The Tree of Life

Edited by Pablo Vargas Rafael Zardoya
Tree of Hexapods showing the phylogenetic relationships among the most significant groups. Colored boxes indicate high taxonomic ranks. Branches with thick lines indicate robust clades, and branches with thin lines less-supported clades. Each number in a green circle indicates the chapter in which a particular clade is also treated. Orange circles mark some nodes and their age. Photographs illustrate principal clades; boxed numbers associate photographs with clades.

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Hexapods
Insects and Their Closely Related Groups
Rolf G. Beutel and Ignacio Ribera

SUMMARY  The Hexapoda (insects in the broadest sense) are the most diverse group of organisms, with approximately one million described species. The most accepted hypothesis is that Hexapoda originated within the traditional “Crustacea,” possibly forming a monophyletic group with Cephalocarida and Remipedia. The entire clade ( paraphyletic “Crustacea” plus Hexapoda) is referred to as Pancrustacea or Tetraconata. Hexapoda includes insects (Insecta, Ectognatha) plus three relatively species-poor orders (Collembola, Protura, and Diplura), the first two possibly forming the Ellipura. There are known fossils of Collembola and other ancestral Hexapoda dating back to the Devonian, more than 400 million years ago. The relationships among the basal Hexapoda are still controversial, although it is generally accepted that Insecta (=Ectognatha) are monophyletic and that Zygentoma are the sister group of Pterygota. Palaeoptera (dragonflies and mayflies) are probably monophyletic and form the sister taxon of Neoptera, the insects able to fold their wings back above the abdomen. Within Neoptera there are three large lineages. The monophyly of Polynoeoptera (grasshoppers, praying mantises, roaches, earwigs, stick insects) is likely but still controversial, whereas it is widely accepted in the case of Acercaria (thrips, bark lice, lice, true bugs, cicadas) and Holometabola (or Endopterygota, insects with complete metamorphosis such as flies, mosquitoes, beetles, butterflies, bees, and ants). Three key innovations that triggered the enormous diversification of Hexapoda seem to have been the ability to fly, the ability to fold back the wings, and complete metamorphosis. The persistence of the main lineages of insects since the Devonian and their ecological and morphological versatility have undoubtedly contributed to making Hexapoda the dominant group in extant terrestrial ecosystems, both in number of species and in biomass and functional diversity.

What is a hexapod?
The hexapods (Greek hex [six] and pod [foot]) are by far the most species rich group of arthropods, with more than a million known species. They are mainly characterized by the subdivision of the body into three tagmata: head, thorax and abdomen. The Hexapoda are secondarily terrestrial Pancrustacea, with specific modifications related to their terrestrial habits, such as the tracheal system, Malpighian tubules, and the formation of a spermatophore. They include the Insecta (or Ectognatha) and three basal wingless groups with low or relatively low diversity, mainly ground-oriented and primarily specialized on life in leaf litter, decaying plant materials and soil substrate: the Collembola, the Protura and the Diplura, traditionally combined as “Entognatha.” The hexapods possess mandibles and other mouthparts (maxillae and labium) that are usually exposed (Ectognatha) or covered by duplicatures of the head (“Entognatha”). The 3-segmented thorax bears three pairs of uniramous legs, and two pairs of wings in most groups of the pterygote insects. The abdomen is primarily composed of 11 segments, but the number varies, with a minimal number of 6 in Collembola. Articulated appendages are usually present, either as an ovipositor in most ectognathous females, as terminal cerci (segment 11), or as a male copulatory apparatus. A lock-and-key mechanism with complex and closely fitting male and female genitalia occurs in different groups of Pterygota, but this is not a general feature of insects. The development of the body plan is primarily ametabolous or hemimetabolous, with immature stages (nymphs or naiads) differing only slightly from the adults. The switch to holometabolous development with complete metamorphosis, larvae strikingly different from the adults, and a pupal stage, was one of the most important steps in hexapod evolution.
The name hexapoda refers to all insect orders, including the entognathous Collembola, Protura, and Diplura. With more than a million described species, hexapods are the group with the highest diversity on this planet. Estimates of the real diversity range between 1.5 and 30 million species, with a number of about 5 million being widely accepted. Approximately 80% of those described belong to the well-supported lineage of Holometabola (=Endopterygota), which contains, among others, four megadiverse orders: Hymenoptera (sawflies, wasps, bees, ants, etc.), Coleoptera (beetles), Diptera (biting flies and flies), and Lepidoptera (moths and butterflies) (see Chapters 33–36 respectively).

The origin of hexapods is not fully clear yet: traditionally they were placed as the closest relatives of Myriapoda (centipedes and millipedes) in the clade “Tracheata.” This group appeared to be well supported by morphological features, all of them more or less closely associated with a secondarily terrestrial lifestyle such as, for instance, the presence of Malpighian tubules and tracheae (the name “Tracheata” refers to this feature). The alternative hypothesis—placement in a clade with the traditional “crustaceans”—was initially suggested by molecular data, and is also supported by some morphological characters. Features of the omatidia and the brain suggest possible affinities with specialized “crustacean” lineages, the Cephalocarida and Remipedia. The group formed by “crustaceans” and hexapods is called Pancrustacea or Tetraconata. The monophyly of this lineage is widely accepted, but the precise placement of Hexapoda is still controversial.

