# Diversity, Form, and Postembryonic Development of Paleozoic Insects

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## Keywords

Hexapoda, Insecta, evolution, deep divergences, functional morphology, metamorphosis

## Abstract

While Mesozoic, Paleogene, and Neogene insect faunas greatly resemble the modern one, the Paleozoic fauna provides unique insights into key innovations in insect evolution, such as the origin of wings and modifications of postembryonic development including holometaboly. Deep-divergence estimates suggest that the majority of contemporary insect orders originated in the Late Paleozoic, but these estimates reflect divergences between stem groups of each lineage rather than the later appearance of the crown groups. The fossil record shows the initial radiations of the extant hyperdiverse clades during the Early Permian, as well as the specialized fauna present before the End Permian mass extinction. This review summarizes the recent discoveries related to the documented diversity of Paleozoic hexapods, as well as current knowledge about what has actually been verified from fossil evidence as it relates to postembryonic development and the morphology of different body parts.

# 1. INTRODUCTION

The Paleozoic Era is a crucial period in evolution; flanked by the Cambrian explosion and the largest extinction event in history, this seemingly alien era was marked by dramatic change. Notably, during the Paleozoic, Earth's earliest terrestrial ecosystems were formed and independently colonized by the earliest land plants (mid-Ordovician, about 475 Mya) and several arthropod groups, including hexapods (34, 173). Parallel colonization of early terrestrial ecosystems appeared in several lineages of arthropods from Euchelicerata, Myriapoda, and Pancrustacea, all during the Silurian (34, 88). Major evolutionary novelties in the history of Pancrustacea, such as the formation of a specialized locomotory tagma (thorax), flight, and complete development (metamorphosis), evolved within the era. Hexapods make up the most species-rich lineage of all life, with current estimates of approximately 5.5 million living species and an unimaginable diversity of extinct species (166). Their evolutionary history is traceable back approximately 410 Mya to the Early Devonian, to basal groups like springtails (Collembola) from Rhynie Chert in Scotland, a locality documenting one of the earliest ecosystems on land (33). Current phylogenetic estimates support the interpretation that Hexapoda is nested within a clade of Pancrustacea and is a sister group of the crustacean class Remipedia (89, 145, 186). Interestingly, the trunk of Remipedia has a small pleural wall containing pleurites, which promote and support limbs (51), particularly those that would be necessary for an eventual invasion of the land.

While the insect faunas of the Mesozoic, Paleogene, and Neogene are considered modern, at least in the general composition of the ordinal lineages, the fauna of the Paleozoic is markedly different from that living today and may be distinguished in many aspects not only relating to their earlier phylogenetic positions, but also reflecting important differences in atmospheric composition, flora, and broader global ecosystem attributes (55). The faunal turnover in response to the End Permian event, approximately 252 Mya, had a distinct impact on the fossil record of hexapods and certainly greatly changed the composition of the global fauna as it is currently understood. This mass extinction drastically affected marine and terrestrial organisms and is largely explained by widespread ocean anoxia and the eruption of the Siberian Traps (107).

Among other changes, this event led to the establishment of new freshwater ecosystems (e.g., lentic habitats with macrophyta) in the early Mesozoic, which were colonized by specialized aquatic insects from several orders (e.g., Ephemeroptera, Plecoptera, Hemiptera, Coleoptera) (178). In addition, there was a remarkable increase in the diversity and abundance of holometabolous insects, such as Coleoptera, Neuroptera, and Mecoptera, during the Triassic.

