

**FIGURE 2** Louse suborders (dorsal view of adults). (A) Amblycera: *Colpocephalum fregili* (Menoponidae), male from the red-billed chough (*Pyrrhocorax pyrrhocorax*). (Adapted from Price and Beer, 1965, *Proc. Entomol. Soc. Wash.* **67**, 7–14.) (B) Ischnocera: *Quadriceps crassipedalis* (Philopteridae), female from the least seed-snipe (*Thinocorus rumicivorus*). (Adapted from Emerson and Price, 1985, *Proc. Entomol. Soc. Wash.* **87**, 395–401.) (C) Rhynchophthirina: *Haematomyzus porci* (Haematomyzidae), male from the red river hog (*Potamochoerus porcus*). (Adapted from Emerson and Price, 1988, *Proc. Entomol. Soc. Wash.* **90**, 338–342.) (D) Anoplura: *Polyplax spinulosa* (Polyplacidae), female of the spiny rat louse from the Norway rat (*Rattus norvegicus*). (Adapted from Kellogg and Ferris, 1915, Leland Stanford Junior University Publication, courtesy of Stanford University Press.)

### See Also the Following Articles

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

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## Phylogeny of Insects

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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 that it reveals 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 because of 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 where resolution appears to be lacking, this lack 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. This 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 among likely sister groups outside Arthropoda. Although traditionally each major arthropod group has been considered monophyletic, most have been suspected of nonmonophyly 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 interrelationships has been a most

**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 forewing, 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 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, e.g., 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.

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 of which was derived from a different nonarthropod 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; however, they lack any evidence of the second antenna of crustaceans or a homologous structure or the mandible comprising a complete limb, rather than the limb base of the crustacean mandible. Proponents of this relationship saw Crustacea either grouping with chelicerates and extinct trilobites, separate from Atelocerata, or forming its sister group, in a clade called 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 some 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, termed Pancrustacea, and exclusion of myriapods. Furthermore, all analyzed molecular sequence data with adequate signal to resolve relationships support Pancrustacea and not 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 of the possible groupings alternative to Pancrustacea. This does not imply that such analyses all identify 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.

If molecular-derived relationships are correct, features understood previously to infer monophyly of Atelocerata must be reconsidered. 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 those Hexapoda possessing these structures. Thus, morphological characters traditionally used to support Atelocerata include states that may be nonhomologous and convergently acquired through terrestriality, not distributed

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across all included taxa, or 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, refutes 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, appears to reflect more accurately phylogeny than much of the earlier external morphological studies.

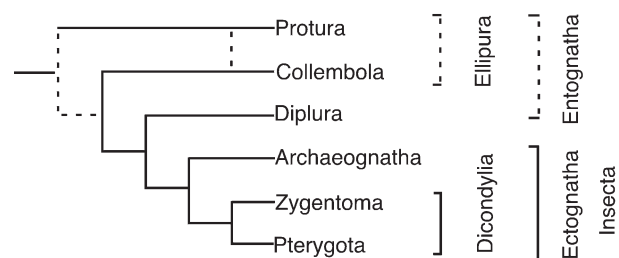
The question remains as to whether part or all of the Crustacea constitute the sister group to Hexapoda. Morphology generally supports a monophyletic Crustacea, but inferences from some molecular data imply paraphyly, including a suggestion that Malacostraca alone are sister to Hexapoda (see below). Combined morphological and molecular data support both Crustacea and Pancrustacea monophyly, and Crustacea monophyly is thus preferred.

### THE EXTANT HEXAPODA

Hexapoda (ranked usually as a 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 three 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 was primitively 11-segmented with up to five exites (outer appendages of the leg), a coxal endite (an inner appendage of the leg), and two 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.

Basal hexapods undoubtedly include taxa whose ancestors were wingless and terrestrial. This grouping is not monophyletic, being based entirely on evident symplesiomorphies or otherwise doubtfully derived characters. Included groups, treated as orders, are Protura, Collembola, Diplura, Archaeognatha, and Zygentoma (Thysanura). True Insecta are the Archaeognatha, the Zygentoma, and the huge radiation of Pterygota (primary winged hexapods). Because Insecta is treated as a class, the successively more distant sister groups Diplura and Collembola (with or without Protura) are of equal rank.

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 a current synthetic view. Traditionally, Collembola, Protura,



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

and Diplura were grouped as “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. However, two different types of entognathy now are 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).

#### 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 all remaining Hexapoda.

#### Collembola (Springtails)

Collembolans are minute to small and soft bodied, often with rudimentary eyes or ocelli. The antennae are four- to six-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 four-segmented. The abdomen is six-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, that is, with segment number constant through development. Collembola form either the sister group to Protura comprising Ellipura or a more strongly supported relationship as sister to Diplura + Insecta.

**Diplura (Diplurans)**

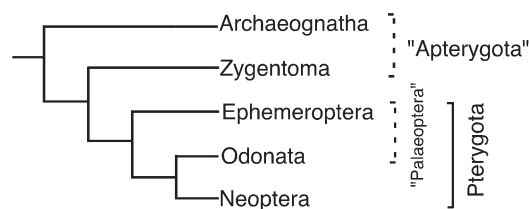
Diplurans are small to medium sized, mostly unpigmented, possessing long, moniliform antennae (like a string of beads), but lacking eyes. The mouthparts are entognathous, with tips of well-developed mandibles and maxillae protruding from the mouth cavity and maxillary and labial palps reduced. The thorax 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 forms the sister group to Insecta.

