presence of a suitable host. Prior to emergence, the adult inside the pupal exoskeleton is termed "**pharate**". Once the pharate adult has eclosed from the pupa, the empty pupal exoskeleton is called an "**exuvium**" (or **exuvia**); in most hymenopterans (ants, bees and wasps) the exuvium is so thin and membranous that it becomes "crumpled" as it is shed.

Pupal mating

Mating in pierid *Catopsilia pyranthe* of male with newly emerged female.

In a few taxa of the Lepidoptera, especially *Heliconius*, pupal mating is an extreme form of reproductive strategy where adults males mate with female pupa about to emerge or with the newly moulted female; this is accompanied by other actions such as capping of the reproductive system of the female with the sphragis, denying access to other males, or by exuding an anti-aphrodisiac pheromone.

Defense

Pupae are usually immovable and are largely defenseless. To overcome this, a common feature is concealed placement. There are some species of Lycaenid butterflies who are protected in their pupal stage by ants. Another means of defense by pupae of other species is the capability of making sounds or vibrations to scare potential predators. A few species use chemical defenses including toxic secretions. The pupae of social hymenopterans are protected by adult members of the hive.

Chrysalis

Common crow (*Euploea core*) chrysalis illustrating the Greek origin of the term : χρυσός (*chrysós*) for gold

A **chrysalis** (Latin *chrysallis*, from Greek χρυσαλλίς = *chrysallís*, pl: *chrysalides*) or **nympha** is the pupal stage of butterflies. The term is derived from the metallic gold-colouration found in the pupae of many butterflies, referred to by the Greek term χρυσός (*chrysós*) for gold.

When the caterpillar is fully grown, it makes a button of silk which it uses to fasten its body to a leaf or a twig. Then the caterpillar's skin comes off for the final time. Under this old skin is a hard skin called a chrysalis.

Because chrysalides are often showy and are formed in the open, they are the most familiar examples of pupae. Most chrysalides are attached to a surface by a Velcro-like arrangement of a silken pad spun by the caterpillar, usually cemented to the underside of a perch, and the *cremaster*, a hook-shaped protuberance from the rear of the chrysalis at the tip of the pupal abdomen by which the caterpillar fixes itself to the pad of silk.

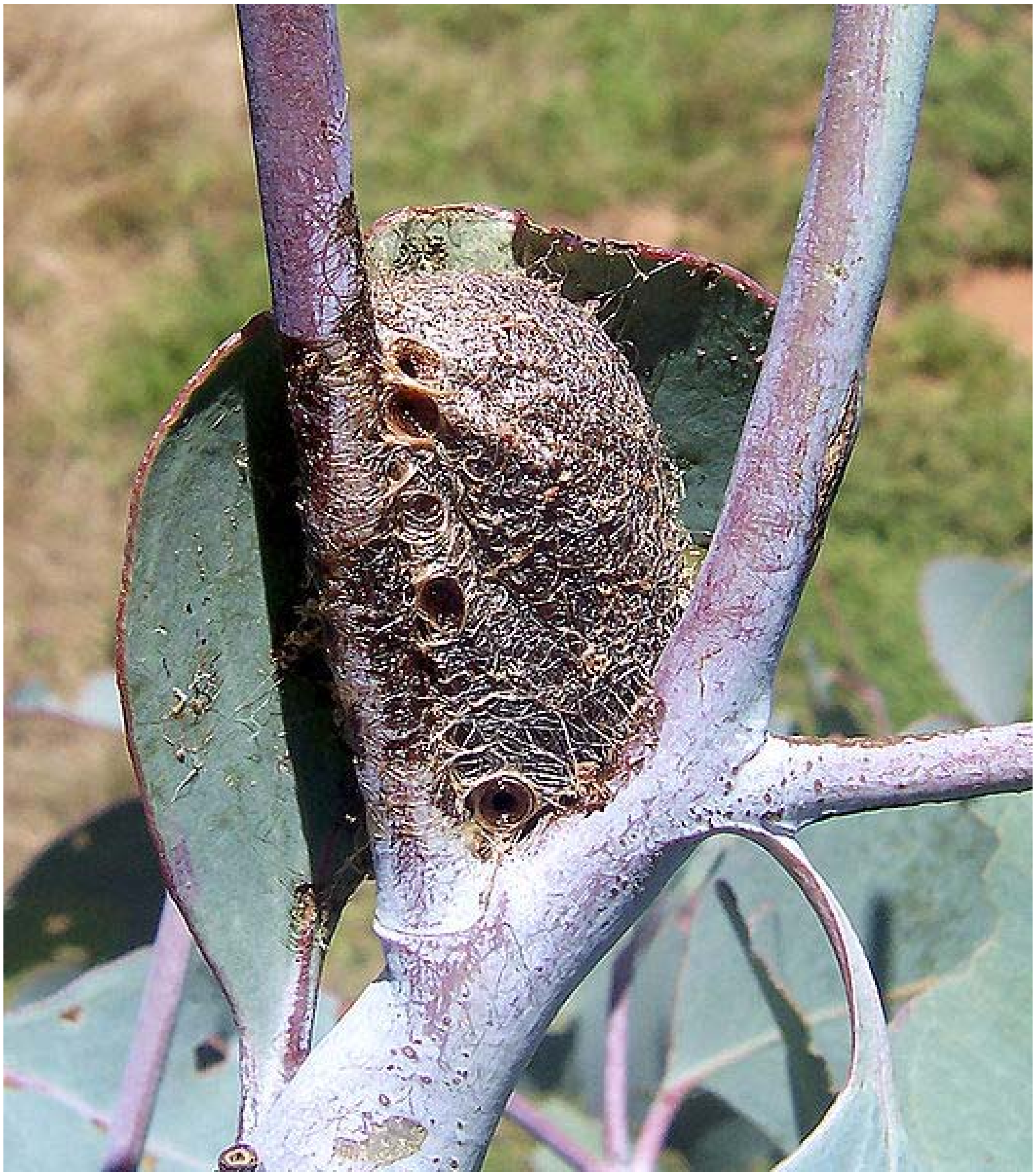
Like other types of pupae, the chrysalis stage in most butterflies is one in which there is little movement. However, some butterfly pupae are capable of moving the abdominal segments to produce sounds or to scare away potential predators. Within the chrysalis, growth and differentiation occur. The adult butterfly emerges (ecloses) from this and expands its wings by pumping haemolymph into the wing veins. This sudden and rapid change from pupa to imago is called metamorphosis but metamorphosis is really the whole series of changes that an insect undergoes from egg to adult.

When the butterfly emerges from the chrysalis, usually it will sit on the empty shell in order to expand and harden its wings. However, if the chrysalis was near the ground (such as if it fell off from its silk pad), the butterfly would find another vertical surface to rest upon and harden its wings (such as a wall or fence).

Moth pupae are usually dark in color and either formed in underground cells, loose in the soil, or their pupa is contained in a protective silk case called a **cocoon**.

It is important to differentiate between pupa, chrysalis and cocoon. The pupa is the stage between the larva and adult stages. The chrysalis is a butterfly pupa. A cocoon is a silk case that moths, and sometimes other insects, spin around the pupa.

Cocoon



The tough brown cocoon of an Emperor Gum Moth

A **cocoon** is a casing spun of silk by many moth caterpillars, and numerous other holometabolous insect larvae as a protective covering for the pupa.

Cocoons may be tough or soft, opaque or translucent, solid or meshlike, of various colors, or composed of multiple layers, depending on the type of insect larva producing it. Many moth caterpillars shed the larval hairs (setae) and incorporate them into the cocoon; if these are urticating hairs then the cocoon is also irritating to the touch. Some larvae attach small twigs, fecal pellets or pieces of vegetation to the outside of their cocoon in an attempt to disguise it from predators. Others spin their cocoon in a concealed location –

on the *underside* of a leaf, in a crevice, down near the base of a tree trunk, suspended from a twig or concealed in the leaf litter.

The silk in the cocoon of the silk moth can be unravelled to get silk fibre which makes this moth the most economically important of all Lepidopterans. The moth is the only completely domesticated Lepidopteran and does not exist in the wild.

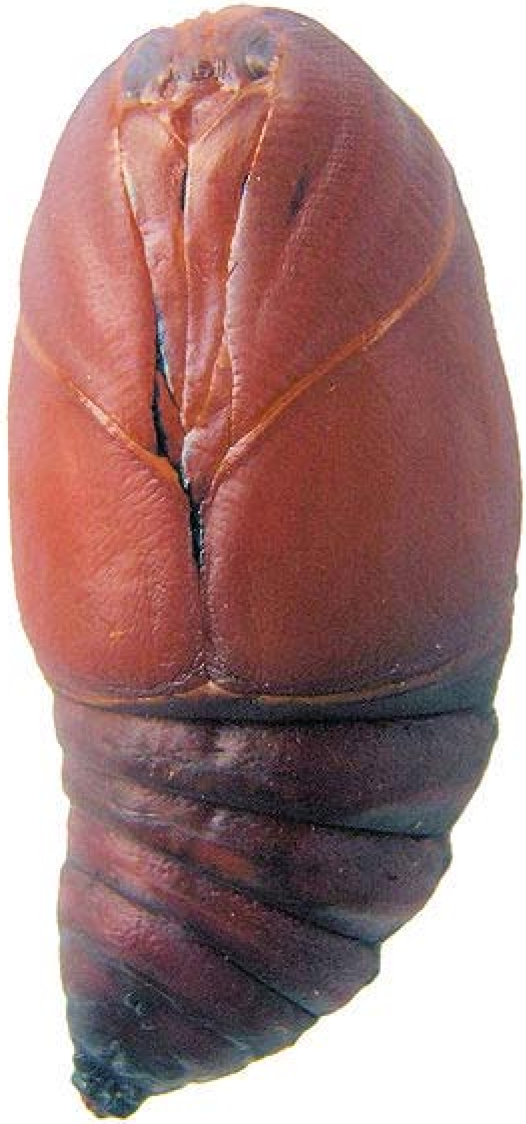
Insects that pupate in a cocoon must escape from it, and they do this either by the pupa cutting its way out, or by secreting fluids that soften the cocoon. Some cocoons are constructed with built-in lines of weakness along which they will tear easily from inside, or with exit holes that only allow a one-way passage out; such features facilitate the escape of the adult insect after it emerges from the pupal skin.

An Emperor Gum Moth caterpillar spinning its cocoon.

Luna moth cocoon and pupa.

Assortment of Luna moth cocoons.

Luna moth emerging from silk cocoon.



Luna moth pupa removed from cocoon.

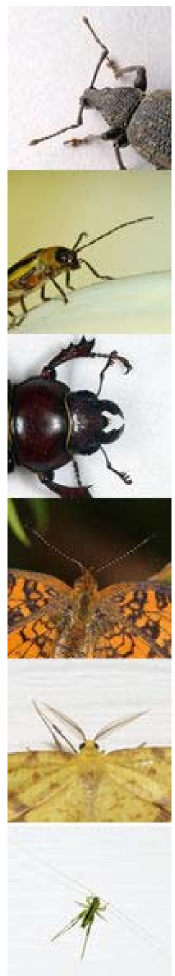
Chrysalis of Gulf Fritillary in Georgetown, South Carolina

Pupation of *Inachis io*

Monarch Butterfly chrysalis

Chapter 6

Phylogeny of Insects



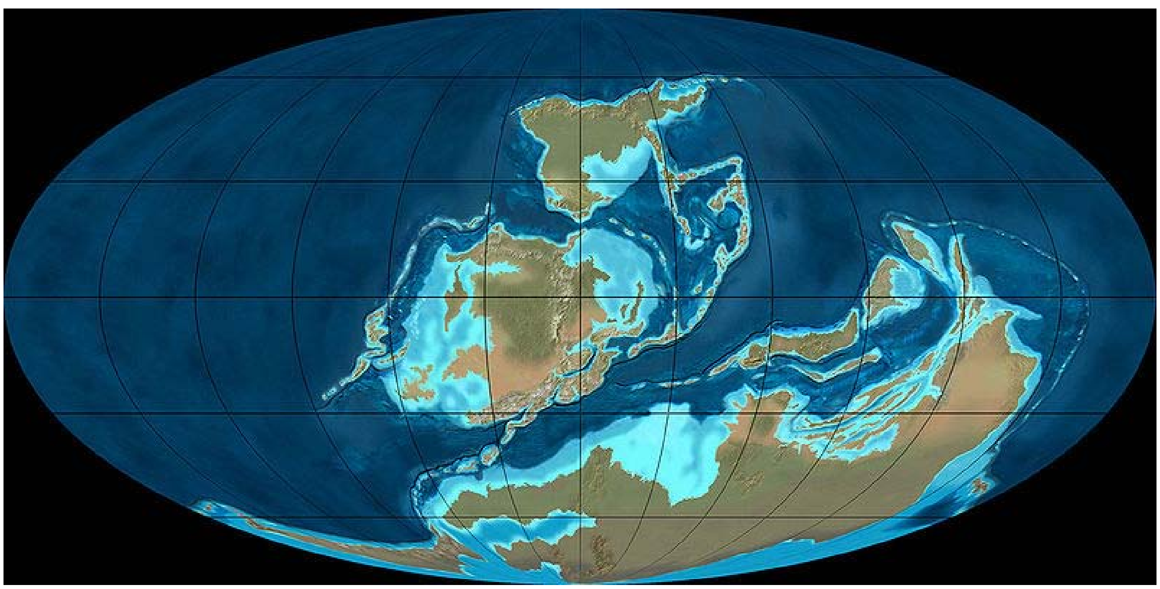
Evolution has produced astonishing variety in insects. Pictured are some of the possible shapes of antennae.

Insects are a highly diverse group of organisms with a worldwide distribution. They have conquered every terrestrial environment and have complex interactions with a wide variety of organisms, including predatory-prey relationships.

Evolutionary history

Devonian

The **Devonian (408-362 mya)** was a relatively warm period, and probably lacked any glaciers with reconstruction of tropical sea surface temperature from conodont apatite implies an average value of 30 °C (86 °F) in the Early Devonian. CO_2 levels dropped steeply throughout the Devonian period as the burial of the newly-evolved forests drew carbon out of the atmosphere into sediments; this may be reflected by a Mid-Devonian cooling of around 5 °C (9 °F). The Late Devonian warmed to levels equivalent to the Early Devonian; while there is no corresponding increase in CO_2 concentrations, continental weathering increases (as predicted by warmer temperatures); further, a range of evidence, such as plant distribution, points to Late Devonian warming. The continent Euramerica (or Laurussia) was created in the early Devonian by the collision of Laurentia and Baltica, which rotated into the natural dry zone along the Tropic of Capricorn, which is formed as much in Paleozoic times as nowadays by the convergence of two great air-masses, the Hadley cell and the Ferrel cell.

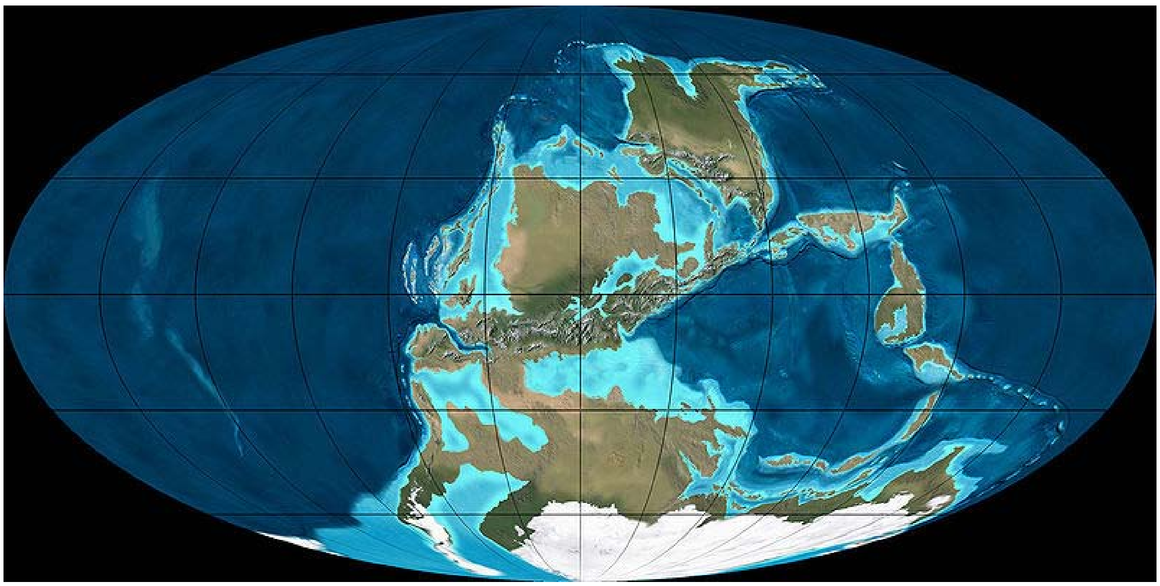


Global paleogeographic reconstruction of the Earth in the late Devonian period 370 million years ago.

The oldest definitive insect fossil is the Devonian *Rhyniognatha hirsti*, estimated at 396-407 million years old. This species already possessed dicondylic mandibles, 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. Like other insects of its time, *Rhyniognatha* presumably fed on plant sporophylls - which occur at the tips of branches and bear sporangia, the spore-producing organs. The insect's anatomy might also give clues as to what it ate. The creature had large mandibles which may or may not have been used for hunting.

Carboniferous

The **Carboniferous (362-290 mya)** is famous for its wet, warm climates and extensive swamps of mosses, ferns, horsetails, and calamites. Glaciations in Gondwana, triggered by Gondwana's southward movement, continued into the Permian and because of the lack of clear markers and breaks, the deposits of this glacial period are often referred to as Permo-Carboniferous in age. The cooling and drying of the climate led to the Carboniferous Rainforest Collapse (CRC). Tropical rain forests fragmented and then were eventually devastated by climate change.



Global paleogeographic reconstruction of the Earth in the late Carboniferous ("Pennsylvanian") period 300 million years ago.

Fossil of *Meganeura sp.*.

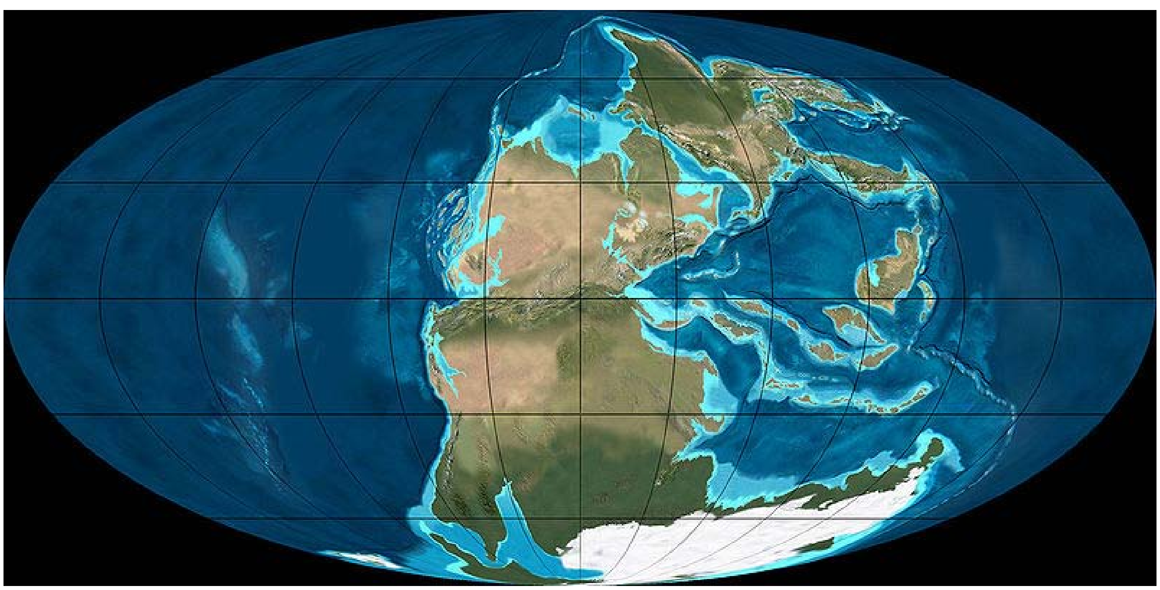
Remains of insects are scattered through out the coal deposits, particularly of wings from cockroaches (**Blattodea**); two deposits in particular are from Mazon Creek, Illinois and Commentary, France. The earliest winged insects are from this time period (Pterygota), including the aforementioned Blattaria, Caloneurodea, primitive stem-group Ephemeropterans, Orthoptera, Palaeodictyopteroidea. In 1940, in Noble County, Oklahoma fossil of Meganeuropsis americana as it represented by the largest complete insect wing ever found.

Very early Blattarians had a large, discoid pronotum and coriaceous forewings wings with a distinct CuP vein (a unbranched wing vein, lying near the claval fold and reaching the wing posterior margin). These where not true cockroahces as they had an ovipositor, although through the Carboniferous, the ovipositor started to diminish. The orders Caloneurodea and Miomoptera are known, with orthoptera and Blattaria to be one of the earliest Neoptera; developing from the upper Caboniferous to the Permian. These insects had wings with similar form and structure: small anal lobes. Species of Orthoptera, or grasshopers and related kin, is an ancient order that still exist till today extending from this time period. From which time even the distinctive synapomorphy of saltatorial, or adaptive for jumping, hind legs is preserved.