The Paleozoic record of hexapods is unevenly biased and largely skewed toward several well-sampled localities, supplemented by isolated finds from a scattering of sites, and marred by prominent gaps (**Figure 1**). This bias is even more obvious when we consider the paleogeographical positions of these well-sampled localities, as most of them are located in the Northern Hemisphere, and few deposits are currently known from the Southern Hemisphere (from the ancient supercontinent of Gondwana). While the majority of Paleozoic insects are known solely from their highly resistant wings, there are some localities, so-called Konservat-Lagerstätten, with exceptional preservation of more complete exoskeletons, allowing for a clearer picture of early insect morphology and its function, as well as insights into paleoecology. Moreover, these localities are usually well sampled, and have yielded hundreds or thousands of insect specimens (e.g., 23, 75, 105). The preservation of Paleozoic insects is largely restricted to compressed fossils reflecting freshwater lacustrine or brackish sedimentary deposits or, less frequently, buried in volcanic ash (e.g., 44, 119, 160). Among the exceptional fossils are those preserved in sphero-siderite concretions (nodules) (147), which partially preserve three-dimensional reliefs of the original insect body, allowing microcomputed tomographic reconstructions (43, 120, 126). Compressed fossils can also
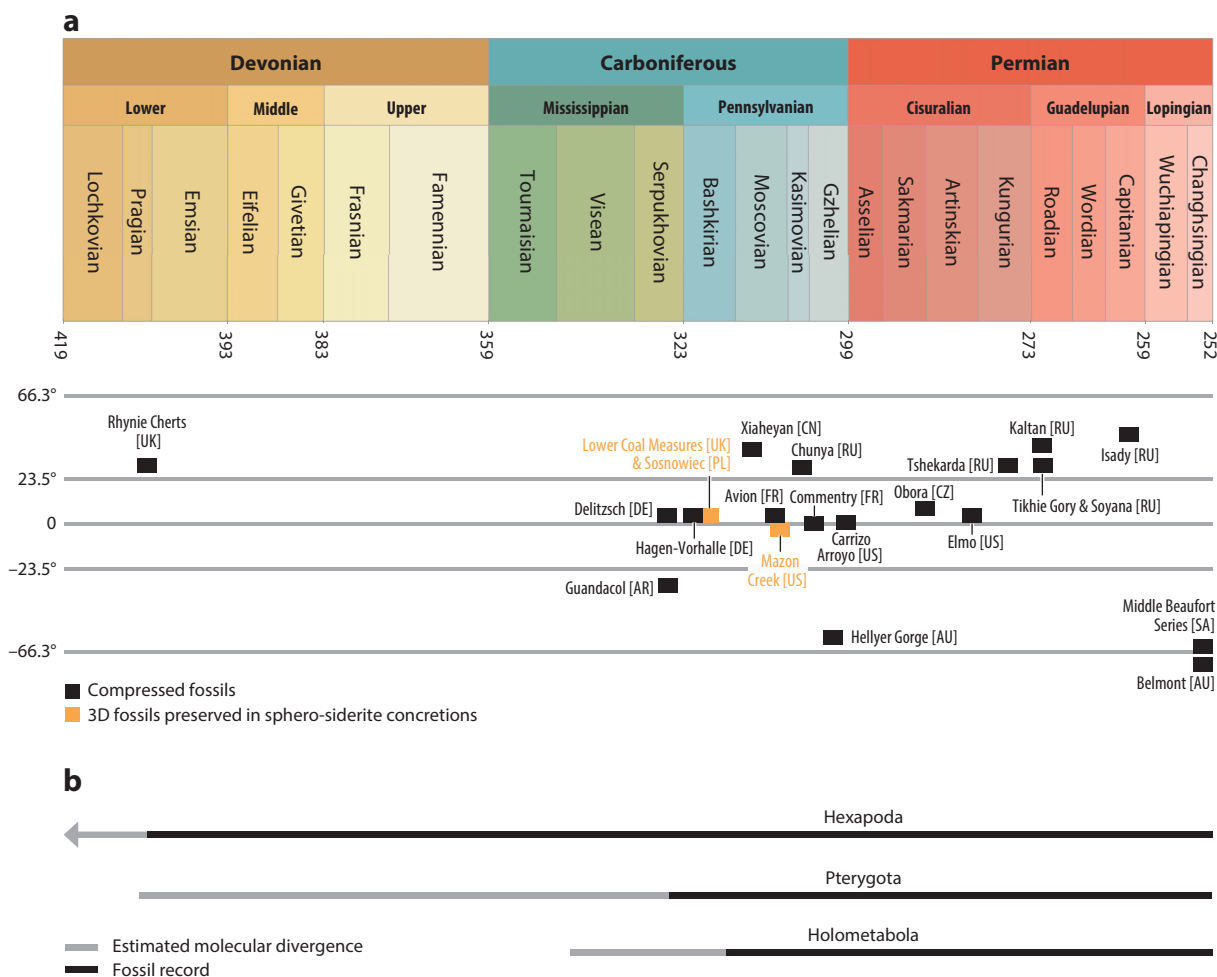
**Figure 1**

