Section 1

INTRODUCTION TO THE ARTHROPODS

Chapter 1

INSECTS AND THEIR RELATIVES

Insects are invertebrate animals within the class Insecta and the phylum Arthropoda of the kingdom Animalia. Phylum Arthropoda consist of more than insects, of course, but to most people all arthropods are 'bugs,' those small but annoying and damaging organisms that lack fur and feathers, and therefore seem rather alien. Arthropods have jointed legs and generally are hard to the touch because they wear their skeleton externally. Think about shrimp, crabs, and lobsters if you are having trouble envisioning this, as they are arthropods, too. However, most people don't think of shrimp, crabs, and lobsters as bugs. To most people bugs are insects, ticks, spiders, centipedes, millipedes and similar terrestrial organisms. Here we will learn about the true insects and their near relatives, and you will learn what distinguishes bugs from similar organisms.

NAMING OF TAXA

But first we need to discuss the naming of organisms. The purpose of naming always has been largely practical. We need to have a way of identifying and describing organisms accurately but concisely. Secondly, we want to describe the relationship of organisms to other organisms, usually by giving their biological position from an evolutionary perspective. Initially, organisms typically were grouped according to their appearance, but as we learned more about them and their interrelationships, their positions relative to others often changed. For example, organisms that dwell within ant nests often look quite like ants. Apparently, if you look and smell like an ant, you can gain easy access to ant nests, and the food riches contained there. However, if they are only ant mimics but actually beetles, we want to call them beetles, not ants. So in many cases physical appearance is not adequate, and we need to know about relatedness.

Do you find scientific terminology and the classification of organisms somewhat overwhelming? If you do, you may find it comforting to know that this is normal. All these hard-to-pronounce names are difficult for everyone. Nevertheless, we need to have a way to organize the diversity of life into manageable groups of related organisms or **taxa** (taxon is the singular form). And insects are truly diverse! Figure 1.1 shows the number of species of common groups of animals. There are far more insects species than other animals. I have used a conservative estimate for the number of species of insects, about one million. In all likelihood, the actual number is probably 3–4 million, as most tropical insect species have yet to be named. As you can see, the number of many other animal species such as reptiles, birds, fish, and mammals is almost insignificant compared to insects.

The insects and their relatives are arranged into taxa that organize similar organisms into categories. The principal taxa, in descending (most inclusive to least) order, are:

Kingdom
- Phylum
  - Class
    - Subclass
      - Infraclass
        - Series

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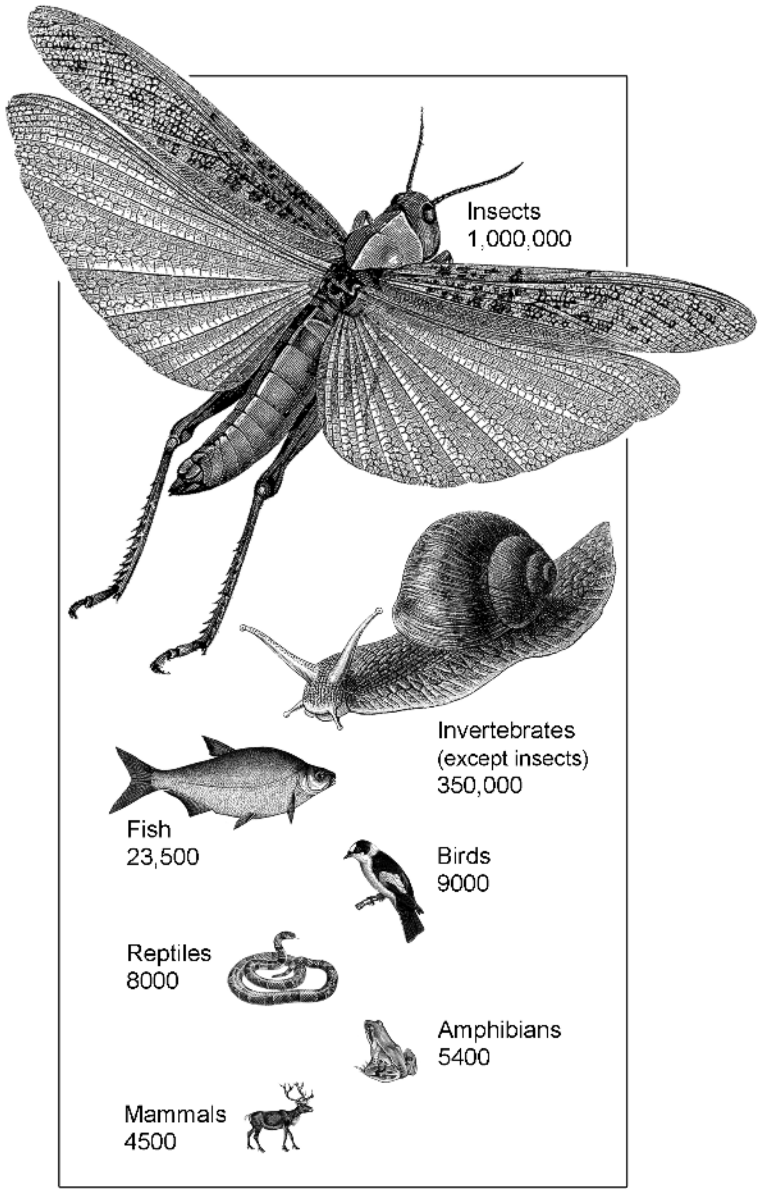


Fig. 1.1. The number of species in some important animal taxa. Note that the size of each image is proportional to the number of species in each group.

Superorder
Order
Suborder
Infraorder
Family
Subfamily
Tribe
Genus
Species

Not all of these categories are always used; the most commonly used taxa are class, order, family, genus and species.

Every organism has a **scientific name**, consisting of a genus and species designation. This two-part name follows a system called **binomial nomenclature**. The rules of binomial nomenclature are standardized to reduce potential confusion, and to confer information about the relatedness of the organism to other organisms. Additional information may be included along with the scientific name. So, you might see something like '*Schistocerca americana* (Drury) (Orthoptera: Acrididae).' The italics signify the genus (which is capitalized) and species (not capitalized). The name following the genus and species is the person who originally described the species; this person is sometimes called the 'author' of the name. If the scientific name (genus and species) is unchanged since the original description, the describer's name lacks parentheses. If the describer's name has been modified (usually this indicates transfer to a different genus) then this change is reflected by the parentheses surrounding the author's name. Therefore, in our example, '(Drury)' signifies that the scientific name has been changed since the original description. In fact, it was originally described as *Libellula americana* by D. Drury in 1773. After studying the genus, however, in 1899 S.H. Scudder placed this species in the genus *Schistocerca*, where it now remains. The names within the next set of parentheses are the order and family designations: order Orthoptera, and family Acrididae. This latter information is not always given, but it is beneficial to do so because it tells you about the relationship of this insect relative to other insects. In this case, *S. americana* belongs to a family that contains many 'short-horned grasshoppers' in an order that contains grasshoppers, crickets and katydids. Sometimes a third italicized name is included: the subspecies.

The **species** is the most fundamental taxon, but for something so fundamental it is surprisingly difficult to define. Most biologists subscribe to the 'biological species concept,' which states that a species is an interbreeding group of organisms that is reproductively isolated from other such groups. Species most often develop through geographic isolation (**allopatric speciation**) from other parts of their interbreeding population. After sufficient isolation and incremental change they can no longer interbreed so they become a new species. Often accompanying this isolation are changes in appearance or behavior, which helps us to identify that they are different species. Sometimes the changes are so subtle that we have trouble identifying groups as being different. Conversely, sometimes we are fooled by the different appearance of organisms into thinking that they are different species when they are only environmentally induced differential expressions of the same species (polyphenisms, see Chapter 2). Geography is not the only means of isolation leading to formation of new species, of course. Another important means occurs when species adopt different host plants, leading to isolation based on feeding behavior, as this can result in host specific associative mating. Speciation that occurs without geographic isolation occurring is called **sympatric speciation**. Sympatric speciation also commonly results when insects become separated in time (developing at different times of the year) or from the use of different chemical attractants (pheromones).

Species that have populations differing in appearance are sometimes divided into subspecies. A **subspecies** is usually little more than a color variant, and can interbreed successfully with other subspecies in the same species. Subspecies may be indicative of speciation in progress, however. Butterflies commonly display regional color variations, so subspecies designations are especially frequent in this taxon.

Other categories also exist, and are used when it is necessary or convenient. For example, the class Insecta, along with the class Entognatha (the collembolans, proturans, diplurans) are often placed together into the superclass Hexapoda. In fact, the entognathans are sometimes considered to be insects. The subclass Pterygota is sometimes divided into two divisions, consisting of the hemimetabolous orders and the holometabolous orders. Also, related families are often grouped into superfamilies. Possibly the only level that can be assessed objectively is the species, and even that can be argued. Species are grouped into genera, genera into families, and so forth, but taxonomists differ in the importance of characters used to cluster the taxa, so different arrangements are possible. The names of most orders end in -ptera; of families in -idae; of subfamilies in -inae, and of tribes in -ini.

Remember, all this naming protocol is simply to create order and to show relatedness. Although it may seem confusing, it is really intended to inform you. Admittedly, it takes a while to catch on.

ARTHOPODA

The Arthopoda are a large (about two to three times all other animal species combined) and diverse phylum. All arthropods have some things in common. Among the characteristics that arthropods share, but which help to separate them from other invertebrates, are:

• bilateral symmetry (the left and right halves are mirror images);
• the integument (external covering) contains a great deal of chitin, a structural polysaccharide, and functions as an external skeleton;
• segmented bodies;
• jointed appendages that assist with walking and feeding; the name 'Arthropoda' is derived from Greek words meaning 'jointed feet';
• a dorsal brain but a ventral nerve cord.

They also have some differences that allow us to separate them into groups (taxa). The principal arthropod taxa of relevance to insects are:

Phylum Arthropoda
- Subphylum Trilobita – trilobites (these are extinct)
- Subphylum Chelicerata
  - Class Merostomata – horseshoe crabs
  - Class Arachnida – arachnids (scorpions, spiders, ticks, mites, etc.)
  - Class Pycnogonida – sea spiders
- Subphylum Crustacea – crustaceans (amphipods, isopods, shrimp, crabs, etc.)
- Subphylum Atelocerata
  - Class Diplopoda – millipedes
  - Class Chilopoda – centipedes
  - Class Pauropoda – pauropods
  - Class Symphyla – symphylans
  - Class Entognatha – collembolans, proturans, diplurans
  - Class Insecta – insects

Trilobites (subphylum Trilobita) have been extinct for 250 million years, but they once were very common and over 17,000 species are known. Probably because they had a tough integument (body covering), they preserved quite well, and are second only to the dinosaurs as well-known fossils.

