

recognition note that populations of head and body lice are separable only statistically on the basis of minor differences in body size; that coloration in human lice is highly variable, with lice often taking on the color of their surroundings; and that hybridization between head and body lice has been demonstrated in the laboratory and is thought to occur in nature.

### See Also the Following Articles

*Lice, Human* ■ *Medical Entomology* ■ *Psocoptera* ■ *Salivary Glands* ■ *Veterinary Entomology*

### Further Reading

- Durden, L. A., and Musser, G. G. (1994). The sucking lice (Insecta, Anoplura) of the world: A taxonomic checklist with records of mammalian hosts and geographical distributions. *Bull. Am. Mus. Nat. Hist.* **218**, 1–90.
- Ferris, G. F. (1951). The sucking lice. *Mem. Pacific Coast Entomol. Soc.* **1**, 1–320.
- Hellenthal, R. A., and Price, R. D. (1991). Biosystematics of the chewing lice of pocket gophers. *Annu. Rev. Entomol.* **36**, 185–203.
- Kim, K. C., Pratt, H. D., and Stojanovich, C. J. (1986). “The Sucking Lice of North America: An Illustrated Manual for Identification.” Pennsylvania State University Press, College Park, PA.
- Peterson, R. K. D. (1995). Insects, disease, and military history: The Napoleonic campaigns and historical perceptions. *Am. Entomol.* **41**, 147–160.
- Price, M. A., and Graham, O. H. (1997). “Chewing and Sucking Lice as Parasites of Mammals and Birds.” USDA Technical Bulletin No. 1849.
- Price, R. D., Hellenthal, R. A., Palma, R. L., Johnson, K. P., and Clayton, D. H. (2003). “The Chewing Lice: World Checklist and Biological Overview.” Illinois Natural History Survey Special Publication 24.
- Zinsser, H. (1934). “Rats, Lice and History: A Study in Biography.” Little Brown, Boston, MA.

by shared derived development of the hind wing as a haltere (balancing organ).

**paraphyletic** Referring to a taxonomic group (called a grade) derived from a single ancestor but not containing all descendants; grades share ancestral features (e.g., Mecoptera relative to Siphonaptera).

**polyphyletic** Referring to a taxonomic group derived from more than one ancestor and recognized by the possession of one or more features evolved convergently. For example, if the primitively wingless silverfish were united with secondarily wingless grasshoppers, beetles, and flies, the resulting group would be polyphyletic.

**sister groups** Species or monophyletic groups that arose from the stem species of a monophyletic group by a singular, identical splitting event. For example, the Lepidoptera and Trichoptera are sister groups; they shared a common ancestor that gave rise to no other lineage.

**synapomorphy (-ic)** A derived state shared among the members of a monophyletic group, in contrast to a **symplesiomorphy**—a shared ancestral (plesiomorphic) state from which phylogenetic relationships cannot be inferred.

**taxon (pl. taxa)** The general name for a taxonomic group at any rank.

**taxonomic rank** The classificatory level in the taxonomic hierarchy, for example, species, genus, family, order. No rank is absolute, and comparisons between ranks of different organisms are inexact or even misleading; despite this, traditional ranks used for insects—notably orders and families—have useful didactic and synoptic value.

## Phylogeny of Insects

Peter S. Cranston, Penny J. Gullan  
*University of California, Davis*

### Specialized Terms

**apomorphy (-ic)** A feature of an organism in the derived state, contrasted with an alternative one in the ancestral (primitive) state—a **plesiomorphy (-ic)** For example, with the character of forewing development, the sclerotized elytron is an apomorphy for Coleoptera, and the alternative, a conventional flying fore wing, is a plesiomorphy at this level of comparison.

**cladogram** Diagrammatic illustration of the branching sequence of purported relationships of organisms, based on distribution of shared derived features (synapomorphies).

**monophyletic** Referring to a taxonomic group (called a clade) that contains all descendants derived from a single ancestor and recognized by the possession of a shared derived feature(s). For example, the clade Diptera is monophyletic, recognized

Ideas concerning the phylogenetic relationships among the major taxa of arthropods, and the included insects, are dynamic. Although there is a single evolutionary history, efforts to uncover this phylogeny vary between different researchers, techniques, and character systems studied. No technique or character system alone can guarantee to reveal the true relationships of the studied taxa; in actuality, convergent (homoplastic) similarity that confuses relationships is common to all data. The evidence behind traditional systems, representing perhaps the thorough understanding of a single character system rather than an integration of all knowledge, sometimes cannot withstand detailed scrutiny. Molecular sequence data often appear to overturn previous ideas derived from morphological interpretation, but may be misleading due to undersampling, unrecognized sampling of alternative gene duplicates (paralogs), and/or inappropriate analyses. In this article, the different sources of evidence for the phylogenies that we have chosen to portray are assessed critically. Well-founded and less well-founded traditional, even refuted, relationships are discussed, and if resolution appears to be lacking, this inadequacy is identified.

### RELATIONSHIPS OF THE HEXAPODA TO OTHER ARTHROPODA

Insects belong to arguably the most successful major lineage of the phylum Arthropoda, the joint-legged animals. The latter clade comprises myriapods (centipedes, millipedes, and their relatives),

chelicerates (horseshoe crabs and arachnids), crustaceans (crabs, shrimps, and relatives), and hexapods (the six-legged arthropods, Insecta, and their relatives). Lobopods (onychophorans) sometimes have been included, but now almost universally are considered to lie outside of Arthropoda. Although traditionally each major arthropod group has been considered monophyletic, most have been suspected of non-monophyly by at least a few investigators. Results of molecular analyses have provided frequent challenges, particularly in suggesting the possible paraphyly of myriapods and of crustaceans. Even if considered monophyletic, estimation of inter-relationships has been a most contentious issue in biology, with almost every possible higher-level relationship finding some support. A once influential “Mantonian” view proposed three groups of arthropods, each derived from a different non-arthropod group, namely Uniramia (lobopods, myriapods and insects, united by single-branched legs), Crustacea, and Chelicerata. More recent morphological and molecular studies reject this hypothesis, proposing instead monophyly of arthropodization, but postulated internal relationships are diverse. Part of Manton’s Uniramia group—Atelocerata (also known as Tracheata) comprising myriapods and hexapods—finds support from morphological features including the occurrence of a tracheal system, Malpighian tubules, unbranched limbs, eversible coxal vesicles, postantennal organs, and anterior tentorial arms, the lack of any evidence of the second antenna of crustaceans or a homologous structure, and the mandible comprising a complete limb, rather than the limb base of the crustacean mandible. Proponents of this relationship saw either Crustacea grouping with chelicerates and extinct trilobites, separate from Atelocerata, or forming its sister group, in a clade Mandibulata. Among all these schemes, the closest relatives of Hexapoda were proposed to be with, or possibly within, Myriapoda.

In contrast, novel and some rediscovered shared morphological features, including from the nervous system (e.g., brain structure, neuroblast formation and axon development), the visual system (e.g., fine structure of the ommatidia, optic nerves), and the process and control of development, especially segmentation, argued for a close relationship of Hexapoda to Crustacea, a group termed Pancrustacea, excluding myriapods. Furthermore, all analyzed molecular sequence data with adequate signal to resolve relationships supports Pancrustacea rather than Atelocerata. As more nuclear, mitochondrial gene order and protein-encoding gene data have been examined, for an ever-wider set of taxa, little or no support has been found for any alternative to Pancrustacea. This does not imply that such analyses all recover Pancrustacea—sometimes certain “problematic” taxa have had to be removed, even from sparsely sampled data sets, and evidently certain genes do not retain strong phylogenetic signal from very old radiations.

Clearly features understood previously to infer monophyly of Atelocerata must be re-considered. Postantennal organs occur in Hexapoda, but only in Collembola and Protura, and are suggested to be convergent with the organs in Myriapoda. Shared absence of features (such as lack of second antenna) cannot be taken as positive evidence of relationship. Malpighian tubules also are present (surely convergently) in arachnids, and evidence for homology between their structure in hexapods and myriapods remains inadequately studied. Coxal vesicles are not developed in all clades and may not be homologous in Myriapoda and in those Hexapoda possessing these structures. Thus, morphological characters traditionally used to support Atelocerata include states that may be non-homologous and convergently acquired associated with development of terrestriality, are not distributed across all included taxa, or are inadequately surveyed across the immense morphological diversity of the arthropods.

A major finding from molecular embryology, that the developmental expression of a homeotic gene (*Dll—Distal-less*) in the mandible of studied insects was the same as in sampled crustaceans, challenges the independent derivation of hexapod mandibles from those of crustaceans. This developmental homology for mandibles substantiates an earlier morphological hypothesis, and undermines Manton’s argument for arthropod polyphyly. In summary, data derived from the neural, visual, and developmental systems, even though sampled across relatively few taxa, appear to reflect more accurately phylogeny than data from many earlier studies of external morphology.

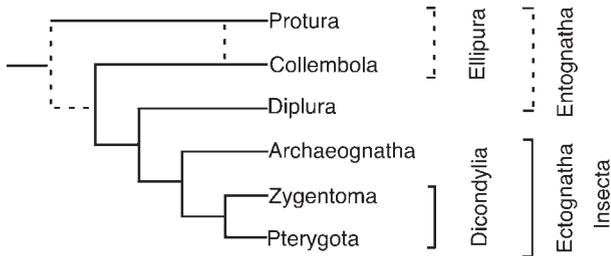
The question remains as to whether part or all Crustacea constitutes the sister-group to Hexapoda. Morphology generally supports a monophyletic Crustacea, but recent molecular data imply paraphyly, with only part of the Crustacea (generally either Malacostraca alone or Branchiopoda alone) being sister to Hexapoda.

### THE EXTANT HEXAPODA

Hexapoda (ranked usually as superclass) contains all six-legged arthropods; diagnosis includes possession of a unique tagmosis, namely specialization of successive body segments that more or less unite to form sections or tagmata: head, thorax, and abdomen. The head is composed of a pregnathal region (often considered to be 3 segments) and 3 gnathal segments bearing mandibles, maxillae and labium respectively; the eyes are variously developed, and sometimes absent. The thorax comprises 3 segments each of which bears one pair of legs, and each thoracic leg has a maximum of 6 segments in extant forms, but is argued to have been primitively 11-segmented with up to 5 exites (outer appendages of the leg), a coxal endite (an inner appendage of the leg) and 2 terminal claws. Primitively the abdomen has 11 segments plus a telson or homolog; abdominal limbs, if present, are smaller and weaker than those of the thorax, and primitively occurred on all segments except the 10th.

Hexapods undoubtedly include taxa whose ancestors were wingless and terrestrial. The extant non-insect hexapods, treated as orders, are Protura (proturans), Collembola (springtails), and Diplura (diplurans). Recent data from ribosomal RNA gene sequences suggest that this grouping of three orders, traditionally named the Entognatha, may be monophyletic, in contrast to results of previous morphological analyses. True Insecta are the Archaeognatha (bristletails), the Zygentoma (=Thysanura; silverfish), and the huge radiation of Pterygota (primary winged hexapods). Insecta is treated as a class, and if monophyly of the Entognatha is confirmed, then it also would be a class, although at present most classifications recognize each of the Collembola, Diplura, and Protura as classes of equal rank to Insecta.