Timeline for the early fossil record of hexapods. (*a*) Major Paleozoic localities and their paleogeographical positions. (*b*) Estimated molecular divergences for the main clades Hexapoda, Pterygota, and Holometabola, as suggested by Misof et al. (92), and their fossil records.

be documented by photographic and computing techniques such as reflectance transformation imaging using multi-lighting conditions to image the surface relief (16). Fine structural details and surface microstructures of some compressed fossils are also accessible using environmental scanning electron microscopy (ESEM) (109, 127, 153). Amber, the best medium for preservational fidelity, is also known from the Carboniferous and has been geochemically identified as the resin typically found in modern conifers. Critically, no arthropod inclusions have ever been discovered (21). Nonetheless, the hope of finding such inclusions remains, and the study of them could be a potential new pathway for future research.

It is from the Paleozoic that we have our first glimpses into the intimate association between early insects and vascular plants. Evidence of early herbivory, and even pollinivory, come from pollen grains preserved in the guts of Permian hypoperlids and paoliids (137). In addition, an abundance of trace fossils documents complex interactions between insects and plants, such as

the earliest evidence of exo- and endophytic oviposition, galls on *Psaronius* tree ferns caused by holometabolan larvae (e.g., 13, 82, 84; see also 86).

Data on diversity patterns as measured at the familial level were first evaluated by Labandeira & Sepkoski (85) and found to be consistent with major geological events. Nicholson et al. (104) analyzed a large data set of fossil insects and demonstrated that basal families of winged insects (Palaeoptera, Polyneoptera, Paraneoptera) had higher origination and extinction rates than the apterygote or primary wingless insect groups (e.g., Archaeognatha and Zygentoma). In contrast, the extinction rates of the megadiverse Holometabola were lower, and the group exhibited a recent slowdown in their otherwise high net diversification rate. There has been a more or less continuous increase in insect diversity at the family level (32), but with some variations. From the Pennsylvanian to the Middle Permian, 93 families appeared, but the number of recorded families decreased during the Middle and Late Permian to only 68 at the Permian-Triassic boundary. Many Paleozoic groups were successively replaced after the mid-Permian by others that were similar ecologically (often from among the eumetabolous insects), such as the replacement of Palaeodictyopterida by the Hemiptera, both of which have stylate mouthparts specialized for piercing and sucking plant tissue. Such patterns have led several researchers to consider the End Permian extinction to be more of a faunal turnover for insects than the mass extinction that it represented for almost all other lineages of life (83, 144).

In this review, we strive to bring attention to the understudied insect fauna of the Late Paleozoic by reviewing the diversity and morphological disparity across different orders. We focus on the importance of Paleozoic insects for resolving insect phylogeny and establishing an accurate timescale for evolutionary events, the direct evidence that these animals provide for understanding the evolution of major body structures and pathways of postembryonic development, and interesting areas for future investigation.