**Class Insecta (True Insects)**

Insects range from minute to large (0.2 to 300 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 the abdomen, but variably reduced or absent (e.g., in many immature stages). Larval/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 comprising the primarily wingless taxa Archaeognatha + Zygentoma is paraphyletic and rejected (Fig. 2).

**ARCHAEOGNATHA (ARCHAEOGNATHANS, BRISTLE-TAILS)** Archaeognathans are medium-sized, elongate



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

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 mandible, one with two neighboring condyli each, and elongate seven-segmented maxillary palps. Often coxae II and III or III of legs bear a coxal stylet, tarsi two- to three-segmented. The abdomen, which continues in an even contour from the humped thorax, bears ventral muscle-containing styles (representing reduced limbs) on segments 2 to 9 and generally one or two pairs of eversible vesicles medial to the styles on segments 1 to 7. Cerci are multisegmented and shorter than the median caudal appendage. Sperm transfer is indirect via sperm droplets attached to a silken line or by stalked spermatophores. Development occurs without change in body form.

The two families of recent Archaeognatha, Machilidae and Meinertellidae, form an undoubted monophyletic group, whose position at the base of Ectognatha and as sister group to Dicondylia (Zygentoma + Pterygota) should be carefully investigated (Figs. 1 and 2).

**ZYAGENTOMA (THYSANURA, SILVERFISH)** Zygentomans (thysanurans) are medium-sized, dorsoventrally flattened apterygotes with almost 400 species in four 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 five-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 to 9, sometimes on 2 to 9, 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.

**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 to 11 abdominal segments lack styles and vesicular appendages, and only most Ephemeroptera 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).

**Informal Grouping "Palaeoptera"** 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 convexity/concavity opposite to that of the adjacent main veins) and a network of crossveins. This wing venation and articulation, substantiated

by paleontological studies on similar features, has suggested that Odonata and Ephemeroptera form a monophyletic group, Palaeoptera, which is a sister group to Neoptera, which contains all remaining extant and primarily winged orders. However, reassessment of morphology of extant basal lineages and much existing molecular evidence reject a monophyletic Palaeoptera. Here Ephemeroptera is treated as sister to Odonata + Neoptera, with Odonata alone as the sister group to Neoptera, giving a higher classification of Pterygota into three Divisions.

**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 nonfunctional, 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. The retention of a subimago (subadult stage) is unique. Nymphs (larvae) are aquatic and the mandible articulation, which is intermediate between monocondyly 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 render phylogenetic reconstruction difficult. Ephemeroptera traditionally has been divided into two suborders: Schistonota (with nymphal forewing pads separate from each other for over half their length), containing the superfamilies Baetoidea, Heptagenioidea, Leptophlebioidea, and Ephemerioidea, and Pannota (“fused back”—with more extensively fused forewing pads), containing Ephemerelloidea and Caenoidea. Recent studies suggest that this concept of Schistonota is paraphyletic. Families Baetiscidae and Prosopistomatidae, whose nymphs have unusually developed thoracic shields, have been withdrawn from the Caenoidea and are placed now in the suborder Catapacea.

**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 behavior, 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.

Traditionally odonatologists have recognized three groups of taxa, Zygoptera (damselflies), Anisozygoptera, and Anisoptera (dragonflies), generally ranked as suborders. Assessment of their monophyly or paraphyly relies 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 that Zygoptera is a

grade on the way to Anisozygoptera, which itself is a grade on the way to Anisoptera. A well-supported view, including information from the substantial fossil record, has Zygoptera probably paraphyletic, Anisozygoptera undoubtedly paraphyletic, and Anisoptera as the monophyletic sister group to some extinct anisozygopterans.

Zygoptera contains three broad suprafamilial groupings, the Coenagrionoidea, Lestoidea, and Calopterygoidea. The first is centered around the family Coenagrionidae, but the group is made paraphyletic by excision of Eurasian Platynemididae (for their dilated tibiae), South American Pseudostigmatidae (for their huge size), Platystictidae (for a narrow wing), and Protoneuridae and Isostictidae (for wings narrowed in a different way). Those latter two families differ only in the degree of wing narrowing, and the narrower one, Australasian Isostictidae, often is treated as a subfamily of the less narrow one, Protoneuridae.

The Calopterygoidea usually is regarded as centered around Calopterygidae. This specious family is made paraphyletic by excision of Chlorocyphidae (whose frons has a unique shape), Dicteriadidae (with legs lacking setae), Euphaeidae (a Southeast Asian variant on Calopterygidae, with abdominal gills in the larvae), and South American Polythoridae, with brightly colored wings.

Lestoidea contains the families Lestidae and Synlestidae, which clearly are related to each other. Perilestidae may belong here, and the enigmatic Hemiphlebiidae may be sister to this grouping. The quite different-looking Megapodagrionidae are related in some way to Amphipterygidae and Lestoidea (the latter being an unstable mix of small genera allocated to either Lestoidea or Calopterygoidea).

Among Anisoptera four major lineages can be recognized, but their relationships to each other are obscure. Three aeshnid families, Aeshnidae, Neopetaliidae (evidently a subset of Aeshnidae), and Cordulegastridae (aeshnids with a secondarily elongate ovipositor), form a clade. The small (10 species) but very distinct Petaluridae forms a distinctive group. Gomphidae forms a large family all on its own. The superfamily Libelluloidea traditionally is divided into two large families, Cordulidae and Libellulidae, but the limits of each division are unclear, and no single character separates them. Chlorogomphidae, Macromiidae, and Synthemistidae are small, local “families” often separated out as near the corduliids.

Sister to Anisoptera is the minor suborder Anisozygoptera containing one extant genus with two species.