Palaeodictyopteroidea is a large and diverse group includes 50% of all known Paleozoic insects. Containing many of the primitive features of the time: very long cerci, an ovipositor, and wings with little or no anal lobe. Protodonata, as its name implies, is a primitive paraphyletic group similar to Odonata; although lacks distinct features such as a nodus, a pterostigma and a arculus. Most were only slightly larger than modern dragonflies, but the group does include the largest known insects, such as the late Carboniferous *Meganeura monyi*, *Megatypus*, and the even larger later Permian *Meganeuropsis permiana*, with wingspans of up to 71 centimetres (2.33 ft). They where probably the top predators for some 100 million years.

Permian

The **Permian (290-245 mya)** was a relatively short period, however a very important period at least. During this time period, all the Earth's major land masses were collected into a single supercontinent known as Pangaea. Pangaea straddled the equator and extended toward the poles, with a corresponding effect on ocean currents in the single great ocean ("Panthalassa", the "universal sea"), and the Paleo-Tethys Ocean, a large ocean that was between Asia and Gondwana. The Cimmeria continent rifted away from Gondwana and drifted north to Laurasia, causing the Paleo-Tethys to shrink. At the end of the Permian, the biggest mass extinction in the history history took place, collectively called the Permian–Triassic extinction event: 30% of all insect species became extinct, however, it is the only mass extinction of insects in Earth's history until today.



Global paleogeographic reconstruction of the Earth in the late Permian period 260 million years ago.

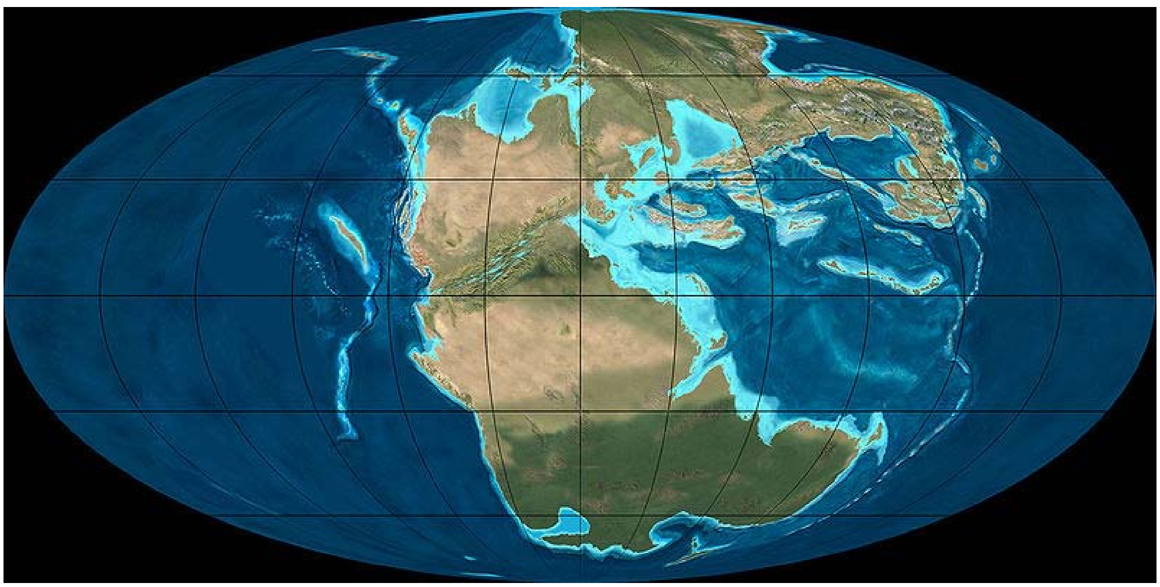
2007 study based on DNA of living beetles and maps of likely beetle evolution indicated that beetles may have originated during the Lower Permian, up to 299 million years ago. In 2009, a fossil beetle was described from the Pennsylvanian of Mazon Creek, Illinois, pushing the origin of the beetles to an earlier date, 318 to 299 million years ago. Fossils from this time have been found in Asia and Europe, for instance in the red slate fossil beds of Niedermoschel near Mainz, Germany. Further fossils have been found in Obora, Czechia and Tshekarda in the Ural mountains, Russia.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 were made in the Wellington formation of Oklahoma and were published in 2005 and 2008. Some of the most important fossil deposits from this era are from Elmo, Kansas (260 mya); others include New South Wales, Australia (240 mya) and central Eurasia (250 mya).

During this time, many of the species from the Carboniferous diversified, and many new orders developed, including: Protelytroptera, primitive relatives of Plecoptera (Paraplecoptera), Psocoptera, Mecoptera, Coleoptera, Raphidioptera, and Neuroptera. The last four being the first definitive records of the Holometabola. By the Pennsylvanian and well into the Permian, by far the most successful were primitive Blattoptera, or relatives of cockroaches. Six fast legs, two well developed folding wings, fairly good eyes, long, well developed antennae (olfactory), an omnivorous digestive system, a receptacle for storing sperm, a chitin skeleton that could support and protect, as well as form of gizzard and efficient mouth parts, gave it formidable advantages over other herbivorous animals. About 90% of insects were cockroach-like insects ("Blattopterans"). The dragonflies *Odonata* were the dominant aerial predator and probably dominated terrestrial insect predation as well. True Odonata appeared in the Permian and all are amphibious. Their prototypes are the oldest winged fossils, go back to the Devonian, and are different from other wings in every way. Their prototypes may have had the beginnings of many modern attributes even by late Carboniferous and it is possible that they even captured small vertebrates, for some species had a wing span of 71 cm.

The oldest known insect that resembles species of Coleoptera date back to the Lower Permian (270 mya), though they instead have 13-segmented antennae, elytra with more fully developed venation and more irregular longitudinal ribbing, and an abdomen and ovipositor extending beyond the apex of the elytra. The oldest true beetle, that is having features that include 11-segmented antennae, regular longitudinal ribbing on the elytra, and having genitalia that are internal. The earliest beetle-like species had pointed, leather like forewings with cells and pits. Hemiptera, or true bugs had appeared in the form of Arctiniscytina and Paraknightia. The later had expanded parapronotal lobes, a large ovipositor, and forewings with unusual venation, possibly diverging from Blattoptera. The orders Raphidioptera and Neuroptera are grouped together as Neuropterida. The one family of putative Raphidiopteran clade (Sojanoraphidiidae) has been controversially placed as so. Although the group had a long ovipositor distinctive to this order and a series of short crossveins, however with a primitive wing venation. Early families of Plecoptera had wing venation consistent with the order and its recent decendents. Psocoptera was first appeared in the Permian period, they are often regarded as the most primitive of the hemipteroids.

Triassic

The **Triassic (245-208 mya)** was a period when arid and semiarid savannas developed and when the first mammals, dinosaurs, and pterosaurs also appeared. During the Triassic, almost all the Earth's land mass was still concentrated into Pangaea. From the east a vast gulf entered Pangaea, the Tethys sea. The remaining shores were surrounded by the world-ocean known as Panthalassa. The supercontinent Pangaea was rifting during the Triassic—especially late in the period—but had not yet separated. The climate of the Triassic was generally hot and dry, forming typical red bed sandstones and evaporites. There is no evidence of glaciation at or near either pole; in fact, the polar regions were apparently moist and temperate, a climate suitable for reptile-like creatures. Pangaea's large size limited the moderating effect of the global ocean; its continental climate was highly seasonal, with very hot summers and cold winters. It probably had strong, cross-equatorial monsoons.



Global paleogeographic reconstruction of the Earth in the late Triassic period 220 million years ago.

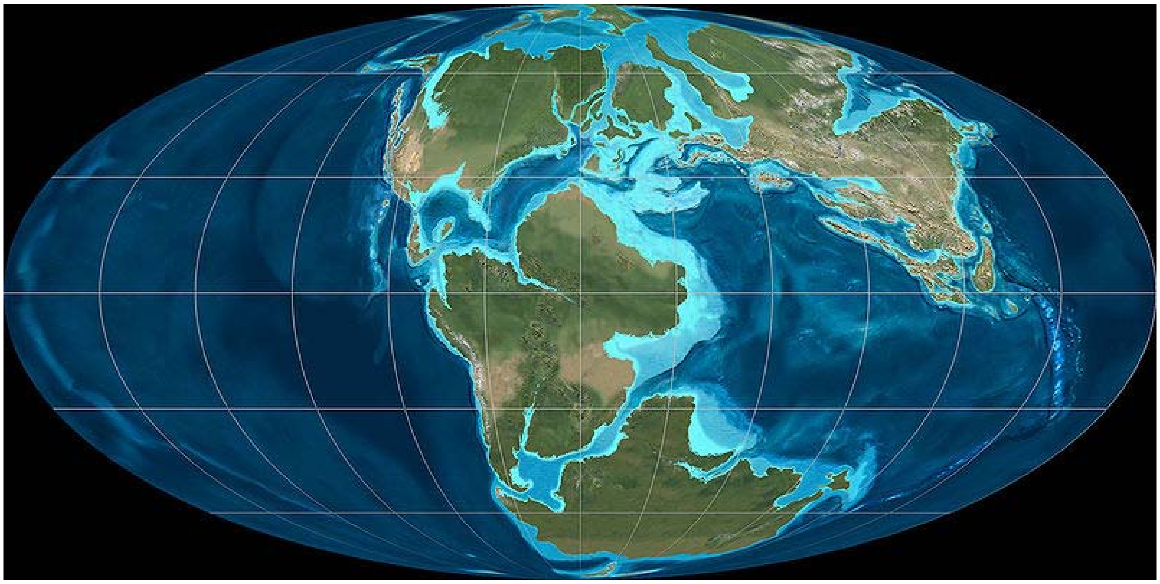
As a consequence of the P-Tr Mass Extinction at the border of Permian and Triassic, there is only little fossil record of insects including beetles from the Lower Triassic. However, there are a few exemptions, like in Eastern Europe: At the Babiy Kamen site in the Kuznetsk Basin numerous beetle fossils were discovered, even entire specimen of the infraorders Archostemata (e.i., **Ademosynidae**, **Schizocoleidae**), Adephaga (e.i., **Triaplidae**, **Trachypachidae**) and Polyphaga (e.i., **Hydrophilidae**, **Byrrhidae**, **Elateroidea**) and in nearly a perfectly preserved condition. 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. Further records are known from Khey-Yaga, Russia in the Korotaikha Basin. There are many important sites from the Jurassic, with more than 150 important sites with beetle fossils, the majority being situated in Eastern Europe and North Asia. In North America and especially in South

America and Africa the number of sites from that time period is smaller and the sites have not been exhaustively investigated yet. Outstanding fossil sites include [[Solnhofen] in Upper Bavaria, Germany, Karatau in South Kazakhstan, the Yixian formation in Liaoning, North China 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.

Around this time, during the Late Triassic, mycetophagous, or fungus feeding species of beetle (e.i. **Cupedidae**) appear in the fossil record. In the stages of the Upper Triassic representatives of the algophagous, or algae feeding species (e.i. **Triaplidae** and **Hydrophilidae**) begin to appear, as well as predatory water beetles. The first primitive weevils appear (e.i. **Obrienidae**), as well as the first representatives of the rove beetles (e.i. **Staphylinidae**), which show no marked difference in physique compared to recent species. This was also around the first time evidence of diverse freshwater insect fauna appeared. Some of the oldest living families also appear around during the Triassic, including from Hemiptera: Cercopidae, Cicadellidae, Cixiidae, and Membracidae; from Coleoptera: Carabidae, Staphylinidae, and Trachypachidae; from Hymenoptera: Xyelidae; From Diptera: Anisopodidae, Chironomidae, and Tipulidae. The first flies (**Diptera**), Hymenoptera, and true dragonflies (**Odonata**), Heteroptera, and Thysanoptera. The first true species of Diptera are known from the Middle Triassic, becoming widespread during the Middle and Late Triassic . A single large wing from a species of Diptera in the Triassic (10 mm instead of usual 2-6 mm) was found in Australia (Mt. Crosby). This family Tilliardipteridae, despite of the numerous 'tipuloid' features, should be included in Psychodomorpha sensu Hennig on account of loss of the convex distal 1A reaching wing margin and formation of the anal loop.

Jurassic

The **Jurassic (208-145 mya)** was important in the development of birds, one of insects major predators. During the early Jurassic period, the supercontinent Pangaea broke up into the northern supercontinent Laurasia and the southern supercontinent Gondwana; the Gulf of Mexico opened in the new rift between North America and what is now Mexico's Yucatan Peninsula. The Jurassic North Atlantic Ocean was relatively narrow, while the South Atlantic did not open until the following Cretaceous Period, when Gondwana itself rifted apart. The global climate during the Jurassic was warm and humid. Similar to the Triassic, there were no larger landmasses situated near the polar caps and consequently, no inland ice sheets existed during the Jurassic. Although some areas of North and South America and Africa stayed arid, large parts of the continental landmasses were lush. The laurasian and the gondwanian fauna differed considerably in the Early Jurassic. Later it became more intercontinental and many species started to spread globally.



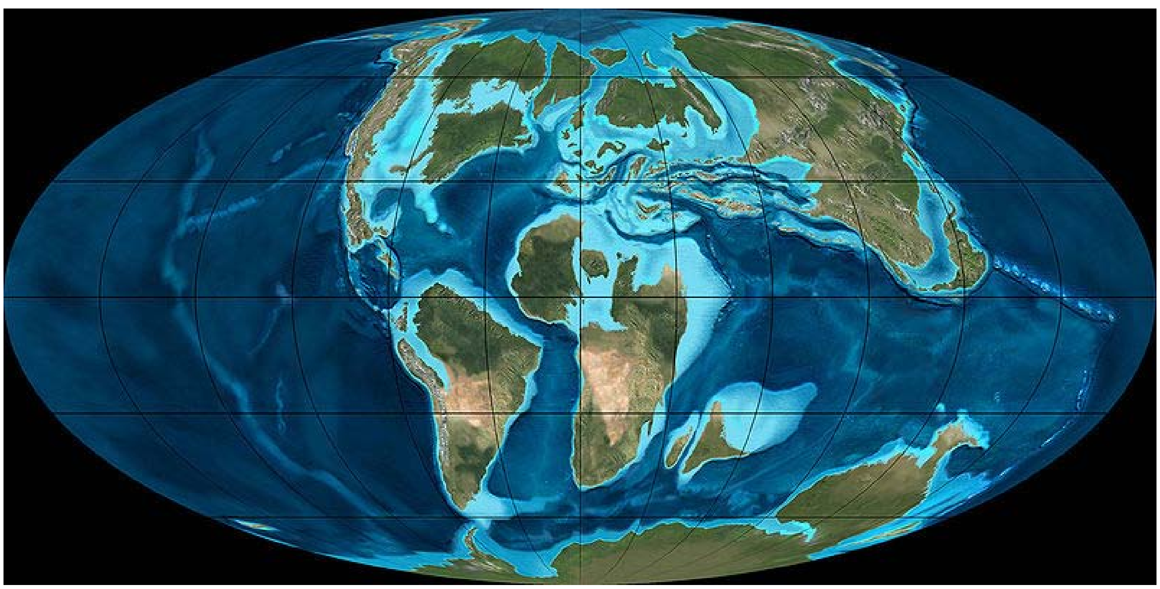
Global paleogeographic reconstruction of the Earth in the late Jurassic period 150 million years ago.

There are many important sites from the Jurassic, with more than 150 important sites with beetle fossils, the majority being situated in Eastern Europe and North Asia. In North America and especially in South America and Africa the number of sites from that time period is smaller and the sites have not been exhaustively investigated yet. Outstanding fossil sites include [[Solnhofen] in Upper Bavaria, Germany, Karatau in South Kazakhstan, the Yixian formation in Liaoning, North China 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. Numerous deposits of other insects occur in Europe and Asia. Including Grimmen and Solnhofen, German; Solnhofen being famous for findings of the earliest birds (e.i., Archeopteryx). Others include Dorsect, England; Issyk-Kul, Kirghizstan; and the most productive site of all, Karatau, Kazakhstan.

During the Jurassic (210-145 mya) there was a dramatic increase in the known diversity of family-level Coleoptera. This includes the development and growth of carnivorous and herbivorous species. Species of the superfamily **Chrysomeloidea** are believed to have developed around the same time, which include a wide array of plant host ranging from cycads and conifers, to angiosperms. Close to the Upper Jurassic, the portion of the **Cupedidae** decreased, however at the same time the diversity of the early plant eating, or phytophagous species increased. Most of the recent phytophagous species of Coleoptera feed on flowering plants or angiosperms.

Cretaceous

The Cretaceous (145-65 mya) had much of the same insect fauna as the Jurassic until much later on. During the Cretaceous, the late-Paleozoic-to-early-Mesozoic supercontinent of Pangaea completed its tectonic breakup into present day continents, although their positions were substantially different at the time. As the Atlantic Ocean widened, the convergent-margin orogenies that had begun during the Jurassic continued in the North American Cordillera, as the Nevadan orogeny was followed by the Sevier and Laramide orogenies. Though Gondwana was still intact in the beginning of the Cretaceous, it broke up as South America, Antarctica and Australia rifted away from Africa (though India and Madagascar remained attached to each other); thus, the South Atlantic and Indian Oceans were newly formed. Such active rifting lifted great undersea mountain chains along the welts, raising eustatic sea levels worldwide. To the north of Africa the Tethys Sea continued to narrow. Broad shallow seas advanced across central North America (the Western Interior Seaway) and Europe, then receded late in the period, leaving thick marine deposits sandwiched between coal beds. At the peak of the Cretaceous transgression, one-third of Earth's present land area was submerged. The Berriasian epoch showed a cooling trend that had been seen in the last epoch of the Jurassic. There is evidence that snowfalls were common in the higher latitudes and the tropics became wetter than during the Triassic and Jurassic. Glaciation was however restricted to alpine glaciers on some high-latitude mountains, though seasonal snow may have existed farther south. Rafting by ice of stones into marine environments occurred during much of the Cretaceous but evidence of deposition directly from glaciers is limited to the Early Cretaceous of the Eromanga Basin in southern Australia.



Global paleogeographic reconstruction of the Earth in the late Cretaceous period 90 million years ago.

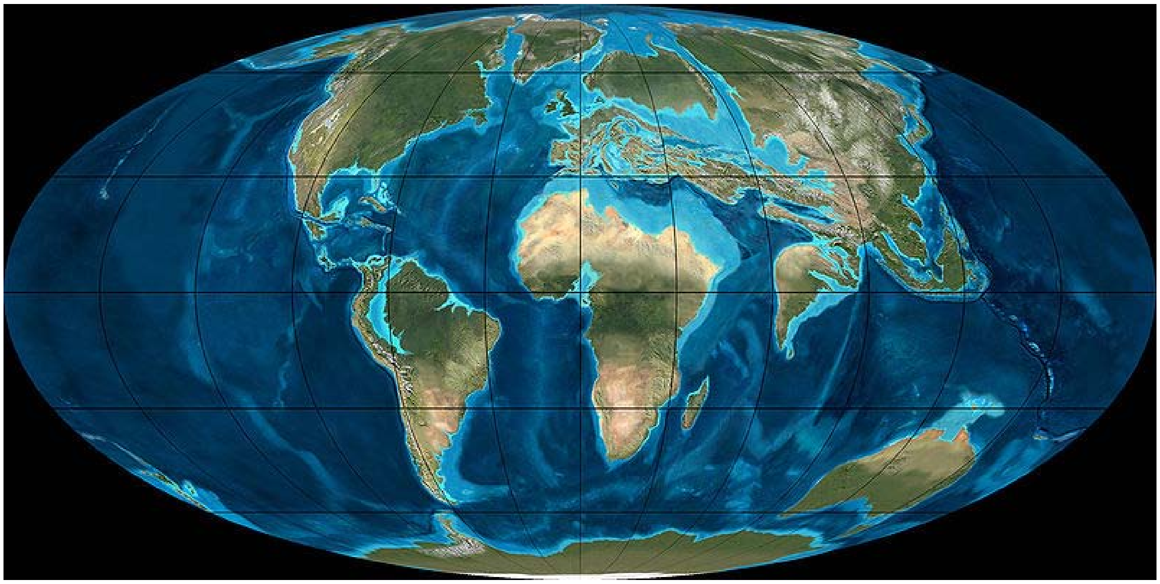
Fossil of a grasshopper (or other Orthopteran). Found in the Lower Cretaceous Santana Formation, near Nova Olinda, Brazil. Whole rock specimen is about 8 cm in diameter.

There is a large number of important fossil sites worldwide containing beetles from the Cretaceous. Most of of them are located in Europe and Asia and belong to the temperate climate zone during the Cretaceous. A few of the fossil sites mentioned in the chapter Jurassic also shed some light on the early cretaceous beetle fauna (e.g. the Yixian formation in Liaoning, North China). Further important sites from the Lower Cretaceous include the Crato Fossil Beds in the Araripe basin in the Ceará, North Brazil as well as overlying Santana formation, with the latter was situated near the paleoequator, or the position of the earth's equator in the geologic past as defined for a specific geologic period. In Spain there are important sites near Montsec and Las Hoyas. In Australia the Koonwarra fossil beds of the Korumburra group, South Gippsland, Victoria is noteworthy. Important fossil sites from the Upper Cretaceous are Kzyl-Dzhar in South Kazakhstan and Arkagala in Russia.