The monophyly of Hexapoda is almost universally accepted. It was challenged in a study based on mitochondrial genomes, but other investigations based on extensive molecular data sets (transcriptomes) unambiguously support a clade Hexapoda. The hexapods are primarily wingless. The body is subdivided into three tagmata: the head, with sense organs, mouthparts, and the brain; the thorax, with three pairs of 6-segmented legs; and the 11-segmented abdomen, with the fat body, genital organs, and a large part of the digestive tract. The oldest known fossils are from Early Devonian deposits (approximately 400 Mya). One of them can be clearly assigned to Collembola, the springtails, and displays characteristic features of this specialized group. A dicondylic mandible from the same fossil site shows that the most basal splits within Hexapoda had already taken place. This suggests an origin of the group in the Silurian. The placement in Pancrustacea clearly implies an aquatic origin, but aquatic stem-group hexapods are still unknown.

**Characteristics of Hexapod Genomes**

Some species of holometabolous insects are among the most commonly used model organisms. The fruit fly *Drosophila melanogaster* (Diptera), the honeybee *Apis mellifera* (Hymenoptera), some disease-transmitting mosquitoes (*Anopheles, Aedes, Diptera*), and the flour beetle (*Tribolium, Coleoptera*) have been widely used since the earliest genetic investigations. They contributed to the clarification of some important developmental and evolutionary mechanisms relevant for many living organisms (see Chapters 30–36). Since T. H. Morgan chose *Drosophila melanogaster* as the model organism for his ground-breaking genetic studies, a milestone in the biology of the twentieth century, thousands of researchers all over the world have based

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**Box 29.1 Morphological characters unique to hexapods**

- Body subdivided into three tagmata: head (with one pair of antennae), postcephalic body with a 3-segmented thorax (with three pairs of legs), and an abdomen with 11 segments
- Presence of a large fat body, mainly concentrated in the abdomen
- Complete fusion of the second maxilla to form a lower lip, the labium
- Midgut gland absent

**Box 29.2 Hexapods by the numbers**

- Number of species: approximately 1,000,000 described; estimated between 1.5 and 30 million, probably around 5 million
- Number of orders: 40
- Oldest fossils: *Rhyniella praecursor* (Collembola) and *Rhyniognatha hirsti* (Dicondylia), Devonian, in Scotland, about 400 million years old
- Largest species: some tropical species of stick insects (*Phasmida*) can reach a length of about 25 cm (*Pharmacia, Phobaeticus*)
- Smallest species: some parasitic wasps (*Hymenoptera*), approximately 0.2 mm long (family Myrmicidae)
- Shortest adult life: some mayflies (*Ephemeroptera*) live only few hours as adults, or even only minutes (for instance, some species of the genus *Dolania*)
- Longest life cycle: cicadas of the genus *Magicicada* have a developmental cycle of 17 years under normal conditions, and emerge synchronously in very large numbers
their investigations on this inconspicuous fly (or on closely related species). It is conceivable that it is the most intensively studied metazoan species (excluding humans), with the best-known physiology, genetics, and developmental biology. More recently, entire genomes of a larger sample of Hexapoda have been elucidated, and this has made it possible to do comparative studies of genome evolution for a very extensive branch of the tree of life. The mitochondrial genomes of Hexapoda are generally largely conserved, with relatively few gene arrangement changes from the presumptive arthropod body plan. The main differences are found in noncoding areas, which can vary greatly in length, and in the position of the tRNAs. The endoparasitic Strepsiptera apparently display a number of genetic peculiarities (see Box The Strepsiptera problem). Recently, when the entire genome of a basal species of the group was sequenced, the long-disputed system-
The Strepsiptera problem

The Strepsiptera (approximately 600 known species) are a small group with a worldwide distribution. The females are neotenic, and in the vast majority of species, endoparasites of other insects. The winged males do not feed and live only for a few hours. The extremely modified morphology (with strong miniaturized larvae of approximately 200 µm or less) and a highly aberrant life cycle have attracted the interest of researchers for more than 200 years. In the earliest descriptions, males of Strepsiptera were identified as hymenopterans close to ichneumonid wasps, which are also endoparasites of other insects as larvae. When the larviform females were discovered, alternative systematic affinities were suggested, close to Diptera (because of their wings modified as halteres), Lepidoptera, or within polyphagan Coleoptera, as a family (Stylolopidae) close to other groups with parasitic larvae. More recently, even their placement within Holometabola was discussed. Features differing from typical holometabolans are the appearance of compound eyes and external wing buds before the pupal stage, and the presence of an abdominal segment 11 and cerci in the larvae. A position close to Diptera was proposed based on analyses of ribosomal genes, but this was apparently an analytical artifact caused by their isolation (long branch attraction). A recent analysis of complete genomes including basal representatives of Strepsiptera (Mengenillidae) and beetles (Cupedidae) clearly shows that Strepsiptera are the sister group of a monophyletic Coleoptera. Combined with morphological evidence, this settles the Strepsiptera problem after a very long controversy.

Phylogenetic Results Contrasted with Previous Classifications

**Basal orders: Ellipura, Diplura, Archaeognatha, and Zygentoma**

Traditionally, Hexapoda are divided into “Entognatha” and Ectognatha (or Insecta), even though the systematic affinities of the three entognathous orders are still controversial. In the traditional concept, “Entognatha” form a clade divided into Ellipura and Diplura, and the entire lineage is placed as the sister group of Insecta. The Ellipura include Collembola (approximately 6000 species) and Protura (approximately 500 species). In contrast to the “Entognatha” concept, some morphological features and recent analyses of transcriptome data suggest that Ellipura are the sister group to a monophylum comprising the entire rest of Hexapoda—that is, Diplura + Ectognatha (Cercophora). Morphological arguments for Cercophora include the presence of cerci, paired claws, and a sperm axoneme pattern with an additional peripheral ring of nine microtubules. Ellipura are supported by a specific entognathous condition, a ventromedian furrow (linea ventralis), the absence of abdominal spiracles, and possibly the presence of the Tomosvary organ (although a similar structure occurs in Myriapoda). Other molecular studies support the monophyly of “Entognatha,” or a clade “Nonoculata” comprising the completely eyeless Diplura and Protura. It is evident that the entognathous relationships are presently not fully clarified.