The chelicerate arthropods (subphylum Chelicerata) have two principal body segments, the **cephalothorax** (fused head and thorax) and the **abdomen**. They have feeding structures called **chelicerae**, which are often fang-like and good for grasping and piercing, but not for chewing. They also possess **pedipalps**, additional segmented appendages that assist in feeding and which may possess claws. The chelicerate arthropods usually have four pairs of legs, but lack **antennae** (elongate sensory appendages located on the head). The pedipalps, however, often perform sensory functions.

The crustaceans also have a cephalothorax but possess feeding structures called **mandibles**. Mandibles are jaw-like structures that are good for grasping, holding, and masticating food. The number of legs present is variable, but they have two pairs of antennae.

The classes in the subphylum Atelocerata also have mandibles, and variable numbers of legs, but possess only one pair of antennae. The more important arthropods are briefly discussed below prior to a more detailed discussion of insects.

ARACHNIDA

This class is the most important and familiar of the chelicerate classes, containing many familiar forms (Fig. 1.2). They tend to be carnivorous, and often the digestion occurs largely outside the body (predigestion) because enzymes are secreted into the prey, with the resulting fluid taken up. Four pairs of legs are normal, although the occurrence of enlarged pedipalps in some may give the appearance of five pairs of legs. The most important arachnids are:

Order Scorpiones, the scorpions
Order Pseudoscorpiones, the false scorpions
Order Solifugae, the sun spiders or wind scorpions
Order Uropygi, the whip scorpions
Order Aranaea, the spiders
Order Opiliones, the harvestmen or daddy longlegs
Order Acarina, the mites and ticks

The **scorpions** (order Scorpiones) seem to be the oldest terrestrial arthropods, and may have been the first to conquer land. They are nocturnal (night-active) and secretive, hiding by day in burrows and beneath stones and logs. They are found widely in both arid and

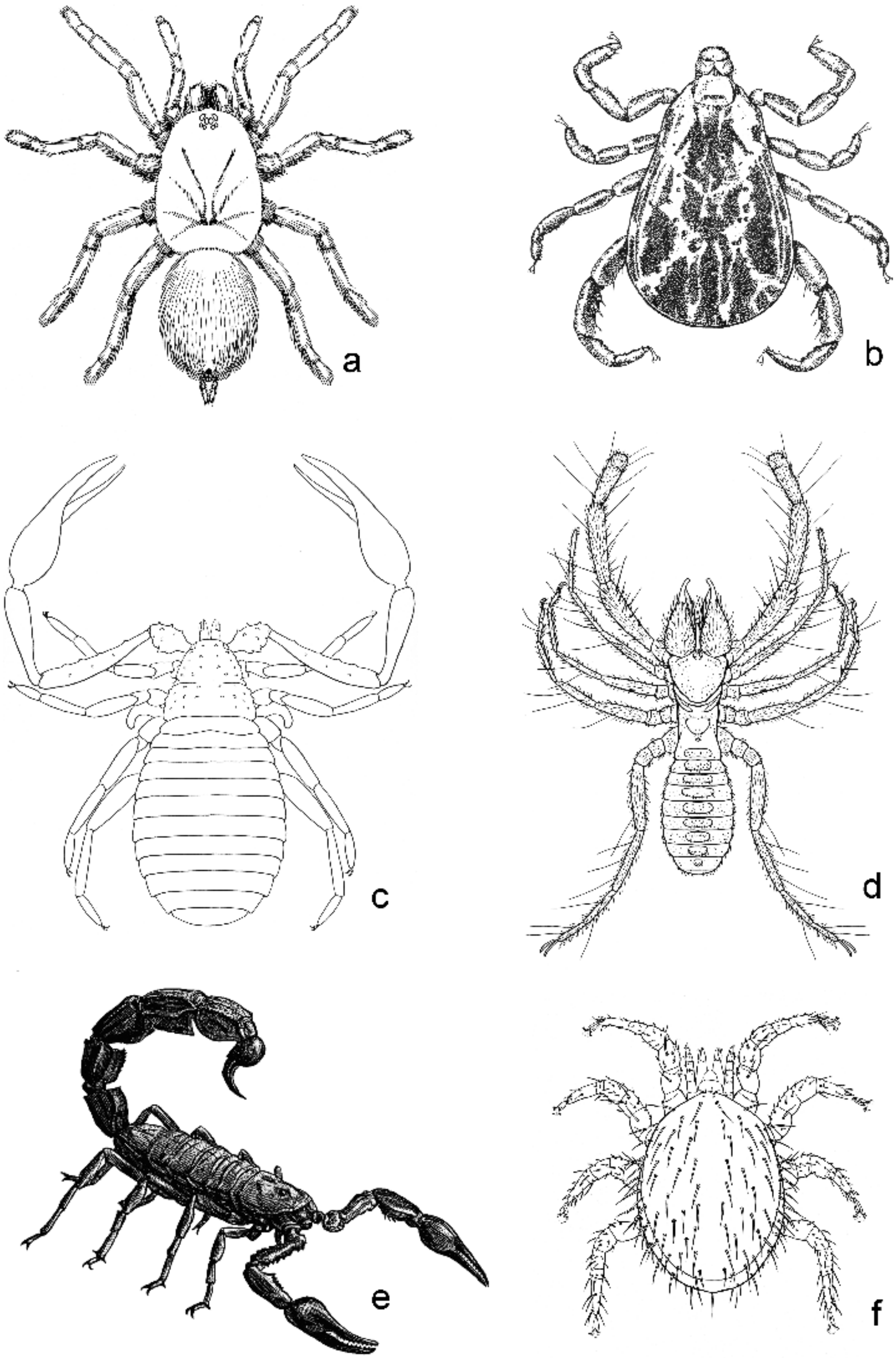


Fig. 1.2. Representative arachnids (phylum Arthropoda, class Arachnida): (a) a spider (order Aranaea); (b) a tick (order Acarina); (c) a pseudoscorpion (order Pseudoscorpiones); (d) a sun spider (order Solifugae); (e) a scorpion (order Scorpiones); (f) a mite (order Acarina).

moist environment. Scorpions are well known for their long abdomen that terminates in a sting apparatus. The venom of scorpions is sufficient to kill many invertebrates, but not usually dangerous to humans, producing pain equivalent to a yellow jacket. A few species, however, are quite dangerous, and can kill a human. In the southwestern USA, species of *Centruroides* fall into this 'quite dangerous' category. The front appendages, which appear to be legs, are really enlarged mouth structures (pedipalps) bearing claws for capturing prey. They feed mostly on arthropods, but occasionally on small vertebrates. Scorpions can be up to 18 cm in length. There are about 2000 species of scorpions.

The **pseudoscorpions** (order Pseudoscorpiones) are smaller than scorpions, barely exceeding 8 mm in length. About 3400 species are known. Superficially they resemble scorpions because they bear enlarged pincer-like pedipalps, but their abdomen is not elongate and they lack a sting apparatus. They are commonly found in leaf debris, but due to their small size often are overlooked. They feed on small arthropods.

The **solifugids** (order Solifugae) live in warm, arid environments, and shelter belowground. They are large, up to 7 cm long. They are best known for their large, conspicuous chelicerae. These are in the form of two pairs of pincers that articulate vertically. Like scorpions, they will feed on both arthropods and vertebrates. Unlike scorpions, they are principally diurnal (day-active). About 1000 species have been described.

The **whip scorpions** (order Uropygi) resemble scorpions except that the abdomen terminates in a long flagellum (the 'whip'). Some are known as 'vinegaroons' because they spray acetic acid as a defensive measure. They vary from small to large in size. Only about 100 species are known.

The **spiders** (order Araneae) are among the most widely known arthopods. This order is quite species-rich, with over 40,000 named species. They range in size from 0.5 mm to perhaps 9 cm. They feed mostly on insects, but sometimes capture small vertebrates, including birds. Many, but not all, depend on production of silk to ensnare prey. Many hunting spiders such as wolf, crab and jumping spiders stalk their prey, and while they may rest within a web or even tie their captured prey with silk, they do not rely on a web for prey capture. The hunting spiders tend to be heavy bodied. In contrast, the web-producing spiders usually have long, slender legs. Spider webs vary in complexity, but most contain both dry and adhesive strands. The chelicerae of all spiders possess poison glands. The venom of most spiders is not toxic to humans, but a few are quite poisonous. The eyes of spiders are more developed than most arachnids, though they are unable to form an image due to insufficient number of receptors. They usually occur in two rows of four eyes. Courtship of spiders is often a complex process. Eggs are often deposited within an egg sac, and when the young **spiderlings** (young spiders) hatch they disperse. A common method of dispersal involves ballooning. When **ballooning**, the spiderling climbs to an elevated location and releases a strand of silk. If the breezes are sufficiently strong to tug on the strand of silk, the spider releases its hold on the substrate and is carried in the wind.

The **harvestmen** or daddy longlegs (order Opiliones) are a small (about 6400 species) but well-known group of long-legged, spider-like arachnids. They vary in size but some are quite large. However, the size is deceptive; the body is always small and the legs are always long. More than most arachnids, harvestmen are omnivorous. Although usually feeding on insects, they also eat dead animal matter and plant material. Thus, unlike spiders, which suck in predigested prey, harvestmen can ingest particulate matter.

The **mites** and **ticks** (order Acarina) are unquestionably the most important arachnids. They occur in all habitats, and often are very numerous. There are about 50,000 described species, but most mites have yet to be described. As might be expected with such a large group, they are quite varied in appearance. Mites feed on economically important plants and animals, and although ticks do not attack plants, ticks are very important ectoparasites of vertebrates. Ticks are second only mosquitoes in importance as vectors of animal disease. Mites are usually only 1 mm in length, whereas ticks can reach up to 3 cm in length. Perhaps the most distinctive feature of ticks and mites is the lack of body segmentation. Abdominal segmentation is not visible, and even the two major body regions are joined imperceptibly. Ticks and mites are discussed more fully in Chapter 10.