## 2. EARLY INSECT DIVERGENCES FROM A PALAEOZOIC PERSPECTIVE

Although molecular phylogenies based on analyses of large transcriptomic or genomic data sets currently provide a reliable picture of relationships, fossils play indispensable roles for the calibration of nodes and unique taxa for breaking long branches among otherwise disparate groups (**Figure 2**). Over the past two decades, there has been an increased emphasis on the calibration of phylogenetic trees using fossils to set a minimum age for nodes. Documentation of deep divergences of hexapod lineages and understanding of the early phases of insect evolution are the major outcomes of phylogenomic studies currently using transcriptomic and genomic data. Whitfield & Kjer (170) evaluated the ancient radiations of the main insect clades at the ordinal level and highlighted major challenges in reconstructing phylogenies based on combinations of molecular and morphological data sets. Of particular concern was a perceived shortness of time spans between divergences, allowing for only a few phylogenetic markers for such relationships to accumulate, followed by long time spans subsequent to divergences. Their analysis indicated that there were several highly disparate groups on long branches initially diverging in a short frame of time, with few character transitions accumulated. They emphasized the methodological limitations of parsimony methods for such data, particularly when coupled with extensive homoplasy. It must be noted that fossil species do not indicate the time of origin of a particular taxon, only the presence of a group at a certain section of time, along with information on the sequence of character transitions (50). Fossils set minimum ages for nodes in calibrated phylogenies and provide unique character combinations that may give resolution to particularly knotty areas in the topology. Two different methodological approaches to incorporate fossils in phylogenies for
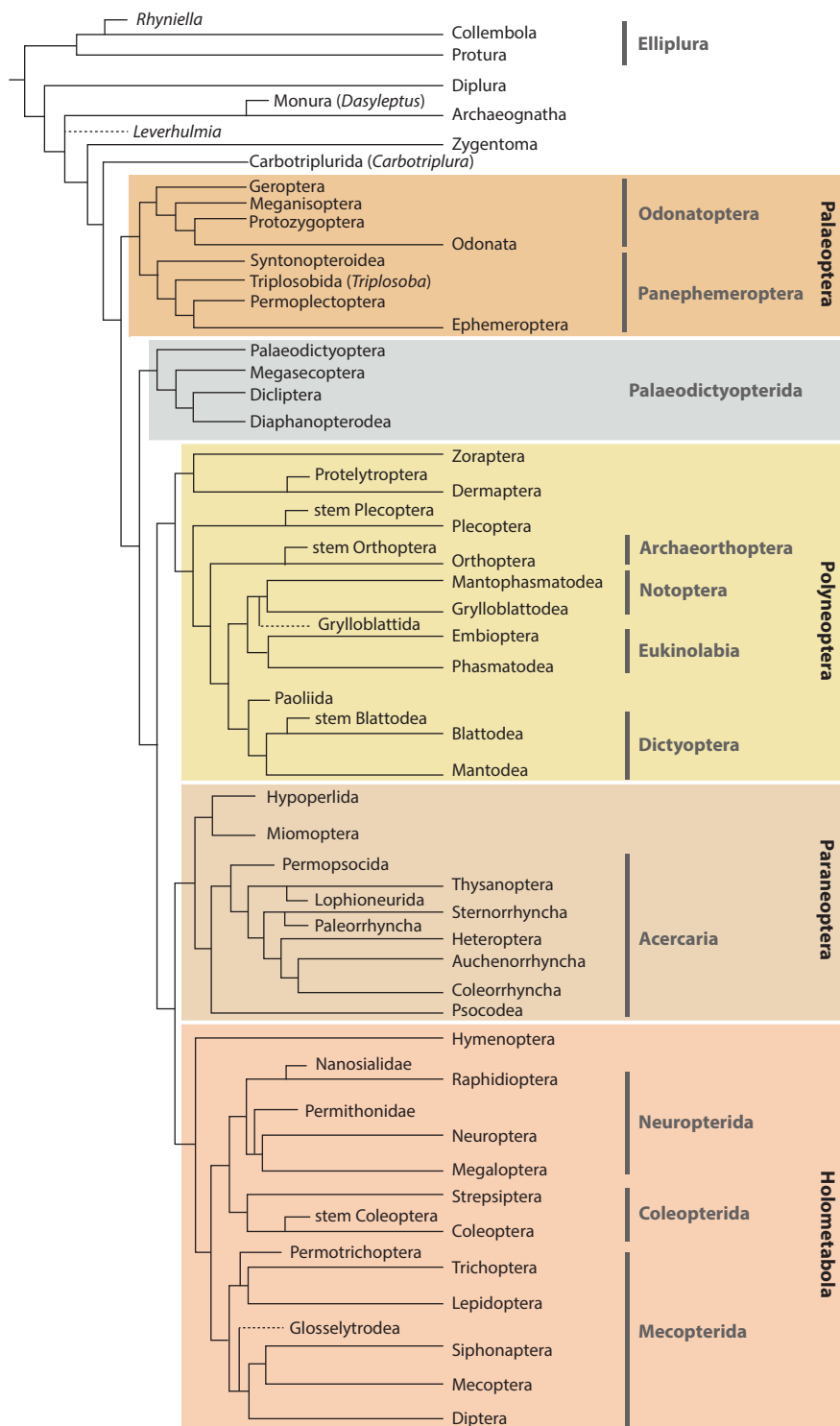
## DIVERGENCE TIMES VERSUS ORIGINS OF HIGHER CLADES