Relationships among the component taxa of Hexapoda are uncertain, although the cladogram shown in Fig. 1 and the classification presented in the sections that follow reflect one current view based on morphology. Traditionally, Collembola, Protura, and Diplura were grouped as the Entognatha, based on the apparently similar morphology of the mouthparts. The mouthparts of Insecta (Archaeognatha+Zygentoma+Pterygota) are exposed (ectognathous), whereas those of Entognatha are enclosed in folds of the head. Two different types of entognathy have been recognized, one shared by Collembola and Protura and the second found only in Diplura. Other morphological evidence indicates that Diplura may be closer to Insecta than to other entognathans and thus Entognatha may be paraphyletic (as indicated by the broken line in Fig. 1). In contrast to the relationships suggested in Fig. 1, nucleotide sequence data from ribosomal RNA genes suggest that the Diplura may be the sister group to Protura, a grouping termed the “Nonoculata” due to



**FIGURE 1** Cladogram depicting one view of relationships among, and inferred classification of, the higher ranks Hexapoda (six-legged Arthropoda). Dashed lines indicate uncertainty in relationships or paraphyly in classification.

the absence of eyes in these hexapods, with the Collembola sister to Diplura+Protura.

### Protura (Proturans)

Proturans are small, delicate, elongate, mostly unpigmented hexapods, lacking eyes and antennae, with entognathous mouthparts consisting of slender mandibles and maxillae that slightly protrude from the mouth cavity. Maxillary and labial palps are present. The thorax is poorly differentiated from the 12-segmented abdomen. Legs are 5-segmented. A gonopore lies between segments 11 and 12, and the anus is terminal. Cerci are absent. Larval development is anamorphic, that is with segments added posteriorly during development. Protura either is sister to Collembola, forming Ellipura in a weakly-supported relationship based on similarity of the entognathous mouthparts and lack of cerci, or is sister to just the Diplura, as suggested by ribosomal RNA genes.

### Collembola (Springtails)

Collembolans are minute to small and soft bodied, often with rudimentary eyes or ocelli. The antennae are 4- to 6-segmented. The mouthparts are entognathous, consisting predominantly of elongate maxillae and mandibles enclosed by lateral folds of head, and lacking maxillary and labial palps. The legs are 4-segmented. The abdomen is 6-segmented with a sucker-like ventral tube, a retaining hook and a furcula (forked jumping organ) on segments 1, 3, and 4, respectively. A gonopore is present on segment 5, the anus on segment 6. Cerci are absent. Larval development is epimorphic, i.e., with segment number constant through development. Collembola form either the sister group to Protura comprising Ellipura, or the sister group to Diplura+Protura, or are sister to Diplura+Insecta, depending on the character data analyzed.

### Diplura (Diplurans)

Diplurans are small to medium-sized, mostly unpigmented, possess long, moniliform antennae (like a string of beads), but lack eyes. The mouthparts are entognathous, with tips of well-developed mandibles and maxillae protruding from the mouth cavity, and maxillary and labial palps reduced. The thorax is poorly differentiated from the 10-segmented abdomen. The legs are 5-segmented and some abdominal segments have small styles and protrusible vesicles.

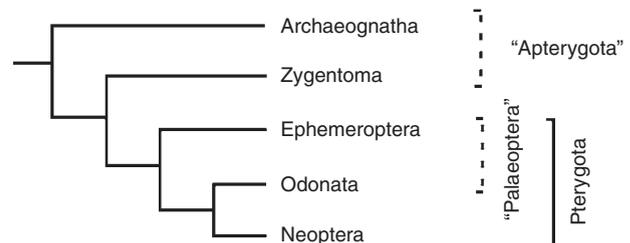
A gonopore lies between segments 8 and 9; the anus is terminal. Cerci are filiform to forceps-like. The tracheal system is relatively well developed, whereas it is absent or poorly developed in other entognath groups. Larval development is epimorphic. Diplura either forms the sister group to Insecta, or is sister to the Protura within the Entognatha.

### Class Insecta (True Insects)

Insects range from minute to large (0.2–360 mm in length) and are very variable in appearance. They typically have ocelli and compound eyes, at least in adults, and the mouthparts are exposed (ectognathous), with the maxillary and labial palps usually well developed. The thorax is variably developed in immature stages, but distinct in adults with degree of development dependent on the presence of wings. Thoracic legs have more than 5 segments. The abdomen is primitively 11-segmented with the gonopore nearly always on segment 8 in the female and segment 9 in the male. Cerci are primitively present. Gas exchange is predominantly tracheal with spiracles present on both the thorax and abdomen, but variably reduced or absent (e.g., in many immature stages). Larval or nymphal development is epimorphic, that is, with the number of body segments constant during development.

The insects may be divided into two groups. Monocondylia is represented by just one small order, Archaeognatha, in which each mandible has a single posterior articulation with the head, whereas Dicondylia (Fig. 1), which contains the overwhelming majority of species, is characterized by mandibles with secondary anterior articulation in addition to the primary posterior one. The once traditional group “Apterygota” for the primarily wingless taxa Archaeognatha + Zygentoma is paraphyletic and rejected (Fig. 2).

**ARCHAEOGNATHA (ARCHAEOGNATHANS, BRISTLE-TAILS)** Archaeognathans are medium-sized, elongate-cylindrical apterygotes, with some 500 species in two extant families. The head bears three ocelli and large compound eyes that are in contact medially. The antennae are multisegmented; the mouthparts project ventrally and can be partially retracted into the head and include elongate mandibles with two neighboring condyles each, and elongate 7-segmented maxillary palps. Coxal styles are present on the legs; the tarsi are 2- to 3-segmented. The abdomen, which continues in an even contour from the humped thorax, bears ventral muscle-containing styles (representing reduced limbs) on segments 2–9, and generally 1–2 pairs of eversible vesicles medial to the styles on segments 1–7. Cerci are multisegmented and shorter than the median caudal appendage. Sperm transfer is indirect via sperm droplets



**FIGURE 2** Cladogram depicting relationships among, and inferred classification of, higher ranks within the Insecta. Dashed lines indicate paraphyly in classification.

attached to silken lines or by stalked spermatophore. Development occurs without change in body form.

The two families of recent Archaeognatha, Machilidae and Meinertellidae, form an undoubted monophyletic group, whose position as sister group to Dicondylia (Zygentoma+Pterygota) (Figs. 1 and 2) appears undisputed.

**ZYGENTOMA (THYSANURA, SILVERFISH)** Zygentomans (thysanurans) are medium-sized, dorso-ventrally flattened apterygotes with almost 400 species in five extant families. Eyes and ocelli are present, reduced, or absent, and the antennae multisegmented. The mouthparts are ventrally to slightly forward projecting and include a special form of double-articulated (dicondylous) mandibles and 5-segmented maxillary palps. The abdomen continues the even contour of the thorax, and includes ventral muscle-containing styles (representing reduced limbs) on at least segments 7–9, sometimes on 2–9, and with eversible vesicles medial to the styles on some segments. Cerci are multisegmented and subequal to the length of the median caudal appendage. Sperm transfer is indirect via a spermatophore that the female picks up from the substrate. Development occurs without change in body form. Zygentoma is the sister group to the Pterygota.

**PTERYGOTA** Pterygotes are winged or secondarily apterous insects, in which the thoracic segments of adults are usually large with the meso- and metathorax variably united to form a pterothorax. The lateral regions of the thorax are well developed. The 8–11 abdominal segments lack styles and vesicular appendages, and only Ephemeroptera ever have a median terminal filament. The spiracles primarily have a muscular closing apparatus. Mating is by copulation. Metamorphosis is hemi- to holometabolous, with no adult ecdysis, except for the ephemeropteran subimago (subadult).

**“Palaeoptera”: An Informal Grouping or a Monophyletic Group of Pterygotes?** Palaeopteran wings are unable to be folded against the body at rest because articulation is via axillary plates that are fused with veins. Extant orders typically have triadic veins (paired main veins with intercalated longitudinal veins of opposite convexity/concavity to the adjacent main veins) and a network of cross-veins. This wing venation and articulation, substantiated by palaeontological studies on similar features, has suggested that Odonata and Ephemeroptera form a monophyletic group, Palaeoptera, sister to Neoptera (all remaining extant and primarily winged orders). However, some assessments of morphology and some molecular evidence reject a monophyletic Palaeoptera. At present, relationships among the Ephemeroptera, Odonata, and Neoptera must be considered unresolved. Here Ephemeroptera is treated as sister to the Metapterygota, the Odonata+Neoptera, with Odonata alone as the sister group to Neoptera, giving a higher classification of Pterygota into three divisions. Metapterygota is defined by the loss of the subimaginal molt, loss of the median caudal filament of the abdomen, fixation of the anterior mandibular articulation, and by features of the wing and leg tracheation.

**Ephemeroptera (Mayflies)** Ephemeroptera has a fossil record dating back to the Carboniferous and is represented today by a few thousand species. In addition to their palaeopteran features, mayflies display a number of unique characteristics including the non-functional, strongly reduced adult mouthparts, the presence of just one axillary plate in the wing articulation, a hypertrophied costal brace, and male forelegs modified for grasping the female during copulatory flight. Subimago (subadult stage) retention

is unique. Nymphs (larvae) are aquatic and the mandible articulation, which is intermediate between monocondylous and the dicondylous ball and socket joint of all higher Insecta, may be diagnostic. Historic contraction of ephemeropteran diversity, and remnant high levels of homoplasy renders phylogenetic reconstruction difficult. Ephemeroptera traditionally was divided into two suborders: Schistonota (with nymphal forewing pads separate from each other for over half their length) containing superfamilies Baetoidea, Heptagenioidea, Leptophlebioidea and Ephemeroidea, and Pannota (“fused back”—with more extensively fused forewing pads) containing Ephemerelloidea and Caenoidea. Recent studies suggest this concept of Schistonota is paraphyletic. Families Baetiscidae and Prosoptomatidae, whose nymphs have unusually developed thoracic shields, have been withdrawn from the Caenoidea and placed now in suborder Carapacea. Currently three or four suborders are recognized: Carapacea (Baetiscidae + Prosoptomatidae), Furcatergalia (the pannote families plus some other families such as Leptophlebiidae), Pisciforma (the minnow-like mayflies), and Setisura (the flat-headed mayflies); sometimes the Setisura are placed in the Pisciforma.

**Odonata (Dragonflies and Damselflies)** Odonates have palaeopteran as well as many additional unique features, including the presence of two axillary plates (humeral and posterior axillary) in the wing articulation and many features associated with specialized copulatory behaviour, including possession of secondary copulatory apparatus on ventral segments 2 and 3 of the male and the formation of a tandem wheel during copulation. The immature stages are aquatic and possess a highly modified prehensile labium for catching prey.

There are nearly 6000 species of odonates. Traditionally, odonatologists recognized three groups of taxa, Zygoptera (damselflies), Anisozygoptera, and Anisoptera (dragonflies), generally ranked as suborders, but the extant Anisozygoptera now are included with Anisoptera in the suborder Epirocta (with living Epiophlebiidae sister to rest of Anisoptera). Assessment of the monophyly or paraphyly of the suborders has relied very much on characters derived from the very complex wing venation, but homology of these features within the odonates and between other insects has been substantially prejudiced by prior phylogenetic ideas. Thus, the Comstock and Needham wing vein naming system implies that the common ancestor of modern Odonata was anisopteran and the zygopteran venation arrived by reduction. In contrast, the Tillyard system implied Zygoptera is a grade on the way to Anisozygoptera, which itself is a grade on the way to Anisoptera. The recent consensus, based on morphological and molecular data, has both Zygoptera and Epirocta monophyletic, and Anisoptera as the monophyletic sister group to some extinct anisozygopterans with Epiophlebiidae (formerly recognized as the only living anisozygopterans) sister to Anisoptera+extinct anisozygopterans.