CRUSTACEA

The **crustaceans** (subphylum Crustacea) are a diverse group numbering about 52,000 described species. The Crustacea are the only large group of arthropods that

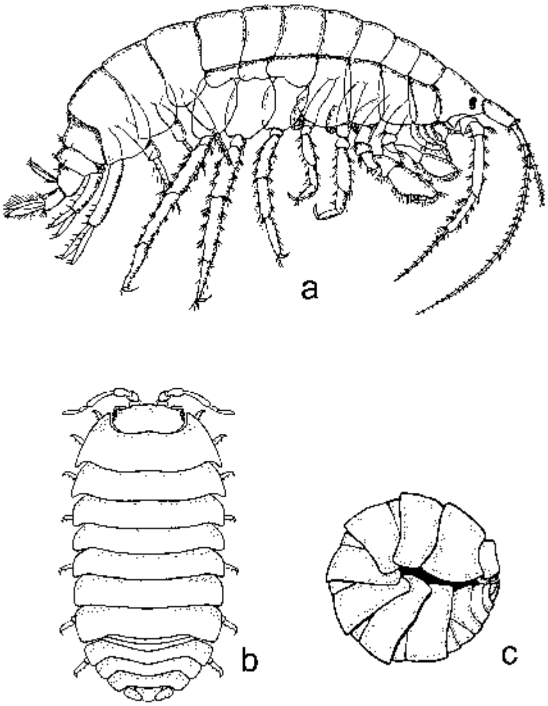


Fig. 1.3. Representative crustaceans (phylum Arthropoda, subphylum Crustacea): (a) a common aquatic crustacean, the amphipod *Gammarus* sp. (class Malacostraca: order Amphipoda); (b, c) common terrestrial crustaceans, woodlice or pillbugs, *Armadillidium* sp. (class Malacostraca: order Isopoda).

are primarily aquatic. Most occupy the marine environment but they are also numerous in fresh-water aquatic habitats. Some are terrestrial, and woodlice (class Malacostraca, order Isopoda), which are sometimes called pillbugs and sowbugs, are examples of common terrestrial crustaceans (Fig. 1.3). Woodlice can be quite important in decomposition of organic materials, and often are quite abundant on the forest floor. However, whereas crustaceans are very abundant in the marine environment, insects dominate terrestrial environments. Small crustaceans can obtain adequate oxygen through their body covering. Larger crustaceans, however, use gills associated with their legs to move water and take up oxygen. Crustaceans may have two body regions (cephalothorax and abdomen), or three (head, thorax, abdomen). Some of the important groups of crustaceans are:

Class Branchiopoda, the tadpole shrimps, water fleas, others
Class Ostracoda, the seed shrimps
Class Copepoda, the copepods
Class Cirripedia, the barnacles
Class Malacostraca, the mantis shrimps, amphipods, isopods, krill, crabs, lobsters, shrimps

Crustaceans are quite variable in appearance, but have two pairs of antennae. The thorax is often covered by a dorsal carapace that may extend over the sides of the animal. The cuticle of the larger crustaceans is calcified, a characteristic lacking in most other arthropods. Some crustaceans swim, but most simply crawl. The adults of most have a pair of compound eyes. Crustacea are significant mostly as a food resource for animals dwelling in aquatic and marine habitats. Some, such as lobsters, crabs, shrimp, and crayfish are economically important food for humans. Many of the terrestrial forms may help in decomposition of detritus, however, and a few consume plants.

DIPLOPODA

Millipedes (class Diplopoda) have numerous legs, but not the thousand suggested by their common name. The occurrence of numerous legs is a characteristic of this group, but none have more than 375 pairs, and most have considerably fewer. In distinguishing this group from the similar-appearing centipedes, the presence of two pairs of legs per body segment is the key character used to identify millipedes (Fig. 1.4). There are about 10,000 species known around the world.

Millipedes are quite diverse morphologically, though they all consist of a long chain of rather uniform body segments, and lack wings. Some are rather short, and may be covered with feather- or scale-like adornment. Others look greatly like woodlice (Isopoda, the pillbugs), and even roll into a ball in the manner of pillbugs. Most, however, are elongate and thin in general body form. There are three basic body regions: the head, which bears a pair of moderately long antennae; the body, consisting of numerous leg-bearing segments, and which normally are rather cylindrical but sometimes bears prominent lateral projections; and the telson, or posterior body segments bearing the anus. The integument is very hard.

The life cycle of millipedes is often long. Many live for a year, but some persist for 2 to 4 years before attaining maturity. In a *Julus* sp. studied in a temperate

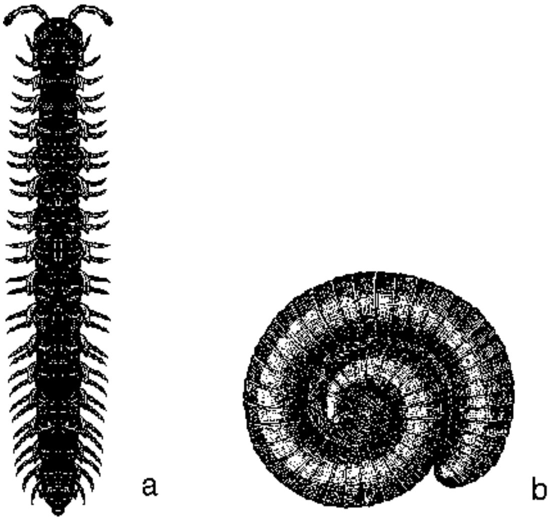


Fig. 1.4. Representative millipedes (phylum Arthropoda, class Diplopoda): (a) normal posture; and (b) coiled defensive posture of *Oxidus* sp.

environment, oviposition took place in April, with instar 6 to 7 attained by winter and instars 8 to 9 by the second winter. They overwintered as instars 9–11, then mated and oviposited the following spring, their third year of life, before they perished.

Adult millipedes vary considerably in size, often measuring from 10–30 mm in length, but in some species exceeding 100 mm. Their color ranges from whitish to brown and black. The sexes are separate. The external genitalia of adult millipedes are located between the second and third pairs of legs. Some adult millipedes have the ability to molt from a sexually active adult to an intermediate stage that is not functional sexually. Parthenogenesis (production of eggs or young without fertilization by males) occurs in some species and some populations, but this is not usual. Millipedes lack a waxy cuticle and are susceptible to desiccation. They have glands, with openings usually located laterally, which secrete chemicals that are toxic and may immobilize predatory arthropods such as spiders and ants.

Millipedes are common animals, and are found wherever there is adequate food. They are detritivores, normally feeding on dead plant material in the form of leaf litter. However, they occasionally graze on roots and shoots of seedlings, algae, and dead arthropods and molluscs. They move rather slowly. They are selective in their consumption of leaf litter, preferring some leaves over others. They also tend to wait until leaves have aged, and are partially degraded by bacteria and fungi. Thus, they function principally as decomposers, hastening the break-up of leaf material into smaller pieces, and incorporating the organic matter into the soil. Whether they derive most of their nutritional requirements from the organic substrate or the microorganisms developing on the substrate is uncertain. Millipedes also tend to consume their own feces, and many species fare poorly if deprived of this food source.

Millipedes sometimes are viewed as a severe nuisance as a result of exceptional abundance in an inappropriate location such as in yards, homes, or commercial or food processing facilities. Millipedes can exist in tremendous quantities in the soil and become a problem only when they come to the surface and disperse as a group. This often occurs following abnormally large rainfall events, though hot and dry conditions also are sometimes suspected to be a stimulus for dispersal. Several species of millipedes are reported to be injurious to plants. Probably the most important is garden millipede, *Oxidus gracilis* Koch (Diplopoda: Paradoxosomatidae). It apparently was accidentally introduced to most temperate areas of the world from the tropics, probably via transport of specimen plants. In cool areas it is principally a greenhouse pest.

Millipedes produce various foul-smelling fluids (sometimes including hydrogen cyanide) from openings along the sides of their body. Despite the formidable chemical defenses of millipedes, several natural enemies are known. Small vertebrates such as shrews, frogs, and lizards eat millipedes. Invertebrate predators such as scorpions (Arachnida), ground beetles (Coleoptera: Carabidae), and rove beetles (Coleoptera: Staphylinidae) also consume millipedes, though ants are usually deterred. Some diseases and parasitic flies also are known to affect millipedes.

The toxic secretions of millipedes do not go unnoticed by wildlife such as the New-World capuchin monkeys, *Cebus* spp. The monkeys anoint themselves with *Orthoporus dorsovittatus* millipede secretions (benzoquinones) by rubbing crushed millipedes over their body. This repels mosquitoes, which are a serious nuisance, but perhaps more importantly this repellent is thought to reduce the probability that monkeys will be infested by bot flies. Some bot flies (Diptera: Oestridae) capture mosquitoes and lay an egg on the mosquito. When the mosquito feeds, the bot fly egg hatches, and the young bot fly enters the wound created by the mosquito's feeding. Thus, reducing the feeding by mosquitoes also reduces the infestation by bot flies. Millipedes, therefore, are natural sources of insect repellency that are used by monkeys to their advantage. Often monkeys will pass a crushed millipede to others in the group, creating a significant social interaction. Malagasy lemurs and some birds also take advantage of millipedes by self-anointing with insect-repellent or insecticidal secretions.

CHILOPODA

Centipedes (class Chilopoda) possess but one pair of legs per segment (Fig. 1.5), a feature that allows them to be easily distinguished from the superficially similar millipedes (Diplopoda). Like many other arthropods, but unlike entognathans and insects, the centipedes bear a head and a long trunk with many leg-bearing segments. The head bears a pair of antennae, and sometimes ocelli, but not compound eyes. The mouthparts are ventral, and positioned to move forward.

Centipedes usually are 1 to 10 cm in length, but may be larger in the tropics, where they can attain a length of up to 26 cm. Covering the mouthparts of centipedes is a pair of poison claws. They are derived from the first pair of trunk appendages, but are involved in feeding. A poison gland is found within the base of the claw. Centipedes are well known for their poison claws, but they have other defenses as well. In some, the posterior-most legs may be used for pinching, and repugnatorial glands on the last four legs are common. As with millipedes, defensive secretions may include hydrocyanic acid. About 3000 species are known.

Life histories of centipedes are poorly known, but longevity is often 3 to 6 years, and it commonly takes more than a year to attain maturity. Some centipedes produce a cavity in soil or decayed wood in which to brood their egg clutch. The female guards the eggs until the young hatch. In the remaining taxa, the eggs are deposited singly in the soil.

Centipedes are predaceous. As might be expected of predators, they move very quickly. Most feed on arthropods, snails, earthworms and nematodes, but even toads and snakes are consumed by some. The antennae and legs are used to detect prey. The poison claws are used to stun or kill the prey. Though painful, the bite of centipedes is normally not lethal to humans, resembling the pain associated with a wasp sting.

Centipedes require a humid environment. Their integument is not waxy, and their spiracles do not close. Hence, they are found belowground, in sheltered environments, or are active aboveground principally at night. Some centipedes have adapted to a marine existence, living among algae, stones and shells in the intertidal zone. Apparently, they can retain sufficient air during high tides, or capture a sufficiently large bubble of air to allow submersion.

