

# Advances in Insect Phylogeny at the Dawn of the Postgenomic Era

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## Abstract

Most species on Earth are insects and thus, understanding their evolutionary relationships is key to understanding the evolution of life. Insect relationships are increasingly well supported, due largely to technological advances in molecular sequencing and phylogenetic computational analysis. In this postgenomic era, insect systematics will be furthered best by integrative methods aimed at hypothesis corroboration from molecular, morphological, and paleontological evidence. This review of the current consensus of insect relationships provides a foundation for comparative study and offers a framework to evaluate incoming genomic evidence. Notable recent phylogenetic successes include the resolution of Holometabola, including the identification of the enigmatic Strepsiptera as a beetle relative and the early divergence of Hymenoptera; the recognition of hexapods as a crustacean lineage within Pancrustacea; and the elucidation of Dictyoptera orders, with termites placed as social cockroaches. Regions of the tree that require further investigation include the earliest winged insects (Palaeoptera) and Polyneoptera (orthopteroid lineages).

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**PCR:** polymerase chain reaction  
**micro-CT:** microcomputer tomography

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## INTRODUCTION

Insects account for most of the species-richness of life on Earth. As a result, their phylogenetic history and diversification are central to understanding the evolution of life more generally. Our knowledge of the history and diversification of insects has expanded greatly in the 30 years since a landmark review of the subject was published in the *Annual Review of Entomology* (68). This progress continues to develop through major conceptual and technological advances in the practice of systematic entomology. The most significant change is the rapid acquisition of large amounts of molecular sequence data from high-throughput genomics, providing an ever-expanding evidence base for reexamination of long-standing controversies in insect phylogeny. Parallel advances in computational biology, bioinformatics, and computation speed have spurred analytical achievements in phylogeny reconstruction. Just a decade ago, when insect systematists were relying largely on easy-to-acquire molecular markers such as mitochondrial genes and ribosomal DNA, the annotated genomes of *Drosophila melanogaster* and *Anopheles gambiae* were published (48, 65). As sequenced genomes accumulated, it became easier to develop taxon-specific primers for conserved genes, and an emphasis on the phylogenetic utility of nuclear protein-coding genes emerged (97, 100). We are now at a turning point where large-scale-targeted polymerase chain reaction (PCR) may no longer be a cost-effective alternative to next-generation sequencing methods that can return hundreds of candidate genes per taxon for phylogenetic analysis. Today, complete genome sequences are available only for critical insect model organisms, yet in the very near future, genomic data for a much broader sampling of insects will rapidly accrue.

With this great increase in molecular data comes a new set of challenges; instead of struggling to add another gene to a data set, we will winnow down large harvests of genes to identify single-copy orthologs to recover phylogeny. We will determine whether “more genes” or “less noise” is the superior approach. Another hurdle in analyzing large data sets is systematic error. Unlike the phylogenetic inaccuracy that results from stochastic error in small genetic samples, systematic error masquerades as strongly supported resolution and results from undetected genetic biases and/or errors inherent in model estimation and algorithm design. As the practice of phylogenetics intersects with the world of comparative genomics, it has become evident that molecular data, even complete genome sequences, are not always an independent solution to resolving the tree of life (93, 105). The entomological advances of this postgenomic era will be characterized by an emphasis on the analytical integration of and congruence among multiple sources of phylogenetic evidence. The progression toward more thoroughly integrative systematics that includes rich new evidence from morphological, paleontological, and molecular data (11, 41, 130), along with methods that enable greater synthesis across data types, will dramatically improve our ability to assess the accuracy of our hypotheses of the evolutionary relationships of insects.

The major outlines of insect phylogeny were first recognized by morphology (46, 68), and even today virtually every evolutionary relationship resolved by molecular data has been at some point previously hypothesized by morphologists. Now, in concert with phylogenomic data, morphology offers not only additional data points, but also an independent estimate of phylogeny that permits both the corroboration of relationships and the placement of fossil taxa. Morphological studies have become increasingly sophisticated, now routinely analyzing hundreds of characters quantitatively, either independently or in combination with molecular data sets (36). In the past decade (e.g., 35), new techniques, such as microcomputer tomography (micro-CT) combined with computer-based three-dimensional reconstruction, have revolutionized insect anatomy. An optimized combination of traditional and innovative techniques and a standardized work-flow has made it possible to acquire well-documented, high-quality morphological data at a greatly accelerated rate (e.g., 7).

The need for phylogenetic resolution within the insect tree of life has never been more acute. Accurate, up-to-date, and accessible studies of biodiversity depend on stable, predictive classifications; in a world faced with rapid climate change and extensive global habitat loss, increasingly accurate knowledge of the Earth's biota is critically important (78). In addition, many insects are important model organisms across scientific disciplines, and comparative studies of these organisms rely on a phylogenetic framework to inform us about genetics, development, medicine, and basic science. As large-scale data acquisition and analysis become more routine, we will necessarily rely on the knowledge of a current best estimate of insect relationships to assess incoming genomic evidence.