**Neoptera** 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) crossveins.

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 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 Basal Neopteran Orders)** [Isoptera, Blattodea, Mantodea, Dermaptera, Grylloblattaria (Grylloblattodia), Plecoptera, Orthoptera, Phasmatodea, Embiidina (Embioptera), Zoraptera, Mantophasmatodea] The relationships of the basal neopteran orders are poorly resolved with several, often contradictory, relationships being suggested by morphology. The 11 included orders may be monophyletic, based on the shared presence of tarsal plantulae (lacking only in Zoraptera) and 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, features of the head skeleton (perforated

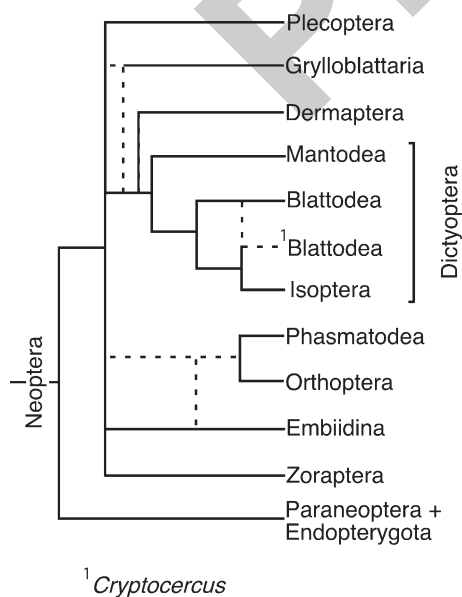
tentorium), mouthparts (paraglossal musculature), digestive system (toothed proventriculus), and female genitalia (shortened ovipositor above a large subgenital plate) demonstrate monophyly of Dictyoptera, substantiated by nearly all molecular analyses. However, as seen below, views on the internal relationships are changing. Dermaptera (earwigs) is 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 one another and to the above groupings are less well understood.

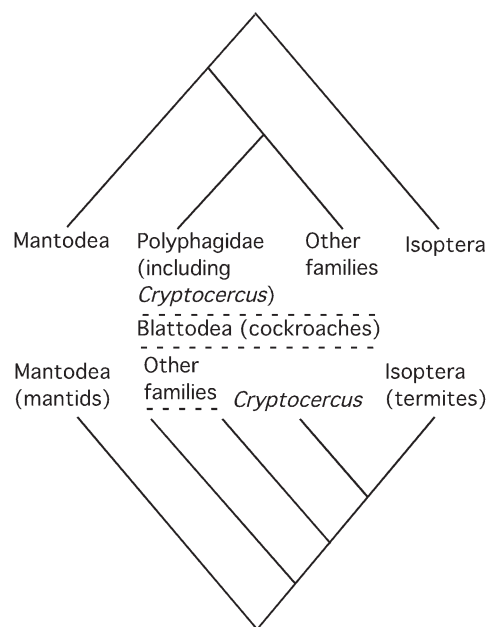
**Isoptera (Termites, White Ants).** Isoptera forms a small order of eusocial hemimetabolous neopterans, with some 2600 described species, living socially with polymorphic caste systems of reproductives, workers, and soldiers. The mouthparts are typically blattoid, being mandibulate but varying between 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- and hind wings are generally similar and 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 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 may have arisen from within the cockroaches, thereby rendering that group paraphyletic. Under this scenario, the (wingless) wood roaches 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 with the reduced diversity of the extant family, which comprises just one species in northern Australia.

**Blattodea (Cockroaches).** Blattodea contains over 3500 species in at least eight families worldwide. They are hemimetabolous, dorsoventrally flattened insects with filiform, multisegmented antennae, and mandibulate, ventrally projecting mouthparts.



**FIGURE 3** Cladogram depicting relationships among, and inferred classification of, orders of Neoptera: Polyneoptera. Dashed lines indicate uncertainty in cladogram.



**FIGURE 4** Cladogram depicting alternative relationships among Dictyoptera. Dashed lines indicate paraphyly in classification.

The prothorax has an enlarged, shield-like pronotum, often covering the head; the meso- and metathorax are rectangular and subequal. The forewings are sclerotized as tegmina, which protect the 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 that the termites arose from within the cockroaches, and the “order” thus is rendered paraphyletic. The sister group of the Isoptera may be *Cryptocercus*, a basal cockroach (Fig. 4). Blatellidae and Blaberidae form a derived sister grouping.

*Mantodea (Mantids)*. Mantodea contains some 2000 species in eight families. They 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 forewings form leathery tegmina with a reduced anal area; the hind wings are broad and membranous, with long unbranched veins and many crossveins, 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 forms the sister group to Blattodea + Isoptera and shares 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 characteristics of visual predation, namely the mobile head with large, separated eyes. Internal relationships of Mantodea are uncertain and little studied.

*Grylloblattaria (Notoptera, Grylloblattodea) (Grylloblattids or Rock Crawlers)*. Grylloblattaria contains one family (Grylloblattidae) with 20 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 are either 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- to 9-segmented cerci. The female has a short ovipositor, and the male genitalia are asymmetrical.

The phylogenetic placement of Grylloblattaria is controversial, as they are generally argued to be relicts that either “bridge the cockroaches and orthopterans” or are “primitive among orthopteroids.” The antennal musculature resembles that of mantids and embiids, mandibular musculature resembles that of Dictyoptera, and the maxillary muscles resemble those of Dermaptera. Embryologically grylloblattids appear closest to the orthopteroids. The only molecular phylogenetic study that included a grylloblattid implied a sister group relationship to Dictyoptera, instead of one lying more basal in the Neoptera as is implied by the morphology. However, sampling in this analysis lacked some important plesiomorphic taxa, such as *Cryptocercus*, *Mastotermes*, and Embiidina. A tentative relationship of Grylloblattaria as sister to Dermaptera + Dictyoptera remains a favored hypothesis.