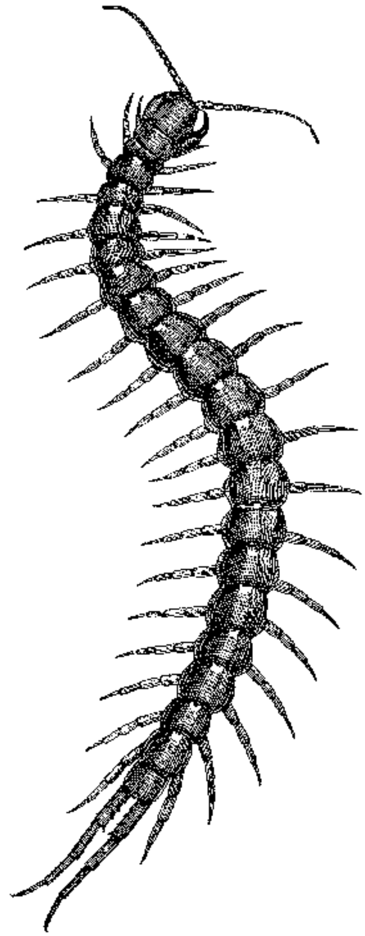


Fig. 1.5. A representative centipede (phylum Arthropoda, class Chilopoda): *Scolopendra* sp.

ENTOGNATHA

The entognathans (class Entognatha) consist of three orders of six-legged arthropods that are closely related to insects: Collembola, Protura, and Diplura. Indeed, sometimes they are included with the insects in the class Insecta. However, it is better to consider the enognathans and insects part of the same superclass, the **Hexapoda**, thereby recognizing that while they are closely related, they are not truly insects. The Entognatha have their mouthparts sunk into the head (**entognathous**), unlike the insects, which have their mouthparts extruded (**ectognathous**). Also, unlike most insects, they lack wings, and the immature forms greatly resemble the adult forms.

Springtails and proturans exhibit **anamorphosis**, a type of development that adds a body segment after a molt. In some cases, the adult stage continues to molt throughout the remainder of its life. Sperm transfer in entognathans is indirect, with sperm deposited in stalked droplets (spermatophores) on the ground. In most cases, sperm uptake by the female is a passive process, but in some of the more advanced species, the male guides the female to his sperm.

Springtails (order Collembola) are a primitive entognathous order of hexapods that are among the most widespread and abundant terrestrial arthropods. They are even found in Antarctica, where arthropods are scarce. Generally they are considered to be useful, as they assist in the decomposition of organic materials, and few are pests. There are about 6000 species of springtails.

Springtails are small animals, measuring only 0.25 to 10 mm in length, and usually less than 5 mm long. They are either elongate or globular in body form (Fig. 1.6). Their color varies greatly, and though often obscure, some are brightly colored. The antennae are short to medium in length, and consist of four to six segments. The compound eyes are small, with only a few facets per eye. The mouthparts are basically the biting (chewing) type, but sometime extensively modified, and somewhat enclosed by the head. The legs are small, and lack extensive modifications. Springtails often are equipped with a jumping apparatus that serves as the basis for the common name. This apparatus consists of a spring-like **furcula** originating near the tip of the abdomen that is flexed ventrally and held by a catch, the **tenaculum**. When the tenaculum releases, the furcula springs with a snap that propels the insect forward. In addition, springtails possess a small ventral tube-like structure on the first abdominal segment, called a **collophore** or ventral tube. The collophore has various functions, including water absorption and excretion, and possibly adhesion to smooth surfaces. The immatures usually resemble the adults in

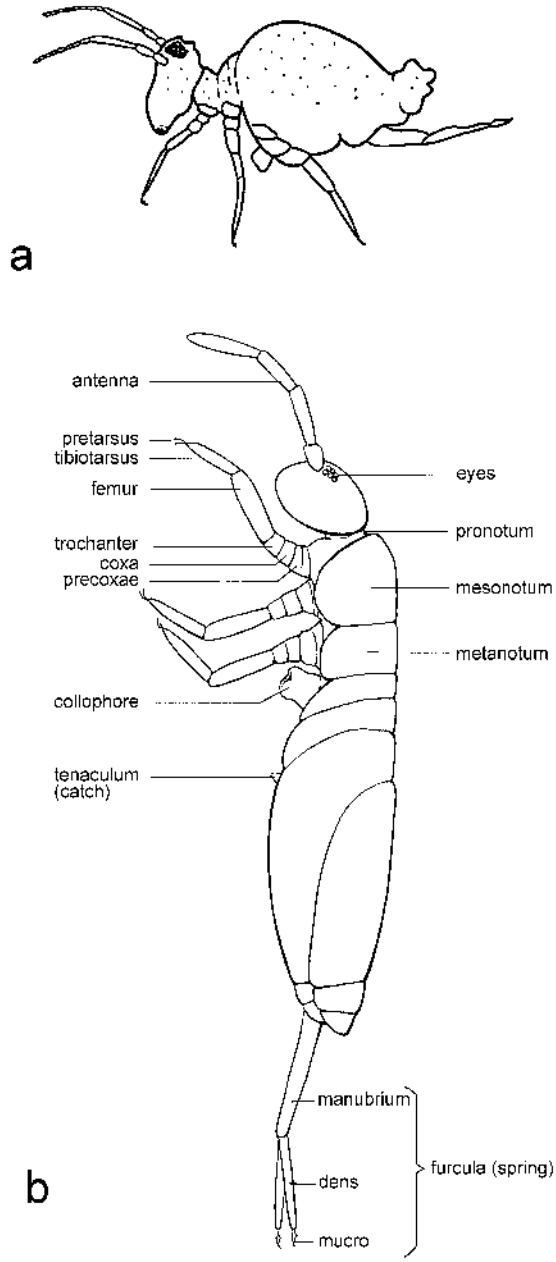


Fig. 1.6. Typical springtails (class Entognatha, order Collembola): (a) lateral view of a globular springtail; (b) diagram of elongate springtail showing key morphological features.

external morphology. There are three major body types found among springtails: globular, elongate, and grub-like.

Springtails occur in numerous habitats, including the water surface of fresh water, the tidal region of salt water, in soil, leaf debris, bird nests, beneath bark, and occasionally on foliage. They feed primarily on lichens, pollen, fungi, bacteria, and carrion, though a few feed on seedling plants or are carnivorous. Springtails often aggregate in large groups, and this can be observed on the surface of water, snow, or on organic material. The purpose or cause of aggregations is unknown.

Proturans (order Protura) are minute soil-inhabiting hexapods that lack eyes and antennae, and possess a 12-segmented abdomen. The first three abdominal segments have small leg-like appendages that are capable of movement. The first pair of legs have enlarged foretarsi that are covered with many types of setae and sensilla and function as antennae. Protura have a worldwide distribution with over 500 described species. Soil animals are not well known, and undoubtedly there are many hundreds of species yet to be found in the tropics as well as temperate areas.

Proturan life history is poorly understood, including their diet. Many species can be found in leaf litter, soil that is rich in organic matter, and dead wood. Most species appear to have modifications for feeding on fungi; however, some species have piercing or grinding structures. Like most soil arthropods, proturans most likely feed on a variety of materials including plants and fungi as well as scavenging on dead arthropods.

Diplurans (order Diplura) number about 660 species from throughout the world, though this group is not well known. They resemble proturans and silverfish (Insecta: Thysanura) but the presence of only two cerci rather than three caudal filaments distinguishes diplurans from silverfish (Fig. 1.7). They are distinguished from proturans by the presence of antennae.

Diplurans are usually less than 10 mm in length, though their size range is 2 to 50 mm. They are elongate, soft-bodied, and brownish. The integument is thin, and few scales are found on these animals. The body regions, including the three thoracic segments, are distinct. The head is distinct, and the antennae long, many-segmented, and slender. Compound eyes and ocelli are absent. The three pairs of legs are similar in appearance and moderately short. The tip of the abdomen bears a pair of cerci. The cerci vary greatly among the taxa, from long, many-segmented antenna-like appendages to stout, rigid forceps used for prey

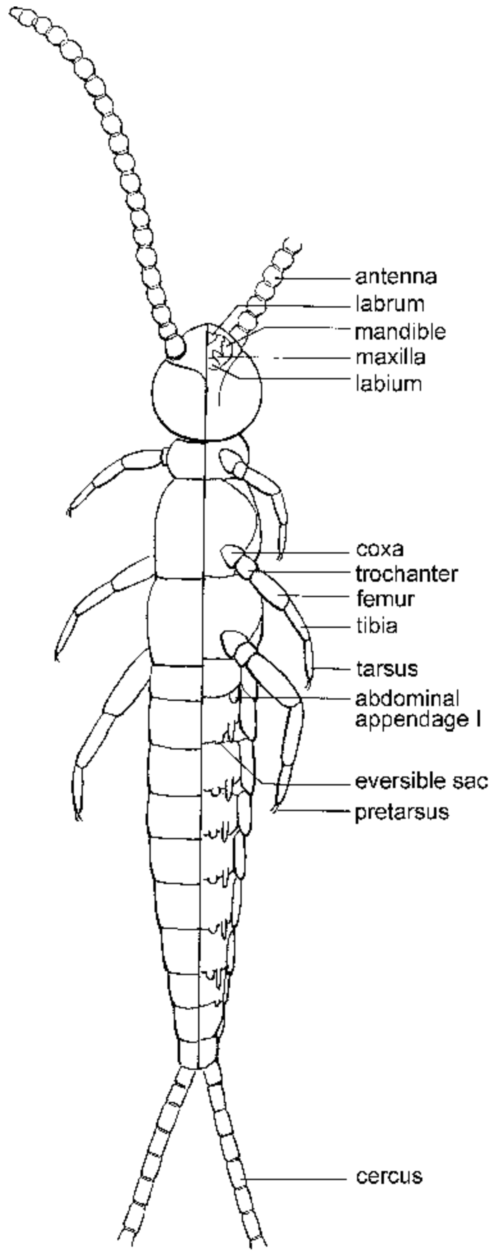


Fig. 1.7. Typical dipluran (class Entognatha, order Diplura) with dorsal view on left and ventral view on right.

capture. Most of the abdominal segments also bear small appendages. The immatures greatly resemble the adult stage, differing principally in the number of antennal segments.

These small animals are found among fallen leaves and in decaying vegetation, under logs and stones, and in soil and caves. They vary in dietary habits; some feed on vegetation whereas others eat other small soil-inhabiting arthropods. Eggs are deposited in the soil. They can be long-lived, with the life span requiring 2–3 years in some species.

INSECTA

The insects (class Insecta) are characterized by having three body regions (head, thorax, abdomen), three pairs of legs attached to the thorax, one pair of antennae, and external mouthparts that include mandibles. Most insects are terrestrial and possess wings, at least in the adult stage. The immature stages often differ considerably from the adult stage. However, as you might expect from a group with over a million species, there is tremendous variability among insects in their structure, physiology and development, and ecology. The following synopsis will attempt to describe some of the common patterns found in their structure, physiology and development, and ecology. Where relevant, some of the important differences among taxa will be noted, but this overview is designed mostly to show the fundamental characteristics of insects.