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**rDNA:** ribosomal DNA

**mtDNA:** mitochondrial DNA

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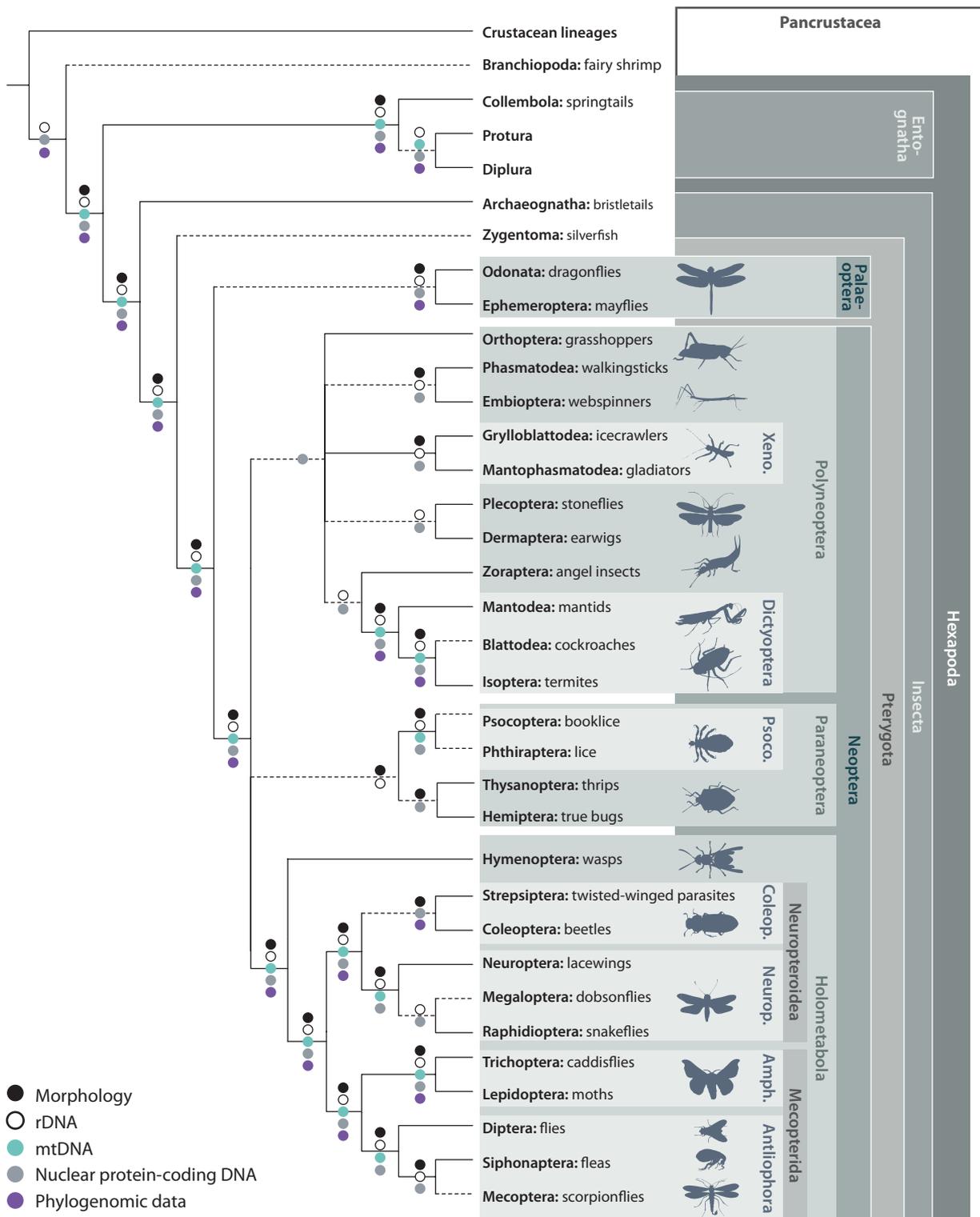
## A REVIEW OF INSECT PHYLOGENY

Mapping the evolutionary relationships of insects, with their stunning diversity, remains a challenge, even in light of new theory and technology (109, 130). Across the tree of all life we are seeing that evolution has taken place in episodic bursts of radiation (108, 130, 135). Whereas the relationships among some lineages are easy to resolve, ancient divergencies and groups that underwent rapid diversification may be difficult, if not impossible, to recover (105). Higher-level insect phylogeny perfectly mirrors this broad evolutionary paradigm of episodic diversification. With the collection of phylogenomic data and the discovery and interpretation of new morphological characters and paleontological data, the relationships among several key orders have been clearly revealed, yet others remain obscured by conflicting evidence.

In recent years, we have seen comparative analyses of complete genomes of insect model organisms (111, 145), analyses of full mitochondrial genomes (16–18), a new understanding of the origin of insects within Arthropoda (85, 97, 110), new evidence for phylogenetic placement of insect orders (55, 111, 131, 134), and phylogenetic arrangements of major insect subgroups (7, 9, 10, 77, 115, 134). These studies add to early molecular work aimed at resolving relationships among insect orders that relied primarily on ribosomal DNA (rDNA) and mitochondrial DNA (mtDNA) (often in combination with morphology). rDNA is a standard, reliable marker, but it can generate results that are highly dependent on character/taxon inclusion and alignment method, whereas mtDNA can be ineffective for deep divergencies. The first broadly sampled study to rely on nuclear protein-coding genes recovered both traditional relationships and controversial hypotheses (56). Here we review the current consensus of higher-level insect phylogeny (largely similar to Reference 66, with new insights and supports) based on a survey of the most recent and modern systematic analyses, with the goal of highlighting notable successes as well as persisting challenges (**Figure 1**).