During the Cretaceous the diversity of **Cupedidae** and **Archostemata** decreased considerably. Predatory ground beetles (**Carabidae**) and rove beetles (**Staphylinidae**) began to distribute into different patterns: whereas the **Carabidae** predominantly occurred in the warm regions, the **Staphylinidae** and click beetles (**Elateridae**) preferred many areas with temperate climate. Likewise, predatory species of **Cleroidea** and **Cucujoidea**, hunted their prey under the bark of trees together with the jewel beetles (**Buprestidae**). The jewel beetles diversity increased rapidly during the Cretaceous, as they were the primary consumers of wood, while longhorn beetles (**Cerambycidae**) were rather rare and their diversity increased only towards the end of the Upper Cretaceous. The first coprophagous beetles have been recorded from the Upper Cretaceous, and are believed to have lived on the excrement of herbivorous dinosaurs, however there is still a discussion, whether the beetles where always tied to mammals during its development. Also, the first species with an adaption of both larvae and adults to the aquatic lifestyle are found. Whirligig beetles (**Gyrinidae**) were moderately diverse, although other early beetles (e.i., **Dytiscidae**) where less, with the most widespread being the species of **Coptoclavidae**, which preyed on aquatic fly larvae.

Paleogene

The **Paleogene (65-56 mya)** comprises the first part of the Cenozoic, which during this time the continents assumed their modern shapes. The fragments of Gondwana (South America, Africa, India and Australia) began to drift northwards. The collision of India with the eurasian landmass led to the folding and formation the Himalayas. Similarly, the Alps were folded in Central Europe by the collision of the African plate with Europe. A land bridge between North America and South America did not yet exist. The Atlantic Ocean continued to widen during the Paleogene. In the North, the last land bridge between North America and Europe broke up during the Eocene. Climate during the Paleogene was warm and tropical as most time during the Mesozoic. The climate in the beginning climate was drier and cooler than in the preceding Cretaceous, but the temperature strongly increased during the Eocene and subtropical vegetation spread up to Greenland and Patagonia. The climate near the poles was cool temperate, in Europe, North America, Australia and the southern part of South America warm temperate. Near the equator there was tropical climate, flanked by hot and arid zones in the north and the south. In the Oligocene, global cooling started. Antarctica was covered by an ice sheet and subsequently, sea levels dropped. Except an intermittent warm period during the late Oligocene, global cooling continued and finally led to the Pleistocene ice age.

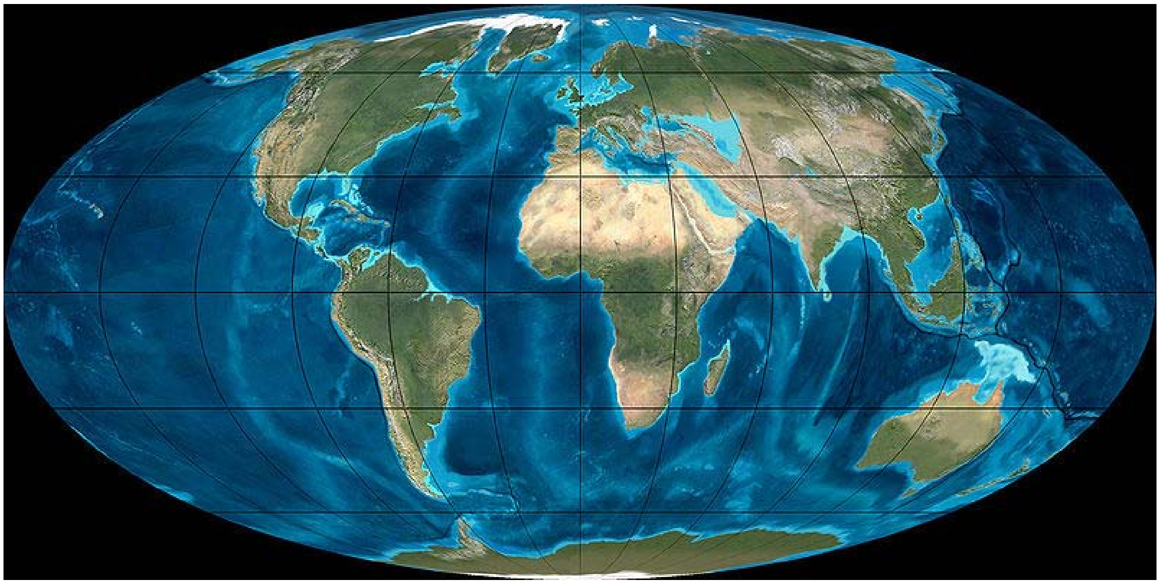


Global paleogeographic reconstruction of the Earth in the middle Paleogene (Eocene) period 50 million years ago.

There are many fossils of beetles known from this era, though the beetle fauna of the Paleocene is comparatively poorly investigated. In contrast, the knowledge on the Eocene beetle fauna is very good. The reason is the occurrence of fossil insects in amber and cay slate sediments. Amber is fossilized tree resin, that means it consists of fossilized organic compounds, not minerals. Different amber is distinguished by location, age and species of the resin producing plant. For the research on the Oligocene beetle fauna, Baltic and Dominican amber is most important. Even with the insect fossils record in general lacking, the most diverse deposit being from the Fur Formation, Denmark; including giant ants and primitive moths (Noctuidae).

The first butterflies are from the Upper Paleogene, while most, like beetles, already had recent genera and species already existed during the Miocene, however, their distribution differed considerably from today's.

Neogene



Global paleogeographic reconstruction of the Earth in the lower Neogene (Miocene) period 20 million years ago.

Phylogeny

The relationships of insects to other animal groups remain unclear. Although more traditionally grouped with millipedes and centipedes, evidence has emerged favouring closer evolutionary ties with the crustaceans. In the Pancrustacea theory, insects, together with among others Malacostraca, make up a monophyletic group (sharing a common ancestor): this is today a well accepted hypothesis.

Early evidence

The oldest definitive insect fossil is the Devonian *Rhyniognatha hirsti*, estimated at 396-407 million years old. This species already possessed dicondylic mandibles, 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.

The subclass Apterygota (wingless insects) is now considered artificial as the silverfish (order Thysanura) are more closely related to Pterygota (winged insects) than to bristletails (order Archaeognatha). For instance, just like flying insects, Thysanura have so-called dicondylic mandibles, while Archaeognatha have monocondylic mandibles. The reason for their resemblance is not due to a particularly close relationship, but rather because they both have kept a primitive and original anatomy in a much higher degree than the winged insects. The most primitive order of flying insects, the mayflies (Ephemeroptera), are also those who are most morphologically and physiologically similar to these wingless insects. Some mayfly nymphs resemble aquatic thysanurans.

Modern Archaeognatha and Thysanura still have rudimentary appendages on their abdomen called styli, while more primitive and extinct insects known as Monura had much more developed abdominal appendages, as seen here. The abdominal and thoracic segments in the earliest terrestrial ancestor of the insects would have been more similar to each other than they are today, and the head had well developed compound eyes and long antennae. Their body size is not known yet. As the most primitive group today, Archaeognatha, is most abundant near the coasts, it could mean that this was the kind of habitat where the insect ancestors became terrestrial. But this specialization to coastal niches could also have a secondary origin, just as could their jumping locomotion, as it is the crawling Thysanura who are considered to be most original (plesiomorphic). By looking at how primitive cheliceratan book gills (still seen in horseshoe crabs) evolved into book lungs in primitive spiders and finally into tracheae in more advanced spiders (most of them still have a pair of book lungs intact as well), it is possible the trachea of insects was formed in a similar way, modifying gills at the base of their appendages.

So far there is nothing that suggests the insects were a particularly successful group of animals before they got their wings.

Odonata

The Odonata (dragonflies) are also a good candidate as the oldest living member of the Pterygota. Mayflies are morphologically and physiologically more primitive, but the derived and advanced characteristics of dragonflies could have evolved independently in their own direction for a long time. It seems that orders with aquatic nymphs or larvae become evolutionarily conservative once they had adapted to water. If mayflies made it to the water first, this could partly explain why they are more primitive than dragonflies, even if dragonflies have an older origin.

Similarly, stoneflies are the most primitive of the Neoptera, but they were not necessarily the first order to branch off. This also makes it less likely that an aquatic ancestor would have the evolutionary potential to give rise to all the different forms and species of insects that we know today.

Dragonfly nymphs have a unique labial "mask" used for catching prey, and the imago has a unique way of copulating, using a secondary male sex organ on the second abdominal segment. It looks like abdominal appendages modified for sperm transfer and direct insemination have occurred at least twice in insect evolution, once in Odonata and once in the other flying insects. If these two different methods are the original ways of copulating for each group, it is a strong indication that it is the dragonflies who are the oldest, not the mayflies. There is still not agreement about this. Another scenario is that abdominal appendages adapted for direct insemination have evolved three times in insects; once Odonata, once in mayflies and once in the Neoptera, both mayflies and Neoptera choosing the same solution. If so, it is still possible that mayflies are the oldest order among the flying insects. The power of flight is assumed to have evolved only once, suggesting sperm transfer in the earliest flying insects still was done indirectly.

One possible scenario on how direct insemination evolved in insects is seen in scorpions. The male deposits a spermatophore on the ground, locks its claws with the female's claws and then guides her over his packet of sperm, making sure it comes in contact with her genital opening.

When the early (male) insects laid their spermatophores on the ground, it seems likely that some of them used the clasping organs at the end of their body to drag the female over the package. The ancestors of Odonata evolved the habit of grabbing the female behind her head, as they still do today. This action, rather than not grasping the female at all, would have increased the male's chances of spreading its genes. The chances would be further increased if they first attached their spermatophore safely on their own abdomen before they placed their abdominal claspers behind the female's head; the male would then not let the female go before her abdomen had made direct contact with his sperm storage, allowing the transfer of all sperm.

This also meant increased freedom in searching for a female mate because the males could now transport the packet of sperm elsewhere if the first female slipped away. This ability would eliminate the need to either wait for another female at the site of the deposited sperm packet or to produce a new packet, wasting energy. Other advantages include the possibility of mating in other, safer places than flat ground, such as in trees or bushes.

If the ancestors of the other flying insects evolved the same habit of clasping the female and dragging her over their spermathophore, but posterior instead of anterior like the Odonata does, their genitals would come very close to each others. And from there on, it would be a very short step to modify the vestigial appendages near the male genital opening to transfer the sperm directly into the female. The same appendages the male Odonata use to transfer their sperm to their secondary sexual organs at the front of their abdomen.

All insects with an aquatic nymphal or larval stage seem to have adapted to water secondarily from terrestrial ancestors. Of the most primitive insects with no wings at all, Archaeognatha and Thysanura, all members live their entire life cycle in terrestrial environments. As mentioned previously, Archaeognatha were the first to split off from the branch that led to the winged insects (Pterygota), and then the Thysanura branched off. This indicates that these three groups (Archaeognatha, Thysanura and Pterygota) have a common terrestrial ancestor, which probably resembled a primitive model of Apterygota, was an opportunistic generalist and laid spermatophores on the ground instead of copulating, like Thysanura still do today. If it had feeding habits similar to the majority of apterygotes of today, it lived mostly as a decomposer.

One should expect that a gill breathing arthropod would modify its gills to breathe air if it were adapting to terrestrial environments, and not evolve new respiration organs from bottom up next to the original and still functioning ones.

Then comes the fact that insect (larva and nymph) gills are actually a part of a modified, closed trachea system specially adapted for water, called tracheal gills. The arthropod trachea can only arise in an atmosphere and as a consequence of the adaptations of living on land. This too indicates that insects are descended from a terrestrial ancestor.

And finally when looking at the three most primitive insects with aquatic nymphs (called naiads: Ephemeroptera, Odonata and Plecoptera), each order has its own kind of tracheal gills that are so different from one another that they must have separate origins. This would be expected if they evolved from land-dwelling species.

This means that one of the most interesting parts of insect evolution is what happened between the Thysanura-Pterygota split and the first flight.

Evolutionary relationships

Insects have complex evolutionary and ecological relationships with other groups including plants and other animals. For example, 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.

Origin of insect flight

The origin of insect flight remains obscure, since the earliest winged insects currently known appear to have been capable fliers. Some extinct insects (e.g. the Palaeodictyoptera) had an additional pair of winglets attached to the first segment of the thorax, for a total of three pairs.

The wings themselves are thought by many to be highly modified (tracheal) gills. And there is no doubt that the tracheal gills of the mayfly nymph in many species look like wings. By comparing a well developed pair of gill blades in the naiads and a reduced pair of hind wings on the adults, it is not hard to imagine that the mayfly gills (tergaliae) and insect wings have a common origin, and newer research also supports this. The tergaliae are not found in any other order of insects, and they have evolved in different directions with time. In some nymphs/naiads the most anterior pair has become sclerotized and works as a gill cover for the rest of the gills. Others can form a large sucker, be used for swimming or modified into other shapes. But it doesn't have to mean that these structures were originally gills. It could also mean that the tergaliae evolved from the same structures which gave rise to the wings, and that flying insects evolved from a wingless terrestrial species with pairs of plates on its body segments: three on the thorax and nine on the abdomen (mayfly nymphs with nine pairs of tergaliae on the abdomen exist, but so far no living or extinct insects with plates on the last two segments have been found). If these were primary gills, it would be a mystery why they should have waited so long to be modified when we see the different modifications in modern mayfly nymphs.

Theories

When the first forests arose on Earth, new niches for terrestrial animals were created. Spore-feeders and others who depended on plants and/or the animals living around them would have to adapt too to make use of them. In a world with no flying animals, it would probably just be a matter of time before some arthropods who were living in the trees evolved paired structures with muscle attachments from their exoskeleton and used them for gliding, one pair on each segment. Further evolution in this direction would give bigger gliding structures on their thorax and gradually smaller ones on their abdomen. Their bodies would have become stiffer while thysanurans, which didn't evolve flight, kept their flexible abdomen.

Mayfly nymphs must have adapted to water while they still had the "gliders" on their abdomen intact. So far there is no concrete evidence to support this theory either, but it is one that offers an explanation for the problems of why presumably aquatic animals evolved in the direction they did.

Leaping and arboreal insects seems like a good explanation for this evolutionary process for several reasons. Because early winged insects were lacking the sophisticated wing folding mechanism of neopterous insects, they must have lived in the open and not been able to hide or search for food under leaves, in cracks, under rocks and other such confined spaced. In these old forests there weren't many open places where insects with huge structures on their back could have lived without experiencing huge disadvantages. If insects got their wings on land and not in water, which clearly seems to be the case, the tree canopies would be the most obvious place where such gliding structures could have emerged, in a time when the air was a new territory. The question is if the plates used for gliding evolved from "scratch" or by modifying already existing anatomical details. The thorax in Thysanura and Archaeognatha are known to have some structures connected to their trachea which share similarities to the wings of primitive insects. This suggests the origin of both the wings and the spiracles are related.

Gliding requires universal body modifications, as seen in present-day vertebrates such as some rodents and marsupials, which have grown wide, flat expansions of skin for this purpose. The flying dragons (genus *Draco*) of Indonesia has modified its ribs into gliders, and even some snakes can glide through the air by spreading their ribs. The main difference is that while vertebrates have an inner skeleton, primitive insects had a flexible and adaptive exoskeleton.

It is clear that there would have been some animals living in the trees, as animals are always taking advantage of all available niches, both for feeding and protection. At the time, the reproductive organs were by far the most nutritious part of the plant, and these early plants show signs of arthropod consumption and adaptations to protect themselves, for example by placing their reproductive organs as high up as possible. But there will always be some species who will be able to cope with that by following the their food source up the trees.

Knowing that insects were terrestrial at that time and that some arthropods (like primitive insects) were living in the tree crowns, it seems less likely that they would have developed their wings down on the ground or in the water.

In a three dimensional environment such as trees, the ability to glide would increase the insects' chances to survive a fall, as well as saving energy. This trait has repeated itself in modern wingless species such as the gliding ants who are living an arboreal life. When the gliding ability first had originated, gliding and leaping behavior would be a logical next step, which would eventually be reflected in their anatomical design.

The need to navigate through vegetation and to land safely would mean good muscle control over the proto-wings, and further improvements would eventually lead to true (but primitive) wings.

While the thorax got the wings, a long abdomen could have served as a stabilizer in flight.

It is also worth remembering that some of the earliest flying insects were large predators. This isn't surprising since there weren't yet any other predators hunting in the air: it was therefore a totally new ecological niche. Some of the prey were without a doubt other insects, as insects with proto-wings would have radiated into other species even before the wings were fully evolved. From this point onwards, the arms race could continue: the same predator/prey co-evolution which has existed as long as there have been predators and prey on earth; both the hunters and the hunted were in need of improving and extending their flight skills even further to keep up with the other.

Insects that had evolved their proto-wings in a world without flying predators could afford to be exposed openly without risk, but this changed when carnivorous flying insects evolved. It is unknown when they first evolved, but once these predators had emerged they put a strong selection pressure on their victims and themselves. Those of the prey who came up with a good solution about how to fold their wings over their backs in a way that made it possible for them to live in narrow spaces would not only be able to hide from flying predators (and terrestrial predators if they were on the ground) but also to exploit a wide variety of niches that were closed to those who couldn't fold their wings in this way. And today the neopterous insects (those that can fold their wings back over the abdomen) are by far the most dominant group of insects.

The water-skimming theory suggests that skimming on the water surface is the origin of insect flight. This theory is based on the fact that the first fossil insects, the Devonian *Rhyniognatha hirsti*, is thought to have possessed wings, even though the insects closest evolutionary ties are with crustaceans, which are aquatic.

Life cycle

Mayflies

Another primitive trait of the mayflies are the subimago; no other insects have this winged yet sexually immature stage. A few specialized species have females with no subimago, but retain the subimago stage for males.

The reasons the subimago still exists in this order could be that there hasn't been enough selection pressure to get rid of it; it also seems specially adapted to do the transition from water to air.

The male genitalia are not fully functional at this point. One reason for this could be that the modification of the abdominal appendages into male copulation organs emerged later than the evolution of flight. This is indicated by the fact that dragonflies have a different copulation organ than other insects.

As we know, in mayflies the nymphs and the adults are specialized for two different ways of living; in the water and in the air. The only stage (instar) between these two is the subimago. In more primitive fossil forms, the preadult individuals had not just one instar but numerous ones (while the modern subimago do not eat, older and more primitive species with a subimagos were probably feeding in this phase of life too as the lines between the instars were much more diffuse and gradual than today). Adult form was reached several moults before maturity. They probably didn't have more instars after becoming fully mature. This way of maturing is how Apterygota do it, which moult even when mature, but not winged insects.

Modern mayflies have eliminated all the instars between imago and nymph, except the single instar called subimago, which is still not (at least not in the males) fully sexually mature. The other flying insects with incomplete metamorphosis (Exopterygota) have gone a little further and completed the trend; here all the immature structures of the animal from the last nymphal stage are completed at once in a single final moult. The more advanced insects with larvae and complete metamorphosis (Endopterygota) have gone even further. An interesting theory here is that the pupal stage is actually a strongly modified and extended stage of subimago, but so far it is nothing more than a theory. Interestingly enough there are some insects within the Exopterygota, thrips and whiteflies (Aleyrodidae), who have evolved pupae-like stages too.

Distant ancestors

The distant ancestor of flying insects, a species with primitive proto-wings, had a more or less ametabolous life cycle and instars of basically the same type as thysanurans with no defined nymphal, subimago or adult stages as the individual became older. Individuals developed gradually as they were growing and moulting, but there were probably no big changes in between instars.

Modern mayfly nymphs do not acquire gills until after their first moult. Before this stage they are so small that there is no need for gills to extract oxygen from the water. This could be a trait from the common ancestor all flyers evolved from. An early terrestrial insect would have no need for paired outgrowths from the body before it started to live in the trees (or in the water, for that matter), so it would not have any.

This would also affect the way their offspring looked like in the early instars, resembling earlier ametabolous generations even after they had started to adapt to a new way of living, in a habitat where they actually could have some good use for flaps along their body. Since they matured in the same way as thysanurans with plenty of moultings as they were growing and very little difference between the adults and much younger individuals (unlike modern insects, who are hemimetabolous or holometabolous), there probably wasn't much room for adapting into different niches depending on age and stage. Also, it would have been difficult for an animal already adapted to a niche to make a switch to a new niche later in life based on age or size differences alone when these differences were not significant.