The springtails (Collembola) are an ancient group with well-preserved Early Devonian fossils. Morphologically, it is highly derived, with unique autapomorphies such as the ventral tube of the first abdominal segment and a conspicuous jumping device, the furculum, at the apex of the 6-segmented abdomen. The furculum is normally kept below the abdomen and held in its resting position by the retinaculum, a small process of the third abdominal segment. The release of the furculum results in a catapulting effect, flinging the insect over a considerable distance with great velocity. Springtails are small (maximum length 6 mm) and can be extremely abundant in suitable habitats, such as leaf litter on a forest floor (up to 100,000 individuals...
als per 1 m³). They feed mainly on decaying organic matter and can play an important role in the formation of humus. With approximately 6000 known species, Collembola are quite diverse and more flexible in their habitat choice than the other apterygote groups, which are mostly confined to leaf litter or similar microhabitats. Some springtail species are aquatic, whereas others live in caves or tree canopies or along glaciers. Distribution is worldwide and the group is found in extreme latitudes. Springtails belong to one of the very few hexapod groups inhabiting Antarctica.

The Protura are very small insects (less than 2 mm), eyeless and normally unpigmented. They have completely lost their antennae and use the forelegs as tactile organs (functional quadrupedalism). Proturans are the only insects with anamorphic development. They live in soil and rotting organic materials. Many aspects of their biology and ecology are unknown.

The monophyly of Diplura (approximately 800 known species) is supported by the specific entognathous condition and the absence of the primary mandibular joint. Most species are largely unpigmented and small, but the largest species of the subgroup, a japygoid, reaches a length of approximately 5 cm. Like proturans, they are eyeless and live cryptically under bark and in leaf litter and similar microhabitats. In the ancestral body plan, cerci are always present and multisegmented; they are modified as unsegmented sclerotized hooks in the predaceous Japygidae, similar to what happens in the unrelated Dermaptera. As in the other primarily wingless hexapods, fertilization is external, with a spermatophore usually deposited on a stalk or thread formed by secretions.

The monophyly of Ectognatha (=Insecta) is undisputed and strongly supported by a series of apomorphies: a flagellar antenna, of which only the first segment, or scapus, has muscles (the rest of the antennal segments are the pedicellus, with Johnston’s organ, and a multisegmented flagellum); the presence of a tentorial bridge (corpotentorium); the subdivision of the tarsus, with a far-reaching reduction of the pretarsus; the ovipositor formed by appendages of the abd...
dominal segments 8 and 9; the terminal filament; and the formation of an embryonic amniotic cavity. The Archaeognatha (approximately 390 species) are the insect group with the maximum number of preserved plesiomorphies. A conspicuous feature is the large leg-like maxillary palp, arguably a plesiomorphic feature, as this also occurs in the extinct Monura. Archaeognatha is the sister group of Dicondylia, a clade comprised of Zygentoma and Pterygota. The most important dicondylian apomorphy is the second (anterior) mandibular joint, with a socket on the mandible and a condyle on the head capsule. Archaeognatha have a worldwide distribution, which, as in Collembola, includes the arctic regions. They feed on plant material in different states of decay. Their general body habitus is very similar to that of the silverfish, the Zygentoma.

The Dicondylia comprise the Zygentoma (silverfish) and Pterygota, the insects with wings. Recently, the paraphyly of Zygentoma was questioned based on a possible placement of Lepidotrichidae as the sister group of the remaining Zygentoma + Pterygota, based on morphological and molecular data. Lepidotrichidae is known from Baltic amber, and a single extant species, Tricholepidion gertschi, was discovered in California about 50 years ago. Recent analyses of transcripomes have unambiguously supported a clade Zygentoma, including Lepidotrichidae. Typical silverfish are characterized by distinctly reduced eyes (though not in Tricholepidion), a drop-shaped body with long cerci and a terminal filament, loss of most or all abdominal styli and coxal vesicles (not in Tricholepidion), and more or less cryptic habits. One species, Lepisma saccharina, is a regular inhabitant of houses, especially of moist kitchens or bathrooms. Zygentoma are primarily inhabitants of leaf litter and soil, but also live in rock crevices and caves. They feed on detritus and more or less decaying plant materials. As in the other apterygote hexapods, fertilization is external, with a spermatophore often attached by a silk thread to a substrate.