### Holometabola: A Success Story

Holometabola—insects that undergo complete metamorphosis—are what make insects the most diverse lineage of life on Earth. Approximately 80% of their species richness is concentrated in four superradiations: beetles, flies, bees and wasps, and moths and butterflies. After centuries of debate, there is general agreement on the evolutionary relationships among the 11 included holometabolan orders, resolving one of the most substantial branches of the tree of life. The recent widely accepted phylogeny of Holometabola (= Endopterygota) is a primary example of the success and progress resulting from integrative systematics and emphasizes the importance of corroborating results from independent data types. The initial approach to resolving Holometabola was driven by the sudden availability of sequenced genomes from insect model organisms from each major holometabolan lineage: *Apis mellifera* (honey bee), *Tribolium castaneum* (red flour



beetle), *Bombyx mori* (silkworm), and *Drosophila melanogaster* (fruit fly) (111, 145). Although initially acquired for their importance to other fields of biology, these model organism genomes have now revealed the evolutionary relationships of these superdiverse lineages, and the resulting phylogenetic framework can facilitate comparative studies across scientific disciplines (145).

One notable success within Holometabola involves the resolution of the controversial Strepsiptera problem. Until just a few years ago, the enigmatic, parasitic Strepsiptera were considered the most phylogenetically ambiguous insect order, with even their placement within Holometabola in question (69). Strepsipterans are fascinating endoparasites of other insects with primarily wingless, legless females that never leave their host (except in the family Menginillidae). Hypotheses regarding the Strepsiptera problem varied from traditional morphology-based classifications that placed the parasites as close relatives to beetles (or as beetles themselves) (9, 10), to a combined molecular/morphological study that placed them as the sister group to flies (Halteria) on the basis of rDNA and putative homology between the hind halteres of flies and the fore halteres of Strepsiptera (132, 133). The latter finding implied that a homeotic mutation, a change in the genes that dictate segment order, was responsible for the divergence of flies and strepsipterans. Halteria instigated intense debate and became the best-known empirical example of long-branch attraction (52) and an important case study for the complexities of ribosomal alignments (60). Amid great controversy, multiple reanalyses and several genetic studies failed to find evidence to unite flies and strepsipterans (14, 45, 107), and the Strepsiptera problem persisted without much additional data or further elucidation.

Now, a close relationship between Strepsiptera and Coleoptera (beetles), joined in the clade Coleopterida, appears well established from both molecular and morphological data and brings a controversial chapter in insect phylogenetics to a close (although the refinement of this relationship remains a pressing issue). A recent phylogenetic analysis across holometabolans orders, based on nuclear protein-coding genes, found strong support for a sister-group relationship between Strepsiptera and Coleoptera (134). This result was confirmed by analyses of an extensive morphological data set (7, 36, 73) and by two subsequent molecular studies (56, 77). Alternative placements of Strepsiptera were also proposed (83) and placed Strepsiptera either as a sister group to Neuropterida (Neuroptera: lacewings, Raphidioptera: snakeflies, and Megaloptera: dobsonflies) or as a subordinate group of polyphagan beetles.

Although each of these aforementioned studies recovers Strepsiptera as a close beetle relative with varying placement within Neuropteroidea (Coleopterida + Neuropterida), they do not all equally sample the four extant beetle suborders; thus leaving open the question, Are strepsipterans an order-level sister group to beetles, or are they actually highly derived beetles that originated from within Coleoptera? Neuropterida-Strepsiptera morphological synapomorphies are lacking (7), however. Although Coleoptera and their included suborders are strongly supported (9, 10), strepsipteran placement as a polyphagan subgroup is a possible alternative (24). Some males of the polyphagan family Rhipiphoridae strongly resemble strepsipterans, and both groups possess a highly active triungulin larval instar. In addition, the reversal of features in the highly specialized

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### Figure 1

This tree represents the best current estimate of insect relationships based on a review of recent literature. Dashed lines indicate tenuously supported relationships or possible nonmonophyly (in the case of terminal branches). The types of data supporting each node are displayed if a node was recovered by a particular line of evidence alone or in a combined analysis. Phylogenomic data refer to a molecular data set of at least 20 kb, to data collected through EST harvests, or to large-scale genome comparison. Abbreviations: EST, expressed sequence tag; mtDNA, mitochondrial DNA; rDNA, ribosomal DNA; Amph., Amphiesmenoptera; Coleop., Coleopterida; Neurop., Neuropterida; Psoco., Psocodea; Xeno., Xenonomia.

parasitic Strepsiptera cannot be fully excluded. Future work to clarify the origin of Strepsiptera must emphasize increased taxon sampling within Neuropteroidea, specifically Coleoptera, to discern whether twisted-winged parasites are truly a unique lineage deserving of order status or whether they are simply highly derived polyphagan beetles.

All these studies support an emerging consensus on the phylogeny of the holometabolan orders, including new evidence for the previously ambiguous phylogenetic placement of Hymenoptera (bees, wasps, and ants). Initially, two phylogenomic projects with limited taxon sampling but large numbers of genes found conflicting placements for Hymenoptera: Mitochondrial genomes supported a sister-group relationship between Hymenoptera and Mecoptera (Lepidoptera, Trichoptera, Diptera, Mecoptera, and Siphonaptera) (22), whereas 185 nuclear genes provided the first convincing evidence for Hymenoptera as the earliest-branching lineage of Holometabola (111). The basal position of Hymenoptera has been confirmed by every molecular study that has since addressed the question (56, 77, 83, 134, 145), including a large phylogenomic study (of arthropod relationships; 177 genes) (85) and a new analysis of mitochondrial genomes (18). Furthermore, recent morphological analyses also unequivocally place Hymenoptera as the sister group to the rest of Holometabola (7). Hymenoptera display a remarkable mixture of unique, highly specialized features along with characters preserved across nonholometabolan insects, a high number of Malpighian tubules, well-developed glossae and paraglossae in adults (including muscles), and a fully developed orthopteroid ovipositor (7).