CLASSIFICATION OF INSECTS

The classification of insects is often debated, but a common arrangement and the derivation (from Greek or Latin) for the names of the taxa in the class Insecta follow. Also, the vernacular (common) name is given for each order.

- Class Insecta
  - Subclass Apterygota: Greek *a* (without) + *pteron* (wings)
    - Order Archeognatha: Greek *archaios* (primitive) + *gnathos* (jaw) – the bristletails
    - Order Zygentoma: Greek *zyg* (bridge) + *entoma* (insect) – the silverfish
  - Subclass Pterygota: Greek *pteron* (wing)
    - Infraclass Paleoptera: Greek *palaios* (ancient) + *pteron* (wing)
      - Order Ephemeroptera: Greek *ephermeros* (short-lived) + *pteron* (wing) – the mayflies
      - Order Odonata: Greek *odon* (tooth) (referring to the mandibles) – the dragonflies and damselflies
    - Infraclass Neoptera: Greek *neos* (new) + *pteron* (wing)
      - Series Exopterygota: Greek *exo* (outside) + *pteron* (wing)
        - Superorder Plecopteroidea
          - Order Plecoptera: Greek *plecos* (plaited) + *pteron* (wing) – the stoneflies
          - Order Embiidina: Latin *embios* (lively) – the webspinners
        - Superorder Orthopteroidea
          - Order Phasmida: Latin *phasma* (apparition or specter) – the stick and leaf insects
          - Order Mantodea: Greek *mantos* (soothsayer) – the mantids
          - Order Mantophasmatodea: from Mantodea + Phasmatodea – the gladiators
          - Order Blattodea: Latin *blatta* (cockroach) – the cockroaches
          - Order Isoptera: Greek *iso* (equal) + *pteron* (wing) – the termites
          - Order Grylloblattodea: Latin *gryllus* (cricket) + *blatta* (cockroach) – the rock crawlers
          - Order Orthoptera: Greek *orthos* (straight) + *pteron* (wing) – the grasshoppers, katydids, and crickets
          - Order Dermaptera: Greek *derma* (skin) + *pteron* (wing) – the earwigs
          - Order Zoraptera: Greek *zoros* (pure) + *a* (without) + *pteron* (wing) – the angel insects
        - Superorder Hemipteroidea
          - Order Psocoptera: Latin *psocos* (book louse) + Greek *pteron* (wing) – the barklice, booklice, or psocids
          - Order Thysanoptera; Greek *thysanos* (fringed) + *pteron* (wing) – the thrips
          - Order Hemiptera: Greek *hemi* (half) + *pteron* (wing) – the bugs
          - Order Phthiraptera: Greek *phtheir* (louse) + *a* (without) + *pteron* (wing) – the chewing and sucking lice
      - Series Endopterygota: Greek *endo* (inside) + *pteron* (wing)
        - Superorder Neuropteroidea
          - Order Megaloptera: Greek *megalo* (large) + *pteron* (wing) – the alderflies and dobsonflies

Order Raphidioptera: Greek *raphio* (a needle; referring to the ovipositor) + *pteron* (wing) – the snakeflies
Order Neuroptera: Greek *neuron* (nerve) + *pteron* (wing) – the lacewings, antlions, and mantidflies
Superorder Coleopteroidea
Order Coleoptera: Greek *coleos* (sheath) + *pteron* (wing) – the beetles
Order Strepsiptera: Greek *strepti* (twisted) + *pteron* (wing) – the stylopids
Superorder Panorpoidea
Order Mecoptera: Greek *mecos* (length) + *pteron* (wing) – the scorpionflies
Order Trichoptera: Greek *trichos* (hair) + *pteron* (wing) – the caddisflies
Order Lepidoptera: Greek *lepido* (scale) + *pteron* (wing) – the butterflies and moths
Order Diptera: Greek *di* (two) + *pteron* (wing) – the flies
Order Siphonaptera: Greek *siphon* (tube) + *a* (without) + *pteron* (wing) – the fleas
Superorder Hymenopteroidea
Order Hymenoptera: Greek *hymen* (membrane) + *pteron* (wing) – the wasps, ants, bees, and sawflies

CHARACTERISTICS OF THE MAJOR GROUPS OF INSECTS

The major groups of insects are characterized by a number of fundamental differences. Some of the major differences, and the relationships of taxa, are shown diagrammatically in Fig. 1.8. Characteristics of the insect orders most important to wildlife are shown in Table 1.1. Additional information on the important insect families is provided in Chapters 5 (Insects important as food for wildlife) and 10 (Arthropods as parasites of wildlife).

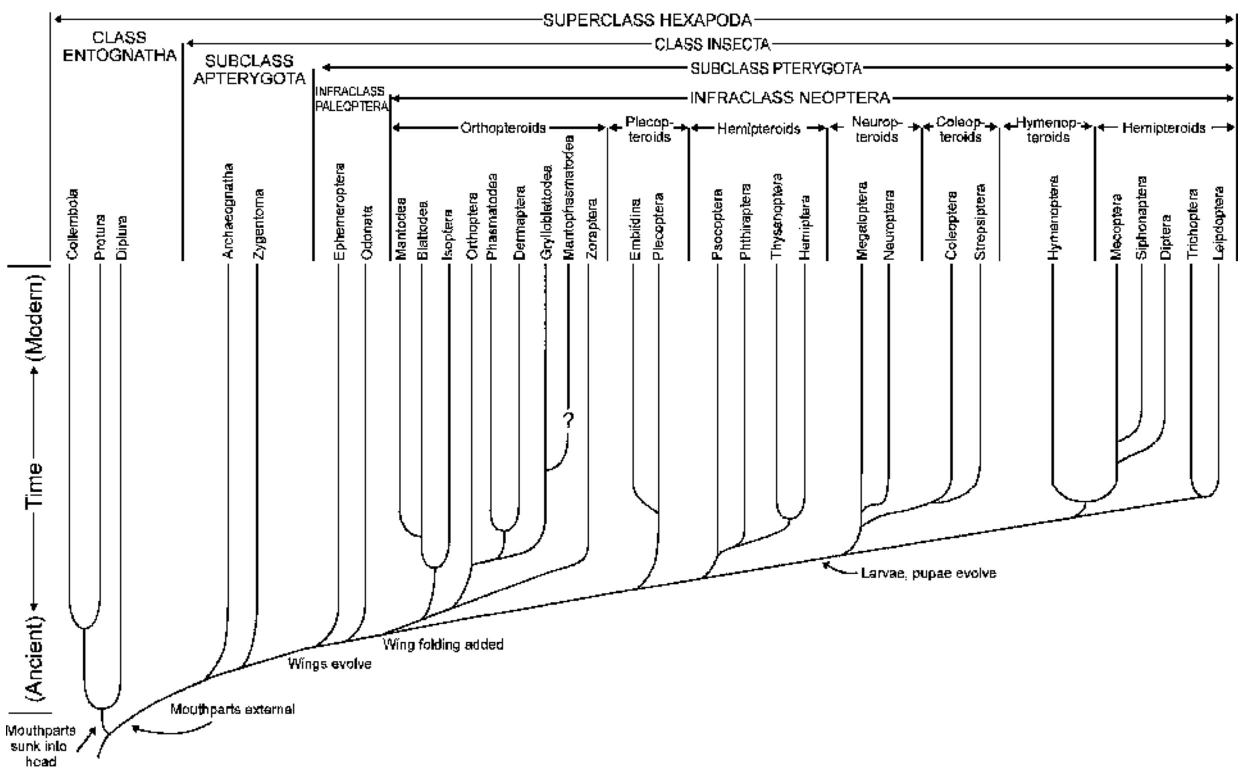
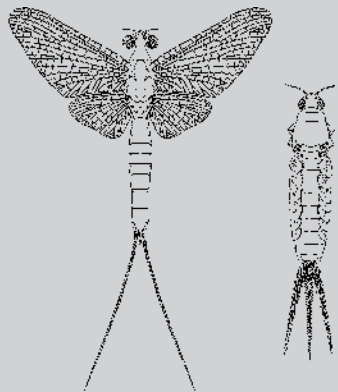
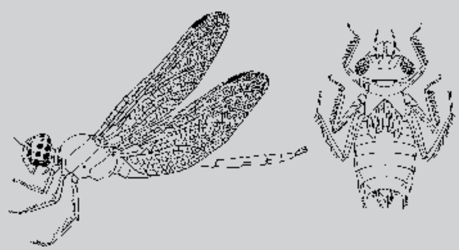
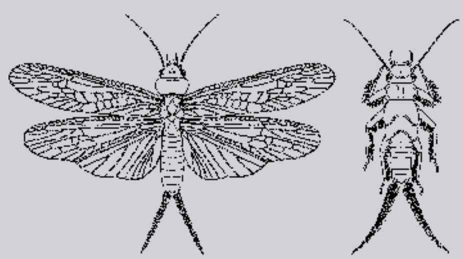
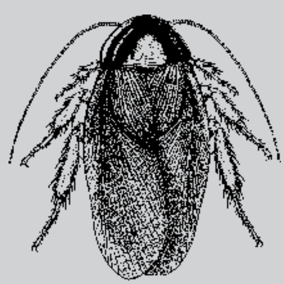


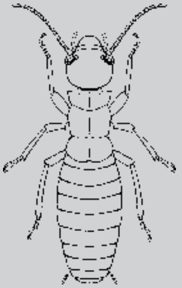
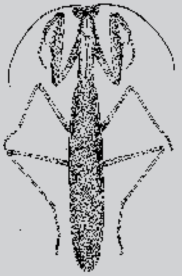
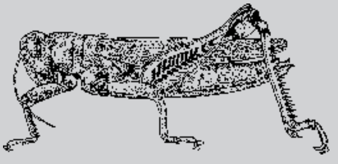
Fig. 1.8. Diagram of the possible phylogeny of the hexapods, showing relationships among the major groups and the temporal occurrence of major evolutionary steps in insect structure and development.

Table 1.1. The orders of insects most important to wildlife, and the key characteristics of the adult stage.