So they had to specialize and focus their whole existence on improving a single lifestyle in a particular niche. The older the species and the single individuals became, the more would they differ from their original form as they adapted to their new lifestyle better than the generations before. The final body design was no longer achieved while still inside the egg, but continued to develop for most of the life, causing a bigger difference between the youngest and oldest individuals. Assuming that mature individuals most likely mastered their new element better than did the nymphs who had the same lifestyle, it would appear to be an advantage if the immatures reached adult shape and form as soon as possible. This may explain why they evolved fewer but more intense instars and a stronger focus on the adult body, and the differences between the adults and the first instars were greater, instead of just gradually growing bigger as earlier generations had done. This evolutionary trend explains how they went from ametabolous to hemimetabolous insects.

Reaching maturity and a fully grown body became only a part of the development process, gradually also a new anatomy and new abilities only possible in the later stages of life, were included. The anatomy they were born and grew up with had limitations the adults who had learned to fly didn't have. If they couldn't live their early life the way adults did, immature individuals had to adapt to the best way of living and surviving despite their limitations till the moment came when they could leave them behind. This would be a starting point in the evolution where imago and nymphs started to live in different niches, some more clearly defined than others. Also, a final anatomy, size and maturity reached at once with a single final nymphal stage meant less waste of time and energy, and also made a more complex adult body structure. These strategies obviously became very successful with time.

Late Carboniferous and Early Permian insect orders include both several current very long-lived groups (mayflies, (Ephemeroptera), dragonflies (Odonata), cockroaches (Blattodea), and Orthoptera (grasshoppers and their relatives)) and a number of Paleozoic forms. During this era, some giant dragonfly-like forms – e.g. *Meganeura* and *Meganeuropsis* (Order Protodonata) and *Mazothairos* (Order Palaeodictyoptera) – reached wingspans of 55 to 70 cm (22 to 28 in), making them far larger than any living insect. Also their nymphs must have had a very impressive size. This gigantism may have been due to higher atmospheric oxygen levels (up to 80% above modern levels during the Carboniferous) that allowed increased respiratory efficiency relative to today. The lack of flying vertebrates could have been another factor.

Most extant 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.

The remarkably successful Hymenopterans appeared in the Cretaceous but achieved their diversity more recently, in the Cenozoic. A number of highly successful insect groups — especially the Hymenoptera and Lepidoptera (butterflies), as well as many types of Diptera (flies) and Coleoptera (beetles) — evolved in conjunction with flowering plants, a powerful illustration of co-evolution.

Many modern insect genera developed during the Cenozoic; insects from this period on are often found preserved in amber, often in perfect condition. Such specimens are easily compared with modern species. The study of fossilized insects is called paleoentomology.

Chapter 7

Earwig

Earwigs Temporal range: 208–0 Ma Late Triassic to Recent	

Female common earwig, *Forficula auricularia*

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Hexapoda
Class:	Insecta
Order:	**Dermaptera** De Geer, 1773

Suborders

- †Archidermaptera
- Arixeniina
- Forficulina
- Hemimerina

Synonyms

- Euplecoptera
- Euplexoptera
- Forficulida

Earwigs make up the insect order **Dermaptera**, found throughout the Americas, Eurasia, Australia and New Zealand. It is one of the smaller insect orders, with only 1,800 recorded species in 12 families. Typical earwigs have characteristic cerci, a pair of forceps-like pincers on their abdomen, and membranous wings folded underneath short forewings, hence the scientific name for the order, which translates literally as "skin wings." Some groups within the earwig order are tiny parasites on mammals and lack the typical pincers. Earwigs rarely fly, even though they are capable of doing so.

Earwigs are nocturnal; they 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 undergo an average of 5 molts over the course of a year, their average life expectancy, before they become adults. Many earwig species display maternal care, which is uncommon among insects. Female earwigs are known to take care of 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.

Earwig fossils have been found in different places. Some of those specimens are now included in the extinct suborder Archidermaptera dating back to the Late Triassic. Many orders of insect have been theorized to be closely related to earwigs by many authors, though Grylloblattaria is the most likely.

Etymology

The scientific name for the order, *Dermaptera*, is Greek in origin, stemming from the words *dermatos*, meaning skin, and *pteron*, 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". The name may be related to the old wives' tale that earwigs burrowed into the brains of humans through the ear and laid their eggs there. Earwigs are predisposed to hiding in warm humid crevices and may indeed occasionally crawl into the human ear canal (much like any other small organism).

Wicga is in turn related to *wiggle,* and ultimately to other words implying movement, including *way* and *vehicle,* all from PIE *wegh-.* Other languages have words based on the same premises: German *Ohrenkneifer*, *Ohrwurm*, or *Ohrenhöhler*; Dutch *oorwormen* or *oorwurmen*; French *perce-oreille* (ear-piercer, literally pierce-ear); Danish *ørentvist*; Slovak *ucholak* (*ucho* = ear, *lak* = scare); Persian *Güsh Kar Kon* ("That which brings deafness to the ear") (*Güsh* = ear, *Kar* = Deaf); Romanian *urechelniţă* (ureche = ear); Bulgarian ухолазка (ухо = ear, лазка = crawler); as well as Hungarian *fülbemászó* and Navajo *Jeeʼiighááh* ("crawler-into-the-ear"). The German word *Ohrwurm* has the derived meaning of earworm. Hungarian also uses phrases such as *fülbemászó dallam* (meaning "a catchy melody"), but these are unrelated to the insect's meaning.

English uses "to earwig" as a slang verb, *to earwig* meaning either "to attempt to influence by persistent confidential argument or talk". or "to eavesdrop".

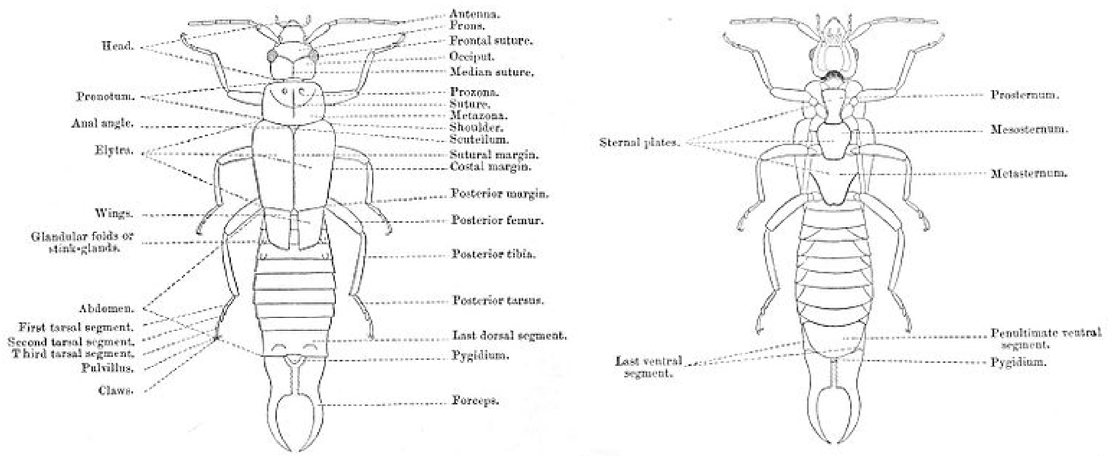
Distribution

An earwig from the Western Ghats

Earwigs are fairly abundant and can be found virtually everywhere, especially throughout the Americas and Eurasia. The common earwig was introduced into North America in 1907 from Europe and now occur throughout North America, but tend to be more common in the southern and southwestern states. The only native species of earwig found in the north is the spine-tailed earwig (*Doru aculeatum*), 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), Labiidae, Anisolabididae, and Labiduridae.

Few earwigs survive winter outdoors in cold climates. They can be found in tight crevices in woodland, fields and gardens. Out of about 1,800 species, about 25 occur in North America, 45 in Europe (including 7 in Britain), and 60 in Australia.

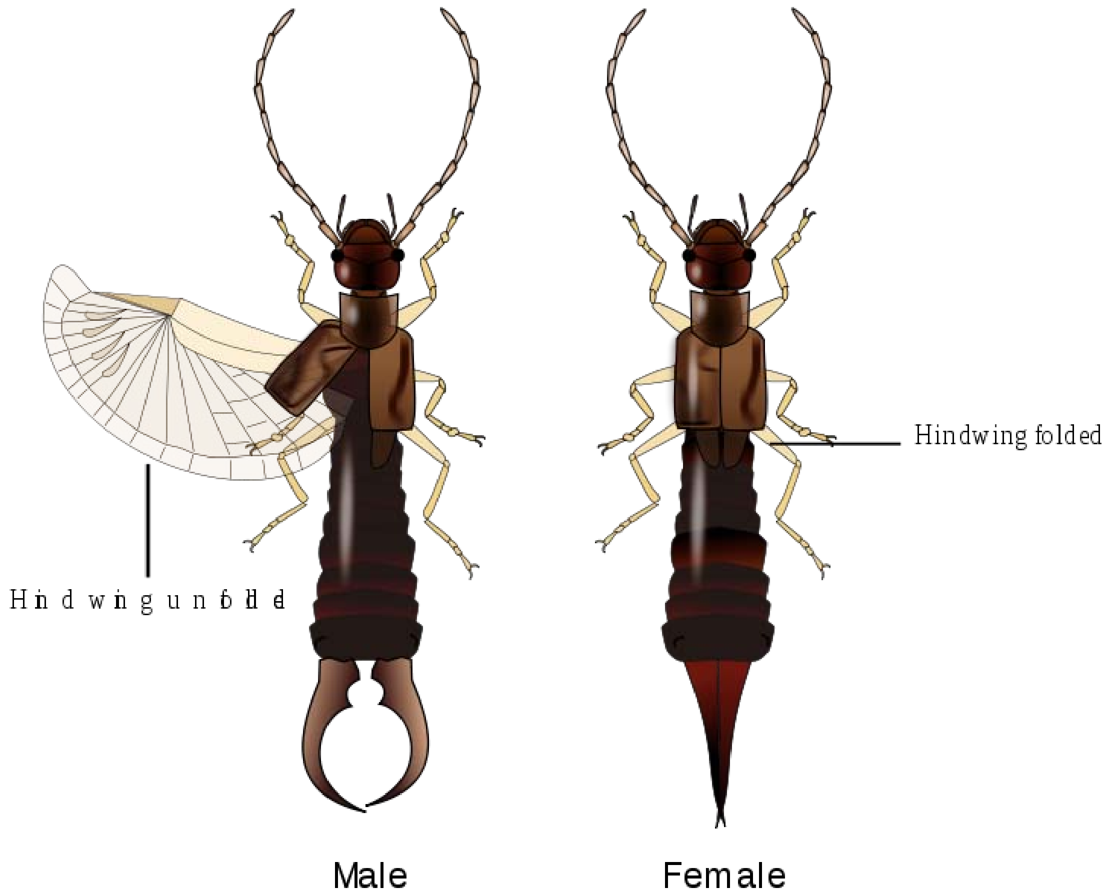
Morphology



Male earwig, external morphology.

Most earwigs are flattened (to fit inside tight crevices, such as under bark) with an elongated body generally 7–50 millimetres (0.28–2.0 in) long, though some can grow longer, such as the Saint Helena earwig which reaches 80 mm (3.1 in) long. Earwigs are characterized by the cerci, or the pair of forceps-like pincers on their abdomen; male earwigs have curved pincers, while females have straight ones. These pincers are used to capture prey, defend themselves and fold their wings under the short tegmina. The antennae are thread-like with at least 10 segments or more.

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 suborders Arixeniina and Hemimerina have no wings and are blind with filiform segmented cerci. 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. The epizoic species, sometimes considered as ectoparasites, are wingless.



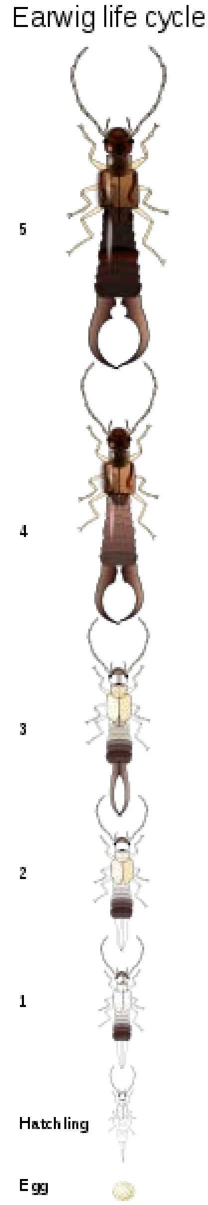
Earwig diagram with wings extended and closed

Internal

The neuroendocrine system consist of what typical insect would. There is a Brain, a subesophageal ganglion, three thoratic ganglia, and six abdominal ganglia; a ganglion being a mass of neurons. Strong neuron connects connect the neurohemal corpora cardiaca to the brain and frontal ganglion, where the closely related median corpus allatum produces Jeuvenile 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, albeit, earwigs lack gastric caecae which specialize in many species of insects for digestion. Long, slender (extratory) malpighian tubules can be found between the juntion of the mid- and hind gut.

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; or 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.

Life cycle and reproduction



The life cycle and development of a male earwig from egg to each instar

Earwig 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 fall, and can be found together in the fall and winter. The male and female will live in a chamber in debris, crevices, or soil 2.5 mm deep. 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. When first laid, the eggs are white or cream-colored and oval-shaped, but right before hatching they become kidney-shaped and brown. Each egg is approximately 1 mm (0.04 in) tall and 0.8 mm (0.03 in) wide.

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. 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 vigorously defend the eggs from predators, not eating unless an egg goes bad. 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.

Female earwig in its nest, with eggs

Female earwig in its nest with newly-hatched young

The eggs hatch within 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 in about July. The nymphs feed on food regurgitated by the mother, and on their own molts. If the mother dies before the nymphs are ready to leave, the nymphs may eat her.

After five to six instars, the nymphs will molt into adults. The male's forceps will become curved, while the females' 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 the

South Africa. Food typically consist of a wide array of living and dead plant and animal matter. For protection from predators, the species *Doru taeniatum* of earwigs can squirts foul-smelling yellow liquid in the form of jets from sent 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.

Ecology

Earwigs are mostly scavengers, but some are omnivorous or predatory. 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.

A male of *Forficula auricularia* feeding on flowers.

The common earwig is one of the few insects that actively hunt for food and are omnivorous, eating arthropods, plants, and ripe fruit. To a large extent, this species is also a scavenger, feeding on decaying plant and animal matter if given the chance. Insects seen to have been caught include largely plant lice, but also large insects such as bluebottle flies. Plants that they feed on typically include clover, dahlias, zinnias, butterfly bush, hollyhock, lettuce, cauliflower, strawberry, 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.

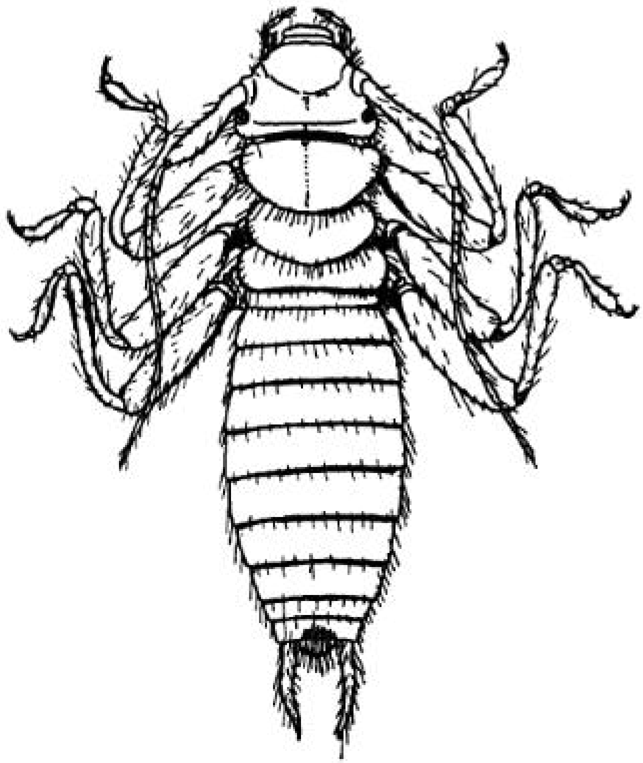
Species of the suborders Arixeniina and Hemimerina are generally considered epizoic, or living on the outside of other animals, mainly mammals. In the Arixeniina, family Arixeniidae, species of the genus *Arixenia* are normally found deep in the skin folds and gular pouch of Malaysian hairless bulldog bats (*Cheiromeles torquatus*), apparently feeding on bats' body or glandular secretions. On the other hand, species in the genus *Xenarina* (still of the suborder Arixeniina) are believed to feed on the guano and possibly the guanophilous arthropods in the bat's nest, 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.

Earwigs are generally nocturnal, and typically hide in small, dark, and often moist areas in the daytime. They can usually be seen patrolling 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. 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. Some people erroneously believe that earwigs burrow into people's ears; that is mostly a myth, although earwigs may crawl into ears and some can bite, as other insects do (see above). Picnic tables, compost and waste bins, patios, lawn furniture, window frames, or anything with minute spaces (even artichoke blossoms) can potentially harbor them.

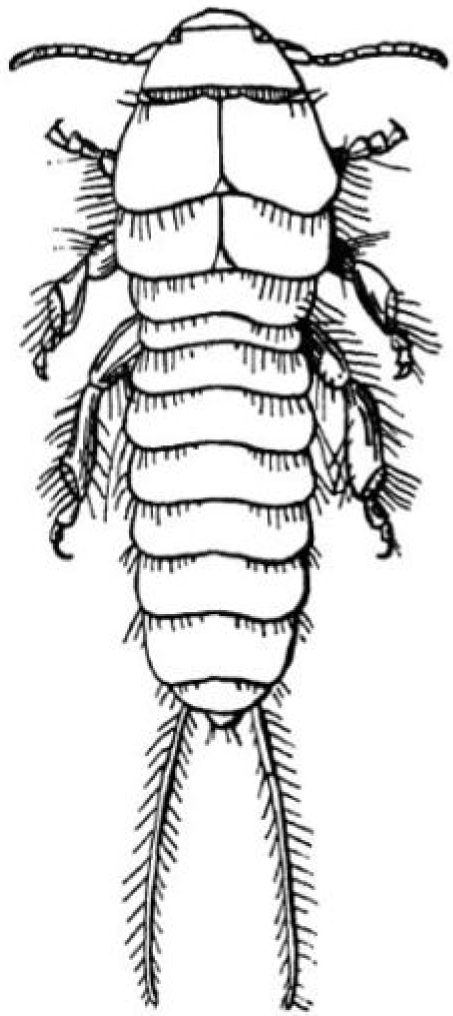
Predators and parasites

Earwigs are regularly preyed upon by birds, but (like many other insect species) are also prey for insectivorous mammals, amphibians, lizards, centipedes and spiders. European naturalists have observed bats preying upon earwigs. The primary insect predators that prey on the earwig are parasitic species of Tachinidae, or tachinid flies, whose larvae are endoparasites of the earwig. One species of tachinid fly, *Triarthria setipennis*, has been demonstrated to be successful as a biological control of earwigs for almost a century. Another tachinid fly and parasite of earwigs, *Ocytata pallipes*, has shown promise as a biological control agent as well. The common predatory wasp, the yellow jacket (*Vespula maculifrons*), preys upon earwigs when abundant. A small species of roundworm, *Mermis nigrescens*, is known to occasionally parasitize earwigs that have consumed roundworm eggs with plant matter. At least 26 species of parasitic fungus from the order Laboulbeniales have been found on earwigs. The eggs and nymphs are also cannibalized by other earwigs. A species of tyroglyphoid mite, *Histiostoma polypori* (Histiostomatidae, Astigmata), has been observed on common earwigs, sometimes in great densities; however, this mite feeds on earwig cadavers and not its live earwig transportation. Hippolyte Lucas observed scarlet acarine mites on European earwigs.

Evolution



Arixenia esau from the suborder Arixeniina



Hemimerus hanseni from the suborder Hemimerina

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. 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. The most likely, and most closely resembling, related order of insects is Grylloblattaria, theorized by Giles in 1963. However, other arguments have been made by other authors linking them to Phasmida, Embioptera, Plecoptera, and Dictyoptera.

Archidermaptera is believed to be sister to the remaining earwig groups. This suborder has tarsi with five segments (unlike the three found in the other suborders) as well as unsegmented cerci like Hemimerina and Arixenina; however, no fossil Hemimerina and Arixenina are known. Species in Hemimerina 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.

Some evidence of early evolutionary history is the structure of the antennal heart, a separate circulatory organ consisting of two ampullae, or vesicles, that are attached to the frontal cuticle to the bases of the antennae. 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.

Taxonomy

Distinguishing characteristics

The characteristics which distinguish the order Dermaptera from other insect orders are:

- *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, 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.

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. Hemimerina also has two genera, *Hemimerus* and *Araeomerus*, with a total of 11 species.

Phylogeny

A female of the common earwig in a threat pose

Dermaptera (= Euplecoptera, Euplexoptera, or Forficulida) is relatively small compared to the other orders of Insecta, with only about 1,800 species, 3 suborders and 11 families, not including the one extinct suborder **Archidermaptera** and its extinct family **Protodiplatyidae**. 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 suggests that Forficulina is paraphyletic through the exclusion of Hemimerina which should instead be nested within the Forficulina.