Holometabola, excluding Hymenoptera, are composed of two main lineages: Neuropteroidea (Neuropterida, Coleoptera, Strepsiptera) and Mecoptera (Amphiesmenoptera and Antliophora). Neuropteroidea require further resolution not only in the exact placement of Strepsiptera, but within the arrangement of the Neuropterida. Neuropteridans, lacewings, snakeflies, and dobsonflies, include three orders of archaic, large-winged predators that exhibit ancient morphologies; the greatest species richness is within the lacewings. Traditional classifications and a recent extensive morphological study (7) place Neuroptera (Neu) as the sister group to the Raphidioptera (Raph) + Megaloptera (Meg) (46). Alternatively, a sister-group relationship between Megaloptera and Neuroptera is purported on the basis of morphology and a shared aquatic larval stage inferred for their most recent common ancestor (3). Molecular work of the past decade, as with morphological data, offers no robust support for any single alternative topology, thus highlighting this area as a current enigma of the insect tree of life. Molecular studies, with limited support, agree with the traditional morphological hypothesis of Neu + (Raph + Meg) (83, 134), as well as recovering (Neu + Raph) + Meg (27, 56) and (Neu + Meg) + Raph (18, 43). Studies that have included morphological characters conflict in their arrangement of the orders but have found Megaloptera to be paraphyletic (7, 136). Expanded taxon sampling, in combination with a broader sample of genes to get beyond the minimal and nonconclusive signal of rDNA and mtDNA, respectively, is the next important step in elucidating these relationships.

Mecoptera, the largest lineage within Holometabola, include the traditionally well-founded Amphiesmenoptera (Lepidoptera: butterflies and moths, and Trichoptera: caddisflies) and Antliophora (Diptera: flies, Mecoptera: scorpionflies, and Siphonaptera: fleas). Both superorders are well supported in recent molecular studies (56, 83, 134), and morphologically, the union of moths and caddisflies is supported by shared features such as setulose wings, similar venation, and larvae with silk-producing mouthparts. Within Antliophora, recent molecular evidence supports a monophyletic Mecoptera with Siphonaptera as its sister group as the closest relatives of Diptera (56, 83, 134). Mecoptera, excluding Siphonaptera, were also retrieved in a morphology-based study (7). This stands in contrast to the widely accepted hypothesis that fleas are actually mecopterans, sister group to the wingless family of snow scorpionflies, Boreidae (60, 61, 131). The expansion of Mecoptera to include Siphonaptera is supported primarily by rDNA and mtDNA,

as well as some aspects of morphology such as winglessness and oogenesis (but see 8). Of the aforementioned studies, however, only one (131) has an extensive taxon sample for scorpionflies and fleas, thus emphasizing the need for an additional broadly sampled phylogenetic study focused on Antliophora.

### **Origin of Hexapods: Achievements of Phylogenomic Data**

Another successful and significant paradigm shift within insect systematics has been the emerging discovery that insects are a crustacean lineage, members of the Pancrustacea clade ('Crustacea' + Hexapoda) (39, 60, 61, 82, 85, 97, 99, 110). This new view stands in contrast to longstanding classifications supported by morphology that place Myriapoda (millipedes and centipedes), or one of their members, as the closest relatives of insects (66), together called Tracheata (= Atelocerata, Antennata). However, as molecular evidence grows in unequivocal support of Pancrustacea, reinterpretations of morphological characters contribute support as well (15, 40, 42, 110, 119). The strong support for Pancrustacea implies an evolutionary scenario for the origin of Hexapoda strikingly different from that traditionally hypothesized for Tracheata, including the independently acquired terrestrial habits of both insects and myriapods. In addition, an entire suite of shared characters that were once considered to belong uniquely to Tracheata (insects + myriapods) instead appear to have evolved independently in two disparate lineages (15) in response to the common environmental pressures of a terrestrial life. These include the tracheal system, Malpighian tubules at the midgut-hindgut border, completely fused second maxillae, a movable head with specialized neck musculature, undivided coxae, the loss of the ventral food rim, the loss of exopodites, and other features. However, a critical and formal evaluation of these characters is required.

The new clarity that phylogenomic approaches offer in some lineages can simultaneously reveal uncertainty in other lineages. The same large-scale phylogenomic work on Arthropoda that has supported the monophyly of Pancrustacea has highlighted uncertainty in the arrangement of crustacean lineages, particularly which crustacean is closest to the hexapods. Now, no fewer than four different sister taxa have support on the basis of at least one analysis. Results from both multigene and phylogenomic analyses suggest a close relationship between Branchiopoda and Hexapoda (1, 28, 81, 85, 99), whereas another phylogenomic study inferred Remipedia + Cephalocarida as the sister group to Hexapoda (100). Morphological synapomorphies support Remipedia + Hexapoda (32), Malacostraca + Hexapoda (44), and Malacostraca + Remipedia + Hexapoda (33), indicating general incongruence between recent molecular and morphological hypotheses.