**Neoptera** All winged and secondarily wingless insects except for the two palaeopteran orders belong to this large clade of the Pterygota. Neopteran insects diagnostically have wings capable of being folded back against their abdomen when at rest, with wing articulation deriving from separate movable sclerites in the wing base, and wing venation with fewer (or lacking completely) triadic veins and mostly lacking anastomosing (joining) cross-veins.

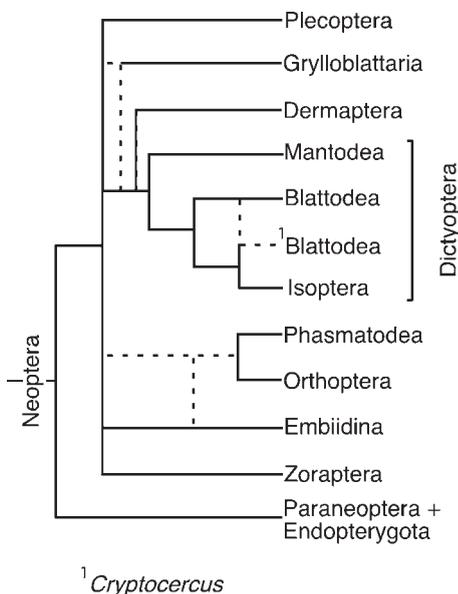
The phylogeny (and hence classification) of the neopteran orders is still the subject of debate, mainly concerning (a) the placement of many extinct orders described only from fossils of variably adequate

preservation, (b) the relationships among the Polyneoptera (orthopteroid and plecopteroid orders), and (c) the relationships of the highly derived Strepsiptera.

However, the summary that follows reflects one possibility among current interpretations, based on both morphology and molecules. No single or combined data set provides unambiguous resolution of insect order-level phylogeny, and there are several areas of controversy (such as the position of the Strepsiptera) arising from both inadequate data (insufficient or inappropriate taxon sampling) and character conflict within existing data. In the absence of a robust phylogeny, ranking is somewhat subjective and “informal” ranks abound.

A group of up to 11 orders termed the orthopteroid-plecopteroid assemblage (if monophyly is uncertain) or Polyneoptera (if monophyletic) is considered to be sister to the remaining Neoptera. The remaining neopterans can be divided readily into two monophyletic groups, namely Paraneoptera and Endopterygota (= Holometabola). These three clades may be given the rank of subdivision.

**Polyneoptera (or Orthopteroid–Plecopteroid Assemblage of Neoptera)** [Isoptera, Blattodea, Mantodea, Dermaptera, Grylloblattaria (=Grylloblattodea or Notoptera), Plecoptera, Orthoptera, Phasmatodea, Embiidina (= Embioptera), Zoraptera, Mantophasmatodea] The relationships of these neopteran orders are poorly resolved with several, often contradictory, relationships being suggested by morphology. The 11 included orders may form a monophyletic group, based on the shared presence of tarsal plantulae (lacking only in Zoraptera) and by limited, but increasing, molecular information. Within Polyneoptera, only the grouping comprising Blattodea (cockroaches), Isoptera (termites), and Mantodea (mantids)—the Dictyoptera (Fig. 3)—is robust. Although each of these three orders is distinctive, certain features of the head skeleton (perforated tentorium), mouthparts (paraglossal musculature), digestive system (toothed proventriculus), and female genitalia (shortened ovipositor above a large subgenital plate) demonstrate monophyly of Dictyoptera, substantiated by nearly all molecular analyses. However, as seen below, views on the internal relationships



**FIGURE 3** Cladogram depicting relationships among, and inferred classification of, orders of the Polyneoptera (Neoptera). Dashed lines indicate uncertainty in relationships. Mantophasmatodea not included.

are changing. Dermaptera (earwigs) may be sister to Dictyoptera, and Grylloblattaria (rock crawlers; now apterous, but with winged fossils) may be sister to this grouping.

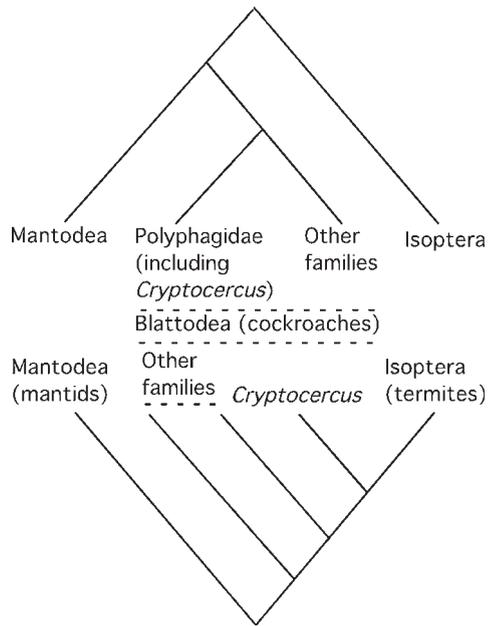
Some molecular data suggest that Orthoptera (crickets, katydids, grasshoppers, locusts, etc.), Phasmatodea (stick insects or phasmids), and Embiidina (webspinners) may be closely related, forming Orthopteroidea in the sense of Hennig. The relationships of Plecoptera (stoneflies), orthopteroids, Zoraptera (zorapterans), and the recently discovered Mantophasmatodea to each other and to the above groupings are less well understood.

**Isoptera (Termites, White Ants)** Isoptera forms a small order of eusocial hemimetabolous neopterans, with more than 2600 described species, living socially with polymorphic caste systems of reproductives, workers, and soldiers. The mouthparts are typically blattoid, being mandibulate but varying among castes, with some soldiers having bizarre development of mandibles or a nasus (snout). The compound eyes are frequently reduced, the antennae are long and multisegmented, and the fore wings and hind wings are generally similar, membranous, and have restricted venation. *Mastotermitidae* (Mastotermitidae) has complex wing venation and a broad hind wing anal lobe and is exceptional among termites in that the female has a reduced blattoid-type ovipositor. The male external genitalia are weakly developed and symmetrical, in contrast to the well complex, symmetrical genitalia of Blattodea and Mantodea.

Isopteran relationships are somewhat controversial, although they have always been considered to belong in Dictyoptera close to Blattodea. Recent studies that include the structure of the proventriculus and molecular sequence data suggest that termites arose from within the cockroaches, thereby rendering the latter group paraphyletic. Under this scenario, the (wingless) woodroaches of North America and eastern Asia (genus *Cryptocercus*) form the sister group to Isoptera. This contrasts with alternative suggestions that the semisociality (parental care and transfer of symbiotic gut flagellates between generations) of *Cryptocercus* was convergent with certain features of termite sociality, and independently originated within the true cockroaches. These two contrasting views are shown in Fig. 4. The social system and general morphology of *Mastotermitidae* suggests a cockroach-like condition, and most phylogenies place this group as sister to remaining extant Isoptera. Of considerable interest is the wide distribution and species richness of Mastotermitidae in Cretaceous times, compared to the reduced diversity of the extant family, which comprises just one species in northern Australia.

**Blattodea (Cockroaches)** Blattodea contains about 4000 species in at least seven families worldwide. They are hemimetabolous, dorsoventrally flattened insects with filiform, multisegmented antennae, and mandibulate, ventrally projecting mouthparts. The prothorax has an enlarged, shield-like pronotum, often covering the head; the meso- and metathorax are rectangular and subequal. The fore wings are sclerotized as tegmina, which protect membranous hind wings folded fan-like at rest beneath the tegmina and characterized by many vein branches and a large anal lobe; wings are often reduced. Often the legs are spiny and the tarsi are 5-segmented. The abdomen has 10 visible segments, with a subgenital plate (sternum 9), bearing in the male well-developed asymmetrical genitalia, with one or two styles, and concealing the reduced 11th segment. Cerci have 1 or, usually, many segments; the female ovipositor valves are concealed beneath tergum 10.

Although long considered an order (and hence monophyletic), convincing evidence has been produced by several independent researchers that the termites arose from within the cockroaches, and



**FIGURE 4** Cladogram depicting alternative relationships among Dictyoptera. Dashed lines indicate paraphyly in classification. The lower cladogram shows that most recent consensus view.

the “order” thus is rendered paraphyletic. The sister group of the Isoptera appears to be the cockroach genus *Cryptocercus* (Fig. 4).

**Mantodea (Mantids)** Mantodea contains some 2300 species in 8–14 families. Mantids are hemimetabolous predators, with males generally smaller than females. The small, triangular head is mobile, with slender antennae, large, widely separated eyes and mandibulate mouthparts. The prothorax is narrow and elongate, with the meso- and metathorax shorter. The fore wings form leathery tegmina with a reduced anal area; the hind wings are broad and membranous, with long unbranched veins and many cross-veins, but often are reduced or absent. The forelegs are raptorial, whereas the mid and hind legs are elongate for walking. The abdomen has a visible 10th segment, bearing variably segmented cerci. The ovipositor is predominantly internal and the external male genitalia are asymmetrical.

Mantodea form the sister group to Blattodea+Isoptera, and share many features with Blattodea such as strong direct flight muscles and weak indirect (longitudinal) flight muscles, asymmetrical male genitalia and multisegmented cerci. Derived features of Mantodea relative to Blattodea involve modifications associated with predation, including leg morphology, an elongate prothorax, and features associated with visual predation, namely the mobile head with large, separated eyes, and several peculiarities of the proventriculus. Internal relationships of Mantodea have been uncertain, and many of the existing families and subfamilies have been shown to be paraphyletic based on recent molecular data.

**Grylloblattaria (Notoptera, Grylloblattodea) (Grylloblattids or Rock Crawlers)** Grylloblattaria contains one family (Grylloblattidae) with fewer than 30 species, restricted to western North America and central to eastern Asia, and particularly tolerant of cold and high elevations. Grylloblattids are moderate-sized, soft-bodied insects with anteriorly projecting mandibulate mouthparts and compound eyes that either are reduced or absent. The antennae are multisegmented and the mouthparts mandibulate. The quadrate prothorax is larger

than the meso- or metathorax, and the wings are absent. The legs are adapted for running, with large coxae and 5-segmented tarsi. There are 10 visible abdominal segments with rudiments of segment 11, including 5–9-segmented cerci. The female has a short ovipositor, and the male genitalia are asymmetrical.

The phylogenetic placement of Grylloblattaria is controversial, generally being argued to be relictual, either “bridging the cockroaches and orthopterans” or “primitive amongst orthopteroids.” The antennal musculature resembles that of mantids and embiids, mandibular musculature resembles Dictyoptera, and the maxillary muscles those of Dermaptera. Embryologically grylloblattids appear closest to the orthopteroids. Some molecular phylogenetic data place the Grylloblattaria as sister to the Mantophasmatodea.

**Dermaptera (Earwigs)** Dermaptera is a worldwide order, modest in size, with an unstable family classification and about 1900 species. Adult earwigs are elongate and dorsoventrally flattened with mandibulate, forward-projecting mouthparts, compound eyes ranging from large to absent, no ocelli, and short annulate antennae. The tarsi are 3-segmented with a short second tarsomere. Many species are apterous or, if winged, the fore wings are small, leathery, and smooth, forming unveined tegmina, and the hind wings are large, membranous, semi-circular, and dominated by an anal fan of radiating vein branches connected by cross-veins; when at rest, the hind wings are folded fan-like and then longitudinally, protruding slightly from beneath the tegmina.