**Pterygota, or winged insects: The basal groups**

The monophyly of Pterygota is strongly supported by morphological and molecular data. The two pairs of wings and associated structures are undoubtedly autapomorphic. The fact that this is the most important single novelty in insect evolution is not affected by the controversy on the origin of wings (see *Evolutionary Tendencies* on pp. 348–349). In traditional classifications, Pterygota were subdivided into Palaeoptera (Odonata, dragonflies and damselflies, and Ephemeroptera, mayflies), which are unable to fold back their wings, and Neoptera (the remaining Pterygota orders) characterized by a folding mechanism at the wing base. However, alternative sister group relationships between Ephemeroptera and Neoptera (“Chia-stomyaria”) and between Odonata and Neoptera (“Metapterygota”) have been suggested. The former concept was mainly based on the dominant role of indirect flight muscles and the internal fertilization with a postabdominal aedeagus; the latter on modifications at the mandibular base and tracheal system. Recent analyses based on molecular and morphological data have revived the Palaeoptera. Odonata and Ephemeroptera appear to form the monophyletic sister group of Neoptera, but the alternative concepts cannot be ruled out with certainty at the moment.

Ephemeroptera (approximately 2500 species) have aquatic larvae and winged, short-lived adults. The duration of aquatic postembryonic development can vary from some months to several years. The adults have reduced mouthparts and a degenerated digestive tract. They do not feed during their very short life span—in some cases only few hours (the name Ephemeroptera refers to this)—which is sufficient for copulating and depositing eggs on the water surface or below the water. Hatching of the adults is synchronized, and in some cases this leads to mass emergence with thousands or millions of individuals. The nymphs are characterized by lateral abdominal tracheal gills and long cerci. The presence of a terminal filament is a unique plesiomorphy among the pterygote group. Another unique feature, probably also plesiomorphic, is the subimago, a winged preimaginal stage not present in any other pterygote group. Molting of a winged stage is likely associated with evolutionary costs. The loss of the subimago, which is short-lived but highly exposed to predators, probably occurred independently in Odonata and Neoptera.

One of the most important evolutionary innovations in Hexapoda is the ability to fold back the wings (neopterism), in contrast to Palaeoptera, which hold their wings either vertically above the abdomen (mayflies, damselflies) or extended laterally (dragonflies). This novelty is linked with modifications at the wing base (e.g., a subdivided median plate) and a specific muscle that causes a rotation in the wing joint. The folding enables neopteran insects to penetrate narrow spaces (e.g., under bark), and thus to stay in microhabitats which provide a moist atmosphere (reduced water loss) and protection from many predators (e.g., birds).

The monophyly of Neoptera is undisputed, but relationships among the main lineages were one of the most serious problems in systematic entomology, especially concerning the lower neopteran orders. Traditionally, Neoptera are subdivided into Polynoeoptera, Aceraria (or Paraneoptera), and Holometabola. The monophyly of Aceraria and Holometabola is widely accepted, but that of Polynoeoptera is very uncertain. In particular, the phylogenetic position of Plecoptera and Zoraptera are controversial, as is that of some
other orders, notably Grylloblattodea (Notoptera, ice crawlers), Dermaptera, and Embioptera. Recent studies based on morphological and molecular data tentatively support a clade Polyneoptera, and there has been considerable progress in clarifying the relationships among the orders.

Plecoptera (stoneflies, approximately 1700 species) are terrestrial as adults and aquatic as naïads (larvae). Functionally quadrupedal, they are only modest fliers and are always found close to bodies of water. The naïads usually prefer cold and oxygen-rich water, and are often found in swift streams in mountain regions (up to 5000 m). The short-lived adults of many species consume little food. The larvae are predators or feed on detritus.

Dermaptera (earwigs, approximately 1800 species) are characterized by cerci modified as forceps (as in the dipluran Japygidae) and strongly shortened and sclerotized forewings. In repose, the hind wings are covered by the forewings and folded in a complicated fan-like manner. Functional wings are present in the body plan but reduced in different subgroups, especially in ectoparasitic forms. Female brood care is a conspicuous characteristic of the group.

The Embioptera (webspinners) are a small group (approximately 300 species), mainly distributed in subtropical and tropical areas. The females are wingless, whereas the males possess simplified similar fore- and hind wings with a basal rupture-facilitating mechanism (body plan). A unique autapomorphy is the presence of large silk glands in the tarsi of the forelegs. They produce galleries under stones or wood with silk-like webs. The webspinners form colonies in their galleries, and as in Dermaptera, females perform brood care.

The Zoraptera (ground lice) are small insects (less than 3 mm) and one of the smallest orders (approximately 40 species), all in the single extant genus Zorotypus (an additional genus is known from Cretaceous amber). The dimorphic ground lice live mostly under bark but also occur in leaf litter, in soil substrate, and in decaying plant materials. Most individuals are wingless, blind, and partially depigmented, but darker forms with well-developed compound eyes and ocelli and functional wings also occur. Zorapterans are gregarious, but do not have division of labor or polymorphism.

The position of Zoraptera is one of the few remaining enigmas in insect systematics (the Zoraptera problem), but at least its placement within Polyneoptera has been resolved, in contrast to a sister group relationship with Acercaria (Paraneoptera), as originally proposed by Hennig. A possible sister group relationship with Embioptera is suggested by features of the wing base and the results of molecular studies, but this needs further confirmation. Preliminary analyses of transcriptome data suggest close affinities with Dermaptera. Zoraptera are characterized by a high uniformity in their general morphology in contrast to an extreme variability of the reproductive system, with a reversal to external transfer of a spermatophore in at least one species.

Well-supported large clades within Polyneoptera are Orthoptera (Caelifera and Ensifera, grasshoppers, crickets, locusts etc., approximately 20,000 species) (Chapter 31) and Dictyoptera (Mantodea, or praying mantises; Isoptera, or termites; and “Blattaria,” or roaches). The monophyly of Dictyoptera is well supported by morphological apomorphies such as a large genital chamber, an ootheca (a robust package containing the eggs), and an additional anterior tentorial bridge, and also by molecular data. A feature shared with Orthoptera and Phasmatodea are tegmina (leathery forewings) and euplantulae (tarsal attachment pads). It is conceivable that both derived characters were present in the body plan of Polyneoptera, with secondary losses occurring in different groups (e.g., loss of wings and vestigial euplantulae in Grylloblattodea).