Order	Common name	Example	Metamorphosis
Ephemeroptera	Mayflies		Hemimetabolous
Odonata	Dragonflies, damselflies		Hemimetabolous
Plecoptera	Stoneflies		Hemimetabolous
Blattodea	Cockroaches		Hemimetabolous

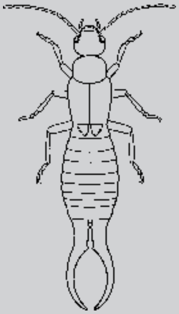
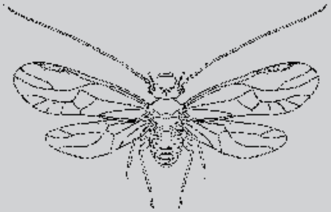
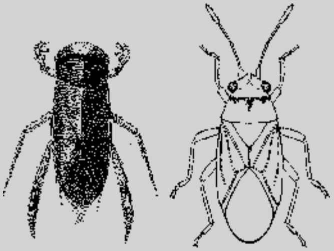
Forewings	Hindwings	Antennae	Mouthparts	Other features
Triangular, membranous, many veins and cross-veins	Smaller, rounded, sometimes absent	Very short, bristle-like	Chewing, but not functional in adults	Two or thee long slender cerci
Long, slender, membranous, many veins and cross-veins	Similar to forewings	Very short, bristle-like	Chewing	Two or more cerci, but very short
Slender, membranous, with many veins	Usually wider than forewings	Long, thread-like	Chewing	Two cerci, length varies, no ovipositor
Usually long, thickened, with few veins	Usually wider than forewings	Long, thread-like	Chewing	Two short cerci, no external ovipositor

Table 1.1. *Continued*

Order	Common name	Example	Metamorphosis
Isoptera	Termites		Hemimetabolous
Mantodea	Mantids or praying mantids		Hemimetabolous
Phasmida	Stick and leaf insects		Hemimetabolous
Orthoptera	Grasshoppers, katydids, crickets		Hemimetabolous

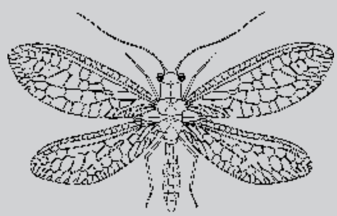
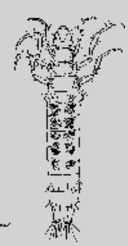
Forewings	Hindwings	Antennae	Mouthparts	Other features
Long, narrow	Long, narrow	Medium length, thread-like	Chewing	Short cerci, no external ovipositor
Long, slender, membranous	Wider than forewings	Medium to long, threadlike	Chewing	Prothorac legs strongly developed and bearing spines
Variable, often lacking	Variable, often lacking	Long, thread-like	Chewing	Cryptic, resembling twigs or leaves
Usually long and slender, thickened, with veins if present	Usually wider than forewings, membranous if present	Medium to long, thread-like	Chewing	Two short cerci, ovipositor present and sometimes long

Table 1.1. *Continued*

Order	Common name	Example	Metamorphosis
Dermaptera	Earwigs		Hemimetabolous
Psocoptera	Barklice, booklice, or psocids		Hemimetabolous
Hemiptera	Bugs, cicadas, leafhoppers, treehoppers, whiteflies, scales, aphids, etc.		Hemimetabolous
Phthiraptera	Chewing and sucking lice		Hemimetabolous

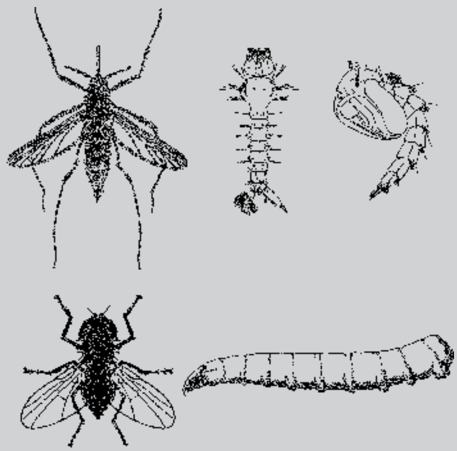
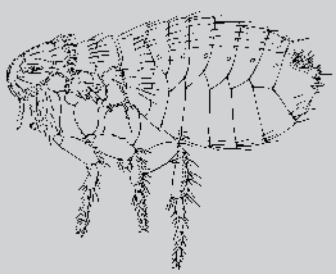
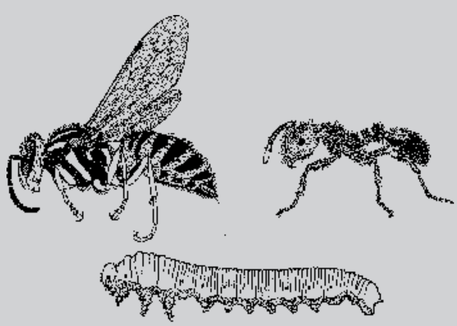
Forewings	Hindwings	Antennae	Mouthparts	Other features
Short, thickened if present	Long, folding, membranous if present	Medium, thread-like	Chewing	Two large, pincer-like cerci, no ovipositor
Membranous, with few veins if present	Smaller, but similar to forewings if present	Long, thread-like	Chewing	No cerci, ovipositor small or absent
Thickened or membranous if present, but often absent	Membranous and shorter than forewings if present, but often absent	Variable length, thread-like	Piercing-sucking	No cerci, ovipositor may be present
None	None	Short	Chewing or piercing-sucking	No cerci, ovipositor present or absent

Table 1.1. *Continued*

Order	Common name	Example	Metamorphosis
Thysanoptera	Thrips		Generally regarded as hemimetabolous, but somewhat intermediate
Megaloptera	Alderflies, dobsonflies, fishflies		Holometabolous
Neuroptera	Lacewings, ant lions		Holometabolous
Coleoptera	Beetles, weevils	 	Holometabolous
Trichoptera	Caddisflies	 	Holometabolous

Forewings	Hindwings	Antennae	Mouthparts	Other features
Very slender with wide fringe of hairs	Very slender with wide fringe of hairs	Short with 6-10 segments	Piercing-sucking, but asymmetrical	Very small, generally less than 5 mm long
Elongate, membranous, with many veins	Similar to forewings	Long, thread-like	Biting	Larvae with paired piercing-sucking mouthparts
Long, membranous, many cross-veins	Similar to forewings	Usually long	Biting	Larvae with paired piercing-sucking mouthparts
Thickened, hardened, veins usually absent	Medium length, membranous, folding if present	Variable in length and shape, often elaborate	Chewing	Larvae may lack legs, often called grubs
Elongate, few cross-veins, many hairs present	Similar to forewings but shorter	Long, thread-like	Chewing	Larvae aquatic, usually build and live within cases

Table 1.1. *Continued*

Order	Common name	Example	Metamorphosis
Lepidoptera	Butterflies, moths		Holometabolous
Diptera	Flies, midges		Holometabolous
Siphonaptera	Fleas		Holometabolous
Hymenoptera	Wasps, bees, ants, sawflies		Holometabolous

Forewings	Hindwings	Antennae	Mouthparts	Other features
Slender to broad, usually covered with scales	Similar to forewings but usually shorter, broader	Long, may be thread-like, plumose, or clubbed	Tubular, siphoning	Larvae usually with prolegs, called caterpillars
Membranous, relatively few veins	Functional wings absent	Often long and thread-like, some short with a bristle	Variable	Larvae legless, often with reduced head and called maggots
None	None	Short	Piercing-sucking	Legless larvae have well-developed head
Membranous, usually long	Membranous, smaller than forewings	Medium length, usually thead-like	Usually chewing, sometimes sucking	Head of larvae well developed, legs variable, may be called grubs

The members of subclass Apterygota lack wings, possess rudimentary abdominal appendages, practice indirect insemination, and molt throughout their life. In contrast, the subclass Pterygota possess wings (or did at one time), generally lack abdominal appendages, practice direct insemination via copulation, and molt only until sexual maturity is attained. So the apterygotes are really quite different from the other insects. They have little or no importance to wildlife. They are rarely seen except in homes where cardboard and other paper products accumulate, especially if accompanied by moisture.

Infraclass Paleoptera consist of primitive insects (evolved early in the lineage of insects), and are comprised of the orders Ephemeroptera and Odonata. The wings often cannot be flexed over the back when the insect is at rest. The immature stages of existing paleopterans live in aquatic habitats. These are important components in aquatic systems, and the adults of Odonata are also important predators.

The infraclass Neoptera, on the other hand, are a diverse groups of relatively modern insects. They can flex their wings over the body. They display development in which the immatures are similar to the mature form (Exopterygota), or the immatures differ markedly in appearance from the adults (Endopterygota).

Superorder Plecopteroidea, consisting of Plecoptera and Embiidina, are closely related to superorder Orthopteroidea. Both suborders have chewing mouthparts; complex wing venation, with the hindwings larger than the forewings; and cerci. They differ, however, in that in the Plecopteroidea the forewings are not thickened, and external male genitalia are lacking. The Plecoptera are important in streams and rivers as a food resource for fish. Embiidina, though interesting, are of little consequence to wildlife.

The members of superorder Orthopteroidea (Polyneoptera) have chewing mouthparts, long antennae, complex wing venation, large hindwings, thickened forewings, large cerci, and nymphs with ocelli. Several orders are considered to be orthopteroids: Phasmida, Mantodea, Mantophasmatodea, Blattodea, Isoptera, Grylloblattodea, Orthoptera, Dermaptera, and Zoraptera. In many older classification systems, they were all considered to be part of the order Orthoptera. This is a relatively primitive group. Many of these taxa are important herbivores, predators, or detritivores, so they are important in ecosystem function. Orthoptera and Isoptera are among the most important sources of wildlife food.

Superorder Hemipteroidea (Paraneoptera) are also a large group, consisting of the orders Psocoptera, Hemiptera, Thysanoptera, and Phthiraptera. Unlike the Orthopteroidea, they lack cerci, and have stylet-like structures associated with their mouthparts (though in Psocoptera, chewing mouthparts are preserved). Some groups are well designed for piercing the host and sucking liquids. Though this and the preceding superorders are considered to be hemimetabolous, many Thysanoptera and a few Hemiptera are physiologically holometabolous. The Psocoptera, Hemiptera, and Thysanoptera are important plant feeders. A few Hemiptera and all of the Phthiraptera feed on wildlife.

The superorder Neuropteroidea are holometabolous, and consist of the orders Megaloptera, Raphidioptera, and Neuroptera. Both aquatic and terrestrial forms occur in this superorder. The wings tend to bear numerous cells. Megaloptera and Raphidioptera are small taxa, and not very important. Neuroptera are best known for the predatory members of the order that feed on terrestrial insects, especially aphids.

Superorder Coleopteroidea consist of the orders Coleoptera and Strepsiptera. They are similar in that the metathorax is developed for flight, and bears functional wings. The forewings of the Coleoptera are reduced to hard wing coverings, and even more reduced in the Strepsiptera, to small club-like appendages. They contrast strongly in that the Coleoptera are the largest order, and Strepsiptera one of the smaller orders. The Coleoptera are very diverse and important ecologically. Only a very few can be viewed as injurious to wildlife, but many are important in ecosystem function and as wildlife food. The Strepsiptera are relatively unimportant parasites of insects.