The five species of suborder Arixeniina are commensals or ectoparasites of bats in Southeast Asia. A few species of semi-parasites of African rodents have been placed in a suborder Hemimerina. These earwigs are blind, apterous, have rod-like forceps, and exhibit pseudoplacental viviparity. Recent morphological study of Hemimerina suggests derivation from within Forficulina, rendering that suborder paraphyletic. The relationships of Arixeniina to more “typical” earwigs (Forficulina) are uninvestigated. Within Forficulina, only four (Karshiellidae, Apachyidae, Chelisochidae, and Forficulidae) of nine families proposed appear to be supported by synapomorphies. Other families may not be monophyletic, as much weight has been placed on plesiomorphies, especially of the penis specifically and genitalia more generally, or homoplasies (convergences) in furcula form and wing reduction.

The relationship of Dermaptera to other polyneopteran orders is uncertain, although a sister group relationship to Dictyoptera has been suggested based on morphology, including many features of the wing venation.

**Plecoptera (Stoneflies)** Plecoptera contains some 16 families and more than 2000 species, predominantly living in temperate and cool areas. The adult is mandibulate with filiform antennae, bulging compound eyes, two or three ocelli, and subequal thoracic segments. The fore wings and hind wings are membranous and similar except that the hind wings are broader; when folded, the wings partly wrap the abdomen and extend beyond the abdominal apex; aptery and brachyptery are frequent. The abdomen is soft and visibly 10-segmented, although remnants of segments 11 and 12 are present, including cerci. Nymphs have many (up to 33) aquatic instars, which have fully developed mandibulate mouthparts, and wings pads first become visible when half-grown.

Monophyly of the order is supported by a few morphological features, including in the adult the looping and partial fusion of gonads and male seminal vesicles, and the absence of an ovipositor. In nymphs the presence of strong, oblique, ventrolongitudinal muscles running intersegmentally allowing lateral undulating swimming, and the probably widespread “cercus heart,” an accessory circulatory

organ associated with posterior abdominal gills, support the monophyly of the order. Gills may be present in nymphal Plecoptera on almost any part of the body, or may be absent, causing problems of homology of gills among families, and between Plecoptera and other orders. Whether Plecoptera are derived from an aquatic or terrestrial ancestor is debatable.

The phylogenetic position of Plecoptera is certainly amongst “lower Neoptera,” possibly as sister group to the remainder of Neoptera. However, some molecular and combined molecular plus morphological evidence tends to support a more derived position with the Polyneoptera.

Internal relationships have been proposed as two predominantly vicariant suborders, the austral Antartoperlaria and northern Arctoperlaria. The monophyly of Antartoperlaria is argued based on the unique sternal depressor muscle of the fore trochanter, lack of the usual tergal depressor, and presence of floriform chloride cells, which may have a sensory function. Some of the included taxa are the large-sized Eustheniidae and Diamphipnoidae, the Gripopterygidae and Austroperlidae—all families with a southern hemisphere “Gondwanan”-type distribution. Recent molecular studies support this clade.

The sister group Arctoperlaria lacks defining morphology, but is united by a variety of mechanisms associated with drumming (sound production) associated with mate finding. The component families Scopuridae, Taeniopterygidae, Capniidae, Leuctridae, and Nemouridae (including Notonemouridae) are essentially distributed in the northern hemisphere with a lesser radiation of Notonemouridae into the southern hemisphere. Molecular studies suggest the paraphyly of Arctoperlaria, with most elements of Notonemouridae forming the sister group to the remainder of the families. Relationships amongst extant Plecoptera are proving important in hypothesising the origins of wings from “thoracic gills” and in tracing the possible development of aerial flight from surface flapping with legs trailing on the water surface, and forms of gliding.

**Zoraptera (Zorapterans)** Zoraptera is one of the smallest (32 species) and probably the least known pterygote order. Zorapterans are small, rather termite-like insects, found worldwide in tropical and warm temperate regions except Australia. Their morphology is simple, with biting, generalized mouthparts, including 5-segmented maxillary palps and 3-segmented labial palps. Sometimes both sexes are apterous, and in alate forms the hind wings are smaller than the fore wings; the wings are shed as in ants and termites. Wing venation is highly specialized and reduced.

Traditionally the order contained only one family (Zorotypidae) and one genus (*Zorotypus*), but has been expanded to include seven genera delimited predominantly on wing venation. This subdivision of *Zorotypus* is not accepted by some authors. The phylogenetic position of Zoraptera based on morphology has been controversial, ranging through membership of the hemipteroid orders, sister to Isoptera, an orthopteroid, or a blattoid, or sister to Embiidina. Analysis of major wing structures and musculature suggests that Zoraptera belongs in the blattoid lineage. Although the wing shape and venation resembles that of narrow-winged Isoptera, cephalic and abdominal characters indicate an early divergence from the blattoid stock, prior to the divergence of Dermaptera, and much before the origin of the Dictyoptera lineage.

**Orthoptera (Grasshoppers, Locusts, Katydid, Crickets)** Orthopterans belong to at least 30 families and more than 20,000 species, and mostly are medium-sized to large insects with hind legs often enlarged for jumping (saltation). The compound eyes are well developed, the antennae are elongate and multisegmented, and the prothorax is large with a shield-like pronotum curving downward laterally. The

fore wings form narrow, leathery tegmina, and the hind wings are broad, with numerous longitudinal and cross-veins, folded beneath the tegmina by pleating; aptery and brachyptery are frequent. The abdomen has 8–9 annular visible segments, with the 2 or 3 terminal segments reduced, and 1-segmented cerci. The female has a well-developed ovipositor formed from highly modified abdominal appendages.

Virtually all morphological evidence, and much of the molecular data suggest that the Orthoptera form the sister group to Phasmatodea. Some authors have united the orders, but the different wing bud development, egg morphology, and lack of auditory organs in phasmatids suggests separation. Molecular evidence indicates Embiidina may be sister to the orthopteran-phasmatid clade.

The division of Orthoptera into two monophyletic suborders, Caelifera (grasshoppers and locusts—predominantly day-active, fast-moving, visually acute, terrestrial herbivores) and Ensifera (katydids and crickets—often night-active, camouflaged or mimetic, predators, omnivores, or phytophages) is supported on morphological and molecular evidence. Grylloidea probably are the sister group (but highly divergent, with a long branch separation) of the remaining ensiferan taxa, Tettigoniodea, Hagloidea, and Stenopelmatoidea. In Caelifera, a well-supported recent proposal for four higher taxa, namely [Tridactyloidea (Tetrigoidea (Eumastacoidea+“higher Caelifera”))] reconciles molecular evidence with certain earlier suggestions from morphology. The major grouping of acridoid grasshoppers (Acridoidea) lies in the unnamed clade “higher Caelifera,” which also includes superfamilies Tanaoceroidea, Pyrgomorphoidea, Pneumoroidea, and Trigonopterygoidea.

**Phasmatodea (= Phasmida) (Phasmatids, Phasmids, Stick Insects or Walking Sticks, Leaf-insects)** Phasmatodea are a worldwide, predominantly tropical order of more than 3000 species of hemimetabolous insects, conventionally classified in three families (although some workers raise many subfamilies to family rank). Body shapes are variations on elongate cylindrical and stick-like or flattened, or often leaf-like. The mouthparts are mandibulate. The compound eyes relatively small and placed anterolaterally, with ocelli only in winged species, and often only in males. The antennae are short to long, with 8–100 segments. The prothorax is small, and the mesothorax and metathorax are long in wingless species, shorter if apterous. The wings, when present, are functional in males, often reduced in females, but with many species apterous in both sexes; the fore wings form short leathery tegmina, whereas the hind wings are broad with a network of numerous cross-veins and with the anterior margin toughened to protect the folded wing. The legs are elongate, slender, and adapted for walking, with 5-segmented tarsi. The abdomen is 11-segmented, with segment 11 often forming a concealed supra-anal plate in males or a more obvious segment in females.

Phasmatodea are sister to Orthoptera in the orthopteroid assemblage. Novel support for this grouping comes from the dorsal position of the cell body of salivary neuron 1 in the subesophageal ganglion and presence of serotonin in salivary neuron 2. Phasmatodea are distinguished from the Orthoptera by their body shape, asymmetrical male genitalia, proventricular structure and lack of rotation of nymphal wing pads during development. The higher classification of the Phasmatodea is poorly studied and current schemes are not based on phylogenetic relationships. The genus *Timema* (Timematidae) is considered to be sister to all other phasmatids, which are placed in Euphasmatodea (= Euphasmida).

**Embiidina (Embioptera) (Embiids, Webspinners)** Embiidina comprise some 400 described species (perhaps up to an order of magnitude more remain undescribed) in at least eight families. The

body is elongate, cylindrical, and somewhat flattened in males. The head has kidney-shaped compound eyes that are larger in males than females, and lacks ocelli. The antennae are multisegmented and the mandibulate mouthparts project forwards (prognathy). All females and some males are apterous, but if present, the wings are characteristically soft and flexible, with blood sinus veins stiffened for flight by blood pressure. The legs are short, with 3-segmented tarsi, and the basal segment of the fore tarsi is swollen because it contains silk glands. The hind femora are swollen by strong tibial muscles. The abdomen is 10-segmented with rudiments of segment 11 and with 2-segmented cerci. The female external genitalia are simple (no ovipositor), and those of males are complex and asymmetrical.

Embiids are undoubtedly monophyletic based, *inter alia*, on the ability to produce silk from unicellular glands in the anterior basal tarsus. They have a general morphological resemblance to Plecoptera based on reduced phallomeres, a trochantin-episternal sulcus, separate coxopleuron, and premental lobes. However, molecular evidence suggests closer relationship to Orthoptera and Phasmatodea; they also have some similarity to the Dermaptera, notably deriving from their prognathy, and to Zoraptera. Internal relationships amongst the described higher taxa of Embidiina suggest that the prevailing classification includes many non-monophyletic groups. Evidently much further study is needed to understand relationships within Embiidina, and among it and other neopterans.

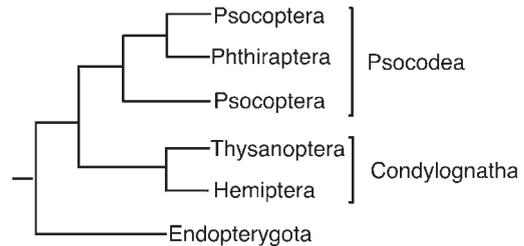
**Mantophasmatodea (Heelwalkers)** Mantophasmatodea was recognized for a species in Baltic amber and two museum specimens representing two species from south-west and east Africa, and freshly collected material from Namibia. Since 2002, at least 20 extant species in three families have been recognized from Africa. All species are apterous and less than 2.5 cm in body length. They have a hypognathous head, generalized orthopteroid mouthparts, and long, multisegmented antennae. The legs have elongate coxae and, characteristically, the distal part of each tarsus is held off the substrate, leading to the common name of “heelwalkers.”

This taxon cannot be placed within any of the existing insect orders, and its phylogenetic relationships based on morphology are unclear, although it has some resemblances to Grylloblattaria, Dictyoptera, and Phasmatodea. Molecular data most strongly support a sister group relationship with the Grylloblattaria, although an analysis of whole mitochondrial genomes of one representative species of several of the hemimetabolous orders found the included phasmatid, rather than the grylloblattid, to be sister to the included species of mantophasmatid.