*Dermaptera (Earwigs)*. Dermaptera is a worldwide order, modest in size, with some 10 families and about 1800 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 three-segmented with a short second tarsomere. Many species are apterous or, if winged, the forewings are small, leathery, and smooth, forming unveined tegmina, and the hind wings are large, membranous, semicircular, and dominated by an anal fan of radiating vein branches connected by crossveins; 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 semiparasites of African rodents have been placed in a suborder,

Hemimerina. These earwigs are blind, are 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 eight 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 the genitalia more generally, or homoplasies (convergences) in furcula form and wing reduction.

A sister group relationship to Dictyoptera is well supported on morphology, including many features of the wing venation.

*Plecoptera (Stoneflies)*. Plecoptera is a minor order of some 16 families, 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- 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 wing pads first become visible when the young are half-grown.

Monophyly of the order is supported by few morphological characters, 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 and 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 between 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 among “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, including as sister to (i) Embiidina or, more likely, (ii) Dermaptera + Dictyoptera.

Internal relationships have been proposed as two predominantly disjunct suborders, the austral *Antarctoperlaria* and northern *Arctoperlaria*. The monophyly of *Antarctoperlaria* 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 the *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) used in mate-finding. The component families *Scopuridae*, *Taeniopterygidae*, *Capniidae*, *Leuctridae*, and *Nemouridae* (including *Notonemouridae*) are essentially of 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 among extant Plecoptera are proving important in hypothesizing 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 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 five-segmented maxillary palps and three-segmented labial palps. Sometimes both sexes are apterous, and in alate forms the hind wings are smaller than the forewings; 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. 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. Analysis of major wing structures and musculature imply that *Zoraptera* belong in the blattoid lineage. Although the wing shape and venation resemble those 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 most are medium-sized to large insects with hind legs 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 forewings form narrow, leathery tegmina, and the hind wings are broad, with numerous longitudinal and crossveins, folded beneath the tegmina by pleating; aptery and brachyptery are frequent. The abdomen has eight or nine annular visible segments, with the two or three terminal segments reduced, and one-segmented cerci. The female has a well-developed ovipositor formed from highly modified abdominal appendages.

Virtually all morphological evidence, and much of the newer molecular data suggest that the Orthoptera form the



sister group to Phasmatodea. Some authors have united the orders, but the different wing-bud development, different egg morphology, and lack of auditory organs in phasmatids suggest separation. Molecular evidence indicates that Embiidina may be sister to the orthopteran–phasmatid clade, but the support for this relationship is weak.

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 is the sister group (but highly divergent, with a long branch separation) of the remaining ensiferan taxa, Tettigoniioidea, Hagloidea, and Stenopelmatoidea. On grounds of some molecular and morphological data Tettigoniidae and Haglidae form a monophyletic group, sister to Stenopelmatoidea and relatives (mormon crickets, wetas, cooloola monsters, and the like), but alternative analyses suggest different relationships, and conservatively, an unresolved group is perhaps appropriate at this stage.

In Caelifera a well-supported recent proposal for four superfamilies, namely [Tridactyloidea (Tetrargoidea (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 the superfamilies Tanaoceroidea, Pyrgomorpoidea, Pneumoroidea, and Trigonopterygoidea.

*Phasmatodea (Phasmatids, Phasmids, Stick Insects or Walking Sticks).* Phasmatodea are a worldwide, predominantly tropical order of more than 2500 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 are relatively small and placed anterolaterally, with ocelli only in winged species and often only in males. The antennae are short to long, with 8 to 100 segments. The prothorax is small, and mesothorax and metathorax are long in wingless species and shorter in apterous ones. The wings, when present, are functional in males, often reduced in females, but with many species apterous in both sexes; the forewings form short leathery tegmina, whereas the hind wings are broad with a network of numerous crossveins 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.

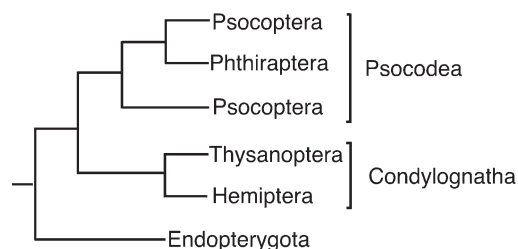
*Embiidina (Embioptera) (Embiids, Webspinners).* Embiidina comprise some 200 described species (perhaps up to an order of magnitude more remain undescribed) in at least eight families. The body is elongate, cylindrical, and somewhat flattened in males. The head has kidney-shaped compound eyes that are larger in males than in females and lacks ocelli. The antennae are multisegmented and the mandibulate mouthparts project forward (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 the males are complex and asymmetrical.

Embiids are undoubtedly monophyletic based on, *inter alia*, 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 a closer relationship to Orthoptera and Phasmatodea; they also have some similarity to the Dermaptera, notably deriving from their prognathy. Internal relationships among the described higher taxa of Embiidina suggest that the prevailing classification includes many nonmonophyletic groups. Evidently much further study is needed to understand relationships within Embiidina and among it and other neopterans.