### **Early Wingless Lineages of Hexapods and Insects: Molecular Data Provide Clarity and Ambiguity**

Ambiguity regarding crustacean relationships extends even to the monophyly of the hexapods. Hexapoda include not only Insecta *sensu stricto* (ectognaths: exposed jaws) but also three early-diverging lineages of minute, wingless entognaths (enclosed jaws: orders Protura, Diplura, and Collembola). Although hexapods (entognaths + Insecta) have long been considered monophyletic primarily on the basis of their shared body plan features—head, thorax, and abdomen and three pairs of thoracic legs (46, 62)—the relationship between entognaths and insects was called into question by an early comparison of partial mitochondrial genomes that found collembolans to be more closely related to crustaceans (19, 90). Hexapod monophyly is difficult to resolve with morphological characters alone because the early-diverging entognath lineages exhibit many traits of reduction coinciding with their habitation in substrate (85). rDNA (60, 79, 82, 86, 129) in addition to recent phylogenomic (85, 122) analyses recovers a monophyletic Hexapoda and newly

converges on the arrangement of Collembola + (Protura + Diplura) (38, 61, 79, 85, 86; but see 19, 98) in contrast to the more traditional Ellipura (Collembola + Protura) (98). Although hexapod monophyly is considered well established, uncertainty remains regarding the relative placement of these early hexapod lineages, leaving the possibility that one alone is the closest relative of Insecta, rendering Entognatha paraphyletic (10, 38, 61, 98). For reviews of hexapod origins and monophyly see References 20 and 42.

Within Insecta, the earliest lineages are the wingless jumping bristletails (Archeognatha: ancient jaws = Microcoryphia) and silverfish (Zygentoma). Members of these two early insect lineages appear largely similar and were previously joined in the order Thysanura, together constituting Apterygota (wingless insects), the sister group to Pterygota (winged insects) (41). Now, the silverfish are found to be closer relatives to winged insects, and together these two groups form Dicondylia (named for the shared trait of mandibles with two points of articulation) (56, 100, 129). The primary unresolved issue that remains for early insect relationships is the placement of the enigmatic silverfish Tricholepidion and thus the monophyly of Zygentoma (9, 30).

### **INTRACTABLE REGIONS: EARLIEST WINGED INSECTS, OR THE PALAEOPTERA PROBLEM**

In contrast to the recent successes in resolving the evolutionary relationships of Holometabola and the origin of Hexapoda, the elucidation of the relationships of the earliest-diverging lineages of winged insects remains a problem for insect phylogenetics despite the application of both phylogenomic and morphological data. Winged insects (Pterygota) are a well-established group. Odonata (dragonflies and damselflies) and Ephemeroptera (mayflies) are the first lineages of winged insects and, in contrast to the great majority of insects, are unable to fold their wings flat over their abdomen and thus have long been grouped together in Palaeoptera (old wings) as sister to all remaining Insecta (Neoptera: new wings). Where the palaeopteran orders fit is a persistently enigmatic phylogenetic question that has been addressed by rDNA, multigene data sets, phylogenomic data (including complete mitochondrial genomes), and morphology, yet palaeopteran relationships have never been murkier. Conflicting evidence from both molecules and morphology has demonstrated support for Palaeoptera (Odonata + Ephemeroptera) as well as hypotheses known as Metapterygota (Odonata + Neoptera) and Chiasmomyaria (Ephemeroptera + Neoptera). The three ancient lineages Ephem, Odo, and Neo appear to have diverged rapidly, leaving few characters to discern their relationships (130). Evolutionary rate heterogeneity across clades and the representation of old lineages by recent extant taxa make this one of the most difficult ancient insect radiations to decipher (130).

Molecular studies based primarily on rDNA conflict in their support for relationships among palaeopteran orders. Much of this conflict may be attributable to alternative alignment, sampling, and analysis strategies (50, 60, 86, 91, 125). Multigene data sets (56, 61) have shown robust support for Palaeoptera monophyly. Conversely, phylogenomic data have produced conflicting results. Simon et al. (115) found strong support for mayflies as the closest relatives to Neoptera (Chiasmomyaria) based on a sample of 125 genes. This finding was both confirmed (Maximum Likelihood) and contested (Bayesian Inference) by a phylogenomic study of arthropods that included single representatives of Odonata and Ephemeroptera (85). Another phylogenomic study of arthropods, based only on nuclear protein-coding genes and including four paleopteroids, recovered Palaeoptera with modest support (100). On the contrary, mitochondrial genomes and several morphological studies recovered Odonata as the closest relatives to Neoptera (Metapterygota) (10, 17, 117, 146). Adult head structures and features related to the mandible support Metapterygota (e.g., 117), whereas characters of the wing base and wing venation support Palaeoptera (70).

Shortcomings of the presently available morphological evaluations include the lack of reliable anatomical data for Odonata and the narrowness of the analyzed data, i.e., only characters related to the flight apparatus. In addition, the assessment of polarity between early winged insects and their wingless ancestors is difficult because wings had a major effect on transforming insect morphology, and it is impossible to use outgroup comparison for characters that did not exist.

The Palaeoptera problem continues. It is one area of insect phylogeny that has received the most attention and sequence data, yet it remains intractable. Palaeopteran relationships have the potential to be an informative case study for exploring and resolving incongruence in phylogenomic analyses, as multiple large-scale molecular studies have shown support for competing hypotheses. Exploring the cause of systematic bias and continuing the search for critical genetic and morphological synapomorphies are important components of future work on this phylogenetically ambiguous region of the insect tree of life.