#### Paraneoptera (Acercaria or Hemipteroid Assemblage)

This group contains Psocoptera+Phthiraptera, Thysanoptera, and Hemiptera and is defined by derived features of the mouthparts, including the slender, elongate maxillary lacinia separated from the stipes, and the swollen postclypeus containing an enlarged cibarium (sucking pump), and the reduction in tarsomere number to three or less.

Within Paraneoptera, the monophyletic superorder Psocodea contains Phthiraptera (parasitic lice) and Psocoptera (book lice and bark lice). Phthiraptera appears to have arisen from within Psocoptera, rendering that group paraphyletic. Although sperm morphology and some molecular sequence data imply the relationship [Hemiptera (Psocodea+Thysanoptera)], a grouping of Thysanoptera+Hemiptera (= superorder Condylgnatha) is supported by head and mouthpart synapomorphies including the stylet mouthparts, features of the wing base, and the sclerotized ring between antennal flagellomeres. Condylgnatha thus forms the sister group to Psocodea (Fig. 5).



**FIGURE 5** Cladogram depicting relationships among, and inferred classification of, Paraneoptera.

**Psocoptera (Bark and Book Lice)** Psocoptera is a worldwide order of cryptic small insects, with a large, mobile head, bulbous postclypeus, and membranous wings held roof-like over the abdomen. About 6000 extant species are described in 39 families. Evidently Psocoptera belong with Phthiraptera in a monophyletic clade Psocodea. However, Psocoptera is rendered paraphyletic by a postulated relationship of some Phthiraptera to the psocopteran family Liposcelididae. Traditionally the order has been divided into three suborders, Psocomorpha (25 families), Troctomorpha (9 families), and Trogiomorpha (5 families); the Psocomorpha and Trogiomorpha have been studied phylogenetically and internal relationships are partly resolved. However, the Liposcelididae (book lice) appears to be the sister group of the just chewing lice (Amblycera).

**Phthiraptera (Lice)** Phthirapterans are wingless obligate ectoparasites of birds and mammals, lacking any free-living stage, with nearly 5000 species in some 28 families. Each of the four lice suborders Anoplura, Amblycera, Ischnocera, and Rhyncophthirina are monophyletic, but the Phthiraptera appears paraphyletic. The latter three suborders have been treated traditionally as a monophyletic Mallophaga (biting and chewing lice) based on their feeding mode and morphology, in contrast to the piercing and blood-feeding Anoplura. Cladistic analysis of morphology has disputed mallophagan monophyly, suggesting the relationship Amblycera [Ischnocera (Anoplura+Rhyncophthirina)]. Molecular data have supported a classification in which Amblycera is sister to Liposcelididae (book lice), suggesting that parasitism arose twice in Psocodea. Resolution of these issues is important in estimation of degree of cospeciation between lice and their bird and mammal hosts.

**Thysanoptera (Thrips)** Thysanoptera is a worldwide order of nearly 6000 species in nine families. The development of thrips is intermediate between hemi- and holometabolous. Their head is elongate and the mouthparts are unique in that the maxillary laciniae formed grooved stylets, the right mandible is atrophied, and only the left mandible forms a stylet; all three stylets together form the feeding apparatus. The tarsi are 1- to 2-segmented, and the pretarsus has an apical protrusible adhesive arolium (bladder or vesicle). Female thrips are diploid, whereas males (if present) are haploid, being produced from unfertilized eggs.

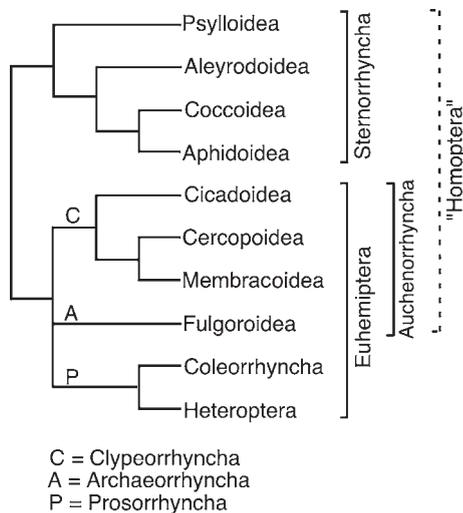
Molecular evidence supports one of the traditional morphological divisions of the Thysanoptera into two suborders, Tubulifera containing the sole, speciose, family Phlaeothripidae, and Terebrantia. Terebrantia includes one very speciose family, Thripidae, plus the smaller Aeolothripidae, Heterothripidae, and Melanthripidae, and four even smaller families. Relationships among families in Terebrantia are poorly resolved, although phylogenies are being generated at lower levels particularly concerning aspects of the evolution of sociality, the

origins of gall-inducing thrips, and of “soldier” castes in Australian gall-inducing Thripidae.

**Hemiptera (Bugs, Cicadas, Leafhoppers, Planthoppers, Spittle Bugs, Aphids, Psylloids, Scale insects, Whiteflies, Moss Bugs, Stink Bugs, etc.)** Hemiptera is the largest of the non-endopterygote orders, with more than 90,000 species in about 140 families. Hemipteran mouthparts diagnostically have the mandibles and maxillae modified as needle-like stylets, lying in a beak-like, grooved labium, collectively forming a rostrum or proboscis within which the stylet bundle contains two canals, one delivering saliva, and the other uptaking fluid. Palps are lacking. The thorax usually has a large prothorax and mesothorax and a small metathorax. Both pairs of wings often have reduced venation; some species are apterous; and male scale insects have only one pair of wings. Legs often possess complex pretarsal adhesive structures. Cerci are lacking.

Hemiptera and Thysanoptera are sister groups within Paraneoptera. Hemiptera used to be divided into two groups, Heteroptera (true bugs) and “Homoptera” (cicadas, leafhoppers, planthoppers, spittle bugs, aphids, psylloids, scale insects, and whiteflies), treated variously as suborders or orders. All homopterans are terrestrial plant feeders and many share a common biology of producing honeydew and being ant-attended. However, although possessing defining features, such as wings held roof-like over the abdomen, forewings in the form of a tegmina of uniform texture, and with the rostrum arising ventrally close the anterior of the thorax, “Homoptera” represents a paraphyletic grade rather than a clade. This view is supported by re-interpreted morphological data and by cladistic analysis of nucleotide sequences from the nuclear small subunit ribosomal RNA gene (18S rRNA). These data also suggest a much more complicated pattern of relationships among the higher groups of hemipterans (Fig. 6).

The rank of the various clades is much disputed and thus the more stable superfamily and family names have been used here. Four suborders appear warranted on phylogenetic grounds; Archaeorrhyncha (= Fulgoromorpha), Clypeorrhyncha (= Cicadomorpha), and Prosorrhyncha collectively form the Euhemiptera, which is the sister group to the fourth suborder, Sternorrhyncha. The latter contains the aphids, psylloids, scale insects, and whiteflies, which are characterized principally by their possession of a particular kind of gut



**FIGURE 6** Cladogram depicting relationships among, and inferred classification of, Hemiptera. Dashed line indicates paraphyly in classification.

filter chamber, a rostrum that appears to arise between the bases of their front legs and, if winged, by absence of vannus and vannal fold in hind wing. Some relationships among Euhemiptera are unsettled. The group called Auchenorrhyncha, morphologically defined by their possession of a tymbal acoustic system, an aristate antennal flagellum, and reduction of the proximal median plate in the wing base, contains two suborders, Archaeorrhyncha (planthoppers, often called Fulgoromorpha) and Clypeorrhyncha (cicadas, leafhoppers, and spittle bugs, often called Cicadomorpha). Molecular data tends to refute the monophyly of Auchenorrhyncha, implying Archaeorrhyncha is closer to Prosorrhyncha than to Clypeorrhyncha, but relationships depend upon sampling and more traditional arrangements are minimally less parsimonious.

Heteroptera (true bugs, including assassin bugs, backswimmers, lace bugs, stink bugs, waterstriders, and others) and its sister group, variously called Coleorrhyncha, Peloridioidea, or Peloridiomorpha and containing only family Peloridiidae or moss bugs, form suborder Prosorrhyncha (sometimes called Heteropterodea). Although small, cryptic, and rarely collected, moss bugs have generated considerable phylogenetic interest due to their combination of ancestral and derived hemipteran features, and their exclusively “relictual” Gondwanan distribution. Heteropteran diversity is distributed amongst some 80 families and almost 40,000 described species, forming the largest hemipteran clade. Heteroptera is most easily diagnosed by the presence of metapleural scent glands, and monophyly is never disputed.

### Endopterygota (or Holometabola) (Coleoptera, Neuroptera, Megaloptera, Raphidioptera, Hymenoptera, Trichoptera, Lepidoptera, Mecoptera, Siphonaptera, Diptera, Strepsiptera)

Endopterygota comprise insects with immature (larval) instars that are very different from their respective adults. Thus development is holometabolous, with a complete metamorphosis separating immature and adult stages. The adult wings and genitalia are internalized in their pre-adult expression, developing in imaginal discs that are evaginated at the penultimate moult. Larvae lack true ocelli. The “resting stage” or pupa is non-feeding, and precedes an often active pharate (“cloaked” in pupal cuticle) adult. Unique derived features are less evident in the adults than in immature stages, but the clade is consistently recovered from morphological, molecular, and combined analyses.

Two or three groups currently are proposed amongst the endopterygotes, of which one of the strongest is a sister group relationship termed Amphiesmenoptera between Trichoptera (caddisflies) and Lepidoptera (butterflies and moths). A plausible scenario of an ancestral amphiesmenopteran taxon has a larva living in damp soil amongst liverworts and mosses followed by radiation into water (Trichoptera) or into terrestriality and phytophagy (Lepidoptera).

A second (usually) strongly supported relationship is between three orders: Neuroptera, Megaloptera, and Rhaphidioptera—Neuropterida (sometimes treated as a group of ordinal rank)—showing a sister group relationship to Coleoptera.

A third postulated relationship—Antliophora—unites Diptera (true flies), Siphonaptera (fleas), and Mecoptera (scorpionflies and hangingflies). Debate continues about the relationships of these taxa, particularly concerning the relationships of Siphonaptera. Fleas were considered sister to Diptera, but molecular and novel anatomical supports a relationship with a curious-looking mecopteran group, the Boreidae or snowfleas.

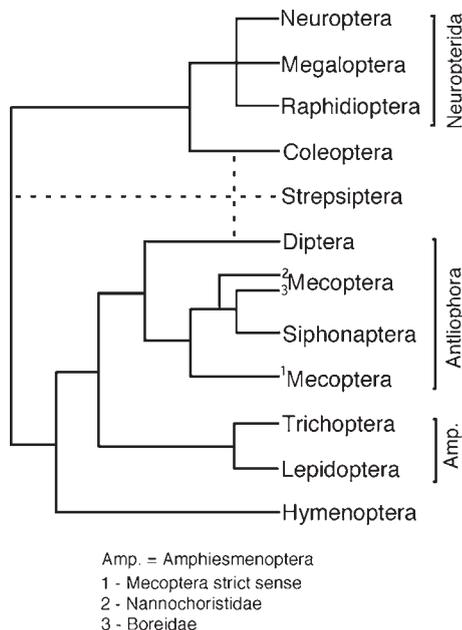
Strepsiptera is phylogenetically enigmatic, but resemblance of their first-instar larvae (called triungula) to certain Coleoptera, notably parasitic Rhipiphoridae, and some wing base features has been cited as indicative of relationship. In contrast, some molecular

evidence as well as haltere development suggest a link between Strepsiptera and Diptera. Strepsiptera is highly derived in both morphological and molecular evolution due to its parasitic lifestyle, and thus possess few features shared with any other taxon. The long-isolated evolution of the genome can create a problem known as “long-branch attraction,” in which nucleotide sequences may converge by chance events alone with those of an unrelated taxon with a similarly long evolution, for the strepsipteran notably with Diptera. The issue remains unresolved.