*Mantophasmatodea.* Mantophasmatodea has been recognized recently for a species in Baltic amber and two museum specimens representing two species from southwest and east Africa and from freshly collected material from Namibia. The taxon cannot be placed within any of the existing orders and initial estimates of relationships are unclear. Some resemblances to Grylloblattarea and Phasmatodea are evident, but more study, including molecular sequencing, is required.

*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 3 or less.

Within Paraneoptera, the monophyletic superorder Psocodea contains Phthiraptera (parasitic lice) and Psocoptera (book lice). Although Phthiraptera is monophyletic, the clade arose 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



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

(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).

*Psocoptera (Plant 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. Some 3000 species are described in 35 families. Evidently Psocoptera belong with Phthiraptera in a monophyletic clade, Psocodea. However, Psocoptera is rendered paraphyletic by a postulated relationship of Phthiraptera to the psocopteran family Liposcelidae. Internal relationships in Psocoptera are poorly known.

*Phthiraptera (Lice)*. Phthirapterans are wingless obligate ectoparasites of birds and mammals, lacking any free-living stage, with some 3000 species in some 17 families. Monophyly of, and relationships among, the traditional suborders Anoplura, Amblycera, Ischnocera, and Rhyncophthirina are poorly understood and nearly all possible arrangements have been proposed. The latter three suborders have been treated 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)]. The only molecular data adduced thus far found unequivocal monophyly only for Amblycera, with a placement that rendered Ischnocera paraphyletic. The data neither supported nor refuted mallophagan monophyly. Resolution of these issues is important in estimation of degree of cospeciation between lice and their bird and mammal hosts.

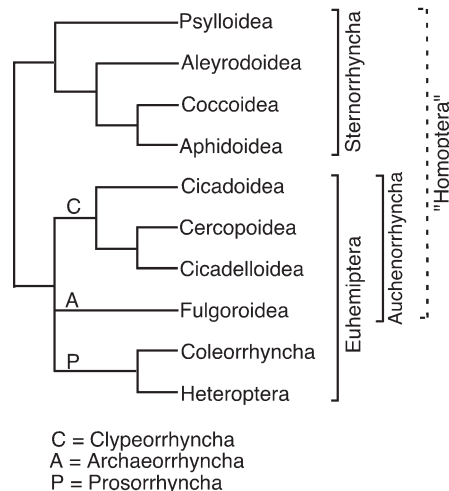
*Thysanoptera (Thrips)*. Thysanoptera is a worldwide order of just over 5000 species in nine families. The development of thrips is intermediate between hemi- and holometabolous. Their head is elongate and the mouthparts are unique in that the maxillary laciniae formed grooved stylets, the right mandible is atrophied, but the left mandible forms a stylet; all three stylets together form the feeding apparatus. The tarsi are one- or two-segmented, and the pretarsus has an apical protrusible adhesive ariolum (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, Terebrantia and Tubulifera, containing the sole, speciose, family Phlaeothripidae. Terebrantia includes three speciose families, Thripidae, Heterothripidae, and Aeolothripidae, and five smaller families. Relationships among families in Terebrantia are poorly resolved, although phylogenies are being generated at lower levels concerning aspects of the evolution of sociality, especially the origins of gall-inducing thrips and of “soldier” castes in Australian gall-inducing Thripidae.

*Hemiptera (Bugs, Cicadas, Leafhoppers, Planthoppers, Spittlebugs, Aphids, Psylloids, Scale Insects, Whiteflies, Moss Bugs)*. Hemiptera is the largest of the nonendopterygote orders, with more than 50,000 species in approximately 100 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 taking up 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, spittlebugs, aphids, psyllids, 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 a rostrum arising ventrally close the anterior of the thorax, “Homoptera” represents a paraphyletic grade rather than a clade. This view is supported by reinterpreted morphological data and by cladistic analysis of nucleotide sequences from the nuclear small subunit ribosomal RNA gene (also called 18S rRNA). These data also suggest a much more complicated pattern of relationships among the higher groups of hemipterans (Fig. 6).

The ranking 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, Clypeorrhyncha, and Prosorrhyncha collectively form the Euhemiptera, which is the sister group to the fourth suborder, Sternorrhyncha. The latter contains the aphids, psyllids, scale insects, and whiteflies, which are characterized principally by their possession of a particular kind of gut filter chamber, a rostrum that appears to arise between the bases of their front legs, and, if winged, the absence of vannus and vannal fold in the hind wing. Some relationships among Euhemiptera are unsettled. A monophyletic Auchenorrhyncha, morphologically defined by their possession of a tymbal acoustic system, an aristate antennal



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

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 spittlebugs, often called Cicadomorpha). Molecular data tend to refute this monophyly, implying that Archaeorrhyncha is closer to Heteroptera, 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 the suborder Prosorrhyncha. 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 among some 75 families, forming the largest hemipteran clade. Heteroptera is most easily diagnosed by the presence of metapleural scent glands, and monophyly is never disputed.

**Endopterygota** (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. The adult wings and genitalia are internalized in their preadult expression, developing in imaginal discs that are evaginated at the penultimate molt. Larvae lack true ocelli. The “resting stage” or pupa is nonfeeding 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 among the endopterygotes, of which one of the strongest is a sister group

relationship termed Amphiesmenoptera between the Trichoptera (caddisflies) and Lepidoptera (butterflies and moths). A plausible scenario of an ancestral amphiesmenopteran taxon has a larva living in damp soil among 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 Raphidioptera—Neuropterida (sometimes treated as a group of ordinal rank)—showing a sister group relationship to Coleoptera.