Panorpoidea is another large superorder, consisting of the orders Mecoptera, Trichoptera, Lepidoptera, Diptera, and Siphonaptera. They share few common characters, however, such as a tendency for a reduced meso- and metasternum, some similar wing vein elements, and the terminal abdominal segments tend to function as an ovipositor. Trichoptera and Diptera are important food resources for fish, and Lepidoptera for birds. Diptera are the most important pests and disease vectors of humans and wildlife.

Lastly, the superorder Hymenopteroidea consist only of the order Hymenoptera, though this is a very divergent, complex group. They bear numerous Malpighian tubules, unlike all other endopterygotes, which have only four to six tubules. Also, their wing venation is often greatly reduced, and wings may be entirely absent in members of some groups. Hymenoptera are important sources of food for birds, mammals, reptiles, and amphibians. Some of the ants and wasps can be troublesome to wildlife, however.

EVOLUTION OF INSECTS

The time line that describes the history of the earth has been divided into large blocks of time, but each large block is normally subdivided, and subdivided again, for convenience (Fig. 1.9). The generally accepted divisions are eon, era, period, epoch, and age. The names given to the block of time often have historical significance, and may be associated with occurrence of different fossils. For example, the Phanerozoic eon also consists of three major divisions: the Cenozoic, the Mesozoic, and the Paleozoic eras. The 'zoic' part of the word comes from the root 'zoo,' meaning animal. 'Cen' means recent, 'Meso' means middle, and 'Paleo' means ancient. These divisions

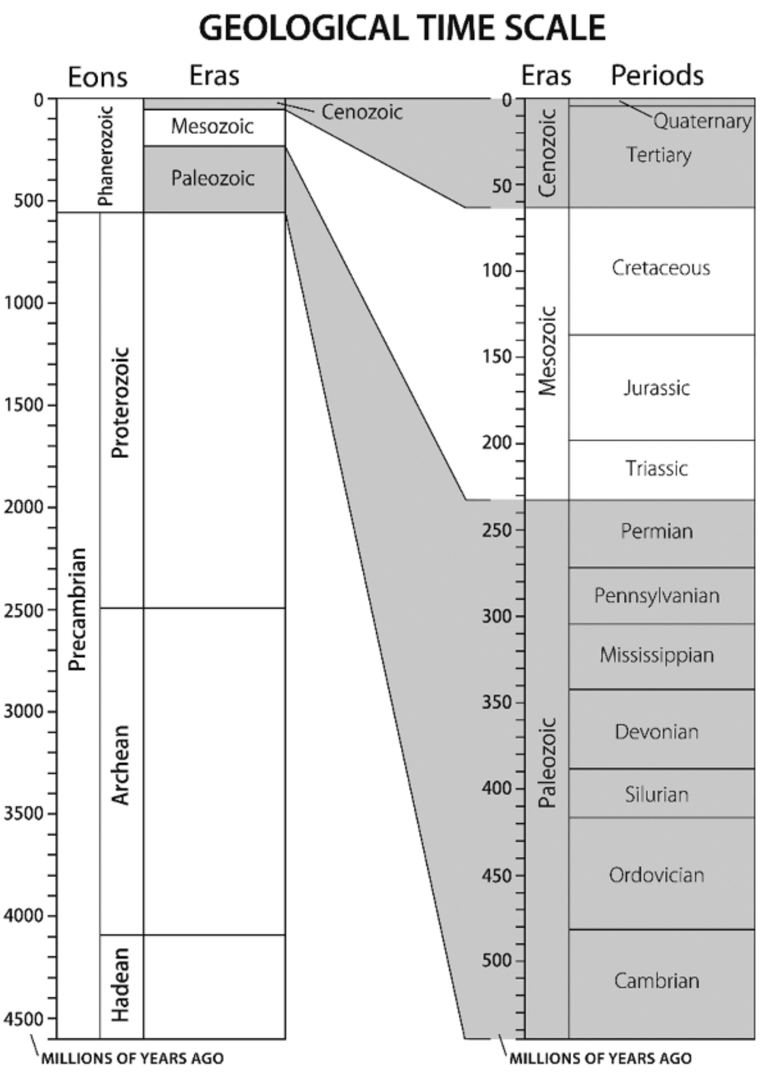


Fig. 1.9. The geological time scale.

reflect major changes in the composition of ancient faunas, with each era associated with domination by a particular group of animals. The Cenozoic has sometimes been called the 'Age of Mammals,' the Mesozoic the 'Age of Dinosaurs,' and the Paleozoic the 'Age of Fishes.' This is not entirely accurate, though there is some basis for these designations. Different spans of time on the geological time scale are usually delimited by major geological or paleontological events, such as mass extinctions. For example, the end of the Cretaceous period of the Mesozoic era is marked by the demise of the dinosaurs and of many marine species. Also, unlike most time lines, the time is expressed not in years from a past event, but from the present. Thus, periods or events are commonly described in millions of years ago (mya).

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

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

The Cenozoic, the most recent era, is divided into two main sub-divisions: the quaternary and the tertiary periods. Most of the Cenozoic is the Tertiary, from 65 million years ago to 1.8 million years ago. The Quaternary includes only the last 1.8 million years. The Cenozoic is particularly interesting to biologists because most of the life forms we see today developed in this period. It has been called the **'age of insects'** due to the development of great diversity, but could also be known as the age of flowering plants, birds, etc., because most of the flora and fauna we see today evolved during this period. The **phylogeny**, or history, origin, and evolution of insects, is shown diagrammatically in Fig. 1.8.

The last 10,000 years (the Holocene) is sometimes known as the 'age of man' and is also the time period since the last major ice age. The time period before the Holocene, the Pleistocene, is noteworthy because though much of the recent flora and fauna is the same as today, some interesting and now extinct megafauna were present, including mastodons, mammoths, sabre-toothed cats, and giant ground sloths. The human species, *Homo sapiens*, also expanded during this time period, and as mentioned previously, there was a significant ice age period.

From an entomological perspective, the Phanerozoic eon (Table 1.2) was an exciting time. Arthropods ventured onto land during the Paleozoic, perhaps 400 mya, though the Silurian entomofauna consisted of primitive myriapods and arachnids. Fossil hexapods have been recovered from the Devonian, most notably springtails from a type of stone called 'chert'. Insects proliferated rapidly during the remainder of the Paleozoic and thereafter. Interestingly, during the Mississippian (also called the Early Carboniferous) we have no fossil evidence of insects, whereas in the Pennsylvanian (also called late Carboniferous) we have numerous records of early (mostly now extinct) insect groups (e.g., protodonata and protorthopterans from deposits in France). At the close of the Paleozoic, the Permian period, the environment of earth was undergoing significant change, most notably a less tropical climate. Numerous insects from many deposits around the world document over a dozen orders of insects, including the occurrence of 'giant' insects.

The Triassic period of the Mesozoic era saw a warming of the earth, and fossil deposits document the occurrence of early insects such as Blattodea and some Orthoptera, Coleoptera, Odonata, Plecop-

Table 1.2. Important time periods of the Phanerozoic eon (543 million years ago to present).

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

tera, Neuroptera and Grylloblattodea. Transition into the Jurassic was not abrupt for insects, and the fossil record documents few marked changes, but increased radiation.

The Cretaceous period is notable for the radiation of angiosperms that took place. Because many insects are intimately associated with plants through plant feeding and pollination, they were profoundly affected by the availability of these new resources. Many of the modern taxa became established during this period, though more modern taxa such as some Diptera and Lepidoptera radiated later in the Cenozoic. One very noteworthy feature of the Cretaceous is the great availability of amber. The spread of resin-producing trees through this period and into the Tertiary provided an excellent preservation medium for insects. Thousands of species and perhaps 30 orders have been recovered from amber deposits around the world. As insects transitioned from the Cretaceous to the Cenozoic era, the earth witnessed the appearance of ‘modern’ insect groups such as termites (Isoptera), scale insects and bat bugs (Hemiptera), fleas (Siphonaptera), lice (Phthiraptera), flies (Diptera), and bees and ants (Hymenoptera).

Insects, or at least arthopods, have existed for perhaps 400 million years, making them among the oldest land animals. Most modern orders of insects had appeared by 250 mya, and some modern families can be traced back at least 120 mya. This is quite old compared to mammals, which did not appear until about 120 mya, with modern orders of mammals appearing only about 60 mya. However, unlike some ancient animals (e.g., coelocanth, *Latimeria chalumnae*) or plants (e.g., ginkgo, *Ginkgo biloba*) they are not all relicts of earlier times. Many evolved relatively recently, and continue to evolve.

The evolution of insects is complex, and aspects of it continue to be debated. As an example of how these strange-looking beasts came to be, consider the development of the general insect body form: the three tagma we now call the head, thorax and abdomen. The theoretical evolution of the insect body form as we know it today, from an annelid-like ancestor, is shown in Fig. 1.10. There are five major steps:

- Initially the organism was worm-like, long, and segmented. This insect ancestor had a ventral mouth and a simple head-like structure called a prostomium that contained the principal sensory organs.

• In the second step, the organism acquired appendages on nearly all the body segments. Antennal organs developed on the prostomium.
• In the third step, the union of the prostomium with other anterior body segments commenced. This was the beginning of the complex, composite head structure found in modern insects.
• In the fourth step, the trunk segments differentiated to form the thorax, which became the body segment responsible for locomotion. The body segments anterior to the thoracic segments continued to differentiate into structures that aided feeding, while the body segments posterior to the thorax differentiated into the abdomen, with greatly diminished appendages.
• Finally, the composite head appeared, consisting of the consolidation of the anterior segment into a single unit but bearing mouthpart appendages derived from several body segments. The thorax bore the legs, and in some lineages wings also evolved here. The abdominal appendages had mostly disappeared.