The position of two major orders of endopterygotes, Coleoptera and Hymenoptera, remains to be considered. Several positions have been proposed for Coleoptera, but current evidence derived from female genitalia and ambivalent evidence from eye structure supports a sister group relationship to Neuropterida. This grouping forms the sister to the remaining Endopterygota in most analyses, although there is some support for Hymenoptera as the sister to all other endopterygote orders. Usually Hymenoptera is treated as sister to Antliophora+Amphiesmenoptera; the many highly derived features of adults, and reductions in larvae, limits morphological justification for the latter position.

Within the limits of uncertainty, the relationships within Endopterygota are summarized in Fig. 7.

**Coleoptera (Beetles)** There are about 350,000 described species of beetles, and the lineage is one of the oldest within the Endopterygota. The major synapomorphic feature of Coleoptera is the development of the fore wings as sclerotized rigid elytra, which extend to cover some or many of the abdominal segments and beneath which the propulsive hind wings are elaborately folded when at rest. Some molecular studies show Coleoptera polyphyletic or paraphyletic with respect to some or all of Neuropterida. However, this is impossible to reconcile with the morphological support for coleopteran monophyly, and a sister group relationship to Neuropterida is accepted.



**FIGURE 7** Cladogram depicting relationships among, and inferred classification of, Endopterygota. Dashed lines indicate three possible alternative placements of Strepsiptera.

Within Coleoptera, four modern lineages (treated as suborders) are recognized: Archostemata, Adephaga, Polyphaga, and Myxophaga. Archostemata includes only the small families Ommatidae, Crowsoniellidae, Cupedidae, and Micromalthidae, and forms the sister group to the remaining extant Coleoptera. The few known larvae are wood-miners with a sclerotized ligula and a large mola on each mandible. Adults have movable hind coxae with usually visible trochantins, and five (not six) ventral abdominal plates (ventrites), but share with Myxophaga and Adephaga wing folding features (apex spirally rolled, major transverse fold crossing vein MP), absence of cervical sclerites, and the external prothoracic pleuron. In contrast to Myxophaga, the pretarsus and tarsus are unfused.

Adephaga is diverse, second in size only to Polyphaga, and include ground beetles, tiger beetles, whirligigs, predaceous diving beetles, wrinkled bark beetles, among others. Larval mouthparts are adapted for liquid-feeding, with a fused labrum and no mandibular mola. Adults have the notopleural sutures visible on the prothorax and have six visible abdominal sterna with the first three fused into a single ventrite which is divided by the hind coxae. Pygidial defense glands are widespread in adults. The most speciose included family is Carabidae, or ground beetles, with a predominantly predaceous feeding habit, but Adephaga also includes the aquatic families, Dytiscidae, Gyrinidae, Haliplidae, and Noteridae, which are algivorous or predaceous. Morphology has suggested that Adephaga is sister group to the combined Myxophaga and Polyphaga, but molecular data (18S rRNA) suggests Adephaga as sister to Polyphaga, with Myxophaga sister to them.

Myxophaga is a clade of small, primarily riparian aquatic beetles, comprising families Lepiceridae, Torridincolidae, Hydrosaphiidae, and Sphaeriidae (= Microsporidae), united by the synapomorphic fusion of the pretarsus and tarsus. The 3-segmented larval antenna, 5-segmented larval legs with a single pretarsal claw, fusion of trochantin with the pleuron, and ventrite structure support a sister group relationship of Myxophaga with the Polyphaga. This has been challenged by some workers, notably because some interpretations of wing venation and folding support [Polyphaga (Archostemata (Myxophaga+Adephaga))].

Polyphaga contains the majority (>90% of species) of beetles, with more than 300,000 described species. The suborder includes rove beetles (Staphylinoidea), scarabs and stag beetles (Scarabaeoidea), metallic wood-boring beetles (Buprestoidea), click beetles, and fireflies (Elateroidea), as well as diverse Cucujiformia, including fungus beetles, grain beetles, ladybird beetles, darkling beetles, blister beetles, longhorn beetles, leaf beetles, and weevils. The prothoracic pleuron is not externally visible, but is fused with the trochantin and remnant internally as a “cryptopleuron.” Thus, one suture between the notum and the sternum is visible in the prothorax in polyphagans, whereas two sutures (the sternopleural and notopleural) often are visible externally in other suborders (unless secondary fusion between the sclerites obfuscates the sutures, as in *Micromalthus*). The transverse fold of the hind wing never crosses MP, cervical sclerites are present, and hind coxae are mobile and do not divide the first ventrite. Female polyphagan beetles have telotrophic ovarioles, which is a derived condition within beetles.

The internal classification of Polyphaga involves several superfamilies or series, whose constituents are relatively stable, although some smaller families (for which rank even is disputed) are allocated to different clades by different authors. Large superfamilies include Hydrophiloidea, Staphylinoidea, Scarabaeoidea, Buprestoidea, Byrrhoidea, Elateroidea, Bostrichoidea, and the grouping Cucujiformia. This latter includes the vast majority of phytophagous (plant-eating)

beetles, united by cryptonephric Malpighian tubules of the normal type, a cone ommatidium with open rhabdom, and lack of functional spiracles on the 8th abdominal segment. Constituent superfamilies of Cucujiformia are Cleroidea, Cucujoidea, Lymexyloidea, Tenebrionoidea, Chrysomeloidea, and Curculionoidea. Evidently, adoption of a phytophagous lifestyle correlates with speciosity in beetles, with Cucujiformia, especially weevils (Curculionoidea), forming a major radiation.

**Neuropterida or Neuropteroid Orders: Megaloptera (Alderflies, Dobsonflies, Fishflies), Raphidioptera (Snakeflies), and Neuroptera (Lacewings, Antlions, Owlflies)** Neuropterida comprises three orders with holometabolous development, with approximately 6500 species of Neuroptera in almost 20 families, 300 of Megaloptera in two widely recognized families, and 220 of Raphidioptera in two families. Adults have multisegmented antennae; large, separated eyes; and mandibulate mouthparts. The prothorax may be larger than the meso- and metathorax, which are about equal in size. Legs sometimes are modified for predation. The fore wings and hind wings are quite similar in shape and venation, with folded wings often extending beyond the abdomen. The abdomen lacks cerci.

Megalopterans are predatory only in the aquatic larval stage; although adults have strong mandibles, they are not used in feeding. Adults closely resemble neuropterans, except for the presence of an anal fold in the hind wing. Raphidiopterans are terrestrial predators as adults and larvae. The adult is mantid-like, with an elongate prothorax, and the head is mobile and used to strike, snake-like, at prey. The larval head is large and forwardly directed. Many adult neuropterans are predators, and have wings typically characterized by numerous crossveins and “twigging” at the ends of veins. Neuropteran larvae usually are active predators with slender, elongate mandibles and maxillae combined to form piercing and sucking mouthparts.

Megaloptera, Raphidioptera, and Neuroptera may be treated as separate orders, or united in Neuropterida, or Raphidioptera may be included in Megaloptera. There is little doubt that Neuropterida is monophyletic with new support from wing base morphology. This latter feature also supplements data supporting the long-held view that Neuropterida forms a sister group to Coleoptera. Each component appears monophyletic, although a doubt remains concerning megalopteran monophyly. There remains uncertainty about internal relationships, which traditionally has Megaloptera and Raphidioptera as sister groups. Recent re-analyses with some new character suites have postulated Megaloptera as sister to Neuroptera and proposed a novel scenario of the plesiomorphy of aquatic larvae (all Megaloptera, Sisyridae in Neuroptera) in Neuropterida.

**Strepsiptera (Twisted-wing Parasites)** Strepsiptera form an enigmatic order of nearly 600 species of highly modified endoparasitoids, most commonly of Hemiptera and Hymenoptera, and show extreme sexual dimorphism. The male has a large head with bulging eyes comprising few large facets and lacks ocelli; the antenna are flabellate or branched, with 4–7 segments; the fore wings are stubby and lack veins, whereas the hind wings are broadly fan-shaped, with few radiating veins; the legs lack trochanters and often also claws. Females are either coccoïd-like or larviform, wingless, and usually retained in a pharate (cloaked) state, protruding from the host. The first-instar larva is a triungulin, without antennae and mandibles, but with three pairs of thoracic legs; subsequent instars are maggot-like, lacking mouthparts or appendages. The pupa, which has immovable mandibles but appendages free from its body, develops within a puparium formed from the last larval instar.

The phylogenetic position of Strepsiptera has been subject to much speculation because modifications associated with their endoparasitoid life style mean that few characteristics are shared with possible relatives. In having posteromotor flight (only metathoracic wings) they resemble Coleoptera, but other attributes traditionally argued to be synapomorphies shared with Coleoptera are suspect or mistaken. However, strepsipterans have a similar life history and triungulin larva to certain beetles, notably the parasitic Rhipiphoridae, in which the adult males have pectinate or flabellate antennae not unlike those of male strepsipterans. The forewing-derived halteres of strepsipterans are gyroscopic organs of equilibrium with the same functional role as the halteres of Diptera, although the latter are derived from the hind wing. Phylogenetic analysis of sequences from the small subunit ribosomal RNA gene (18S rRNA) indicates that Strepsiptera possibly is a sister group to Diptera (if long-branch attraction can be discounted), and some tantalizing information from developmental biology suggests that wings and halteres might be “reverse-expressed” on meso- and metathoracic segments. However, strepsipteran halteres differ in structure from those of Diptera, and Strepsiptera also lack certain other features characteristic of Diptera or the group (Antliophora) to which Diptera belongs. Further data are required to resolve the phylogenetic position of the Strepsiptera.

**Mecoptera (Scorpionflies, Hangingflies)** Mecopterans are holometabolous insects comprising about 550 known species in nine families, with common names associated with the two largest families—Bittacidae (hangingflies) and Panorpidae (scorpionflies). Adults have an elongate ventrally projecting rostrum, containing elongate, slender mandibles and maxillae, and an elongate labium. The eyes are large and separated, the antennae filiform and multisegmented. The fore wings and hind wings are narrow, similar in size, shape, and venation, but often are reduced or absent. The legs may be modified for predation. Larvae have a heavily sclerotized head capsule, are mandibulate, and may have eyes comprising groups of 3–30 stemmata (absent in Panorpidae, indistinct in Nannochoristidae). The thoracic segments are about equal, and have short thoracic legs with fused tibia and tarsus and a single claw; prolegs usually are present on abdominal segments 1–8, and the terminal segment (10) either has paired hooks or a suction disk. The pupa is immobile, mandibulate, and with appendages free.