It is well established that Mantodea are the sister group to the remaining Dictyoptera, that is, the roaches and termites. Roaches (approximately 4000 species) are mainly distributed in the tropical regions and contain some cosmopolitan species (e.g., Periplaneta americana) that are closely associated with human habitations in the broadest sense and can cause great damage as pests of stored products. A major breakthrough in insect systematics was the discovery that Isoptera (approximately 3000 species) are not a separate order, but a specialized subgroup of Blattodea, which implies the paraphyly of the traditional roaches (“Blattaria”). Recent analyses of morphological and molecular data unambiguously place termites (Isoptera) as sister group to the xylophagous and subsoil roach genus Cryptocercus. Therefore, termites are simply specialized roaches with highly developed social systems (eusociality), and are now recognised as a subordinate lineage (Termitoidae) within the more inclusive clade Blattodea. Termites feed on dead plant materials, frequently wood, and they can cause extreme economic damage by destroying wooden constructions, especially in tropical regions, where they reach their highest diversity. They live in colonies that can comprise millions of individuals. Their mounds can be conspicuous elements in tropical landscapes. The social system is characterized by morphologically different sterile castes—workers and soldiers—with a few individuals specialized in reproduction.

The Mantodea (praying mantises, approximately 2300 species) are specialized predators, with strongly modified raptorial forelegs. They occur in warmer regions, with the highest diversity in subtropical and tropical areas.

The Phasmatodea (approximately 3000 species) are generally large phytophagous insects, mainly dis-
Mantophasmatodea, the insect gladiators

In 2002, Klaus Klass and collaborators described a new order of insects, the first in about one hundred years: the Mantophasmatodea, or gladiators (also called heelwalkers or rock crawlers). The description was based on only three specimens from Africa, two of which had been kept in museum collections for more than half a century. They were considered to be immatures of an “orthopteroid” order, but referred to as very rare and enigmatic. They had already been described by Zompro as R haptophasma (incertae sedis), and were finally redescribed by Arillo and Engel as Adicophasma grylloblattoides. In the original description, diagnostic characters were used to exclude their placement in a known order without a formal phylogenetic analysis. Mantophasmatodea are characterized by predaceous habits, an orthognathous head, highly modified attachment structures (e.g., a pan-shaped arolium with acanthae), and female genitalia without an operculum. In a series of studies subsequent to the original description, more structural details were described, and analyses of molecular data were presented, including mitochondrial genomes. Meanwhile, more than twenty species have been described and placed in eight extant genera and three families, but a thorough revision is urgently required. The position of three fossil genera is also unclear. Morphological characters and molecular data consistently suggest placing Mantophasmatodea as sister group to Grylloblattoidea, a clade referred to as Xenonomia.

Mantophasmatodea was the most recent order of insects to be discovered. Its appearance resembles the immature stages of some orthopteroid insects; perhaps for that reason they remained unnoticed until their discovery in the Namibian desert in 2002.

The two very small orders Grylloblattoidea and Mantophasmatodea were discovered late, at the beginnings of the twentieth and twenty-first century, respectively. Grylloblattoidea (approximately 30 species) are restricted to cold areas of the Northern Hemisphere. Mantophasmatodea, the most recent insect order to be discovered, is a small group (approximately 20 species) occurring in southern Africa, but also known from Baltic amber (see Box Mantophasmatodea, the insect gladiators).

The position of Mantophasmatodea has been clarified. Morphological and molecular data strongly suggest a sister group relationship with Grylloblattoidea (Xenonomia). The complete reduction of the wings and the absence of a mandibular mola are potential synapomorphies of both groups. Interestingly, Mantophasmatodea share unusual features of the pretarsal and tarsal attachment structures with basal phasmatodeans (Timematodea, Agathemeridae), an enlarged pan-shaped arolium, and large euplantulae, both densely covered with microtrichia. However, the attachment structures of the ground-oriented Grylloblattoidea are strongly reduced.

A cercaria (Paraneoptera excluding Zoraptera) includes the orders Thysanoptera, Psocoptera, Phthiraptera, and Hemiptera (Heteroptera, or true bugs; Auchenorrhyncha, or cicadas; and Sternorrhyncha, or plant lice in a broad sense; see Chapter 32). The group’s monophyly was seemingly well supported but has been challenged by recent analyses of transcriptome data. The Phthiraptera (lice, approximately 3000 species) and Psocoptera (bark lice, approximately 5500 species) together form a monophyletic unit. The wingless and flattened Lepiscelidae, traditionally placed in Psocoptera, are the sister group of Phthiraptera, which makes the bark lice paraphyletic. The true lice are ectoparasites.
of mammals and birds, with numerous morphological adaptations to this specialized lifestyle. Psocopterans feed on algae, fungi and lichens; some specialized species can damage books (book lice), stored products, and specimens in natural history collections. Thysanoptera (thrips, approximately 5000 species) are very small insects with highly modified narrowed wings with fringes of hairs and a conspicuous eversible arolium. Their mouthparts are strongly asymmetric. Occasionally they can play a role as plant pests.