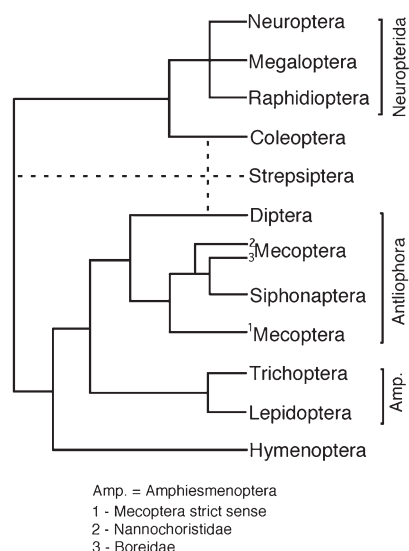
A third, postulated relationship—Antliophora—unites Diptera (true flies), Siphonaptera (fleas), and Mecoptera (scorpionflies and hangingflies). Debate continues about the relationships of these taxa, particularly concerning the relationships of Siphonaptera. Fleas were considered sister to Diptera, but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

Strepsiptera is phylogenetically enigmatic, but resemblance of their first-instar larvae (called triangulins) to certain Coleoptera, notably parasitic Rhipiphoridae, and some wing base features have been cited as indicative of relationship. This placement is becoming less likely, as molecular evidence (and haltere development) suggests a link between Strepsiptera and Diptera. Strepsiptera is highly derived in both morphological and molecular evolution, and thus possesses 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 positions of two major orders of endopterygotes, Coleoptera and Hymenoptera, remain 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. Hymenoptera may be the sister to Antliophora + Amphiesmenoptera; the many highly derived features of adults, and reductions in larvae, limit morphological justification for this position.

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

**Coleoptera (Beetles).** Coleoptera undoubtedly lie among the basal Endopterygota. The major synapomorphic feature of Coleoptera is the development of the forewings 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 the 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 woodminers 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 includes ground beetles, tiger beetles, whirligigs, predaceous diving beetles, and 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, Haliplidae and Noteridae, which are algivorous, and the mycophagous Rhyssodidae. Morphology has suggested that Adephaga is sister group to the combined Myxophaga and Polyphaga, but molecular data (18S rDNA) suggest Adephaga as sister to Polyphaga, with Myxophaga sister to them.

Myxophaga is a clade of small, primarily riparian aquatic beetles, comprising the families Lepiceridae, Torridincolidae, Hydroscaphidae, and Microsporidae, united by the synapomorphic fusion of the pretarsus and tarsus. The three-segmented

larval antenna, five-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 wing venation and folding provide evidence for (Polyphaga (Archostemata (Myxophaga + Adephaga))).

Polyphaga contains the majority (>90% of species) of beetles, with about 300,000 described species. The suborder includes rove beetles (Staphylinioidea), 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, longhorned 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 (whose rank even is disputed) are allocated to different clades by different authors. Large superfamilies include Hydrophiloidea, Staphylinioidea, 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 eighth abdominal segment. Constituent superfamilies of Cucujiformia are Cleroidea, Cucujoidea, 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 comprise three small orders with holometabolous development, with approximately 6000 species of Neuroptera in about 20 families, 300 species of Megaloptera in 2 widely recognized families, and 200 species of Raphidioptera in 2 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- 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 have Megaloptera and Raphidioptera as sister groups. Recent reanalyses 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 and Sisyridae in Neuroptera) in Neuropterida.

*Strepsiptera*. Strepsiptera form an enigmatic order of nearly 400 species of highly modified endoparasites, 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 to 7 segments; the forewings 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 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 instar.

The phylogenetic position of Strepsiptera has been subject to much speculation because modifications associated with their endoparasitic lifestyle 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 synapomorphic with Coleoptera are suspect or mistaken. 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. Molecular sequence studies indicate that Strepsiptera possibly is a sister group to Diptera, and some tantalizing information from

developmental biology suggests that wings and halteres might be “reverse-expressed” on meso- and metathoracic segments.

*Mecoptera* (*Scorpionflies*, *Hangingflies*). Mecopterans are holometabolous insects comprising about 500 known species in nine families, with common names associated with the two largest families—Bittacidae (hangingflies) and Panorpididae (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- 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 compound eyes comprising 3 to 30 ocelli (absent in Panorpididae, 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 to 8, and the terminal segment (10) has either 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, suggest that Siphonaptera arise from within Mecoptera, as a sister group to the “snow fleas” (Boreidae). The phylogenetic position of Nannochoristidae, the southern hemisphere mecopteran taxon currently treated as being of subfamily rank, has a significant bearing on internal relationships within Antliophora. Molecular evidence suggests that it lies as sister to Boreidae + Siphonaptera and therefore is of rank equivalent to the boreids, the fleas, and the residue of Mecoptera—and logically each should be treated as an order or Siphonaptera should be reduced in rank within Mecoptera.

*Siphonaptera* (*Fleas*). Siphonaptera is a highly modified order of holometabolous insects, comprising some 2400 species, all of which are bilaterally compressed, apterous ectoparasites. The mouthparts are specialized for piercing and sucking, lack mandibles, but have an upaired 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 that 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 (snow fleas). Internal relationships of the fleas are under study, and preliminary results imply that monophyly of many families is uncertain.

*Diptera (True Flies).* Diptera is a major order of insects, with perhaps as many as a quarter of a million species in some 120 families. Dipterans are holometabolous and readily recognized by the development of hind (metathoracic) wings as balancers, or halteres (halters), 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 a 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 of a maggot head, retaining only the sclerotized mandibles (“mouth hooks”) and supporting structures.