### **Neoptera: Modest Progress amid Impediments**

Phylogenetic uncertainty remains across much of the midsection of the insect tree of life owing to an apparent rapid diversification of lineages approximately 300–350 mya (41, 61, 130). Although Neoptera are a widely accepted monophyletic group, two of the three putative lineages nested within it, Polyneoptera and Paraneoptera (= Acercaria), at the exclusion of the well-supported Holometabola, lack robust support, and the evolutionary interrelationships among many included orders are largely unconfirmed. There have been, however, some exciting phylogenetic developments in the past decade, including the description of the new polyneopteran order Mantophasmatodea (64), new evidence placing termites within cockroaches (55, 61, 63, 127), the refinement of the placement of the enigmatic order Zoraptera (31, 56, 142), and the union of the orders of lice (143).

### **Polyneoptera: An Unresolved Radiation**

Polyneoptera, traditionally thought to be the earliest-branching lineage of Neoptera, include the orthopteroid orders Plecoptera (stoneflies), Dermaptera (earwigs), Embioptera (web-spinners), Phasmatodea (walking sticks), Mantophasmatodea (gladiators), Grylloblattodea (icecrawlers), Dictyoptera ('Blattodea': roaches, Isoptera: termites, and Mantodea: mantids), Orthoptera (grasshoppers), and possibly Zoraptera (angel insects). Definitive morphological support of relationships among most of these orders is lacking, whereas the vast majority of molecular evidence comes from rDNA (60, 61, 129) and mtDNA (16, 17, 94), which have reached the limits of their phylogenetic utility (130). Major questions regarding the composition and relationships among polyneopteran lineages remain (130), but there is new molecular evidence supporting their monophyly (56).

Among the many outstanding issues of polyneopteran relationships, the relationships of Dictyoptera are a notable success—consensus between morphology and molecules has largely been achieved (27, 55, 63). Dictyoptera have traditionally been considered monophyletic (46), yet the relationships among the termites, cockroaches, and mantids were unclear (27). Shared endosymbionts in the guts of woodroaches (Cryptocercidae) and termites, along with shared morphology, initiated the hypothesis that termites are a roach lineage (75, 76). It is now well established that termites are actually social cockroaches, with the family Cryptocercidae as their closest relative, rendering the Blattodea paraphyletic, and with Mantodea as the sister group to a monophyletic cockroach/termite clade (27, 55–57, 61, 63, 121).

The identification of the new insect order Mantophasmatodea was a recent and exciting find for insect systematists (64). Although new insect species are described regularly, the

magnitude of discovering a new order has been described as the equivalent of discovering bats (D. Vane-Wright, published comment). Called gladiators, these rare, wingless carnivores have a limited African distribution, and even though they were known by both fossils in amber and specimens within collections, they had never been previously described. Evidence from nuclear genes and morphology consistently places them as the closest relative of the Grylloblattodea (10, 56, 61, 121). This clade, called Xenonomia (121), or Chimaeraptera (123), has also gained support in a recent detailed study of head structures (137). In contrast, mtDNA recovers a sister-group relationship between Mantophasmatodea and Phasmatodea (16, 94).

Other putative relationships within Polyneoptera that have been recovered by multiple recent studies are a clade joining Phasmatodea and Embioptera (34, 56, 61, 121) and a tentative sister-group relationship between Plecoptera and Dermaptera (56, 60, 61, 121). Support for these hypotheses is limited, and conflicting evidence was reviewed in Reference 10.

### The Zoraptera Problem

Zoraptera (angel insects) comprise a single family of tiny, aggregating, primarily wingless scavengers often found under wood bark. The morphological knowledge of Zoraptera has greatly increased in recent years (12, 35, 54, 140). Nevertheless, angel insects remain the most phylogenetically ambiguous order of insects. Zoraptera have been placed in both the Polyneoptera and the Acercaria, with affinity to almost every other included order. Although there is no consensus on the evolutionary relationships of Zoraptera, current morphological and molecular data converge on two competing hypotheses: Molecular data, both rDNA and nuclear protein-coding data, support Zoraptera as a close relative of Dictyoptera (56; 129, discussion tree; 142), whereas recent morphological evidence points toward an affinity to Embioptera (31, 140; but see 10, 12, 35). Additional studies recover relationships between Zoraptera and both Paraneoptera (10, 12, 35) and Dermaptera (57, 121), but these hypotheses have not been independently (Paraneoptera) or robustly (Dermaptera) corroborated by molecular data. The 18S used to place Zoraptera as a close relative of Dermaptera (57, 121, 139) was likely a dermapteran contaminant (141).

### Paraneoptera (Acercaria)

Paraneoptera include insects that have primarily sucking mouthparts, such as Hemiptera (true bugs), Thysanoptera (thrips), and Psocodea (Pthiraptera: parasitic lice and Psocoptera: book lice) and have traditionally been considered a monophyly. Although some morphological synapomorphies support the group (e.g., the detachment of the stylet-like lacinia from the stipes), much of the evidence for monophyly relies on the shared loss of external characters (68). rDNA and mtDNA support a primarily monophyletic Paraneoptera (60, 61, 129), yet nuclear protein-coding genes alone recover lice as the closest relative of Holometabola and thrips as the sister group to true bugs (although robust support values are lacking) (56). Morphological data also corroborate a relationship between thrips and true bugs (68, 144). The louse lineage Psocodea are well-established, but molecular and morphological evidence indicates that at least Psocoptera, if not both orders of lice, are paraphyletic (58, 88, 143), with the psocopteran Liposcelidae as the sister group to the pthirapteran Amblycera (58).