**Holometabola**

The monophyly of Holometabola is well established, but their placement within Neoptera is not fully clarified yet. The most widely accepted hypothesis is placement in a clade Eumetabola, which also includes Acarina, but this is still insufficiently supported.

The most prominent characteristic of Holometabola is complete metamorphosis. Larvae and adults differ strikingly in their morphology and usually also in their life habits. The evolutionary interpretation of the origin of holometabolism is controversial (see *Evolutionary Tendencies* on page 348). As an autapomorphy of the group, it is largely undisputed, even though quite similar modes of development have evolved in subordinate groups of Acarina (e.g., Thysanoptera). Another characteristic feature is the absence of ocelli in the larvae, but this feature is shared with Acarina and is possibly a synapomorphy of both lineages. Other holometabolous apomorphies are the invagination of the pterothoracic sternites (*endosterny*) and the absence of muscles and the Johnston’s organ in the larval antenna. Another characteristic feature is the position of the wing buds below the larval cuticle (the name Endopterygota refers to this condition), but distinct convexities are recognizable in the parasitic secondary larvae of Strepsiptera.

The congruent results of recent analyses of morphological and molecular data suggest that the interrelationships of the holometabolous orders are largely clarified. The group can be subdivided into three large clades: Hymenoptera (sawflies, wasps, bees, ants, etc.), Neuroptera + Coleoptera (beetles + Strepsiptera [Box 29.1]), and Mecopterida (Panorpida). The mecopterid orders include Lepidoptera (moths and butterflies) and Trichoptera (caddisflies), which together form the well-supported clade Amphiesmenoptera; and Diptera (flies and biting flies), Mecoptera and Siphonaptera, already united by Hinton and Hennig as Antliophora (*pump bearers*). This concept of Holometabola is largely congruent with the hypothesis suggested by Hinton and Hennig, with the notable exception of the megadiverse Hymenoptera, which are now placed as the first branch within Holometabola, and not as the sister group of Mecopterida. Apomorphies of Holometabola, excluding Hymenoptera, are the modification or reduction of the orthopteroid ovis-positor, the partial or complete reduction of the *glos-sae* and *paraglossae* and associated muscles, and the distinctly reduced number of the Malpighian tubules.

The monophyly of Mecopterida and its two subgroups, Amphiesmenoptera and Antliophora, is widely accepted. The Trichoptera are a medium-sized order (approximately 12,000 known species), with aquatic larvae that form cylindrical protective devices for the largely unsclerotized postcephalic body, using a broad variety of different materials (e.g., sand particles, pine needles, small mollusc shells etc.). The adults are characterized by wings densely covered with hairs, a character reflected by the name Trichoptera. The lepidopteran scales and the hairs on the trichopteran wings are homologous structures.

Within Antliophora, the monophyly of Diptera (approximately 135,000 species) has never been challenged (see Chapter 35), but the relationships of Siphonaptera and Mecoptera have been the subject of controversy. A sister group between the mecopteran family Boreidae (=Neomecoptera, a small group of approximately 30 flightless species distributed in colder areas of the Northern Hemisphere) and the specialized ectoparasitic Siphonaptera has been suggested, based on a single-gene analysis, and some morphological characters seemed to support this. However, the sperm structure and recent analyses of extensive molecular and morphological data sets unambiguously support a clade Mecoptera that includes the enigmatic family Nannochoristidae [=Nannomecoptera]. The Mecoptera (approximately 600 species) have ground-oriented terrestrial larvae (soil substrate, moss, and liverworts), with the notable exception of Nannochoristidae, which probably form the sister group of the remaining Mecoptera. Boreidae are probably the sister group of a well-supported clade Pistillifera (all other mecopteran families), which is characterized by a highly specialized sperm pump with a sclerotized pistil. The name scorpionflies refers to the specific condition of the male genitalia, the last segments of which resemble the tail of a scorpion. The mecopterans have a worldwide distribution, with the highest diversity in tropical areas. They are specialized predators (such as Bittacidae) or omnivorous. A characteristic feature is the nuptial gift offered by the males to the females, either a droplet of sugary secretions (Panorpidae), or a captured insect (Bittacidae). Siphonaptera (fleas, approximately 3,000 species) are ectoparasites of birds and mammals, completely wingless, and morphologically highly modified. The hind legs form a highly efficient jumping apparatus, the body is strongly compressed laterally, and the mouthparts are adapted to sucking blood.

The orders Neuroptera, Megaloptera, and Raphidioptera form a clade, Neuropterida, generally con-
considered to be closely related to the megadiverse Coleoptera (see Chapter 34) or the more inclusive Coleopterida (Coleoptera + Strepsiptera). Recent studies based on extensive morphological and molecular data sets have confirmed the latter hypothesis. The monophyletic origin of Neuropterida is widely accepted but not strongly supported by morphological features. The group is characterized by many preserved plesiomorphies—for instance, large wings with rich venation and without a coupling mechanism; a very complete set of cephalic and thoracic muscles; and a very ancestral pupa, which has even retained an astonishing degree of movability in the case of Raphidioptra. Traditionally, Raphidioptra (camelneck flies) were placed as sister group to Megaloptra (alderflies, dobsonflies). Both groups share derived features, such as a distinctly prognathous head and tarsomeres densely covered with adhesive hairs.