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

Internal relationships among 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 a basal clade, 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 casts doubt on the basal position of the crane flies, but as yet does not produce a robust estimate for any alternative basal grouping. Alternative views based on morphology have suggested that the relictual family Tanyderidae, with complex (“primitive”) wing venation, lies close to the base of the order. In this instance support comes both from the tanyderid larval morphology and from the putative placement in Psychodomorpha, considered a probable basal clade.

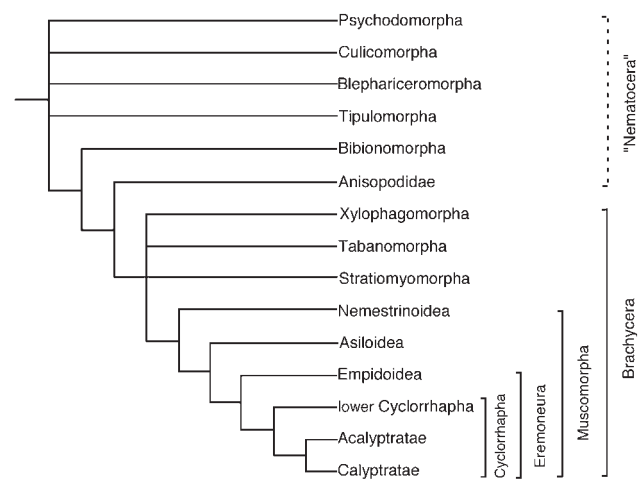
There is strong support for Culicomorpha, comprising mosquitoes (Culicidae) and their relatives (Corethrellidae, Chaoboridae, Dixidae) and their sister group the blackflies, midges, and relatives (Simuliidae, Thaumaleidae, Ceratopogonidae, Chironomidae), and for Bibionomorpha, comprising the fungus gnats (*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 the loss of premandible and, in the adult, 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 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 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 Asiloidea (robber flies, bee flies, and relatives) and Eremoneura (empidoidea 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 genital characters, plus larval features including maxillary reduction and presence of only three instars.

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

*Hymenoptera (Wasps, Bees, Ants, Sawflies, and Wood Wasps).* Hymenoptera contains at least 100,000 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). The hymenopteran head has mouthparts



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

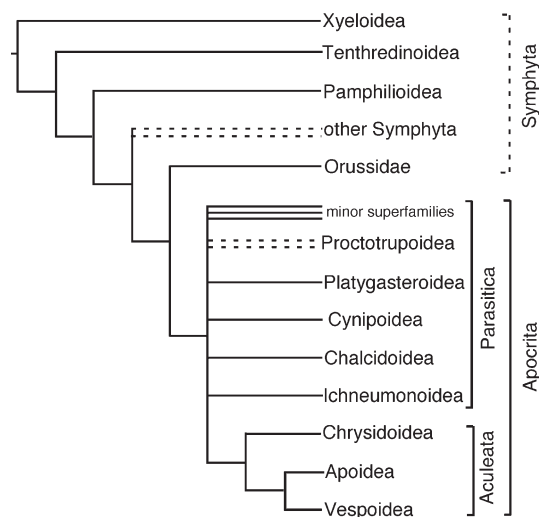
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ventrally directed to forward projecting, ranging from generalized mandibulate (“Symphyta”—woodwasps and sawflies) to sucking and chewing, with mandibles often used for killing and handling prey and, in Apocrita (ants, bees, and wasps), in defense 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 three-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 but is reduced in Apocrita in correlation with body size, such that very small species of 1 to 2 mm have only one divided vein or none. The hind wing has rows of hooks (hamuli) along the leading edge that couple with the hind margin of the forewing 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 to form the sister group to Amphiesmenoptera (Trichoptera + Lepidoptera) + Antliophora (Diptera + Mecoptera/Siphonaptera), although a more basal position in the Holometabola has been advocated. Hymenoptera often are treated as containing two suborders, Symphyta (wood wasps and sawflies) and Apocrita (wasps, bees, and ants). However, Apocrita appears to be sister to one family of symphytan only, the Orussidae, and thus “Symphyta” form a basal paraphyletic group, whose basalmost clade is the Xyeloidea. This is sister to a monophyletic tenthredinoid (sawfly) clade, in turn 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 nonmonophyletic, including Proctotrupoidea, but Proctotrupomorpha, comprising superfamilies Proctotrupoidea, Chalcidoidea, Platygasteroidea, and Cynipoidea, appears to be monophyletic.



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

From morphology, Ichneumonoidea were argued to be sister to Aculeata, but molecular data and reanalysis refute this. The monophyletic aculeates, defined by their distinctive ovipositor construction and loss of female cerci, comprise Chrysididae (Vespoidea + Apoidea). Internal relationships of aculeates, including vespids (wasps), formicids (ants), and apids (bees), and the monophyly of subordinate groups are under scrutiny. Apidae evidently arose from within Sphecidae (digger wasps), but the precise relationships of another significant group of aculeates, Formicidae (ants), within Vespoidea is less well established.

*Trichoptera (Caddisflies)*. Trichoptera contains about 45 extant families containing some 10,000 described species, with estimates of undescribed (mostly Southeast Asian) species diversity some four- to fivefold higher. Trichoptera are holometabolous; the moth-like adult has reduced mouthparts lacking any proboscis, but with three- to five-segmented maxillary palps and three-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 most basal Lepidoptera by the looped anal veins in the forewing and absence of a discal cell. The larva is aquatic, has fully developed mouthparts, has 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 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 the suborder Annulipalpia in its strictest sense, comprising families Hydropsychidae, Polycentropodidae, Philopotamidae, and some close relatives, is well supported by larval and adult morphology—including the presence of an 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, 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* crossvein; hind wings broader than forewings, especially in the anal area; the 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 middorsal 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 the maxillary palp, and eversible oviscapt (egg-laying appendage). Morphological and molecular evidence fail to confirm Spicipalpia monophyly, unless at least 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 Annulipalpia are sister to a paraphyletic Spicipalpia + monophyletic Integripalpia finds support from some morphological and molecular data.

