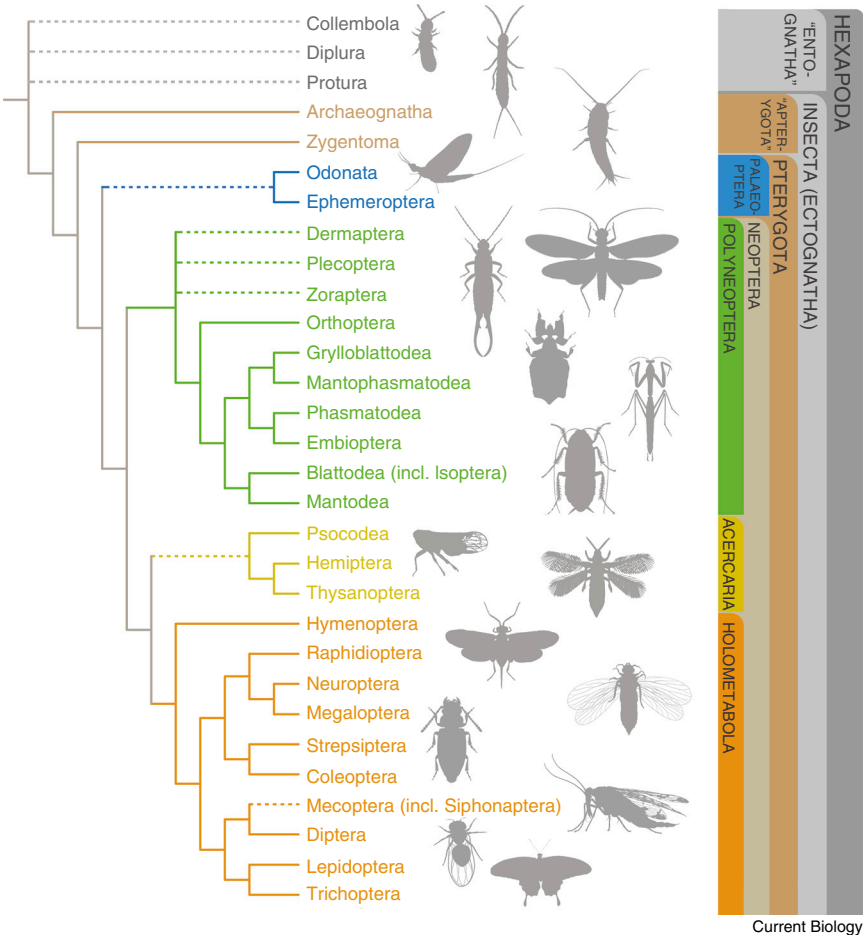

Figure 1. Insect phylogeny.
A best estimate of the relationships among the extant hexapod lineages based on current knowledge, with major clades indicated. Nodes that have traditionally been difficult to resolve with any dataset, molecular or morphological, or relationships incongruent between recent phylogenomic analyses, are indicated with dashed lines. Major contentious relationships include interrelationships of the early-diverging hexapod clades Collembola, Diplura, and Protura; monophyly of Palaeoptera; early branching events within Polyneoptera, particularly the position of Zoraptera; the monophyly of Acercaria with respect to Psocodea; and interrelationships within Mecoptera, specifically the placement of Siphonaptera. Silhouettes depict representatives of major insect orders (from top to bottom): Collembola, Diplura, Zygentoma, Ephemeroptera, Dermaptera, Plecoptera, Phasmatodea, Mantodea, Blattodea, Hemiptera, Thysanoptera, Hymenoptera, Neuroptera, Coleoptera, Mecoptera, Diptera, and Lepidoptera.

resolving relationships deep in the insect tree[58]), or when better-fitting evolutionary models were used[48], fleas were found to be nested within scorpionflies, as sister to the enigmatic Southern Hemisphere family Nannochoristidae, corroborating evidence from Mesozoic fossil species[59] and some morphological data[48]. With the knowledge that fleas represent the largest radiation of scorpionflies, they are now regarded as a member of Mecoptera[48].

Tricky nodes in insect phylogeny

Although many traditional insect clades have been corroborated by phylogenomic analyses[30,43,55,60], there remain contentious nodes that are as difficult to resolve today as they were three decades ago (Figure 1). These long-lasting controversies, relating to deeply nested nodes in hexapod phylogeny, arguably hold the key to our understanding of the origin and early radiation of insects and their resistance to resolution reflects notorious challenges associated with resolving ancient radiations[61].

While the monophyly of hexapods is strongly supported, the earliest branching events within their phylogeny remain controversial[12]. The three non-insect hexapod groups, Collembola, Protura, and Diplura, were combined into the clade 'Entognatha' by Hennig[3] based on their shared possession of mouthparts deeply enclosed within the head (among other characters). However, morphological support for this grouping is equivocal[62,63], and results of molecular phylogenetic analyses vary considerably, with Diplura recovered either as a sister group to insects or to Protura[23,30,64,65]. These uncertainties obscure the origin of the hexapod body plan and our understanding of the morphological adaptations that underpinned their successful colonisation of land. Likewise, the origin of wings and flight in insects also remains elusive. The insect orders Odonata (dragonflies and damselflies) and Ephemeroptera (mayflies) were placed into the clade Palaeoptera, characterised by their inability to fold their wings over their abdomen, which distinguishes them from the remaining winged insects (Neoptera)[66]. However, the monophyly of Odonata and Ephemeroptera has been the subject of much debate, with the results of some morphological[4,67–69] and molecular analyses[11,30,70] suggesting that Palaeoptera may be paraphyletic with respect to Neoptera, and that Ephemeroptera may be representing the sister group of Neoptera[11]. Furthermore, the phylogeny of one of the three major radiations of neopterous insects, Polyneoptera (grasshoppers, roaches, mantises, stick insects, and their kin), has similarly remained difficult to resolve. While phylogenomic datasets now strongly support Zoraptera (a species-poor group of gregarious insects known mostly from the Tropics) as a member of Polyneoptera[30,60,71], its relationships to the early diverging polyneopteran orders Dermaptera (earwigs) and Plecoptera (stoneflies) have remained elusive[19,30,60].

Besides the refractory nature of many old controversies in insect phylogeny, phylogenomic studies have proposed unexpected relationships, such as the non-monophyly of hemipteroid insects (Acercaria or Paraneoptera, i.e., true bugs, thrips and their kin)[30,43]. These relationships require further testing, not least as they stand in stark contrast to available morphological[41] and mitogenomic evidence[72]. There are similar incongruences at