Primarily aquatic larvae and modified genital segments have been suggested as synapomorphies of Megaloptra and Neuroptera (lacewings, ant lions, etc.). This hypothesis was also supported in molecular studies based on single genes, and also in recent analyses of transcriptomes. Raphidioptra are a small group (approximately 220 species) restricted to the Northern Hemisphere. They typically live in temperate-zone forests. They are characterized by a strongly elongated prothorax (less so in the larvae) and a greatly elongated, parallel-sided and prognathous head (the common name snake flies is based on these features). Raphidioptra are specialized predators (mainly feeding on aphids) as larvae and adults, but in contrast to the neuropteran Mantispidae they lack raptorial forelegs. Megaloptra are also a small group (approximately 300 species). They are mainly characterized by plesiomorphic aquatic larvae with lateral abdominal tracheal gills. The short-lived adults do not feed, at least not on solid substrates. Species of the family Corydalidae can reach a body length of approximately 10 centimeters. Megaloptra (lace wings, ant lions, etc., approximately 6000 species) are characterized by unique larval sucking jaws formed by the mandibles and maxillae. The larvae of Nevorthidae and Sisyridae are aquatic, and those of Osmyliidae semiaquatic. The terrestrial larvae of Myrmeleontidae are known for their specialized ambush strategy (ant lions). The adults are highly diverse in their habitats, with forms resembling dragonflies, butterflies, or praying mantises.

Evolution of Characters

Despite of the relative morphological uniformity of hexapods, there exist numerous character systems with a very complex evolution. This includes adaptations to specific habitats (e.g., tree canopies, under bark, caves, rivers), extreme sexual dimorphism, adaptations to parasitism, a highly modified feeding apparatus, chemical mimesis, and others. The appendages are arguably the most variable structures. These include the antennae, mouthparts (mandibles, maxillae, labium), legs, wings, and especially the male copulatory organs. Fossorial legs or swimming legs have evolved independently within different lineages, and highly specialized raptorial legs in the hemimetabolous Mantodea, the holometabolous Mantispidae and some groups of Hemiptera. The wings can be modified in many different ways, for instance, as sclerotic elytra (Coleoptera), leathery tegmina (several groups of Polyneoptera), or halteres, gyroscopic sense organs. The mouthparts can be modified in many different ways and are strongly reduced in some groups (e.g., adult mayflies). Piercing, sucking mouthparts have evolved independently within Phthiraptera (lice), Hemiptera (bugs in the broadest sense), Diptera, and Siphonaptera (fleas). The highest diversity is found in the genital apparatus, notably in males. This is likely related to a form of selective pressure different from that affecting the general morphology. A lock-and-key mechanism occurs in some groups (e.g., geometrid moths) but one of the main triggers of the evolution of highly diverse genitalia is apparently cryptic female choice.

Evolutionary Tendencies

The origin of flight

The development of functional wings was arguably the most important evolutionary novelty in hexapod evolution. It is widely accepted that the ability to fly with a highly specific pterothoracic apparatus is an autapomorphy of Pterygota, and that the resulting improved dispersal capacity and escape mechanism have contributed to the extreme species richness. Excellent flying abilities have very likely resulted in accelerated diversification in groups such as Hymenoptera and Diptera. Despite the great interest in the flight apparatus of insects, its functional aspects were not well understood for a long time, and the evolutionary origin of wings is still a matter of controversy. Traditionally it is assumed that the wings of Pterygota originated as stiff lateral duplicatures of dorsal sclerites of the thoracic segments, which originally included the prothorax. They were initially used as gliding devices before articulated wings evolved, making active flight possible for extant pterygote insects. In an alternative hypothesis, it is assumed that aquatic immature stages belong to the body plan of Pterygota (they are terrestrial in Archaeognatha and Zygentoma), and that wings evolved from articulated lateral appendages primarily functioning as gills. The proto-wings supposedly allowed ancestral pterygotes to glide on the water surface, propelled by air currents. Ensuing optimizations of these
structures finally led to functional meso- and meta-thoracic wings and to active flight. This hypothesis is tentatively supported by the existence of certain pteropteran species that use their wings as sails to move on the water surface. Many modifications of the flight apparatus have evolved within Pterygota. The two most fundamental ones are the exclusive use of direct flight muscles in Odonata, and the dominant role of indirect flight muscles in all other groups of Pterygota including Ephemeroptera. Other important variations are functional (e.g., Auchenorrhyncha, Hymenoptera) or anatomical dipterism (Strepsiptera, Diptera), or the transformation of the forewings into leathery tegmina (e.g., roaches and Orthoptera), partly sclerotized hemelytra (Heteroptera), or entirely sclerotized elytra (Coleoptera).

The origin of the metamorphosis

Metamorphosis is a common strategy in the animal kingdom, enabling immatures and adults to use different habitats and food resources. This usually requires specific morphological and physiological adaptations, but has the advantage of reduced intraspecific competition. In insects there are distinctly different types of metamorphosis, ranging from minimal variation between immature stages and the adults (Polynoeoptera and most groups of Acercaria) to complete transformation in Holometabola. Complete metamorphosis is likely one factor that has contributed to the unparalleled diversification of Holometabola, which comprise about 80% of all hexapod species.

There are different hypotheses concerning the evolutionary origin of holometabolous development. Traditionally, larval stages of Holometabola are considered equivalent to the nymphs of *hemimetabolous* insects. Alternatively, the holometabolous larval stages can be considered homologues to the protonymph in hemimetabolous development—so to speak *free-living embryos*—and the holometabolous pupa (the last immature stage, which displays compound eyes and wing buds for the first time) (**Figure 29.1**) equivalent to hemimetabolous nymphal stages. The latter interpretation conforms better to physiological aspects (hormonal control) and anatomical data, and at present, it is more widely accepted.