We know something about the evolution of insects because in some cases they are well preserved in mineral deposits or in amber. When insects perish in lakes or marine environments, they may settle to the bottom and be covered with very fine sediments. If they do not decompose and are undisturbed for millions of years, they become fossilized. If uncovered later, we may find a cast or mold of the insect showing

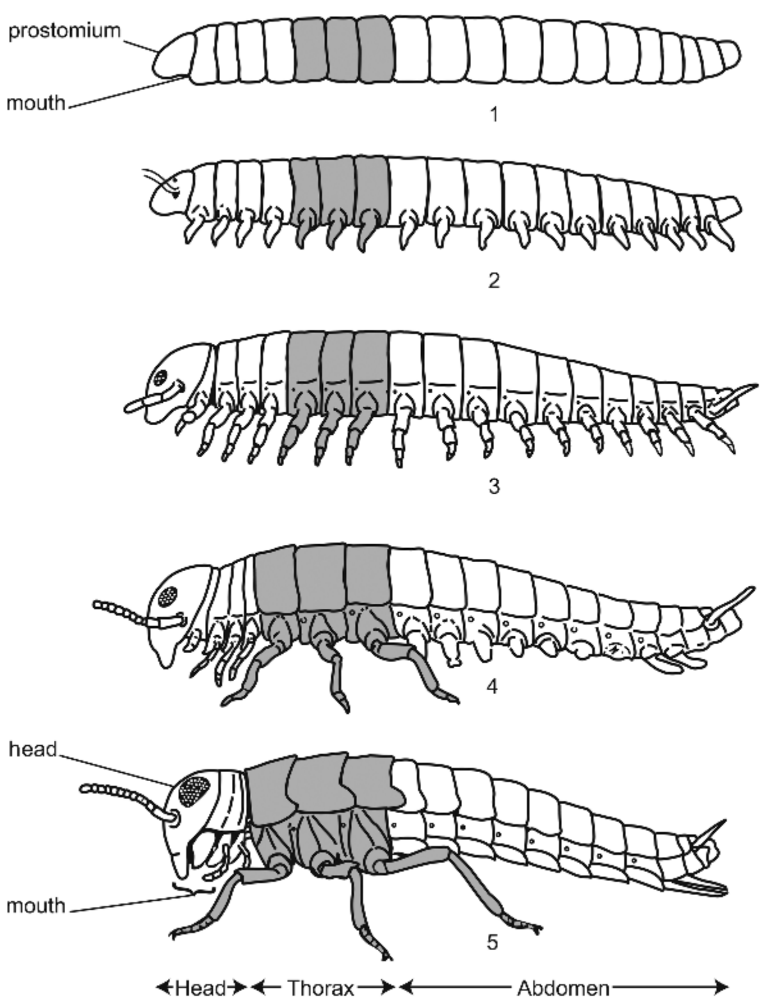


Fig. 1.10. The possible evolution of body form in insects, beginning with an annelid-like ancestor. See text for details. (adapted from Snodgrass 1993).

its form and some relief (such as the venation of the wings), but no color; these are called impressions. However, sometimes the remains of the cuticle are preserved, so some aspects of color are apparent; these are called compressions. The part of insects that preserves well is the hard exoskeleton. The sections of exoskeleton are connected by soft, membranous tissue, which provides the insect with the opportunity for mobility. These soft tissues do not preserve well, so they disappear, leaving sections of insects behind to be preserved. Therefore, often we find just pieces or sections of insects rather than entire, intact bodies. However, sometimes the entire body is replaced by minerals, providing three-dimensional artifacts; this is called petrification. The most celebrated insect fossils are likely amber inclusions. Amber is ancient tree resin. When the resin was fresh, it was sticky, much like present-day exudates of conifers. Insects sometimes became entangled in the surface of the sticky tree exudates, and eventually were engulfed by the flowing resin. This resulted in preservation of insects from up to 250 mya. Amber inclusions often provide nearly perfect detail, including color, so they are exceptionally valuable for studying ancient life.

Why have insects been so successful at persisting, speciating, and exploiting resources relative to other forms of life? The inordinate abundance and diversity of insects is spectacular, and several factors seem to be of paramount importance:

• ***Size.*** The small size of insects allows them to exploit nearly all food resources. For example, a single seed may support the complete dietary needs of an insect.

• ***Longevity.*** Insects often complete develop (mature) quickly. This allows insects to take advantage of transient resources. For example, flies may complete their larval development is as little as 3–4 days, before fruit, dung, or standing water disappears.

• ***Exoskeleton.*** The body plan of insects includes an integument (body covering) that provides a support structure (equivalent to the skeleton of vertebrate animals), protection (essentially a layer of armor that deters predation), and resistance to water loss (the integument has an external layer of wax). This is a very efficient combination that makes insects tougher and hardier than most other animals.

• ***Wings.*** The occurrence of wings in insects provides the unusually good opportunity to disperse; this allows them to take advantage of transient resources, to escape predation, and to find mates. Food, predation, and reproduction are the major factors governing the abundance of animals. No other invertebrates have wings, and few other animals, only birds and bats. Many have speculated that the evolution of wings in birds and bats is directly related to their insectivorous habits.

• ***Ectothermy.*** Insects do not have a constant body temperature, unlike mammals and birds. This feature reduces their energetic (food) requirements because they do not have to burn calories to maintain body temperatures, and allows them to survive long periods without food during inclement weather.

• ***Diapause.*** Insects can undergo arrested development, which means that their progression toward developmental maturity and reproduction ceases temporarily. During diapause, their metabolism falls to a very low level, allowing them to survive long periods of inclement weather and the absence of food.

• ***Chemoreception.*** Insects have highly developed chemical senses. Everyone knows that bloodhounds and many other animals can smell odors that humans cannot perceive. Insects are even more sensitive to odors. Unlike humans, who are vision-dependent, the world of insects is based more on odors. For example, although we might not be able to see into dense vegetation, insects can perceive hosts that are hidden from view because they have such an acute sense of smell. Thus, they are unusually well adapted to find hosts and mates, and to communicate to one another by releasing and sensing chemicals.

• ***Evolutionary precedence.*** Organisms can monopolize resources by evolutionary precedence. It is difficult for organisms to displace other organisms that are already well adapted for a certain niche. For example, insects have made virtually no progress in exploiting marine resources because crustaceans and other marine organisms have monopolized this environment. Similarly, because insects were among the first terrestrial organisms to exploit the terrestrial environment, it is very difficult for other organisms to displace insects in terrestrial environments.

• ***Flowering plants***. The flowering plants, or angiosperms, radiated (evolved into new species) at the same time insects were radiating. It is difficult to know which was more important in this radiation of plant and insects, but clearly there often is an interdependency of insects and terrestrial plants. Certainly angiosperms provided niches that did not exist previously, allowing insects to speciate.

INSECT BIOGEOGRAPHY

The study of spatial patterns of animal and plant occurrence is called **biogeography**. **Ecological biogeography** is concerned with the occurrence of organisms in relation to their environment. For example, the changing distribution of organisms in relation to global warming is an increasingly important aspect of ecological biogeography. The other major form of biogeography is historical biogeography. **Historical biogeography** is the distribution of taxa in relation to the geological history of the earth. Here we are mostly concerned about historical biogeography as background to the zoogeographic realms.

The tenets of historical biogeography have long been postulated, but it was not until the 1960s that geologists gained full understanding of the movement of continents, and provided a geological mechanism for patterns of biodiversity that had long puzzled biologists. Basically, the earth's crust has been in constant motion since its formation, resulting in the movement of the land masses. This movement is called continental drift, and resulted in the formation of mountain ranges where crustal elements collided, and troughs where crustal elements diverged.

A single large land mass existed on earth about 250 million years ago, called Pangaea. Pangaea broke up into two supercontinents, Laurasia in the northern hemisphere and Gondwana in the southern hemisphere. These, in turn, broke into the modern continents, which continue their slow movement. The significance of continental drift is that there are biological similarities in flora and fauna derived from earlier times when continents were physically joined, and they do not necessarily correspond to the modern continents. Thus, for example, the fauna of Africa and South America share some common ancestry despite their current geographic distance.

Entomologists commonly make reference to **zoogeographic realms** (or regions or provinces) that relate to historical biogeography. The fauna within a realm share common phylogeny, and developed in relative isolation from other realms. Traditionally, the zoogeographic realms are:

- ***Australian realm***. Australia and nearby islands;
- ***Oriental realm***. India and Southeast Asia through Indonesia;
- ***Ethiopian realm***. Central and southern Africa;
- ***Palearctic realm***. Europe and Asia except for Southeast Asia, and including the Arabian Peninsula and Northern Africa;
- ***Nearctic realm***. North America except for southern Mexico and Central America;
- ***Neotropical realm***. South and most of Central America, including the Caribbean region.

The major realms are shown in Fig. 1.11. The Nearctic and Palearctic realms are often combined into the **Holarctic realm**, as the fauna are really quite similar, despite the present distances between the continents. Also, sometimes the realms are divided further, reflecting smaller areas with unusual fauna. For example, Madagascar is often given a separate designation, as is the southern tip of Africa, and both of these areas have unique flora and fauna.

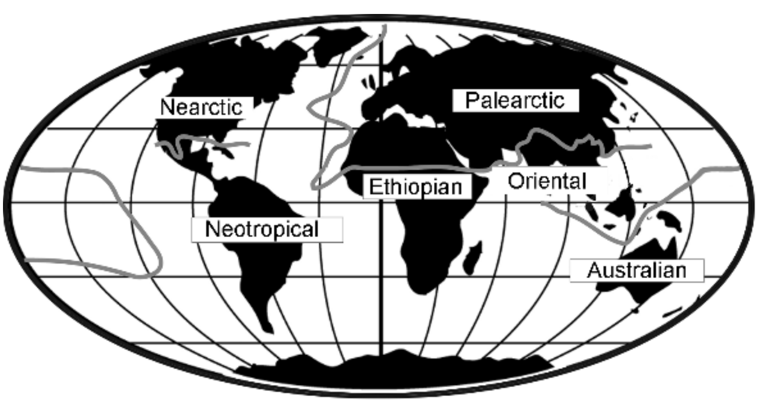


Fig. 1.11. The major zoogeographic realms on earth.

SUMMARY

- Insects are named and categorized into like groups to facilitate information access. The scientific name is based on binomial nomenclature, and all insects have genus and species designations that comprise their scientific name.
- The phylum Arthropoda is composed of organisms with jointed legs and an external skeleton. In addition to insects, it consists of several important classes including the arachnids (spiders, ticks, mites, scorpions), crustaceans (isopods, shrimps, crabs, etc.), millipedes, centipedes, and entognathans.
- The entognathans (class Entognatha) consist of three orders of six-legged arthropods that are closely related to insects: Collembola, Protura, and Diplura. Indeed, sometimes they are considered to be insects. They differ from insects in having their mouthparts sunk into the head (entognathous), unlike the insects, which have their mouthparts extruded (ectognathous). Also, unlike most insects, they lack wings, and the immature forms greatly resemble the adult forms.
- The class Insecta displays three body regions, three pairs of legs, one pair of antennae, and mouthparts containing mandibles. They are extremely diverse, but many possess wings. Presently, 30 orders of insects are recognized, and nearly one million species have been described.
- Insects seem to have evolved about 400 million years ago, during the Paleozoic Era. The modern orders were present 250 million years ago. Insects are much older than mammals, which first appeared about 120 million years ago. Modern orders of mammals appeared about 60 million years ago.
- We know something about the evolution of insects because they are well preserved in mineral deposits and in amber. Insects underwent spectacular radiation in the Cretaceous Period, 144 to 65 million years ago. Some of the features contributing to the success of insects were their small size, short life span, tough exoskeleton, wings, ectothermic temperature relations, ability to undergo diapause, and well developed chemical senses. Other important factors were evolutionary precedence (they were among the first animals to inhabit the terrestrial environment), and the radiation of angiosperms (which provided many new niches).

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