At lower phylogenetic levels, several interfamily relationships have been explored and congruent findings made, for example, concerning the families of Sericostomatoidea, including several from the landmasses formerly constituting Gondwana, including South Africa. In contrast, relationships of taxa associated with the family Leptoceridae vary dramatically between researchers. Forthcoming molecular evidence may be expected to assist in resolution of some issues and perhaps confuse otherwise robust relationships.

*Lepidoptera (Moths and Butterflies)*. Lepidoptera, with some 140,000 described species in 70 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 that 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 forewings are linked

by either 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 sometimes 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 nonditryisian group. Three of the four suborders are species-poor (Micropterigoidea, Agathiphagoidea, Heterobathmioidea), lie sequentially at the base of the Lepidoptera, and lack the synapomorphy of the megadiverse suborder Glossata, namely the characteristically developed coiled proboscis formed from the fused galea. The 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- and hind wings). Trends in the evolution of Ditrysia include elaboration of the proboscis (haustellum) and the reduction or loss of maxillary palpi. Relationships between the smaller superfamilies (not shown in Fig. 10) and the few highly diverse ones (Tineoidea, Gelechioidea, Tortricioidea, 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

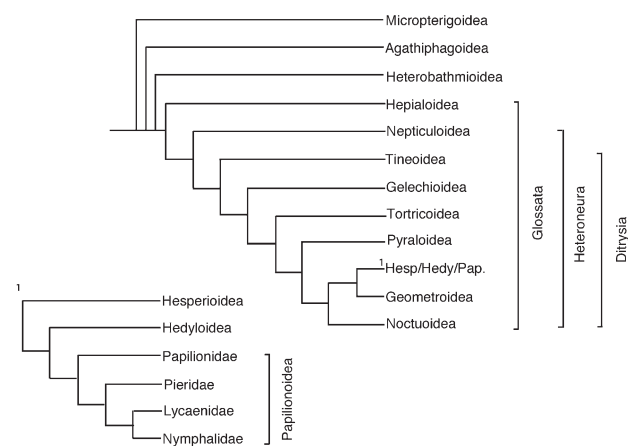


FIGURE 10 Cladogram depicting relationships among, and inferred classification of, Lepidoptera. Only selected superfamilies are depicted.



on the hind wing. To this has been added the neotropical Hedyloidea to form the monophyletic grouping we know as the butterflies.

#### See Also the Following Articles

*Arthropoda and Related Groups* • *Biodiversity* • *Biogeography* • *Fossil Record* • *Insecta, Overview*

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## Physical Control of Insect Pests

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Physical control is one of the four main approaches to crop protection against insects; the other three are the chemical, biological, and biopesticide approaches. From a theoretical and a technical point of view, all of these approaches have limits that make them more or less suitable against a given pest control target. In practice, the relative merits of each approach are also weighted against numerous factors before an actual decision is made regarding the most appropriate method to implement. A majority of agricultural commodities are protected using chemical control but ideally, all components and technologies should be blended optimally and harmoniously into an integrated pest management (IPM) program.

## PHYSICAL CONTROL METHODS

### Definition, Context, and Literature

Physical control methods in crop protection comprise all pest management techniques that rely on the use of physical processes to damage, kill, or induce behavioral changes in target organisms. The primary action may have a direct impact, for example, when insects are killed immediately by mechanical shocks. In other instances, the desired effect is attained through stress responses.

Various physical control methods have been used throughout the long history of plant protection (Table I). With the rapid advances that have occurred in the physical, chemical, and biological sciences since the late 19th century, agriculture has been transformed from a strictly empirical activity, largely based on tradition and aimed primarily at staying off famine, to a quantitative form of agriculture focused on producing a certain amount of food. During this transition, which has been sustained at an increasing rate over the past 50 years, physical control methods have been set aside because of the tremendous success of chemical control. It is only natural that some people should view the use of physical control methods as a step backward to those distant ancestral practices. Thanks to technological advances and greater precision in the implementation of such methods, physical control now has all the necessary attributes for incorporation into IPM strategies.

### Use in Agricultural Production

The different methods of physical control used against crop pests have some common characteristics. One of the characteristics that differentiates physical tactics from the other control methods (Table I) is the absence of persistence. In almost every case, the effect of a treatment is limited to the period of application. When treatment stops, the stressor disappears immediately or dissipates quickly. From the standpoint of exercising control over the treatment and its secondary effects, the absence of a residual action is an advantage. However, this characteristic can also be regarded as a drawback, because the treatment may have to be repeated every few days to control crop pests that emerge and are active for a few days or a few weeks. In such cases, persistent chemicals constitute a much more convenient approach, although they are often undesirable from an environmental standpoint.

In addition to being restricted to the time of application, the impact of a physical control method is limited spatially. Mechanical, pneumatic, electrical, and thermal energies are dissipated locally over a distance of up to a few meters from the site of application. Electromagnetic radiation, which propagates over considerable distances and is subject to numerous restrictions (reserved frequency bands, maximum power, absence of interference), is an exception. Some pesticides have the unfortunate characteristic of dispersing over considerable distances. Similarly, many biological control agents can disperse or become dispersed beyond the treatment area.