Evolution of eusociality

Parental care and social structures occur in different groups of animals, but extreme forms of eusociality have evolved in Hexapoda. Defined in a strict sense, eusociality includes a division of labor (generally with sterile castes) and parental care, and colonies formed by individuals belonging to different generations. Eusociality has evolved in the hemimetabolous termites (Isoptera) and independently in different groups of the aculeatan Hymenoptera (ants, bees, wasps), but tendencies also occur in Sternorrhyncha, Thysanoptera (thrips), and some groups of Coleoptera (see Chapter 34). The existence of sterile individuals or individuals with reduced fertility that apparently sacrifice their own reproductive capacity for the benefit of the group is difficult to explain as an evolutionary phenomenon. Darwin, in his *On the Origin of Species* (1859), suggested the possibility that in these cases, natural selection affects not the individual but the entire colony, which constitutes a superorganism. Twentieth-century researchers favored a more reductionist explanation based on the specific system of sex determination in Hymenoptera, which maximizes the genetic legacy of a sterile individual when it manages to enhance reproduction in their direct female relatives. More recent hypotheses are based on group selection as a primary factor involved in the evolution of eusociality, with secondary effects resulting from the selection of related individuals, but this concept is not generally accepted yet.

Biogeography and Biodiversity

Hexapods are almost entirely (and primarily) absent from marine habitats, but they occur in virtually all terrestrial ecosystems, and also in a broad variety of limnic habitats. With their extreme species richness
and a high density of individuals in many groups, they form an immense biomass and a dominant element of the biosphere. It is apparent that they are a crucial factor in the functioning of most terrestrial ecosystems. Many hexapod species play a highly important role in the recycling of organic materials, as predators or parasites, as a food source for many groups of animals (e.g., spiders, freshwater fish, birds, mammals), and as pollinators of angiosperm plants. With a million described species (out of an estimated five million), the insects comprise about 60% of all known species, and more than 75% of the Metazoa (Animalia). The question of why hexapods were largely unable to invade the marine environment secondarily (rare exceptions are some midges and water striders of the genus Halobates) has been an issue of speculation for a long time. An entire series of possible explanations has been discussed, most of them not very convincing. Physiological limitations have been considered, and also competition with crustaceans. It has recently been noted that in deep water the hexapod tracheal tubes may collapse under the increased hydrostatic pressure, impeding the vertical migration typical of marine zooplankton. Hexapods, permanently confined to the well-illuminated surface layer of water would thus be easy prey for a multitude of predators.

There are cosmopolitan hexapod species, distributed either naturally or by human activities, but there are also many species and groups with restricted distribution that can be used for geological or biogeographic investigations (for instance, in the context of A. Wegener’s theory of continental drift, or A. R. Wallace’s biogeographical hypotheses). Their enormous species richness and ecological versatility make hexapods highly suitable for biodiversity research, including studies of functional biodiversity. However, a solid and detailed knowledge of taxonomy and classification is an indispensable prerequisite. Unfortunately, aside from the dramatic biodiversity crisis we are facing today, the expertise on many groups of hexapods is dwindling rapidly, as a result of low regard for taxonomic studies in the academic environment.

**Differentiation and Speciation**

The enormous species richness of hexapods is an intriguing topic for evolutionary biologists. What factors have triggered this unparalleled diversification? To go beyond ad hoc interpretations, it is necessary first to assess which clades are significantly more diverse than the rest. This leads to the identification of key nodes on the cladogram where there has been an acceleration of diversification, and then to the analysis of potential factors triggering the accelerated rate. Evolutionary novelties that have evolved independently in successful groups are good candidates for study: for instance, the highly efficient flight apparatus in Hymenoptera (functional dipterism) and Diptera (anatomical dipterism). A feature that evolved only once in hexapods, but has doubtlessly contributed immensely to their diversification, is the ability to fly, resulting in an efficient escape mechanism and a greatly improved dispersal ability. This interpretation is supported by the low diversity of all secondarily wingless groups or groups with a tendency to reduce the wings (e.g., Grylloblattodea, Mantophasmatodea, Zoraptera, Embioptera). Another crucial evolutionary novelty was arguably holometabolous development, even though the diversity of different groups of Holometabola is low (Megaloptera, Raphidioptera, Strepsiptera, Mecoptera). It is likely that diversification of the megadiverse holometabolous orders (Hymenoptera, Coleoptera, Lepidoptera, Diptera) was enhanced by successful coevolution with angiosperm plants in the Cretaceous, a phenomenon that probably also affected other groups, especially the phytophagous lineages of Hemiptera. It is apparent that several factors have contributed to the success of insect groups—for example, in the case of Coleoptera, the strong sclerotization of the adults and the extreme ecological versatility of the larvae. A general phenomenon which may have played an important role is sexual selection, but further investigation is required to evaluate its contribution to hexapod diversification.

**Principal Questions Remaining**

Even though there has been great progress in hexapod systematics and evolutionary biology in recent years, there remain many insufficiently clarified questions.

- What is the sister group to Hexapoda within the Pancrustacea?
- What did aquatic stem-group hexapods look like?
- How are the three entognathous orders related to one another?
- What is the evolutionary origin of wings?
- What are the relationships among the major lineages of Polyneoptera?
- What is the position of Zoraptera within Polyneoptera?
- What is the position of Thysanoptera within Hemiptera?
- What are the relationships within Hemiptera?

**Basic Bibliography**