### Advances Within Orders

In addition to the phylogenetic advances made among insect orders, progress has been made toward resolving higher-level relationships within many of the major insect orders. The past

decade has seen an emphasis on multilaboratory collaborations within the systematics community, and modern methods have allowed research teams to tackle larger-scale phylogenetic questions. The National Science Foundation (NSF) Assembling the Tree of Life (AToL) program, as well as the NSF Partnerships for Enhancing Expertise in Taxonomy (PEET) program, has helped catalyze and fund initiatives to revitalize and modernize systematic knowledge and practice. Major new phylogenetic hypotheses have emerged for order-level relationships (e.g., Diptera, 135; Strepsiptera, 95; Coleoptera, 5; Lepidoptera, 89, 101; Hymenoptera, 113, 124; Membracoidea, 25; Trichoptera, 49; Neuroptera, 6, 136; Odonates, 21). Ideally, these large projects, which involve multiple laboratories and data types, have promoted a new systematics paradigm of collaborative data sharing and research coordination to study megadiverse clades. Additional collaborative efforts are critical to address major remaining issues in insect phylogeny as data sets grow in size and complexity.

## INTEGRATIVE PHYLOGENETICS FOR THE POSTGENOMIC ERA

### Phylogenetic Utility of New Genomic Characters

Genome acquisition, comparative genomic analysis, and the application of these data in phylogenetics have been key to the recent progress in resolving long-standing controversies regarding the insect tree of life. Currently, at least 80 insect genomes have been sequenced or are in progress (Genomes On Line Database, 74), and considering the importance of insects as model organisms, vectors of disease, and pests of agriculture, many more will soon be underway (103). Comparative genomics has provided us with a greater understanding of the evolution of insect genomes and offers guidance at different levels to more efficiently harvest genomic data with increased phylogenetic utility (e.g., primer design, gene selection, orthology determination across divergencies). In addition, genomic data can uncover new phylogenetic characters, such as rare genomic changes, that can potentially provide independent corroboration of more standard data types (106). Synteny and gene order, gene duplications, genome rearrangement, indels, and introns, as well as transposable elements, are alternative genetic characters that have demonstrated utility in recovering evolutionary relationships.

Genomic characters play an important role in phylogenetics of many groups, such as mammals (87), birds (29), and Metazoa (120). The use of alternative genomic characters has trickled into insect systematics as well (14, 45, 85, 107), yet their abundance and utility show some limitations not found in younger, less-speciose lineages. Comparative genomics has revealed that insect genomes have undergone rapid change and are more diverse than vertebrate genomes (145). Zdobnov & Bork (145) provide the example that *Drosophila* and *Apis*, who diverged from each other 320 mya, have only 10% of their shared orthologous genes in synteny, whereas the same comparison for human and puffer fish is approximately 50%, even though they diverged from each other 450 mya. Thus, it is likely that many types of genomic characters that have provided resolution within other groups will be more effective at resolving more recently diverging lineages in insects, such as those within orders. This limitation has been demonstrated in mitochondrial genome arrangements (17) and transposable elements (118). MicroRNAs (110, 126), introns (67, 114, 139), and gene duplications (4) are among the genomic characters that have shown promise for insects and their relatives.

### Next-Generation Sequencing

For systematic labs, the use of next-generation sequencing is a bridge to the practice of phylogenomics. Acquisition of genomic data may be less expensive and more time efficient than large-scale

targeted PCR methods, as indicated by reviews of new sequencing technology (59, 104). A recent series of studies on mosquitoes demonstrated a successful and relatively affordable approach to use next-generation sequencing to harvest transcriptome data from nonmodel organisms without reliance on an available closely related genome (37, 47). ESTs (expressed sequence tags) have been used successfully for phylogenetic resolution of several insect groups and their relatives (53, 77, 85, 113).

In the postgenomic era, as genomic data accrue from nonmodel organisms, bioinformatics becomes a new, critical tool for effectively managing, filtering, and vetting the extensive influx of sequences. Complicating factors include the management of extensive amounts of data, filtration and identification of appropriate orthologous markers, taxon sampling limitations due to cost, and computational issues; similar problems are encountered when performing large-scale targeted PCR as well. Indirect gene harvesting methods have been advocated over targeted PCR for some time (92; but see 97) even though next-generation sequencing sacrifices the a priori discernment and selection of applicable, single-copy orthologous markers for the rapid acquisition of copious amounts of sequence data. Nevertheless, marker choice and orthology determination remain of primary importance for accurate phylogeny recovery. At present, there is no broad consensus on how either can best be achieved, yet recent phylogenomic studies and reviews on bioinformatic pipelines for orthology determination are useful guides in determining how to proceed (2, 23, 28, 71, 85, 93, 102). Although the cost of sequencing continues to decrease, the near future still dictates an approach that considers feasibility and affordability trade-offs between the scope of the phylogenetic question, the extent of taxon sampling, and the depth of molecular data collection.

## The Role of Morphology

Morphological systematics continues to play a vital role in the postgenomic era of insect systematics. In addition to providing an independent data set for a critical evaluation of molecular phylogenies (and vice versa), morphological systematics is the basis for reconstructing complex evolutionary scenarios focused on changes at the phenotypic level. Likewise, ontogenetic studies (e.g., 80, 138) and detailed ultrastructural investigations (e.g., 26) will help elucidate the complex mosaic of hexapod evolution. New visualization techniques such as micro-CT scanning (35) are making the study of many more character systems, most importantly those of the internal skeletal and soft anatomy (e.g., Deuterophlebiidae, 112; Osmylidae, 13), tractable. These studies provide exquisitely detailed accounts of the anatomy of phylogenetically critical taxa. Although broad phylogenetic conclusions are difficult to achieve with suites of modified characters owing to lineage-specific adaptations, these studies are necessary first steps that later lead to comprehensive data sets. Some broader phylogenetic comparisons at this level are already providing evolutionary insights (8, 36). Another breakthrough is the application of micro-CT to amber fossils. Recently, the anatomy including internal soft parts of a 40-mya-old strepsipteran fossil was reconstructed almost completely using micro-CT (96). It is conceivable that this new technique will greatly facilitate the placement of fossil taxa crucial for understanding evolutionary history and for which morphology is the only available source of phylogenetic information. Recent fossil discoveries continue to push back the first appearance of major groups (e.g., 84, 116, 128) and further detail the relationships between insects and plants (51, 72).