Suborder Archidermaptera †

Protodiplatyidae

Suborder Arixeniina

Arixeniidae

Suborder Forficulina

Anisolabididae
Apachyidae
Chelisochidae
Diplatyidae
Forficulidae
Karschiellidae
Labiduridae
Labiidae
Pygidicranidae

Suborder Hemimerina

Hemimeridae

Relationship with people

Earwigs are fairly abundant and found in many areas of 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 harm to humans. It is a common urban legend that earwigs crawl into the human ear and lay eggs in the brain. Finding earwigs in the human ear is rare, as most species do not fly and prefer dark and damp areas (such as basements) rather than typical bedrooms.

There is a debate whether earwigs are either harmful or beneficial to crops, as they eat both the insects eating the foliage (such as aphids) and the foliage itself, 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, 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.

Chapter 8

Lepidoptera

Lepidoptera Temporal range: 199–0 Ma Jurassic – Recent	

Clockwise from left to right, Emperor gum moth, Eggfruit Caterpillar moth (*Sceliodes cordalis*), *Abantiades magnificus*, Leopard Lacewing (*Cethosia cyane*) Giant Leopard Moth (*Hypercompe scribonia*), Willowherb Hawkmoth larva (*Proserpinus proserpina*)

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Subclass:	Pterygota

Infraclass:	Neoptera
Superorder:	Endopterygota
Order:	**Lepidoptera** Linnaeus, 1758
Suborders	
Aglossata Glossata Heterobathmiina Zeugloptera	

Lepidoptera is a large order of insects that includes moths and butterflies (called **lepidopterans**). It is one of the most speciose orders in the world, encompassing moths and the three superfamilies of butterflies, skipper butterflies, and moth-butterflies and found virtually everywhere. The term was coined by Linnaeus in 1735 and is derived from Ancient Greek λεπίδος (scale) and πτερόν (wing). Comprising an estimated 174,250 species, in 126 families and 46 superfamilies, the Lepidoptera show many variations of the basic body structure which have evolved to gain advantages in lifestyle and distribution. Recent estimates suggest that the order may have more species than earlier thought, and is among the four largest, most successful orders, along with the Hymenoptera, Diptera, and the Coleoptera.

Lepidopteran species are characterized by more than 20 derived features, some of the most apparent being the scales covering their bodies and wings, and a proboscis. The scales are modified, flattened "hairs", and give butterflies and moths their extraordinary variety of colors. Almost all species have some form of membranous wings, except for a few which have crossvein wings. Like most other insects, butterflies and moths are holometabolous, or undergo complete metamorphosis. Mating and the laying of eggs are carried out by adults, normally near or on host plants for the larvae. The larvae are commonly called caterpillars, and are completely different from their adult moth or butterfly form, having a cylindrical body with a well-developed head, mandible mouth parts, and from 0–11 (usually 8) pairs of prolegs. As they grow, these larvae will change in appearance, going through a series of stages called instars. Once fully matured as larvae, they undergo the pupal stage in their life cycle, which is commonly called a chrysalis for butterflies. A few butterflies and many moth species spin a silk case or cocoon prior to pupating, while others do not, instead going underground.

The Lepidoptera have, over millions of years, evolved a wide range of wing patterns and coloration ranging from drab moths akin to the related order Trichoptera to the brightly colored and complex-patterned butterflies. Accordingly, this is the most recognized and popular of insect orders with many people involved in the observation, study, collection, rearing of and commerce in these insects. A person who collects or studies this order is referred to as a lepidopterist. Many moth and butterfly species are of economic interest by virtue of their important natural role through pollination or the silk they produce.

Butterflies and moths play an important role in the natural ecosystem as pollinators; conversely, their larva are considered very problematic to vegetation in agriculture, as their main source of food is often live plant matter. In many species, the female may produce anywhere from 200 to 600 eggs, while in others the number may go as high as 30,000 eggs in one day. The caterpillars which hatch from this many eggs can mow down entire acres of crops.

Etymology

The word Lepidoptera comes from the Latin word for "scaly wing", from the Ancient Greek λεπίς (*lepis*) meaning scale and πτερόν (*pteron*) meaning wing. Sometimes the term Rhopalocera is used to group the species that are butterflies, from the Ancient Greek ῥόπαλον (*rhopalon*) and κέρας (*kæras*) meaning *club* and *horn* respectively; coming from the shape of the antennae of butterflies.

The origins of the common names of species are varied and often obscure. The English word *butterfly* is from Old English *buttorfleoge*, with many variations in spelling. Other than that, the origin is unknown, although it could be derived from the pale yellow color of many species' wings suggesting the color of butter. The species of Heterocera are commonly called moths. The origins of the English word moth are more clear, which comes from Old English *moððe*" (cf. Northumbrian dialect *mohðe*) from Common Germanic (compare Old Norse *motti*, Dutch *mot* and German *Motte* all meaning "moth"). Perhaps its origins are related to 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.

The etymological origins of the word caterpillar, the larval form of butterflies and moths, are from the early 16th century, from Middle English *catirpel*, *catirpeller*, probably an alteration of Old North French *catepelose*: *cate*, cat (from Latin *cattus*) + *pelose*, hairy (from Latin *pilōsus*).

Distribution and diversity

Diversity of Lepidoptera in each faunal region

	Palearctic	Nearctic	Neotropic	Afrotropic	Indo-australian (comprising Indomalayan and Australian regions)
Estimated number of species	22,465	11,532	44,791	20,491	47,286

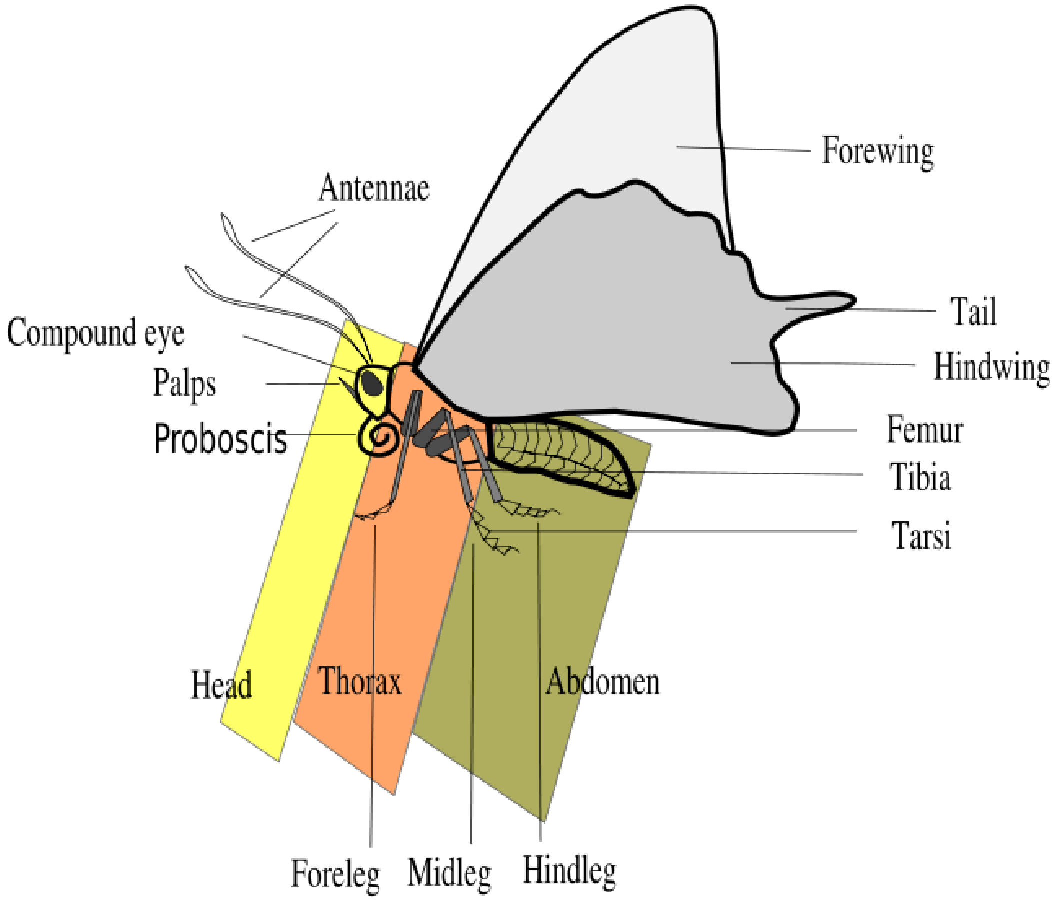
Lepidoptera are among the most successful groups of insects. They are to be found on all continents, except the Antarctic. Lepidoptera inhabit all terrestrial habitats ranging from desert to rain forest, from lowland grasslands to montane plateaus but almost always associated with higher plants, especially angiosperms (flowering plants). Amongst the northern-most of butterflies and moths is the Arctic Apollo (*Parnassius arcticus*) which is found in the Arctic Circle in northeastern Yakutia, at an altitude of 1500 meters above sea level. In the Himalayas, various Apollo species such as *Parnassius epaphus*, besides others, have been recorded to occur up to an altitude of 6,000 meters above sea level.

Some lepidopteran species exhibit symbiotic, phoretic or parasitic life-styles inhabiting the bodies of organisms rather than the environment. Coprophagous pyralid moth species, called as sloth moths, such as *Bradipodicola hahneli* and *Cryptoses choloepi*, are unusual in that they are exclusively found inhabiting the fur of the sloths, mammals found in central and South America. Two species of *Tinea* moths have been recorded as feeding on horny tissue and have been bred from the horns of cattle. The larva of *Zenodochium coccivorella* is an internal parasite of the coccid *Kermes* species. Many species have been recorded as breeding in natural materials or refuse such as owl pellets, bat caves, honey-combs or diseased fruit.

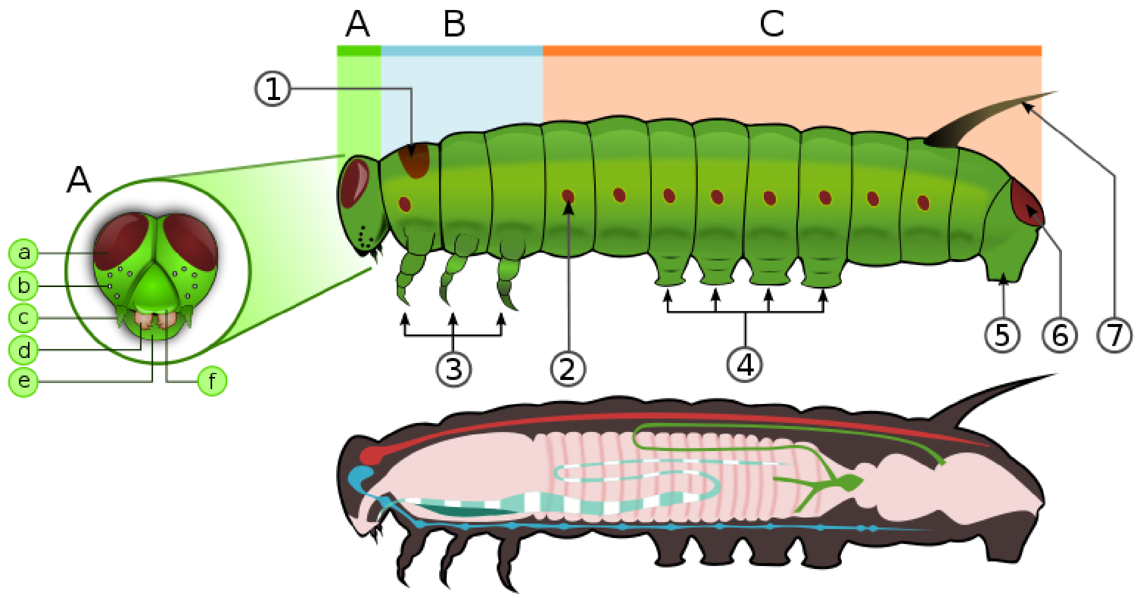
Of the approximately 174,250 lepidopteran species described until 2007, it is estimated that butterflies and skippers comprise approximately 17,950 with moths making up the rest. The vast majority of Lepidoptera are to be found in the tropics but substantial diversity exists on most continents. North America has over 700 species of butterflies and over 11,000 species of moths found in North America while there are about 400 species of butterflies and 20,000 species of moths reported from Australia.

The diversity of Lepidoptera in each faunal region has been estimated by John Heppner in 1991 based partly on actual counts from the literature, partly on the card indexes in the Natural History Museum (London) and the National Museum of Natural History (Washington), and partly on estimates:

External Morphology



Parts of an adult butterfly



A – head, B – thorax, C – abdomen, 1 – prothoracic shield, 2 – spiracle, 3 – true legs, 4 – midabdominal prolegs, 5 – anal proleg, 6 – anal plate, 7 – tentacle, a – frontal triangle, b – stemmata (ocelli), c – antenna, d – mandible, e – labrum.

Lepidoptera are morphologically distinguished from other orders principally by the presence of scales on the external parts of the body and appendages, especially the wings. Butterflies and moths vary in size from microlepidoptera only a few millimeters long, to conspicuous animals with a wingspan of many inches, such as the Monarch butterfly and Atlas moth. The Lepidoptera show many variations of the basic body structure which have evolved to gain advantages in lifestyle and distribution.

Head

The face a caterpillar with the mouthparts showing.

The head is where many sensing organs and the mouth parts are found. Like the adults, the larvae also have a toughened, or sclerotized head capsule. Here, there are two compound eyes, and, unique to Lepidoptera are raised spots or cluster of sensory bristles called chaetosema. even though many taxa have lost one or both of said spots. The antennae have a wide variation in the form amongst species and even between different sexes. The antennae of butterflies are usually filiform and shaped like clubs, while those of moths are with flagellar segments variously enlarged or branched. Some moths have a antennae that are enlarged, or tapered and hooked at the ends.

The maxillary galeae are modified and form an elongated and joined in the form of a proboscis. The proboscis is made of up to one to five segments, usually kept coiled up under the head by small muscles when not being used to suck up nectar from flowers or other liquids. Some moths that are more primitive still have mandibles, or separate moving jaws like their ancestors, these moths form the genus Micropterigidae.

The larvae, caterpillars, have a toughened head capsule, with separate chewing mouthparts. These mouthparts, called mandibles, are used to chew up the plant matter that the larvae eat, rather than a proboscis, which an adult uses to suck liquids. The lower jaw, or labium, is weak but may carry a spinneret, an organ used to create silk. The head is made of large lateral lobes, each having an ellipse of up to six simple eyes.

Thorax

The thorax is made of three fused segments, the prothorax, mesothorax, and metathorax, each with a pair of legs. The first segment contains the first pair of legs. The males of some species in the butterfly family Nymphalidae, the fore-legs are greatly reduced and are not used for walking or perching. The three pairs of legs are covered with scales. Lepidoptera also have olfactory organs on their feet which aid the butterfly in "tasting" or "smelling" out its food. In the larva form there are 3 pairs of true legs, with 0–11 pairs of abdominal legs (usually 8) and hooklets, called apical crochets.

The two pairs of wings are found on the middle and third segment, or mesothorax and metathorax respectively. In the more recent genera, the wings of the second segment or much more pronounced, however some, more primitive form, have similarly sized wings of both segments. The wings are covered in scales arranged like shingles, forming the extraordinary variety seen in color. The mesothorax is designed to have more powerful muscles to propel moth or butterfly through the air, with the wing of said segment having a stronger vein structure. The largest superfamily, Noctuidae, has the wings modified to act as Tympanal or hearing organs

The larvae have an elongated soft body that may have hair-like or other projections, 3 pairs of true legs, with 0–11 pairs of abdominal legs (usually 8) and hooklets, called apical crochets. The thorax will usually have a pair of legs on each segment. The thorax is also lined with many sphericals on both the mesothorax and metathorax, except for a few aquatic species, who instead have a form of gills.

Abdomen

The abdomen, which is less sclerotized than the thorax, consists of 10 segments with membranes in between allowing for articulated movement. The sternum, on the first segment, is small in some families and is completely lost in others. The last 2-3 segments form the external parts of the species' sex organs. The genitalia of Lepidoptera are highly varied and are often the only means of differentiating between species. Male genitals include a valvae, which are usually large, as they are used to grasp the female during mating. Female genitalia include three distinct sections.

In the females of more primitive moths, there is only one sex organ, which is used for copulation and as a ovipositor, or egg laying organ. 98% of moth species have a separate organ for mating, and an external duct that carries the sperm from the male.

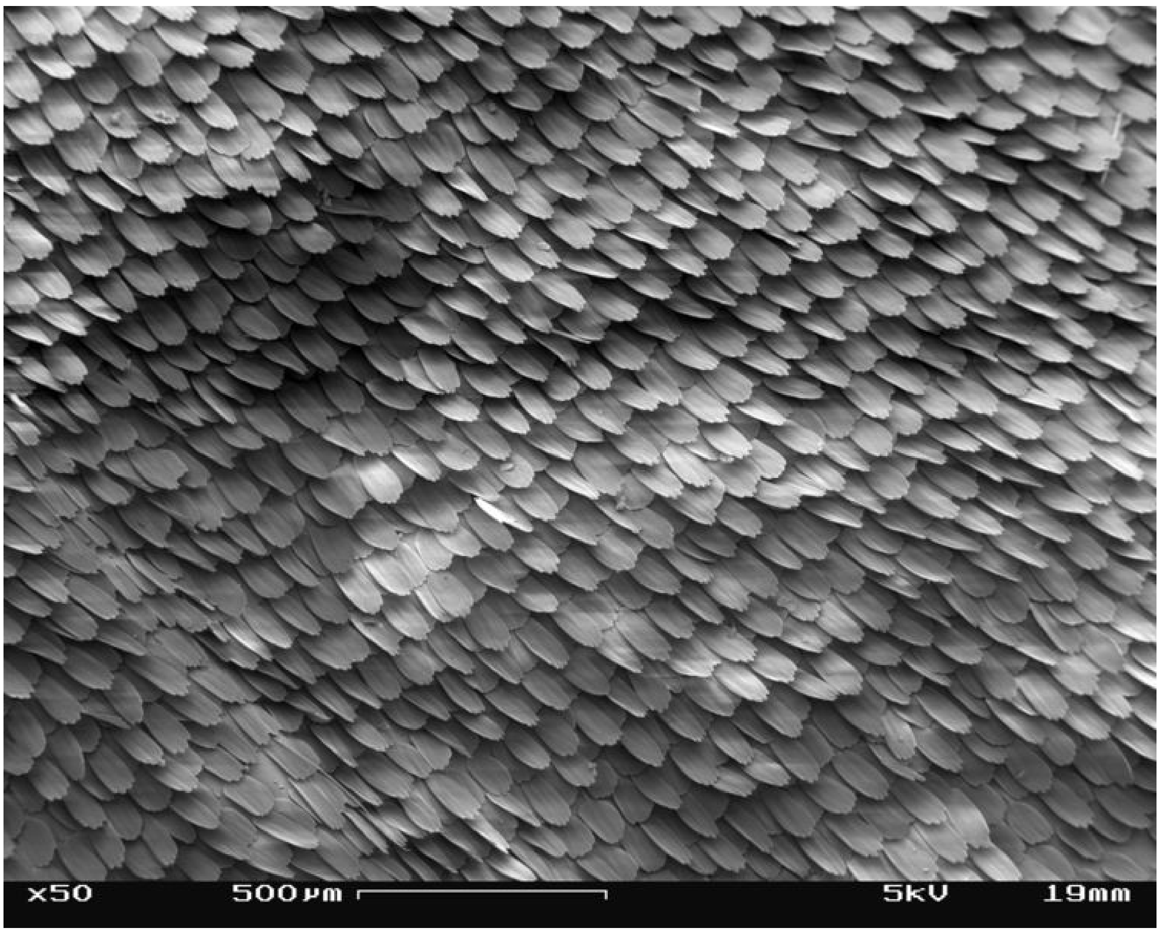
The abdomen of the caterpillar has 4 pairs of prolegs, normally located on the third to sixth segments of the abdomen, and a separate pair of prolegs by the anus, which have a pair of tiny hooks called crotchets. These aid in gripping and walking, especially in species that lack many prolegs (e. g. larvae of Geometridae). In some primitive moths, these prolegs may be on every segment of the body, while prolegs may be lost completely in other groups, which are more adapted to boring and living in sand (e. g., Prodoxidae and Nepticulidae respectively).