There is a tendency in divergence estimation studies to confuse divergence times with the origins of clades as we understand them based on extant species. This is mostly the result of the language used to convey such divergences, the common formula being: Group X and its sister group Y diverged Z Mya, and therefore, X and Y originated Z Mya. Yet such turns of phrase are misleading. A diversification event is a speciation event (higher clades do not themselves speciate), the product of which is two very closely related species—species that in their day would have belonged to a common genus and may have only differed cryptically. Yet the eventual descendant of one, after many generations of subsequent speciation events, will have accumulated a series of changes such that, today, we look at the current descendants and designate them as a separate order from the many descendants of the original sister species. However, at the time of the initial speciation event (the divergence time), those changes had not yet occurred, and the two original sister species would have been little different from one another. Thus, at the time of divergence, the two higher clades as we conceive them based on their descendants would not yet have appeared. In fact, organisms recognizable as a stem group to the crown likely did not appear for a long time subsequent to the divergence event, as the next speciation event is unlikely to have resulted in an immediate appearance of such dramatic changes. In the example of Hymenopterida, we do not expect to find as the product of the divergence event one species that is clearly a stem-Hymenoptera and is sister to another species that is clearly a stem to all other Holometabola. The lineages encompassing what would eventually become Hymenopterida and what would become the other groups of Holometabola diverged at time X, but what we dub the stem-group and crown-group Hymenoptera would only appear much later.

calibration are dominant: total-evidence dating and node dating. A study looking at the early radiation of Hymenoptera found that total-evidence dating was more suitable given that posteriors on divergence times were less sensitive to prior assumptions than they were in node dating (see the sidebar titled Divergence Times versus Origins of Higher Clades) (142). This analysis suggested that the Hymenopterida dates back to the Late Carboniferous (approximately 309 Mya), a conclusion that was in line with the record of stem-group Hymenoptera in coeval strata (101).

Arthropod fossils providing minimum ages for the calibration of their main nodes were recently reevaluated (176), as they represent our best estimates for the earliest occurrence of their clades. A hexapod phylogeny based on 1,478 protein-coding genes provided a robust hypothesis dating the origin of Hexapoda to the Early Ordovician, of insect flight (Pterygota) to the Early Devonian, of major extant lineages to the Mississippian, and of the major diversification of holometabolous insects to the Early Cretaceous (92). Another study analyzed samples from all insect orders and estimated deep divergences using Bayesian inference and maximum likelihood methods to reconstruct phylogenetic relationships (169); its results are congruent with the inferred timescale for various nodes and major historical events, including the increase of atmospheric oxygen in the Late Silurian and the earliest Devonian, the radiation of vascular plants in the Devonian, and the available fossil record of the stem groups of various insect lineages in the Devonian and Carboniferous.