## FUTURE WORK TOWARD THE INSECT TREE OF LIFE

Although great advances have been made toward resolving the insect tree of life, particularly within Holometabola, phylogenetic ambiguity remains for a substantial number of branches, such as the

polyneopteran lineages. As genomic data are brought to bear on these uncertainties, we anticipate further resolution. Yet the case of Palaeoptera makes clear that an increase in sequence data alone is not likely to reveal the relationships among all lineages (93), particularly those that diverged rapidly from one another long ago, leaving little trace of their shared genetic history. Such cases exist at many taxonomic levels and account for several of the most significant evolutionary changes in the insects. Their resolution depends on the use of integrated methods and hypothesis confirmation from congruence among independent data sets. Without corroboration from multiple sources of data, it is often unclear whether a lineage's resistance to resolution is due to rapid ancestral diversification, to inappropriate or insufficient markers (e.g., saturated or noisy), or to systematic bias (e.g., errors in model estimation or analytical methodology). In some cases, we may need to be satisfied with a "bush of life" (105) with multiple plausible histories of particular lineages, but only after the addition and thorough exploration of many new data points and data types. Progress hinges on the selection of orthologous and least-saturated genes, on improved models of sequence evolution to overcome systematic error, and on the continued search for new characters among genomic, morphological, and paleontological data. Ultimately, we look to the combination of robust phylogenetic hypotheses and well-documented morphological transformations at the phenotypic level, along with improved morphological knowledge of fossil taxa, to ultimately guide us to a deeper understanding of insect evolution.

### SUMMARY POINTS

1. Advances in molecular sequencing and computational evolutionary theory, as well as new techniques for the discovery of morphological characters, have furthered resolution of the insect tree of life. Progress in insect systematics in the postgenomic era will rely not only on molecular evidence, but also on integrative methods and corroboration among independent lines of evidence from molecular, morphological, and paleontological sources.
2. Notable phylogenetic successes include the discovery that insects are a crustacean lineage and members of a monophyletic Pancrustacea; the resolution of the relationships of Holometabola, including the enigmatic parasitic order Strepsiptera as a beetle relative and an early-diverging Hymenoptera; and the elucidation of dictyopteran relationships, with the recognition of termites as social roaches.
3. Some regions of the insect tree remain unresolved. Despite the application of extensive phylogenomic data and morphological evidence, the arrangement of the palaeopteran orders (dragonflies and mayflies) and their relationship to Neoptera (the rest of the winged insects) are ambiguous. The Polyneoptera (orthopteroid lineages) and Neuropterida (lacewings, snakeflies and dobsonflies) also remain unclear, yet the utility of phylogenomic data for these groups has yet to be explored. In addition, the monophyly of several orders, Zygentoma, Psocoptera and Pthiraptera, Megaloptera, and Mecoptera, remains in question.
4. Complete genome sequences for nonmodel organisms are the future. Until then, the choice to acquire data by targeted PCR or by high-throughput sequencing is a trade-off of feasibility, affordability, taxon sampling, and depth of data collection. Ongoing challenges for phylogenomics are managing data and bioinformatics, filtering large data harvests to find suitable orthologous markers, overcoming the limitations of extensive computation time and power, and avoiding systematic error (often disguised as robustly supported resolution).

5. Comparative genomics can lead to the discovery of new genomic characters for phylogenetics. Genomic characters such as gene order, genome rearrangement, indels, introns, and transposable elements have been useful in other groups but often present challenges in insects because of their variable genome evolution. More genomic characters should be explored for phylogenetic use in insects both within and among orders.
6. Morphology continues to play a primary role in the postgenomic era. New techniques, such as micro-CT scanning, can reveal new internal characters and uncover details of fossil specimens. Morphological data contribute independent estimates of phylogeny for comparison and corroboration with molecular data, as well as providing the means to incorporate paleontological evidence.
7. Standard phylogenetic characters, sequence data, and morphology will likely not resolve all branches of the insect tree, particularly ancient lineages that diverged rapidly. As we move from reliance on primarily rDNA and mtDNA to a greater emphasis on nuclear protein-coding genes and genomic data sets, we will need to prioritize thorough exploration of our data, with the awareness of systematic error. Further advancement of insect systematics will rely on independent confirmation of phylogenetic hypotheses from molecular, morphological, and paleontological evidence in combination with the discovery of and reliance on new character systems.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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60. Stresses the importance of alignment in rDNA analyses and shows how the exclusion of hypervariable regions could rectify artifactual placements.

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85. Provides a large data set and thorough analyses of arthropods, including recovery of many higher-level insect relationships; also presents a novel pipeline for orthology determination and data filtering.

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93. Addresses many of the pressing issues for systematists in the postgenomic era.

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106. Emphasizes the use of alternate genomic characters for phylogeny resolution, which is of increasing importance in light of systematic error in large data sets.

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