Scales

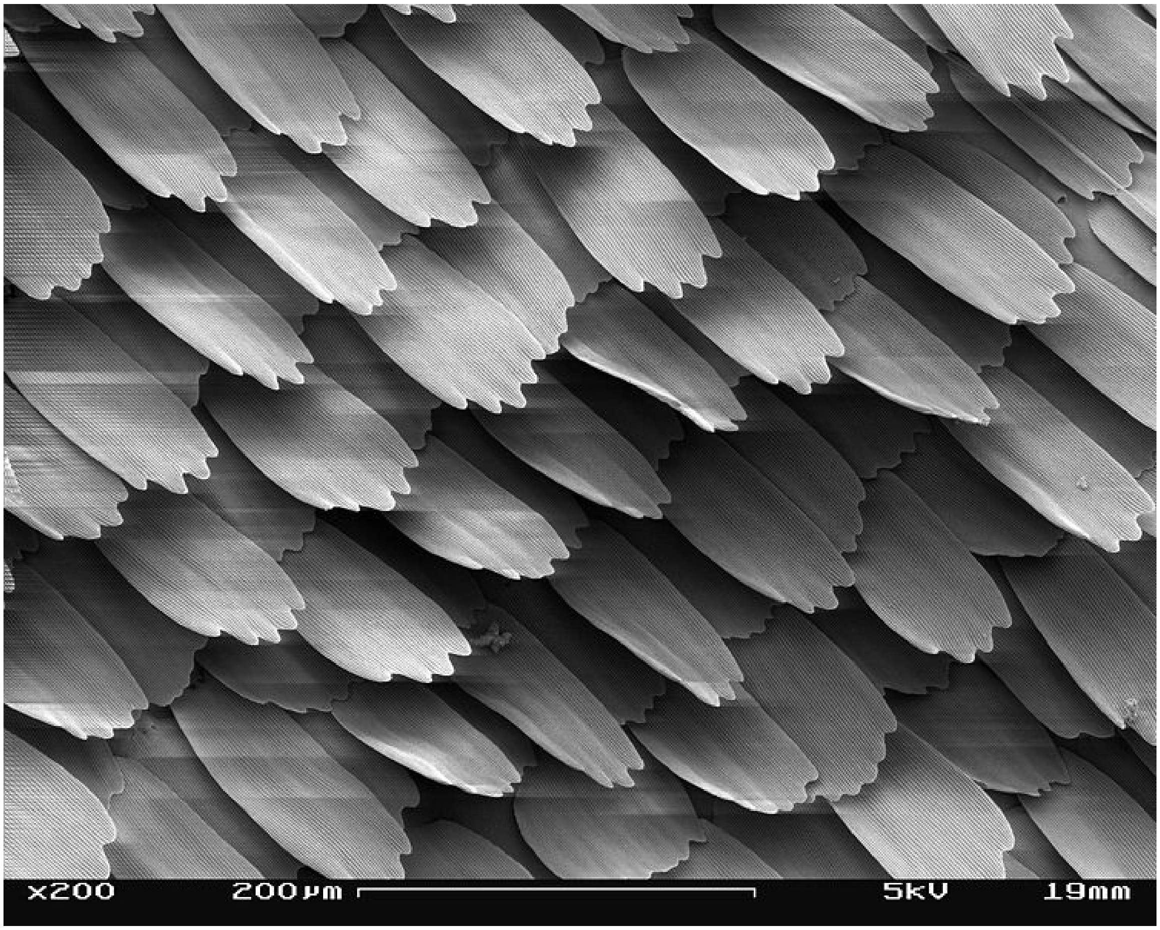
Wing scales form the color and pattern on wings. The scales shown here are lamellar. The pedicel can be seen attached to a few loose scales.

The wings, head parts of thorax and abdomen of Lepidoptera are covered with minute scales, from which feature the order 'Lepidoptera' derives its names, the word "lepteron" in Ancient Greek meaning 'scale'. Most scales are lamellar, or blade-like and attached with a pedicel, while other forms may be hair-like or specialized as secondary sexual characteristics. The lumen or surface of the lamella, has a complex structure. It gives color either due to the pigmentary colors contained within or due to its three-dimensional structure. Scales provide a number of functions, which include insulation, thermoregulation, aiding gliding flight, amongst others, the most important of which is the large diversity of vivid or indistinct patterns they provide which help the organism protect itself by camouflage, mimicry, and to seek mates.

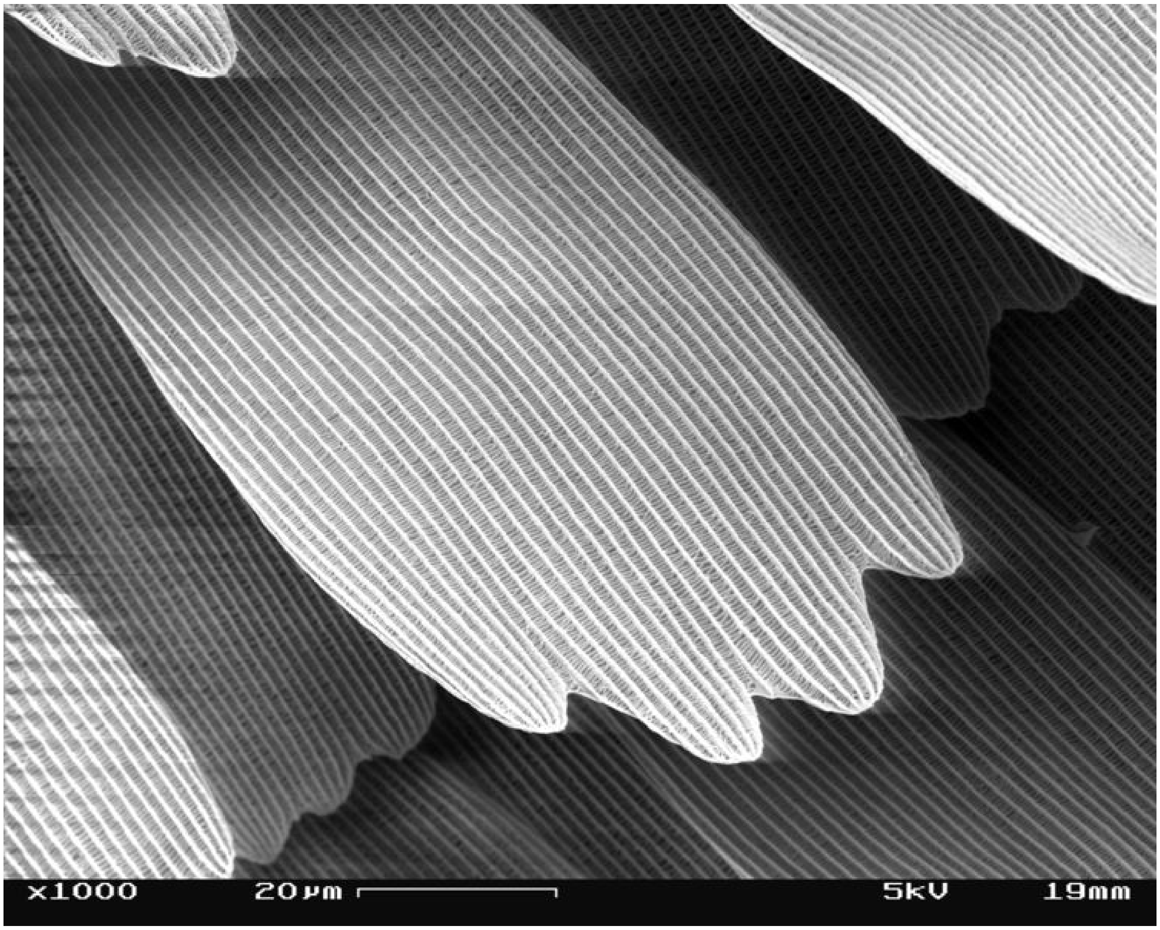
Electron microscopic images of scales



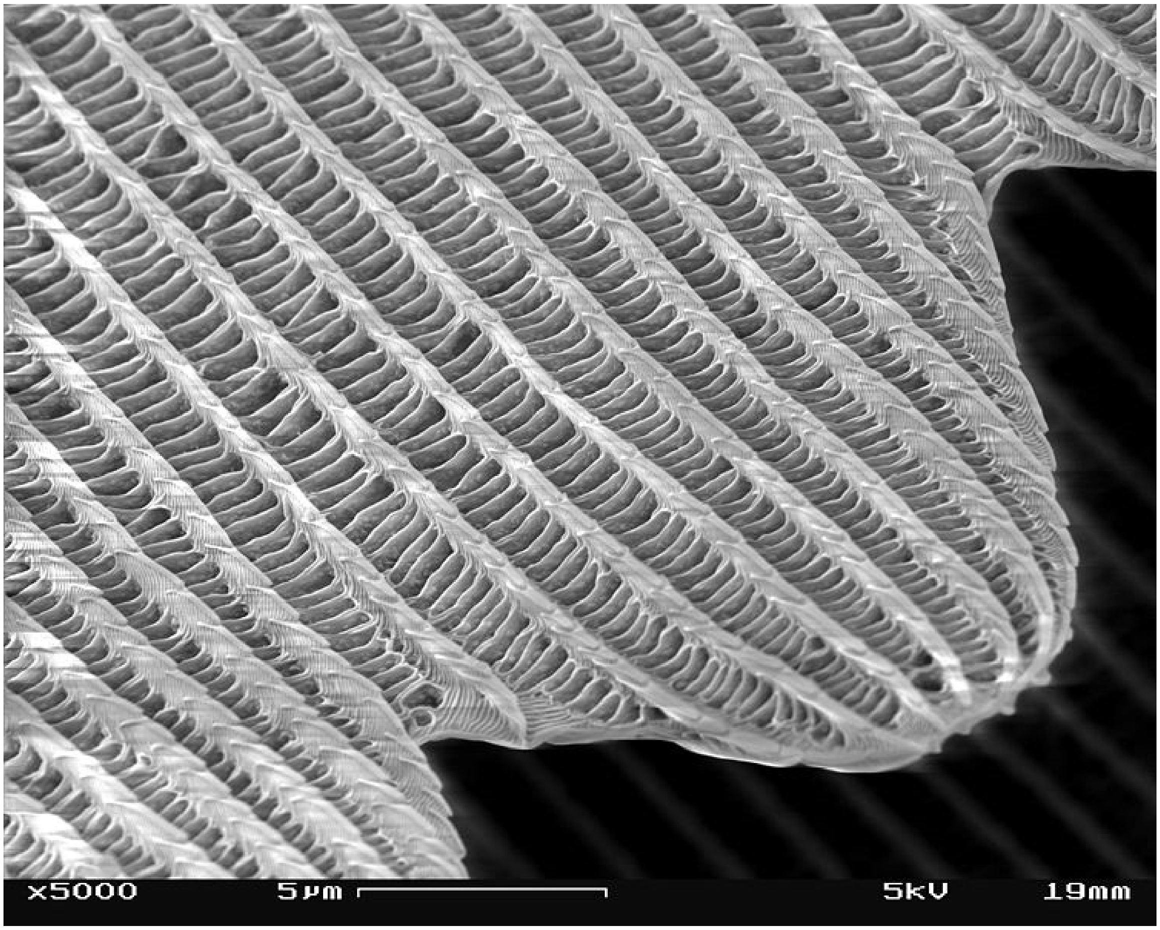
A patch of wing



Scales close up



A single scale

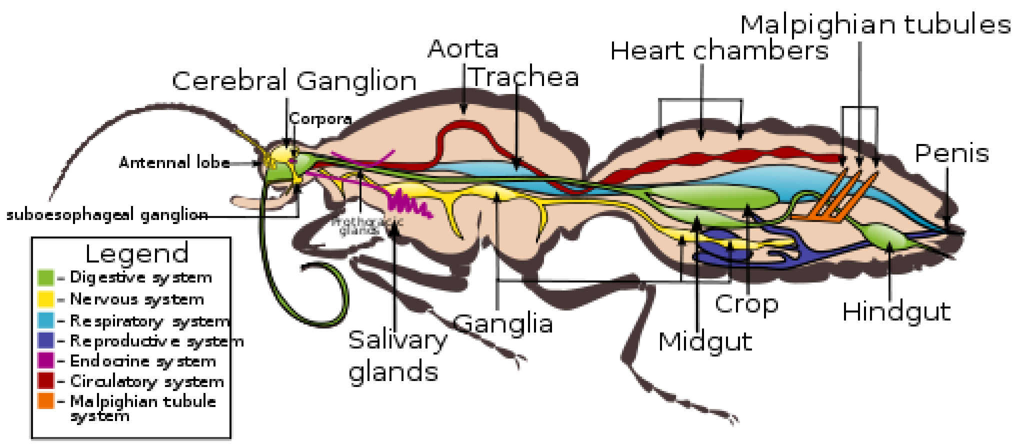


Microstructure of a scale

Internal morphology

In reproductive system of butterflies and moths, the male genitalia are complex and unclear. In females there are three types of genitalia based on the relating taxa: monotrysian, exoporian, and dytresian. In the monotrysian type there is an opening on the fused segments of the sterna 9 and 10, which act as insemination and oviposition. In the exoporian type (in Hepaloidae and Mnesarchaeoidea) there are two separate places for insemination and oviposition, both occurring on the same sterna as the monotrysian type, 9/10. In most species the genitalia are flanked by two soft lobes, although they may be specialized and sclerotized in some species for ovipositing in area such as crevices and inside plant tissue. Hormones and the glands that produce them run the development of butterflies and moths as they go through their life cycle, called the endocrine system. The first insect hormone PTTH (Prothoracicotropic hormone) operates the species life cycle and diapause. This hormone is produced by corpora allata and corpora cardiaca, where it is also stored. Some glands are specialized to perform certain task such as producing silk or producing saliva in the palpi. While the corpora cardiaca produce PTTH, the corpora allata also produces jeuvanile hormones, and the prothorocic glands produce moulting hormones.

In the digestive system, the anterior region of the foregut has been modified to form a pharyngial sucking pump as they need it for the food they eat, which are for the most part liquids. An esophagus follows and leads to the posterior of the pharynx and in some species forms a form of crop. The midgut is short and straight, with the hindgut being longer and coiled. Ancestors of lepidopteran species, stemming from Hymenoptera, had midgut ceca, although this is lost in current butterflies and moths. Instead, all the digestive enzymes other then initial digestion, are immobilized at the surface of the midgut cells. In larvae, long-necked and stalked goblet cells are found in the anterior and posterior midgut regions, respectively. In insects, the goblet cells excrete positive potassium ions, which are absorbed from leaves ingested by the larvae. Most butterflies and moths display the usual digestive cycle, however species that have a different diet require adaptations to meet these new demands.



Internal morphology of adult male Nymphalid species, showing most of the major organ systems, with characteristic reduced fore legs of said species. The corpora include the corpus allatum and the corpus cardiaca.

In the circulatory system, hemolymph, or insect blood, is used to circulate heat in a form of thermoregulation, where muscles contraction produces heat which is transferred to the rest of the body when conditions are unfavorable. In lepidopteran species, hemolymph is circulated through the veins in the wings by some form of pulsating organ, either by the heart or by the intake of air into the trachea. Air is taken in through spiracles along the sides of the abdomen and thorax supplying the trachea with oxygen as it goes through the lepidopteran's respiratory system. There are three different tracheae supplying oxygen diffusing oxygen throughout the species body: The dorsal, ventral, and visceral. The dorsal tracheae supply oxygen to the dorsal musculature and vessels, while the ventral tracheae supply the ventral musculature and nerve cord, and the visceral tracheae supply the guts, fat bodies, and gonads.

Polymorphism

Sexually dimorphic bagworm moths (*Tinea ephemeraeformis*) mating. The female is flightless.

The *Heliconius* butterflies from the tropics of the Western Hemisphere are the classical model for Müllerian mimicry.

Polymorphism is appearance of forms or "morphs" differing in color and number of attributes within a single species. In Lepidoptera, polymorphism can be seen not only between individuals in a population, but also between the sexes as *sexual dimorphism*, between geographically separated populations in *geographical polymorphism* and also between generations flying at different seasons of the year (*seasonal polymorphism* or polyphenism). In some species, the polymorphism is limited to one sex, typically the female. This often includes the phenomenon of mimicry when mimetic morphs fly alongside non-mimetic morphs in a population of a particular species. Polymorphism occurs both at specific level with heritable variation in the overall morphological design of individuals as well as in certain specific morphological or physiological traits within a species.

Environmental polymorphism, which traits are not inherited, is often termed as polyphenism. Polyphenism in Lepidoptera is commonly seen in the form of seasonal morphs especially in the butterfly families of Nymphalidae and Pieridae. An Old World pierid butterfly, the Common Grass Yellow (*Eurema hecabe*) has a darker summer adult morph, triggered by a long day exceeding 13 hours in duration, while the shorter diurnal period of 12 hours or less induces a paler morph in the post-monsoon period. Polyphenism also occurs in caterpillars, an example being the Peppered Moth, *Biston betularia*.

Geographical polymorphism is where geographical isolation causes a divergence of a species into different morphs. A good example is the Indian White Admiral *Limenitis procris* which has five forms, each geographically separated from the other by large mountain ranges. An even more dramatic showcase of geographical polymorphism is the Apollo butterfly (*Parnassius apollo*). Due to the Apollos living in small local populations, having no contact with each other, but because of the strong stenotopic species and weak migration ability interbreeding between populations of one species practically does not occur; they form over 600 different morphs, with the size of spots on the wings of which varies greatly.

Dry-season form

Wet-season form

Sexual dimorphism is the occurrence of differences between males and females in a species. In Lepidoptera, sexual dimorphism is widespread and almost completely determined by genetic determination. Sexual dimorphism is present in all families of the Papilionoidoea and more prominent in the Lycaenidae, Pieridae and certain taxa of the Nymphalidae. Apart from color variation which may differ from slight to completely different color-pattern combinations, secondary sexual characteristics may also be present. Different genotypes maintained by natural selection may also be expressed at the same time. Polymorphic and/or mimetic females occur in the case of some taxa in the Papilionidae primarily to obtain a level of protection not available to the male of their species. The most distinct case of sexual dimorphism is that of adult females of many Psychidae species who have only vestigial wings, legs, and mouthparts as compared to the adult males who are strong fliers with well-developed wings and feathery antennae.

Reproduction and development

Mating pair of *Laothoe populi* (Poplar Hawk-moth) showing two different color variants

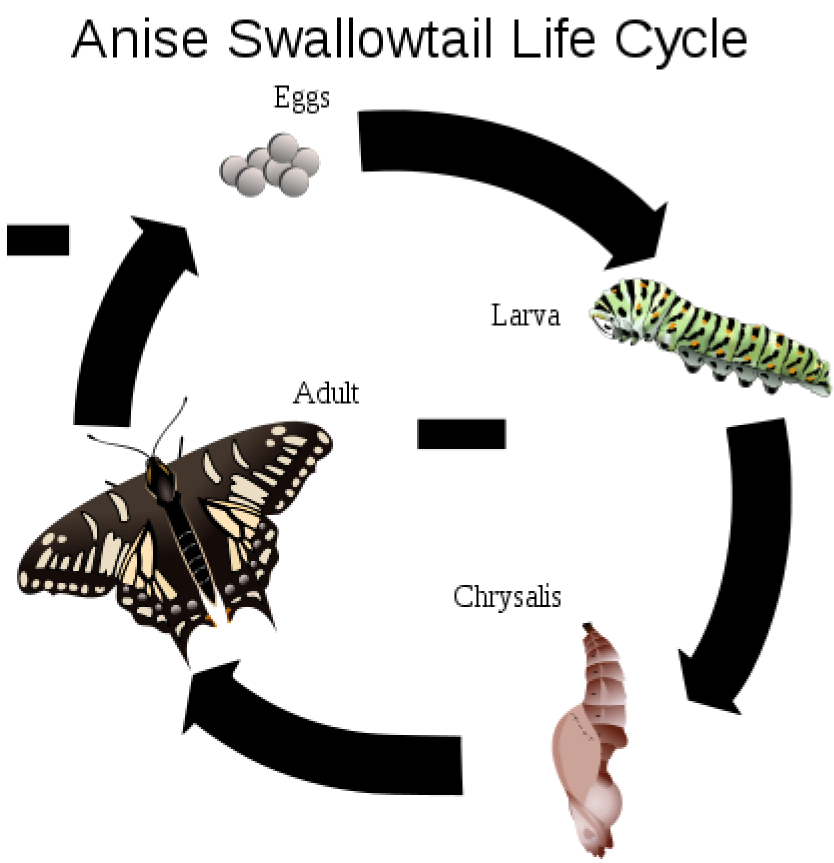
Species of Lepidoptera undergo holometabolism or "complete metamorphosis". Their life cycle normally consists of an egg, larva, pupa, and an imago or adult. The larvae are commonly called caterpillars, and the pupae of moths that are encapsulated in silk are called cocoons while the uncovered pupae of butterflies are called chrysalides.

Mating

Males usually get a head start, and start eclosion or emergence, earlier then females and peak in numbers before females. Both of the sexes are sexually mature by the time of eclosion. Butterflies and moths normally don't associate with each other, except for migrating species, staying relatively asocial. Mating begins with an adult (female or male) attracting a mate, normally using visual stimuli, especially in diurnal species like most butterflies. However, the females of most nocturnal species, including almost all moth species, use pheromones to attract males, sometimes from long distances. Some species engage in a form of acoustic courtship, or attract mates using sound or vibration such as the polka-dot wasp moth, *Syntomeida epilais*.

Adaptations include undergoing one seasonal generation, two or even more, called voltinism (Univoltism, bivoltism and multivism respectively). Most lepidoptera in temperate climates are univoltine, while in tropical climates most have two seasonal broods. Some others may take advantage of any opportunity they can get, and mate continuously throughout the year. These seasonal adaptations are controlled by hormones, and these delays in reproduction are called diapause. Many lepidopteran species, after mating and laying their eggs, die shortly afterwards, having only lived for a few days after eclosion. Others may still be active for several weeks and then overwinter and become sexually active again when the weather becomes more favorable, or diapause. The sperm of the male that mated most recently with the female is most likely to have fertilized the eggs but the sperm from a prior mating may still prevail.