Although some adult Mecoptera resemble neuropterans, strong evidence supports a relationship to Diptera. Intriguing recent morphological studies, plus robust evidence from molecular sequences, suggests that Siphonaptera arise from within Mecoptera, as a sister group to the “snowfleas” (Boreidae). The phylogenetic position of Nannochoristidae, a southern hemisphere mecopteran taxon has a significant bearing on internal relationships within Antliophora. Molecular evidence suggests that it lies as sister to Boreidae+Siphonaptera, and therefore is of equivalent rank to the boreids, fleas, and the residue of Mecoptera—and logically each should be treated as orders, or Siphonaptera should be reduced in rank within Mecoptera.

**Siphonaptera (Fleas)** Siphonaptera is a highly modified order of holometabolous insects, comprising some 2600 species, all of which are bilaterally compressed, apterous ectoparasites. The mouthparts are specialized for piercing and sucking, lack mandibles but have an unpaired labral stylet and two elongate serrate, lacinial stylets that together lie within a maxillary sheath. A salivary pump injects saliva into the wound, and cibarial and pharyngeal pumps suck up the blood meal. Fleas lack compound eyes and the antennae lie in deep lateral grooves. The body is armed with many posteriorly directed

setae and spines, some of which form combs, especially on the head and anterior thorax. The metathorax houses very large muscles associated with the long and strong hind legs, which are used to power the prodigious leaps made by these insects.

After early suggestions that the fleas arose from a mecopteran, the weight of evidence suggested they formed the sister group to Diptera. However, increasing molecular and novel morphological evidence now points to a sister group relationship to a subordinate component of Mecoptera, specifically Boreidae (snowfleas). Molecular phylogenetic study of internal relationships of fleas suggests that at least 10 of 16 families may be monophyletic.

**Diptera (True Flies)** Diptera is a major order of insects, with about 150,000 described species and perhaps more than a quarter of a million species in some 150 families. Dipterans are holometabolous, and readily recognized by the development of hind (metathoracic) wings as balancers, or halteres (halteres), and in the larval stages by lack of true legs and the often maggot-like appearance. Venation of the fore (mesothoracic) flying wings ranges from complex to extremely simple. Mouthparts range from biting-and-sucking (e.g., biting midges and mosquitoes) to “lapping”-type with pseudotracheate labella functioning as a sponge (e.g., house flies). Dipteran larvae lack true legs, although various kinds of locomotory apparatus range from unsegmented pseudolegs to creeping welts on maggots. The larval head capsule ranges from complete, through partially undeveloped, to complete absence in a maggot head that consists only of the sclerotized mandibles (“mouth hooks”) and supporting structures.

Traditionally Diptera had two suborders, Nematocera (crane-flies, midges, mosquitoes, and gnats) with a slender, multisegmented antennal flagellum, and the heavier-built Brachycera (“higher flies” including hover flies, blow flies, and dung flies) with a shorter, stouter, and fewer-segmented antenna. However, Brachycera is sister to only part of “Nematocera”, and thus Nematocera is paraphyletic.

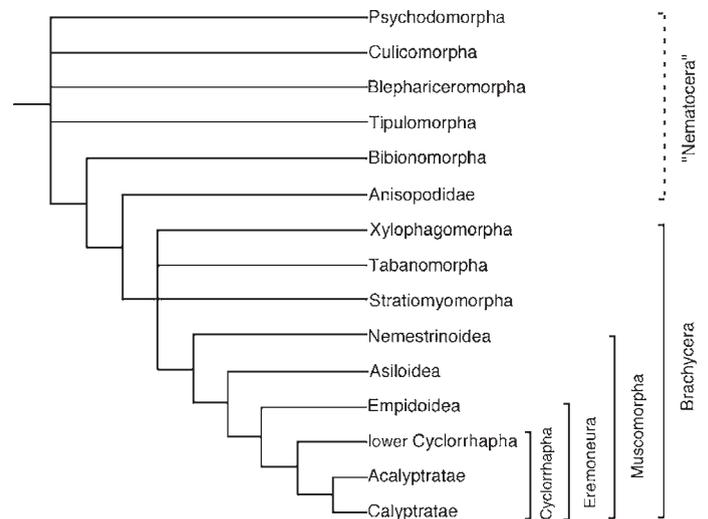
Internal relationships amongst Diptera are becoming better understood, although with some notable exceptions. Ideas concerning “basal” Diptera are inconsistent: traditionally Tipulidae (or Tipulomorpha if subordinate groups are given family rank, but nonetheless undoubtedly monophyletic) is treated as a lineage arising from a basal node, particularly on evidence from the adult wing and other morphology. Such an arrangement is difficult to reconcile with the much more derived larva, in which the head capsule is variably reduced. Furthermore, some molecular evidence places the crane-flies much higher in the dipteran tree as sister to the Brachycera. An alternative view based on morphology is that the relictual family Tanyderidae, with complex (“primitive”) wing venation, arises from close to the basal node of the order. Support for this view also comes from tanyderid larval morphology.

There is strong support for Culicomorpha, comprising mosquitoes (Culicidae) and their relatives (Corethrellidae, Chaoboridae, Dixidae) and their sister group the blackflies, midges, and relatives (Simuliidae, Thaumaleidae, Ceratopogonidae, Chironomidae), and for Bibionomorpha, comprising the fungus gnats (Mycetophilidae *sensu lato*), Bibionidae, Anisopodidae, and possibly Cecidomyiidae. However, in both groups internal relationships remain a matter of debate, which molecular evidence may help to resolve.

Monophyly of Brachycera, comprising “higher flies,” is established by features including in the larva the posterior elongation of the head into the prothorax, the divided mandible, and loss of premandible, and in the adult by the eight or fewer antennal flagellomeres, two or fewer palp segments, and separation of the male genitalia into two parts (epandrium and hypandrium). Possible relationships

of Brachycera include sister to Tipulomorpha, to Psychodomorpha, or even to Culicomorpha (molecular data only), but strong support is provided for sister taxon to the Bibionomorpha or to subordinate Anisopodidae. Brachycera contains four equivalent groups with internally unresolved relationships: Tabanomorpha (with brush on larval mandible and larval head retractile); Stratiomyomorpha (with larval cuticle calcified and pupation in last larval instar exuviae); Xylophagomorpha (with distinctive elongate, conical strongly sclerotized larval head capsule, and abdomen posteriorly ending in sclerotized plate with terminal hooks); and Muscomorpha (adults with tibial spurs absent, flagellum with no more than four flagellomeres and female cercus single-segmented). This latter speciose group contains Nemestrinoidea (bee-flies and relatives), Asiloidea (robber-flies and relatives), and Eremoneura (empidooids and Cyclorrhapha). Eremoneura is a strongly supported clade based on wing venation (loss or fusion of vein  $M_4$  and closure of anal cell before margin), presence of ocellar setae, unitary palp, and several genitalic characters, plus larval feature including maxillary reduction and presence of only three instars.

Cyclorrhaphans, united by their pupation within a puparium formed by the last larval instar cuticle, include a heterogeneous aschizan group including Phoridae and Syrphidae (hoverflies) and the Schizophora defined by the presence of a balloon-like ptilinum that everts from the frons to assist the adult escape the puparium. Higher flies include the ecologically very diverse acalyptrates, and blowflies and relatives (Calypttratae), treated here as sister groups (Fig. 8), but with alternative views suggested.



**FIGURE 8** Cladogram depicting relationships among, and inferred classification of, Diptera. Dashed line indicates paraphyly in classification.

**Hymenoptera (Wasps, Bees, Ants, Sawflies, and Wood Wasps)** This order contains at least 115,000 described species of holometabolous neopterans, varying from minute (e.g. Trichogrammatidae) to large-sized (0.15–120 mm in length), and slender (e.g. many Ichneumonidae) to robust (e.g. certain bees). Hymenoptera often is treated as containing two suborders: “Symphyta” (wood wasps and sawflies; the parentheses indicate a paraphyletic group, as explained below) and “wasp-waisted” Apocrita (wasps, bees, and ants). The hymenopteran head has mouthparts

ventrally directed to forward projecting, ranging from generalized mandibulate (in “Symphyta”) to sucking and chewing with mandibles often used for killing and handling prey, and in Apocrita in defense and nest building. The compound eyes often are large; the antennae are long, multisegmented, and often prominently held forwardly or recurved dorsally. “Symphyta” has a conventional 3-segmented thorax, but in Apocrita the propodeum, abdominal segment 1, is included with the thorax into a mesosoma, or in ants, the alitrunk. The wing venation is relatively complete in large sawflies, is reduced in Apocrita in correlation with body size, such that very small species of 1–2 mm body length have only one divided vein, or none. The hind wing has rows of hooks (hamuli) along the leading edge that couples with the hind margin of the fore wing in flight. In Apocrita, the second abdominal segment (and sometimes also third) forms a constriction, or petiole. Hymenopteran female genitalia include an ovipositor, comprising three valves and two major basal sclerites, which may be long and highly mobile allowing valves to be directed vertically between legs. The ovipositor of aculeate Hymenoptera is modified as a sting associated with a venom apparatus.

Symphytan larvae are eruciform (caterpillar-like) with three pairs of thoracic legs bearing apical claws and with some abdominal legs; most are phytophagous. Apocritan larvae are apodous, with the head capsule frequently reduced but with prominent strong mandibles; larvae may vary greatly in morphology during development (heteromorphosis). Apocritan larvae have diverse feeding habits and may be parasitic, gall-inducing, or fed with prey or nectar and pollen by their parent, or, if a social species, other colony members. Adult hymenopterans mostly feed on nectar or honeydew; only a few consume other insects.

Hymenoptera is considered either to be sister to all other endopterygote orders, or sister to Amphiesmenoptera (Trichoptera+Lepidoptera)+Antliophora (Diptera+Mecoptera/Siphonaptera). However, Apocrita appears to be sister to one family of symphytan only, the Orussidae, and thus “Symphyta” form a paraphyletic group, with the symphytan superfamily Xyeloidea sister to all other hymenopteran

taxa. The monophyletic tenthredinoid (sawfly) clade in turn is sister to weakly supported [Pamphilioidea (Cephoidea (possible grade Siricidae and relatives (Orussidae + Apocrita)))] (Fig. 9).

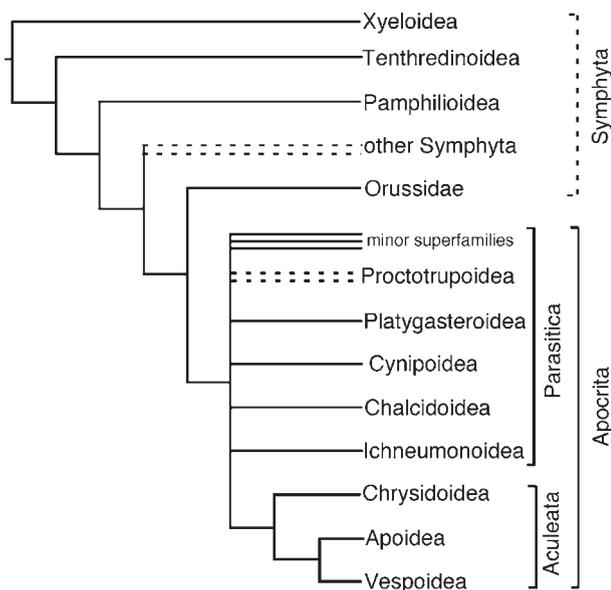
Within Apocrita, aculeate (Aculeata) and parasitic (Parasitica or terebrant) wasp groups were considered each to be monophyletic, but Parasitica evidently is rendered paraphyletic by aculeates originating from somewhere within Parasitica. Some traditional groupings also are non-monophyletic, including Proctotrupoidea, but Proctotrupomorpha comprising superfamilies Proctotrupoidea, Chalcidoidea, Platygastreroidea, and Cynipoidea appears to be monophyletic. From morphology, Ichneumonoidea were argued to be sister to Aculeata, but molecular data and re-analysis refute this. The monophyletic aculeates, defined by their distinctive ovipositor construction and loss of female cerci, comprise [Chrysoidea (Vespoidea+Apoidea)]. Internal relationships of aculeates, including vespids (wasps), formicids (ants), and apids (bees) and the monophyly of subordinate groups are under scrutiny.