Life cycle



The four stages of the life cycle of an Anise Swallowtail

Lepidopteran species like all Endopterygota, are holometabolic, or undergo complete metamorphosis, going through a four-stage life cycle: egg; larva / caterpillar; pupa / chrysalis; and imago (plural: *imagines*) / adult. The morphological characteristics which distinguish the order Lepidoptera from other insect orders are:

Eggs

Lepidoptera usually reproduce sexually and are oviparous (egg-laying), though some species exhibit live birth in a process called ovoviviparity. There are a variety of differences in egg-laying and the number of eggs laid. Some species simply drop their eggs in flight (these species normally have polyphagous larvae, meaning they eat a variety of plants e. g., Hepialids and some nymphalids) while most Lepidoptera will lay their eggs near or on the host plant that the larvae feed on, normally attracted by its odor. The number of eggs laid may vary from only a few to several thousand.

The females of both butterflies and moths select the host plant primarily by chemical cues, where the area and placement is decided by is best fit for the larvae, and which area on the plant is best for oviposition. The moth or butterfly knows this information based on instinct which is inherited genetically.

The egg is covered by a hard-ridged protective outer layer of shell, called the chorion. It is lined with a thin coating of wax which prevents the egg from drying out before the larva has had time to fully develop. Each egg contains a number of micropyles, or tiny funnel-shaped openings at one end, the purpose of which is to allow sperm to enter and fertilize the egg. Butterfly and moth eggs vary greatly in size between species, but they are all either spherical or ovate.

The egg stage lasts a few weeks in most butterflies but eggs laid close to winter, especially in temperate regions, go through a diapause, and hatching may be delayed until spring. Other butterflies may lay their eggs in the spring and have them hatch in the summer. These butterflies are usually northern species (e. g. *Nymphalis antiopa*).

Larvae

The larval form typically lives and feeds on plants.

The larvae or caterpillars are the first stage in the life cycle after hatching. They look very different from the adults and come in a variety of shapes and sizes. The larvae are herbivores, but a few are carnivores (some eat ants or other caterpillars) and detritivores. Different herbivore species have adapted to feed on every part of the plant and are normally considered pests to their host plant; some species have been found to lay their eggs on the fruit and other species lay their eggs on clothing or fur (e. g., *Tineola bisselliella*, the common clothes moth). Some species are carnivorous and others are even parasitic. A species of Geometridae from Hawaii has carnivorous larvae that catch and eat flies. The larvae develop rapidly with several generations in a year; however, some species may take up to 3 years to develop and exceptional examples like *Gynaephora groenlandica* take as long as seven years. The larval stage is where the feeding and growing stages occur, and the larvae periodically undergo hormone-induced ecdysis, developing further with each instar, until they undergo the final larval-pupal molt. Lepidoptera pupa, known as chrysalis, have functional mandibles and with appendages fused or glued to the body in most species, while the pupal mandibles are not functional in others.

The larvae of both butterflies and moths exhibit mimicry to deter potential predators. Some caterpillars have the ability to inflate parts of their head to appear snake-like. Many have false eye-spots to enhance this effect. Some caterpillars have special structures called osmeteria which are averted to produce smelly chemicals. These are used in defense. Host plants often have toxic substances in them and caterpillars are able to sequester these substances and retain them into the adult stage. This helps making them unpalatable to birds and other predators. Such unpalatability is advertised using bright red, orange, black or white warning colors. The toxic chemicals in plants are often evolved specifically to prevent them from being eaten by insects. Insects in turn develop countermeasures or make use of these toxins for their own survival. This "arms race" has led to the coevolution of insects and their host plants.

Wing development

Any form of wings are externally visible on the larva, however when larvae are dissected, developing wings can be seen as disks, which can be found on the second and third thoracic segments, in place of the spiracles that are apparent on abdominal segments. Wing disks develop in association with a trachea that runs along the base of the wing, and are surrounded by a thin peripodial membrane, which is linked to the outer epidermis of the larva by a tiny duct. Wing disks are very small until the last larval instar, when they increase dramatically in size, are invaded by branching tracheae from the wing base that precede the formation of the wing veins, and begin to develop patterns associated with several landmarks of the wing.

Near pupation, the wings are forced outside the epidermis under pressure from the hemolymph, and although they are initially quite flexible and fragile, by the time the pupa breaks free of the larval cuticle they have adhered tightly to the outer cuticle of the pupa (in obtect pupae). Within hours, the wings form a cuticle so hard and well-joined to the body that pupae can be picked up and handled without damage to the wings.

Pupa

Eclosion of *Papilio dardanus*

After about 5 to 7 instars, or molts, certain hormones, like prothoracicotropic hormone, stimulate the production of ecdysone, which initiates insect molting. Then, the larva puparium, a sclerotized or hardened cuticle of the last larval instar, develops into the pupa. Depending on the species, the pupa may be covered in silk and attached to many different types of debris or may not be covered at all. The pupa stays attached to the leaf by silk spun by the caterpillar before it spun the silk for the full pupa. All the features of the adult are easily recognizable in the pupa, externally. All the appendages that are found on the adult head and thorax are found cased inside the cuticle (antennae, mouthparts, etc.), with the wings wrapped around, adjacent to the antennae.

While encased, some of the lower segments are not fused, and are able to move using small muscles found in between the membrane. Moving may help the pupa, for example, escape the sun, which would otherwise kill it. The pupa of the *Cydia deshaisiana*, called the Mexican jumping bean does this. The larvae cut a trapdoor in the bean (species of Sebastiania) and use the bean as a shelter. When there is a sudden rise in temperature, the pupa inside twitches and jerks, pulling on the threads inside. Wiggling may also help to deter parasitoid wasps from laying eggs on the pupa. Other species of moth are able to make clicks to deter predators.

The length of time before the pupa ecloses, or emerges varies greatly. The monarch butterfly may stay in its chrysalis for two weeks, while other species may need to stay for more than 10 months in diapause. The adult will emerge from the pupa either by using abdominal hooks or from projections located on the head. The mandibles found in the most primitive moth families are used to escape from their cocoon (e. g., Micropterigoidea).

Adult

Most lepidopteran species do not live long after eclosion, only needing a few days to find a mate and then lay their eggs. Others may remain active for from one to several weeks or go through diapause, overwintering as monarch butterflies do, or waiting out environmental stress. Some adult species of Microlepidoptera go through a stage where there is no reproductive-related activity lasting through summer and winter, followed by mating and oviposition, or egg laying, in the early spring.

While most butterflies and moths are terrestrial, many species of Pyralidae are truly aquatic with all stages except the adult occurring in water. Many species from other families such as Arctiidae, Nepticulidae, Cosmopterygidae, Tortricidae, Olethreutidae, Noctuidae, Cossidae and Sphingidae are aquatic or semi-aquatic.

Behavior

Flight

Flight is an important aspect of the lives of butterflies and moths and is used for evading predators, searching for food and finding mates in a timely manner as lepidopteran species do not live long after eclosion. It is the main form of locomotion in most species. In lepidoptera, the forewings and hindwings are mechanically coupled and flap in synchrony. Flight is anteromotoric, or being driven primarily by action of the forewings. Although it has been reported that lepidopteran species can still fly when their hindwings are cut off, it reduces their linear flight and turning capabilities.

Lepidopteran species have to be warm, about 77 to 79 °F (25 to 26 °C) in order to fly. They depend on their body temperature being sufficiently high and since they can't regulate it themselves, this is dependent on their environment. Butterflies living in cooler climates may use their wings to warm their bodies. They will bask in the sun, spreading out their wings so that they get maximum exposure to the sunlight. In hotter climates butterflies can easily overheat, so they are usually active only during the cooler parts of the day, early morning, late afternoon or early evening. During the heat of the day they rest in the shade. Some larger thick-bodied moths (e. g. Sphingidae) can generate their own heat to a limited degree by vibrating their wings. The heat generated by the flight muscles warms the thorax while the temperature of the abdomen is unimportant for flight. To avoid overheating some moths rely on hairy scales, internal air sacs, and other structures to separate the thorax and abdomen and keep the abdomen cooler.

Some species of butterfly can reach fast speeds, such as the Southern Dart, which can go as fast as 48.4 km/h. Sphingids are some of the fastest flying insects, some are capable of flying at over 50 km/h (30 miles per hour), having a wingspan of 35–150 mm. In some species, there is sometimes a gliding component to their flight. Flight occurs either as hovering, or as forward or backward motion. In butterfly and in moth species, like hawk moths, hovering is important in that they need to hover over flowers when feeding on the nectar.

Navigation

Timelapse of flying moths, attracted to the floodlights

Navigation is important to lepidoptera species, especially for those that migrate. Butterflies, which have more species that migrate, have been shown to navigate using time compensated sun compasses. They can see polarized light and therefore can orient even in cloudy conditions. The polarized light in the region close to the ultraviolet spectrum is suggested to be particularly important. It is suggested that most migratory butterflies are those that live in semi-arid areas where breeding seasons are short. The life-histories of their host plants also influence the strategies of the butterflies. Other theories include the use of landscapes. Lepidoptera may use coastal lines, mountains and even roads to orient themselves. Above sea it has been observed that the flight direction is much more accurate if the coast is still visible.

Many studies have also shown that moths navigate. One study showed that many moths may use the Earth's magnetic field to navigate, as a study of the moth Heart and Dart suggests. Another study, this time of the migratory behavior of the Silver Y, showed that even at high altitudes the species can correct its course with changing winds, and prefers flying with favourable winds, suggesting a great sense of direction. *Aphrissa statira* in Panama loses its navigational capacity when exposed to a magnetic field, suggesting it uses the Earth’s magnetic field.

Moths exhibit a tendency to circle artificial lights repeatedly. This suggests that they use a technique of celestial navigation called 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 traveling 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, causing airborne moths to come plummeting downwards, and – at close range – which results in a spiral flight path that gets closer and closer to the light source. Other explanations have been suggested, such as the idea that moths may be impaired with a visual distortion called a Mach band by Henry Hsiao in 1972. He stated that they fly towards the darkest part of the sky in pursuit of safety and are thus inclined to circle ambient objects in the Mach band region.

Migration

Monarch butterflies cluster in Santa Cruz. Monarch butterflies migrate to Santa Cruz to spend the winter.

Lepidopteran migration is usually seasonal, the insects moving to escape dry seasons or other disadvantageous conditions. Most lepidopterans that migrate are butterflies, the distance travelled varying from short to very long journeys. Some butterflies that migrate include the Mourning Cloak, Painted Lady, American Lady, Red Admiral, and the Common Buckeye. Particularly famous migrations are those of the Monarch butterfly from Mexico to northern USA and southern Canada, a distance of about 4,000–4,800 km

(2,500–3,000 mi). Other well known migratory species include the Painted Lady and several of the danaine butterflies. Spectacular and large scale migrations associated with the Monsoons are seen in peninsular India. Migrations have been studied in more recent times using wing tags and also using stable hydrogen isotopes.

Moths also undertake migrations, an example being the uraniids. *Urania fulgens* undergoes population explosions and massive migrations that may be not surpassed by any other insect in the Neotropics. In Costa Rica and Panama, the first population movements may begin in July and early August and, depending on the year, may be very massive, continuing unabated for as long as five months.

Communication

Pheromones are commonly involved in mating rituals amongst species, especially moths, but they are also an important aspect of other forms of communication. Usually the pheromones are produced by either the male or the female and detected by members of the opposite sex with their antennae. In many species, a gland between the eighth and ninth segment under the abdomen in the female produces the pheromones. Communication can also occur through stridulation, or producing sounds by rubbing various parts of the body together.

Moths are known to engage in acoustic forms of communication; most often species engage use it in a form of acoustic courtship, attracting mates using sound or vibration. Like most other insects, moths pick up these sounds using tympanic membranes in the abdomen. An example is that of the polka-dot wasp moth (*Syntomeida epilais*), which produce sounds with a frequency above that normally detectable by humans (~20kHZ). These sounds also function as tactile communication, or communication through touch, as they stridulate, or vibrate a substrate like leaves and stems.

Most moths lack bright colors as many species use coloration as camouflage but butterflies engage in visual communication. Female cabbage butterflies, for example, use ultraviolet light to communicate, with scales colored in this range on the dorsal wing surface. When they fly, each down stroke of the wing creates a brief flash of ultraviolet light that the males apparently recognize as the flight signature of a potential mate. These flashes from the wings may attract several males who engage in aerial courtship displays.

Diapause

One of the most important adaptations is diapause, or delay in development in response to regularly and recurring periods of adverse environmental conditions (winter, dry season, etc.). Diapause normally occurs in eggs, or as a reproductive delay in adults. Butterflies like the monarch may undergo diapause during winter, where they undergo a form of hibernation, lying dormant on trees for protection after their large scale migration. Seasonal adaptations such as voltism, where they may reproduce one or more times annually are due to diapause. This response to environmental stress is controlled by hormones and is necessary to survival during unfavorable times, especially in northern areas and high mountains where winter is regular and harsh. For example, in the Mediterranean area, larvae feed during the spring when the vegetation flourishes, then undergo diapause in the summer during drought, and hibernate in the winter.

Ecology

Moths and Butterflies are important in the natural ecosystem. They are integral participants in the food chain, having co-evolved with flowering plants and predators, lepidopteran species have formed a network of trophic relationships between autotrophs and heterotrophs, which are included in the stages of Lepidoptera larvae, pupae and adults. Larvae and pupae are links in the diet of birds and parasitic entomophagous insects. The adults are included in food webs in a much broader range of consumers (including birds, small mammals, reptiles, etc.).

Defense and predation

Papilio machaon caterpillar showing the osmeterium, which emits unpleasant smells to ward off predators

Lepidopteran species are soft bodied, fragile and almost defenseless while the immature stages move slowly or are immobile, hence all stages are exposed to predation. Adult butterflies and moths are predated upon by birds, lizards, amphibians, dragonflies and spiders, besides others. Caterpillars and pupa fall prey, not only to birds but invertebrate predators, small mammals, as well as fungi and bacteria. Parasitoid and parasitic wasps and flies may lay eggs in the caterpillar which would eventually kill it as they hatch inside its body and eat its tissues. Insect-eating birds are probably the worst predators. Lepidoptera, especially the immature stages, are an ecologically important food to many insectivorous birds, such as the Great Tit in Europe.

An "evolutionary arms race" can be seen between predator and prey species. Lepidoptera have developed a number of strategies for defense and protection which include evolution of morphological characters, changes in ecological life-style and in behavior. These include aposematism, mimicry, camouflage, development of threat patterns and displays and so on. Only a few birds, such as the nightjars, hunt nocturnal Lepidoptera and their main enemy are bats. Again, an "evolutionary race" exists which has led to numerous evolutionary adaptations of moths to escape from their main predators, such as the ability to hear ultrasonic sounds, or even to emit sounds in some cases. Lepidoptera eggs are also predated upon. Some caterpillars, such as the zebra swallowtail butterfly larvae, are cannibalistic and may eat other larvae of the same species. Lepidopteran species rely on a variety of strategies.

Some species of lepidoptera are poisonous to predators, such as the Monarch butterfly in the Americas, Atrophaneura species (roses, windmills etc.) in Asia, as well as Papilio antimachus and the birdwings, the largest butterflies in Africa and Asia respectively. 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. 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. Toxic butterflies and larvae tend to develop bright colors, striking patterns as an indicator to predators about their toxicity. This phenomenon is known as aposematism. Other caterpillars emit bad smells to ward off predators. Some caterpillars, especially members of Papilionidae, contain an osmeterium, a Y-shaped protrusible gland found in the prothoracic segment of the larvae. When threatened, the caterpillar emits unpleasant smells from the organ to ward off the predators.

Camouflage and mimicry are also important defense strategies. Some lepidopteran species blend with its surroundings, making them difficult to be spotted by predators. Caterpillars can be shades of green that matches its host plant. Others look like inedible objects, such as twigs or leaves. The larvae of some species, such as the Common Mormon (Papilio polytes) and the Western Tiger Swallowtail look like bird droppings. For example, adult Sesiidae species (also known as *clearwing moths*) have a general appearance that is sufficiently similar to a wasp or hornet to make it likely that the moths gain a reduction in predation by Batesian mimicry. Eyespots are a type of automimicry used by some butterflies and moths. In butterflies, the spots are composed of concentric rings of scales of different colors. The proposed role of the eyespots is to deflect attention to predators. Their resemblance to eyes provokes the predator's instinct to attack these wing patterns.

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* and is most commonly known by the mimicry by the limenitidine Viceroy butterfly of the inedible danaine Monarch. Later research has discovered that the Viceroy is, in fact more toxic than the Monarch and this resemblance should be considered as a case of Müllerian mimicry. 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. The adults of the various species now resemble each other so well that the species cannot be distinguished without close morphological observation and, in some cases, dissection or genetic analysis.

There is evidence moths are able to hear the range emitted by bats, which in effect causes flying moths to make evasive maneuvers because bats are a main predator of moths. Ultrasonic frequencies trigger a reflex action in the noctuid moth that cause it to drop a few inches in its flight to evade attack. Tiger moths in a defense emit clicks within the same range of the bats, which interfere with the bats, and foil their attempts to echolocate it.

Pollination

A Day-flying Hummingbird hawkmoth drinking nectar from a species of Dianthus

Most species of Lepidoptera engage in some form of entomophily (more specifically psychophily and phalaenophily for butterflies and moths respectively), or the pollination of flowers. Most adult butterflies and moths feed on the nectar inside flowers, using their proboscis to reach the nectar hidden at the base of the petals. In the process, the adult brushes against the flower's stamen, on which the flower's reproductive pollen is made and stored. The pollen is transferred on appendages on the adult, who flies to the next flower to feed and unwittingly deposits the pollen on the stigma of the next flower, where the pollen germinates and fertilizes the seeds.

Flowers pollinated by butterflies tend to be large and flamboyant, being pink or lavender in color, frequently having a landing area, and are usually scented, as butterflies are typically day-flying. Since butterflies do not digest pollen (except for Heliconid species), more nectar is offered than pollen. The flowers have simple nectar guides with the nectaries usually hidden in narrow tubes or spurs, reached by the long tongue of the butterflies. Butterflies like the *Thymelicus flavus* have been observed to engage in flower constancy, which means that they are more likely to transfer pollen to other conspecific plants. This can be beneficial for the plants being pollinated, as flower constancy prevents the loss of pollen during different flights and the pollinators from clogging stigmas with pollen of other flower species.

Among the more important moth pollinators are the hawk moths (Sphingidae). Their behavior is similar to hummingbirds: Using rapid wing beats to keep hovered in front of flowers. Most being nocturnal or crepuscular, so moth-pollinated flowers (e. g., *Silene latifolia*) tend to be white, night-opening, large and showy with tubular corollas and a strong, sweet scent produced in the evening, night or early morning. A lot of nectar is produced to fuel the high metabolic rates needed to power their flight. Other moths (e. g., Noctuids, Geometrids, Pyralids) fly slowly and settle on the flower. They do not require as much nectar as the fast-flying hawk moths, and the flowers tend to be small (though they may be aggregated in heads).

Mutualism

Tobacco hornworm caterpillar *Manduca sexta* parasitized by *Braconidae* wasp larvae.

Mutualism is a form of biological interaction where each individual involves benefits in some shape or form. An example of a mutualistic relationship would be the relationship shared by yucca moths (**Tegeculidae**) and their host, yucca flowers (**Liliaceae**). Female yucca moths enter the host flowers, collect the pollen into a ball using specialized maxillary palps, then move to the apex of the pistil where pollen is deposited on the stigma, and lay eggs into the base of the pistil where seeds will develop. The larvae develop in the fruit pod and feed on a portion of the seeds. Thus, both insect and plant benefit, forming a highly mutualistic relationship. Another form of mutualism occurs between some larvae of butterflies and certain species of ants (e. g. Lycaenidae). The larvae communicate with the ants using vibrations that are transmitted through a substrate, such as the wood of a tree or stems, as well as using chemical signals. The ants provide some degree of protection to these larvae and they in turn gather honeydew secretions.

Parasitism

There are only 41 known species of parasitoid lepidoptera (1-Pyralidae; 40-Epipyropidae). The larvae of the Greater and Lesser wax moths feed on the honeycomb inside bee nests and may become pests; they are also found in bumblebee and wasp nests, albeit to a lesser extent. In northern Europe the wax moth is regarded as the most serious parasitoid of the bumblebee, and is found only in bumblebee nests. In some areas in southern England as many as eighty percent of nests can be destroyed. Other parasitic larvae are known to prey upon cicadas and leaf hoppers.

In reverse, moths and butterflies may be subject to parasitic wasps and flies, which may lay eggs on the caterpillars which hatch and feed inside its bodyresulting in death. Although, in a form of parasitism called idiobiont, the adult paralyzes the host, so not to kill it but for it to live as long as possible, so the parasitic larvae may benefit the most. Another form of parasitism, is koinobiont, where the species live of their host while inside or endoparasitic. These parasites live inside the host caterpillar throughout all its life cycle, or may affect it later on as an adult. In other orders, koinobionts include flies, a majority of coleopteran, and many hymenopteran parasitoids. Some species may be subjected to a variety of parasites, such as the Gypsy moth (*Lymantaria dispar*) which is attacked by a series of 13 species, in 6 different taxa throughout its whole life cycle.

In response to a parsitoid egg or larvae in the caterpillar's body, the plasmatocytes, or simply the host's cells can form a multilayered capsule that eventually cause the endoparasite to asphyxiate, and die. The process is called encapsulation, and is one of the caterpillar's only means of defense against parasitoids.

Other biological interactions

A few species of Lepidoptera are secondary consumers, or predators. These species typically prey upon the eggs of other insects, aphids, scale insects, or ant larvae. Some caterpillars are cannibals, and others prey on caterpillars of other species (e. g. Hawaiian *Eupithecia*). Those of the 15 species in Eupithecia that mirror inchworms, are the only known species of butterflies and moths that are ambush predators. There are 4 known species that eat snails. For example, the Hawai'ian caterpillar, (*H. molluscivora*), uses silk traps, in a manner similar to that of spiders to capture certain species of snails (typically Tornatellides).

Larvae of some species of moths of Tineidae, Gelechioidae and Noctuidae, besides others, feed on detritus, or organic material that is not living, such as fallen leaves and fruit, fungi, and animal products and turn it into humus. Well known species include the cloth moths (*Tineola bisselliella*, *T. pellionella*, and *T. tapetzella*), which feed on detritus containing keratin, including hair, feathers, cobwebs, bird nests (particularly of Domestic Pigeons, *Columba livia domestica*) and fruits or vegetables. These species are important to ecosystems as they remove substances that would otherwise take a long time to decompose.

Evolution and systematics

History of study

Lepidoptera collection in Cherni Osam Natural Sciences Museum, Troyan, Bulgaria

Linnaeus in *Systema Naturae* (1758) recognized three divisions of the Lepidoptera: *Papilio*, *Sphinx* and *Phalaena*, with seven subgroups in *Phalaena*. These persist today as 9 of the superfamilies of Lepidoptera. Other works on classification followed including those by Michael Denis & Ignaz Schiffermüller (1775), Johan Christian Fabricius (1775) and Pierre André Latreille (1796). Jacob Hübner described many genera, and the

Lepidopteran genera were catalogued by Ferdinand Ochsenheimer and Georg Friedrich Treitschke in a series of volumes on the Lepidopteran fauna of Europe published between 1807 and 1835. Gottlieb August Wilhelm Herrich-Schäffer (several volumes, 1843–1856), and Edward Meyrick (1895) based their classifications primarily on wing venation. Sir George Francis Hampson worked on the 'Microlepidoptera' during this period and Philipp Christoph Zeller published *The Natural History of the Tineinae* also on Microlepidoptera (1855).

Among the first entomologists to study fossil insects and their evolution was Samuel Hubbard Scudder (1837–1911), who worked on butterflies. He published a study of the Florissant deposits of Colorado, including the exceptionally preserved *Prodryas persephone*. Andreas V. Martynov (1879–1938) recognized the close relationship between Lepidoptera and Trichoptera in his studies on phylogeny.

Major contributions in the 20th century included the creation of the monotrysia and ditrysia (based on female genital structure) by Borner in 1925 and 1939. Willi Hennig (1913–1976) developed the cladistic methodology and applied it to insect phylogeny. Niels P. Kristensen, E. S. Nielsen and D. R. Davis studied the relationships among monotrysian families and Kristensen worked more generally on insect phylogeny and higher Lepidoptera too. While it is often found that DNA-based phylogenies differ from those based on morphology, this has not been the case for the Lepidoptera; DNA phylogenies correspond to a large extent to morphology-based phylogenies.

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: Microlepidotera and Macrolepidoptera, Heterocera and Rhopalocera, Jugatae and Frenatae, Monotrysia and Ditrysia.

Fossil record

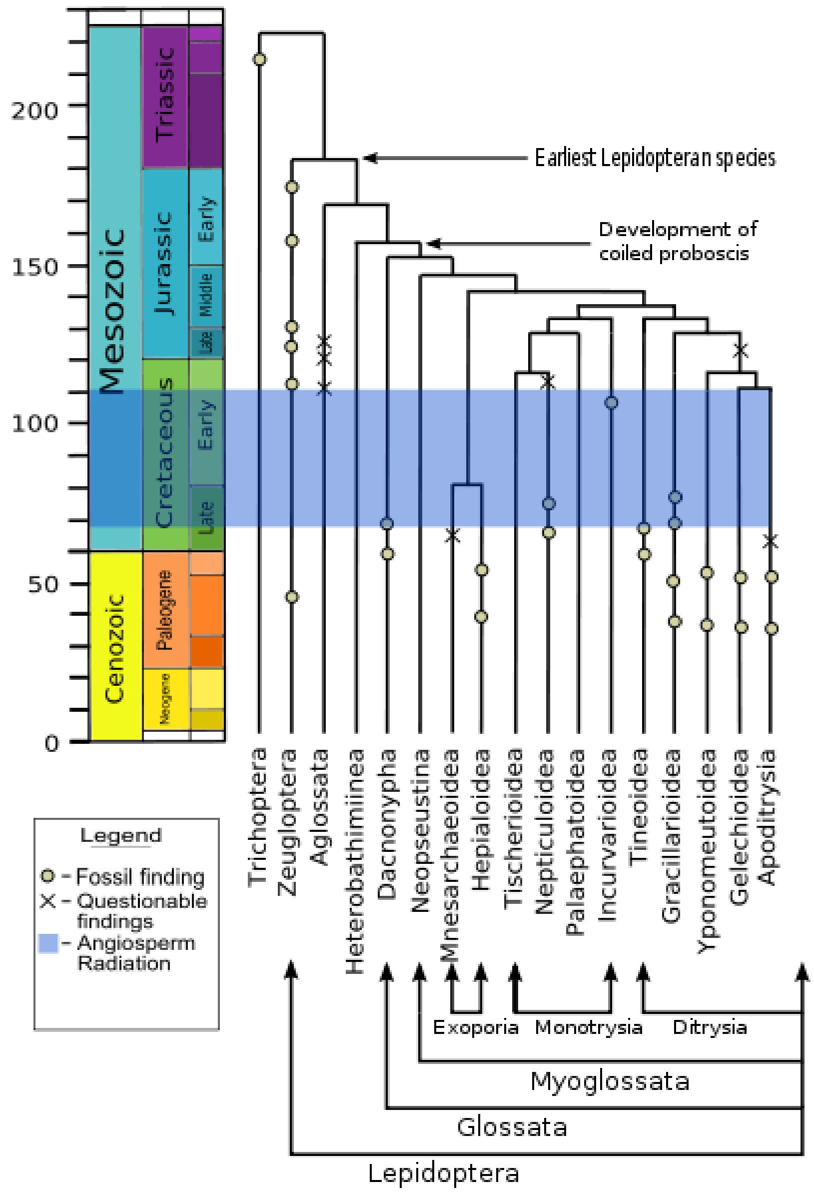
1887 engraving of *Prodryas persephone*, a fossil Lepidopteran from the Eocene.

The fossil record for Lepidoptera is lacking in comparison to other winged species, and tending not to be as common as some other insects in the habitats that are most conducive to fossilization, such as lakes and ponds, and their juvenile stage has only the head capsule as a hard part that might be preserved. The location and abundance of the most common moth species are indicative that mass migrations of moths occurred over the Palaeogene North Sea, which is why there is a serious lack of moth fossils. Yet there are fossils, some preserved in amber and some in very fine sediments. Leaf mines are also seen in fossil leaves, although the interpretation of them is tricky.

Putative fossil stem group representatives of Amphiesmenoptera (the clade comprising Trichoptera and Lepidoptera) are known from the Triassic. The earliest known fossil lepidopteran is *Archaeolepis mane* from the Jurassic, about 190 million years ago in Dorset, UK. The fossil belongs to a small primitive moth-like species, and its wings are showing scales with parallel grooves under a scanning electron microscope and a characteristic wing venation pattern shared with Trichoptera (Caddisflies). Only two more sets of Jurassic lepidopteran fossils have been found, as well as 13 sets from the Cretaceous, which all belong to primitive moth-like families. Many more fossils are found from the Tertiary, and particularly the Eocene Baltic amber. The oldest genuine butterflies of the superfamily Papilionoidea have been found in the Paleocene MoClay or

Fur Formation of Denmark. The best preserved fossil lepidopteran is the Eocene *Prodryas persephone* from the Florissant Fossil Beds.

Phylogeny



Phylogenetic hypothesis of major lepidopteran lineages superimposed on the geologic time scale. Angiosperm radiation spans 130-95 mya from the earliest angiosperms, to angiosperm domination of vegetation.

Lepidoptera and Trichoptera (caddisflies) are more closely related than any other taxa, sharing many similarities that are lacking in other insect orders; for example the females of both orders are heterogametic, meaning they have two different sex chromosomes, whereas in most species the males are heterogametic and the females have two identical sex chromosomes. The adults in both orders display a particular wing venation pattern on their forewings. The larvae of both orders have mouth structures and gland with which they make and manipulate silk. Willi Hennig grouped the two sister orders into the Amphiesmenoptera superorder. This group probably evolved in the Jurassic, having split from the now extinct order Necrotaulidae.

Micropterigidae, Agathiphagidae and Heterobathmiidae are the oldest and most basal lineages of Lepidoptera. The adults of these families do not have the curled tongue or proboscis, that are found in most members order, but instead have chewing mandibles adapted for a special diet. Micropterigidae larvae feed on leaves, fungi, or liverworts (much like the Trichoptera). Adult Micropterigidae chew the pollen or spores of ferns. In the Agathiphagidae, larvae live inside kauri pines and feed on seeds. In Heterobathmiidae the larvae feed on the leaves of *Nothofagus*, the southern beech tree. These families also have mandibles in the pupal stage, which help the pupa emerge from the seed or cocoon after metamorphosis.

The Eriocraniidae have a short coiled proboscis in the adult stage, and though they retain their pupal mandibles with which they escaped the cocoon, their mandibles are non-functional thereafter. Most of these non-ditrysian families, are primarily leaf miners in the larval stage. In addition to the proboscis, there is a change in the scales among these basal lineages, with later lineages showing more complex perforated scales.

With the evolution of the Ditrysia in the mid-Cretaceous, there was a major reproductive change. The Ditrysia, which comprise 98% of the Lepidoptera, have two separate openings for reproduction in the females (as well as a third opening for excretion), one for mating, and one for laying eggs. The two are linked internally by a seminal duct. (In more basal lineages there is one cloaca, or later, two openings and an external sperm canal.) Of the early lineages of Ditrysia, Gracillarioidea and Gelechioidea are mostly leaf miners, but more recent lineages feed externally. In the Tineoidea, most species feed on plant and animal detritus and fungi, and build shelters in the larval stage.

The Yponomeutoidea is the first group to have significant numbers of species whose larvae feed on herbaceous plants, as opposed to woody plants. They evolved about the time that flowering plants underwent an expansive adaptive radiation in the mid-Cretaceous, and the Gelechioidea that evolved at this time also have great diversity. Whether the processes involved co-evolution or sequential evolution, the diversity of the Lepidoptera and the angiosperms increased together.

In the so-called "Macrolepidoptera", which constitutes about 60% of lepidopteran species, there was a general increase in size, better flying ability (via changes in wing shape and linkage of the forewings and hindwings), reduction in the adult mandibles, and a change in the arrangement of the crochets (hooks) on the larval prolegs, perhaps to improve the grip on the host plant. Many also have tympanal organs, that allow them to hear. These organs evolved eight times, at least, because they occur on different body parts and have structural differences. The main lineages in the Macrolepidoptera are the Noctuoidea, Bombycoidea, Lasiocampidae, Mimallonoidea, Geometroidea and Rhopalocera. Bombycoidea plus Lasiocampidae plus Mimallonoidea may be a monophyletic group. The Rhopalocera, comprising the Papilionoidea (butterflies), Hesperioidea (skippers), and the Hedyloidea (moth-butterflies), are the most recently evolved. There is quite a good fossil record for this group, with the oldest skipper dating from 56 million years ago.

Taxonomy

Taxonomy is the classification of species in selected taxa, the process of naming being called nomenclature. There are over 120 families in lepidoptera, in 45 to 48 superfamilies. Lepidoptera have always been, historically, classified in five suborders, one of which is of primitive moths that never lost the morphological features of its ancestors. The rest of the moths and butterflies make up ninety-eight percent of the other taxa, making Ditrysia. More recently, new findings of new taxa and larvae and pupa have aided in detailing the relationships of primitive taxa, phylogenetic analysis showing the primitive lineages to be paraphyletic compared to the rest of Lepidoptera lineages. Recently lepidopterists have abandoned clades like suborders, and those between orders and superfamilies.

- Zeugloptera is a clade with Micropterigoidea being its only family. Species of Micropterigoidea are practically living fossils, being one of the most primitive lepidopteran species, still retaining mandible mouthparts, unlike other clades of butterflies and moths. About 120 species are known worldwide, with more than half the species in the genus *Micropteryx* in the Paleartic region. There are only 2 known in North America (*Epimartyria*), with many more being found Asia and the southwest Pacific, particularly New Zealand with about 50 species.

- Glossata contains a a majority of the species, with the most obvious difference is non-functioning mandibles, and elongated maxillary galeae or the proboscis. The basal clades still retaining some of the ancestral features of the wings such as similarly shaped fore- and hindwings with relatively complete venation. Glossata also contains the division Ditrysia, which contains 98% of all described species in Lepidoptera.

- Aglossata is is the second most primitive lineage of lepidoptera; being first described in 1952 by Lionel Jack Dumbleton. **Agathiphagidae** and **Heterobathmiina** are the only families in Aglossata. Agathiphagidae only contains about 2 species in its genus Agathiphaga.. *Agathiphaga queenslandensis* and *Agathiphaga vitiensis*, being found along the north-eastern coast of Queensland, Australia, and in Fiji to Vanuatu and the Solomon Islands, respectively.

- Heterobathmiina was first described by Kristensen and Nielsen in 1979. There are about 10 species, which are day-flying, metallic moths, confined to southern South America, the adults eat the pollen of *Nothofagus* or Southern Beech and the larvae mine the leaves.

Relationship to people

In culture

Death's-head Hawkmoth (*Acherontia lachesis*), an old bleached specimen still showing the classical skull-shaped head

Artistic depictions of butterflies have been used in many cultures including as early as 3500 years ago, in Egyptian hieroglyphs. Today, butterflies are widely used in various objects of art and jewelry: mounted in frames, embedded in resin, displayed in bottles, laminated in paper, and in some mixed media artworks and furnishings. Butterflies have also inspired the "butterfly fairy" as an art and fictional character, including in the *Barbie Mariposa* film.

In many cultures the soul of a dead person is associated with the butterfly. As in Ancient Greece, where the word for butterfly ψυχή (psyche) also means *soul* and *breath*. In Latin, as in Ancient Greece, the word for "butterfly" papillio was associated with the soul of the dead. The skull-like marking on the thorax of the Death's-head Hawkmoth has helped these moths, particularly *A. atropos*, earn a negative reputation, such as associations with the supernatural and evil. The moth has been prominently featured in art and movies such as *Un Chien Andalou* (by Buñuel and Dalí) and *The Silence of the Lambs*, and in the artwork of the Japanese metal band Sigh's album *Hail Horror Hail*. According to *Kwaidan: Stories and Studies of Strange Things*, by Lafcadio Hearn, a butterfly was seen in Japan as the personification of a person's soul; whether they be living, dying, or already dead. One Japanese superstition says that if a butterfly enters your guestroom and perches behind the bamboo screen, the person whom you most love is coming to see you.

However, large numbers of butterflies are viewed as bad omens. When Taira no Masakado was secretly preparing for his famous revolt, there appeared in Kyoto so vast a swarm of butterflies that the people were frightened — thinking the apparition to be a portent of coming evil.

In the ancient Mesoamerican city of Teotihuacan, the brilliantly colored image of the butterfly was carved into many temples, buildings, jewelry, and emblazoned on incense burners in particular. The butterfly was sometimes depicted with the maw of a jaguar and some species were considered to be the reincarnations of the souls of dead warriors. The close association of butterflies to fire and warfare persisted through to the Aztec civilization and evidence of similar jaguar-butterfly images has been found among the Zapotec, and Maya civilizations.

Caterpillar hatchling of the Grey Dagger (Acronicta psi) eating leaves from a tree.

As pests

The larvae of many Lepidopteran species are major pests in agriculture. Some of the major pests include Tortricidae, Noctuidae, and Pyralidae. The larvae of the Noctuidae genus *Spodoptera* (armyworms) and *Helicoverpa* (corn earworm) can cause extensive damage to certain crops. *Helicoverpa zea* larvae (cotton bollworms or tomato fruitworms) are polyphagous, meaning they eat a variety of crops, including tomatoes and cotton.

Butterflies and moths are one of the largest taxa to solely feed and be dependent on living plants, in terms of the number of species, and they are in many ecosystems make up the largest biomass to do so. In many species, the female may produce anywhere from 200 to 600 eggs, while in some others it may go as high as 30,000 eggs in one day. This creates many problems for agriculture, where many caterpillars can mow down acres of vegetation. Some reports estimate that there have been over 80,000 caterpillars of several different taxa feeding on a single oak tree. In some cases, phytophagous larvae can lead to the destruction of entire trees in relatively short periods of time.

Ecological ways of removing pest lepidoptera species are becoming more economically viable, as research has shown ways like introducing parasitic wasp and flies. For example *Sarcophaga aldrichi*, which the larvae feed upon the larvae of the Forest Tent Caterpillar Moth. Pesticides can affect other species other than the species they are targeted to eliminate, damaging the natural ecosystem. Another good biological pest control method is the use of pheromone traps. A pheromone trap is a type of insect trap that uses pheromones to lure insects. Sex pheromones and aggregating pheromones are the most common types used. A pheromone-impregnated lure is encased in a conventional trap such as a Delta trap, water-pan trap, or funnel trap.

Species of moths that are detrivores would naturally eat detritus containing keratin, such as hairs or feathers. Well known species are cloth moths (*T. bisselliella*, *T. pellionella*, and *T. tapetzella*), feeding on foodstuffs that people find economically important, such cotton, linen, silk and wool fabrics as well as furs; furthermore they have been found on shed feathers and hair, bran, semolina and flour (possibly preferring wheat flour), biscuits, casein, and insect specimens in museums.

As beneficial

Even though most butterflies and moths affect the economy negatively, some species are a valuable economic resource. The most prominent example is that of the Domesticated silkworm moth (*Bombyx mori*), the larvae of which make their cocoons out of silk which can be spun into cloth. Silk is and has been an important economic resource throughout history. The species *Bombyx mori* has been domesticated to the point where it is completely dependent on mankind for survival. A number of wild moths such as *Bombyx mandarina*, and *Antheraea* species, besides others, provide commercially important silks.

The preference of the larvae of most Lepidopteran species to feed on a single species or limited range of plants is used as a mechanism for biological control of weeds in place of herbicides. The pyralid cactus moth was introduced from Argentina to Australia, where it successfully suppressed millions of acres of Prickly pear cactus. Another species of the Pyralidae, called the alligator weed stem borer (*Arcola malloi*), was used to control the aquatic plant known as alligator weed (*Alternanthera philoxeroides*) in conjunction with the alligator weed flea beetle; in this case, the two insects work in synergy and the weed rarely recovers.

Breeding butterflies and moths, or butterfly gardening, has become an ecologically viable process of introducing species into the ecosystem for the better of benefiting it. Butterfly ranching in Papua New Guinea permits nationals of that country to 'farm' economically valuable insect species for the collectors market in an ecologically sustainable manner.

As food

Beondegi, silkworm pupae steamed or boiled and seasoned for taste, for sale by a street vendor in South Korea

Lepidoptera feature prominently in entomophagy as food items on almost every continent. While in most cases, adults, larvae or pupae are eaten as staples by indigenous people, beondegi or silkworm pupae are eaten as a snack in Korean cuisine while Maguey worm is considered a delicacy in Mexico. In the Carnia region of Italy, children catch and eat *Zygaena* moths in early summer. The ingluvies, despite having a very low cyanogenic content, serves as a convenient, supplementary source of sugar to the children who can include this resource as a seasonal delicacy at minimum risk.

Health

Some larvae of both moths and butterflies have a form of hair that has been known to be a cause of human health problems. Caterpillar hairs sometimes have venomous toxins in them and species from approximately 12 families of moths or butterflies worldwide can inflict serious human injuries (Urticarial dermatitis and atopic asthma to osteochondritis, consumption coagulopathy, renal failure, and intracerebral hemorrhage). Skin rashes are the most common, but there have been fatalities. *Lonomia* is a frequent cause of economization in humans in Brazil, with 354 cases reported between 1989 and 2005. Lethality ranging up to 20% with death caused most often by intracranial hemorrhage.

These hairs have also been known to cause kerato-conjunctivitis. The sharp barbs on the end of caterpillar hairs can get lodged in soft tissues and mucus 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. This becomes a particular problem in an indoor setting. The hairs 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.