**Trichoptera (Caddisflies)** Trichoptera contains about 45 extant families containing some 13,000 described species, with estimates of undescribed (mostly SE Asian) species diversity some four- to fivefold higher. Trichoptera are holometabolous; the moth-like adult has reduced mouthparts lacking any proboscis, but with 3–5 segmented maxillary palps and 3-segmented labial palps. The antennae are multisegmented and filiform and often as long as the wings. The compound eyes are large, and there are two or three ocelli. The wings are haired or less often scaled, and differentiated from all but the earliest lineages of Lepidoptera by the looped anal veins in the fore wing, and absence of a discal cell. The larva is aquatic, has fully developed mouthparts, three pairs of thoracic legs (each with at least five segments), and lacks the ventral prolegs characteristic of lepidopteran larvae. The abdomen terminates in hook-bearing prolegs. The tracheal system is closed, and is associated with tracheal gills on most abdominal segments. The pupa is also aquatic, enclosed in a retreat often made of silk, and possesses functional mandibles to aid in emergence from the sealed case.

Amphiesmenoptera (Trichoptera+Lepidoptera) is now unchallenged, despite earlier suggestions that Trichoptera arose from within Lepidoptera. Proposed internal relationships within the Trichoptera range from stable and well supported, to unstable and anecdotal. Monophyly of suborder Annulipalpia in its strictest sense, comprising families Hydropsychidae, Polycentropodidae, Philopotamidae, and some close relatives, is well supported by larval and adult morphology — including presence of annulate apical segment of both adult maxillary and larval palp, absence of male phallic parameres, presence of papillae lateral to the female cerci, and in the larva by the presence of elongate anal hooks and reduced abdominal tergite 10.

The monophyly of the case-making Integripalpia (comprising families Phryganeidae, Limnephilidae, Leptoceridae, Sericostomatidae, and relatives) is supported *inter alia* by the absence of the *m* cross-vein, hind wings broader than forewings especially in the anal area, female lacking both segment 11 and cerci, and larval character states including the usual complete sclerotization of the mesonotum, hind legs with lateral projection, lateral and mid-dorsal humps on abdominal segment 1, and short and stout anal hooks.

Monophyly of a third putative suborder, Spicipalpia, is more contentious. Defined for the Glossosomatidae, Hydroptilidae, and Rhyacophilidae (and perhaps the Hydrobiosidae), the proposed uniting features are the spiculate apex of the adult maxillary and labial palps, ovoid second segment of maxillary palp, and eversible oviscapt (egg laying appendage). Morphological and molecular evidence fail to confirm Spicipalpia monophyly, unless at least



**FIGURE 9** Cladogram depicting relationships among, and inferred classification of, Hymenoptera. Only major superfamilies are depicted. Dashed lines indicate uncertainty in relationships or paraphyly in classification.

Hydroptilidae is removed. All possible relationships between Annulipalpia, Integripalpia, and Spicipalpia have been proposed, often associated with scenarios concerning the evolution of case-making. An early idea that the Annulipalpia is sister to a paraphyletic Spicipalpia+monophyletic Integripalpia finds support from some morphological and molecular data.

**Lepidoptera (Moths and Butterflies)** Lepidoptera, with some 160,000 described species in more than 120 families, is one of the major orders of Holometabola. Adults range from very small to large, with wings always covered in scales. The head bears a long, coiled proboscis formed from greatly elongated maxillary galeae; large labial palps usually are present, but other mouthparts are absent, except mandibles are present primitively in some groups. The compound eyes are large, and ocelli frequently are present. The multisegmented antennae are often pectinate in moths and knobbed or clubbed in butterflies (Papilionoidea+Hedyloidea+Hesperioidea). The wings are completely covered with a double layer of scales (flattened modified macrotrichia), and the hind and fore wings are linked either by a frenulum, jugum, or simple overlap. Lepidopteran larvae have a sclerotized, head capsule with mandibulate mouthparts, usually six lateral ocelli, and short 3-segmented antennae. The thoracic legs are 5-segmented with single claws, and the abdomen is 10-segmented with short prolegs on some segments. Silk gland products are extruded from a characteristic spinneret at the median apex of the labial prementum. The pupa usually is contained within a silken cocoon.

The basal radiation of this large order is considered well enough resolved to serve as a test for the ability of particular molecules to recover phylogenetic signal. Although over 98% of the species of Lepidoptera belong in Ditrysia (Fig 10), the morphological diversity is concentrated in a small non-ditryisian group. Three of the four suborders are species-poor (represented by families Micropterigidae, Agathiphagidae, and Heterobathmiidae, respectively), branch sequentially at the base of the Lepidoptera, and lack the synapomorphy of the mega-diverse suborder Glossata, namely the characteristically developed coiled proboscis formed from the fused galeae. Highly speciose Glossata contains a comb-like basal series of species-poor taxa, and a subordinate clade (Neolepidoptera) defined by the possession in the larva (caterpillar) of abdominal prolegs with muscles and apical crochets (hooklets). Much of the glossatan diversity is found in the derived Ditrysia, defined by the unique two genital openings in

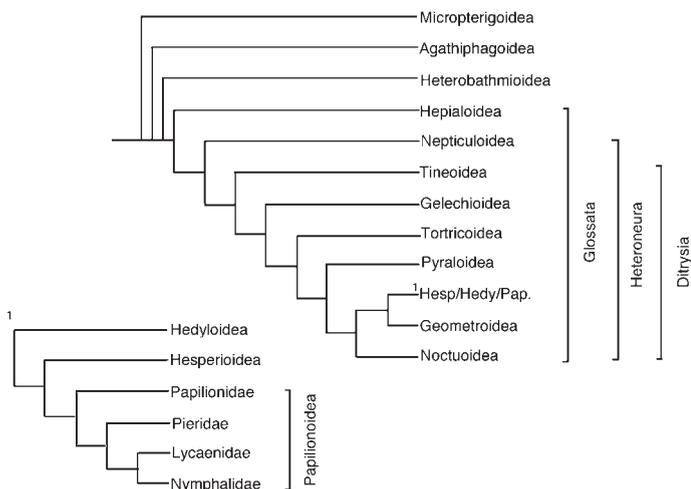
the female, one the ostium bursae on sternite 8, the other the genitalia proper on sternites 9 and 10. Additionally the wing coupling is always frenulate or amplexiform and not jugate, and the wing venation tends to be heteroneuran (with venation dissimilar between fore wings and hind wings). Trends in the evolution of Ditrysia include elaboration of the proboscis (haustellum) and the reduction or loss of maxillary palpi. Relationships among the smaller superfamilies (not shown in Fig. 10), and the few highly diverse ones (Tineoidea, Gelechioidea, Tortricoidea, Pyraloidea, Noctuoidea, and Geometroidea) are not well understood and susceptible to change. However, one of the best-supported relationships in Ditrysia is the grouping of Hesperioidea (skippers) and Papilionoidea (butterflies), united by their clubbed, dilate antennae, lack of frenulum in the wing and large humeral lobe on the hind wing. To this has been added the Neotropical Hedyloidea to form the monophyletic grouping we know as the butterflies (Fig 10).

### See Also the Following Articles

Arthropoda and Related Groups ■ Biodiversity ■ Biogeographical Patterns ■ Fossil Record ■ Insecta, Overview

### Further Reading

- Beutel, R., and Haas, F. (2000). Phylogenetic relationships of the suborders of Coleoptera (Insecta). *Cladistics* **16**, 103–141.
- Bitsch, C., and Bitsch, J. (2000). The phylogenetic interrelationships of the higher taxa of apterygote hexapods. *Zool. Scr.* **29**, 131–156.
- Grimaldi, D., and Engel, M. S. (2005). "Evolution of the Insects." 755 pp. Cambridge University Press, Cambridge.
- Kristensen, N. P. (1999). Phylogeny of endopterygote insects, the most successful lineage of living organisms. *Eur. J. Entomol.* **96**, 237–253.
- Kristensen, N. S., Scoble, M. J., and Karsholt, O. (2007). Lepidoptera phylogeny and systematics: The state of inventorying moth and butterfly diversity. In "Linnaeus Tercentenary: Progress in Invertebrate Taxonomy" (Z.-Q. Zhang, and W. A. Shear, eds.). *Zootaxa*, **1668**, pp. 699–747.
- Luan, Y. X., Mallatt, J. M., Xie, R. D., Yang, Y. M., and Yin, W. Y. (2005). The phylogenetic positions of three basal-hexapod groups (Protura, Diplura, and Collembola) based on ribosomal RNA gene sequences. *Mol. Biol. Evol.* **22**, 1579–1592.
- Lyal, C. H. C. (1985). Phylogeny and classification of the Psocodea, with particular reference to the lice (Psocodea: Phthiraptera). *Syst. Entomol.* **10**, 145–165.
- Mallatt, J., and Giribet, G. (2006). Further use of nearly complete 28S and 18S rRNA genes to classify Ecdysozoa: 37 more arthropods and a kinorhynch. *Mol. Phylogenet. Evol.* **40**, 772–794.
- Schultz, J. W., and Regier, J. C. (2000). Phylogenetic analysis of arthropods using two nuclear protein-encoding genes supports a crustacean-hexapod clade. *Proc. R. Soc. Biol. Sci. B* **267**(1447), 1011–1019.
- Sharkey, M. J. (2007). Phylogeny and classification of Hymenoptera. In "Linnaeus Tercentenary: Progress in Invertebrate Taxonomy" (Z.-Q. Zhang, and W. A. Shear, eds.). *Zootaxa*, **1668**, pp. 521–548.
- Sorensen, J. T., Campbell, B. C., Gill, R. J., and Steffen-Campbell, J. D. (1995). Non-monophyly of Auchenorrhyncha ("Homoptera"), based upon 18S rDNA phylogeny: eco-evolutionary and cladistic implications within pre-Heteropteroidea Hemiptera (s.l.) and a proposal for new monophyletic suborders. *Pan-Pacific Entomol.* **71**, 31–60.
- von Dohlen, C. D., and Moran, N. A. (1995). Molecular phylogeny of the Homoptera: A paraphyletic taxon. *J. Mol. Evol.* **41**, 211–223.
- Whitfield, J. B., and Kjer, K. M. (2008). Ancient rapid radiations of insects: Challenges for phylogenetic analysis. *Annu. Rev. Entomol.* **53**, 449–472.
- Yeates, D. K., Wiegmann, B. M., Courtney, G. W., Meier, R., Lambkin, C., and Pape, T. (2007). Phylogeny and systematics of Diptera: Two decades of progress and prospects. In "Linnaeus Tercentenary: Progress in Invertebrate Taxonomy" (Z.-Q. Zhang, and W. A. Shear, eds.), Vol. 1668, pp. 565–590. *Zootaxa*.



**FIGURE 10** Cladogram depicting relationships among, and inferred classification of, Lepidoptera. Only selected superfamilies are depicted.