Integrated morphological and phylogenomic studies of various insect groups (clades) have used fossils for calibrations to clarify the timescale of the principal nodes. A phylogenomic study using transcriptome data for Odonata and employing the most inclusive set of fossils assembled for calibration (64) indicated that crown-group Odonata diverged from ancient relatives during the Permian, in accordance with the presence of two families of the stem-Odonata in the Middle Permian (97, 131). A large-scale phylogenomic analysis, similarly calibrated with fossils, found support for a terrestrial ancestor to Polyneoptera, as well as Pterygota, in all developmental stages and

indicated that it was likely that wings did not evolve in species living in an aquatic environment, particularly given the derived position of Plecoptera (175). Phylogenetic analyses of Dictyoptera calibrated with fossils bearing distinct synapomorphies of their respective lineages corroborated most hypotheses regarding major lineages of this superordinal complex (41, 87). The diversification of Dictyoptera has alternated between periods of high diversification, as in the Pennsylvanian, and periods of high extinction rates, most notably at the Permian–Triassic boundary (27). Phylogenomic relationships among major lineages of Orthoptera, again including divergence-time estimates, have focused on exploring the evolution of acoustic communication (161), and a related work looked at rates of evolution and constraints on the mitochondrial genomes of Orthoptera, estimating a divergence between Caelifera and Ensifera in the latest Permian (25). Admittedly, the selection of fossils for calibrations in these two studies has been criticized, particularly for the presence of crown-group Ensifera in the Middle Permian (94).

Paraneopteran insects represent approximately 10% of insect diversity, and a phylogenetic analysis of 2,395 protein-coding, single-copy genes derived from transcriptomes provided strong support for a tree congruent with previous classification schemes (56). This study recovered monophyly of Psocodea, Thysanoptera, and Hemiptera and supported the seemingly bizarre sister grouping of Psocodea and Holometabola (92), although such a relationship was contradicted by further analyses (169, 175), as well as morphological analyses (53, 183). Dates from these studies based on fossil calibrations suggest early divergences between Psocodea and Holometabola, between Thysanoptera and Hemiptera, and even between Sternorrhyncha and (Heteroptera + Auchenorrhyncha + Coleorrhyncha) in the Late Devonian, over 365 Mya. These calculated divergences are widely out of step with our fossil evidence, from which we have only stem-group Thysanoptera, Hemiptera and Holometabola no earlier than the Late Carboniferous (99, 101, 103). These divergence times may be accurate for the speciation event between the species ancestral to the lineages giving rise to groups such as Thysanoptera and Hemiptera, but not for organisms that we would classify as stem- or crown-group members.

## 3. MAJOR HEXAPOD LINEAGES IN THE PALEOZOIC

### 3.1. Early Ametabolous Hexapods (Collembola, Archaeognatha, Zygentoma)

Defining the phylogenetic relationships of ametabolous hexapods from the Late Paleozoic is difficult due to the scarcity of well-preserved fossils and controversial interpretations of decisive traits. Primary wingless hexapods like springtails or bristletails are recorded among the arthropods colonizing early terrestrial habitats at least by the early Devonian. The earliest record comes from the famous Lower Devonian Konservat-Lagerstätte of Rhynie (approximately 411 Mya) located in Aberdeenshire, Scotland. This site presents a window into early terrestrial ecosystems: land plants; fungi; lichens; and a spectrum of eukaryotes and prokaryotes, including symbiotic associations (mycorrhiza), all preserved in remarkable anatomical detail (33). *Rhyniella praecursor* is a definitive springtail (Collembola) of the Arthropleona, and, in fact, springtails are the most common hexapod preserved at Rhynie. Among the diversity of specimens tentatively attributed to *R. praecursor*, there are likely three different groups of springtails, demonstrating an early diversification of Collembola (31). The highly fragmentary *Rhyniognatha hirsti* is represented by a largely cleared and crushed head capsule, with prominent mandibles and apodemes. Although *R. hirsti* is considered an early insect, its placement among Hexapoda remains uncertain, as there are traits consistent with Chilopoda; at the same time, it cannot be definitively excluded from among the insects (39, 46). *Leverhulmia mariae* is another fragmentary fossil (found in the coeval Windyfield chert) bearing five pairs of abdominal styli (leglets) and seemingly having close affinities to Archaeognatha or Zygentoma (42).
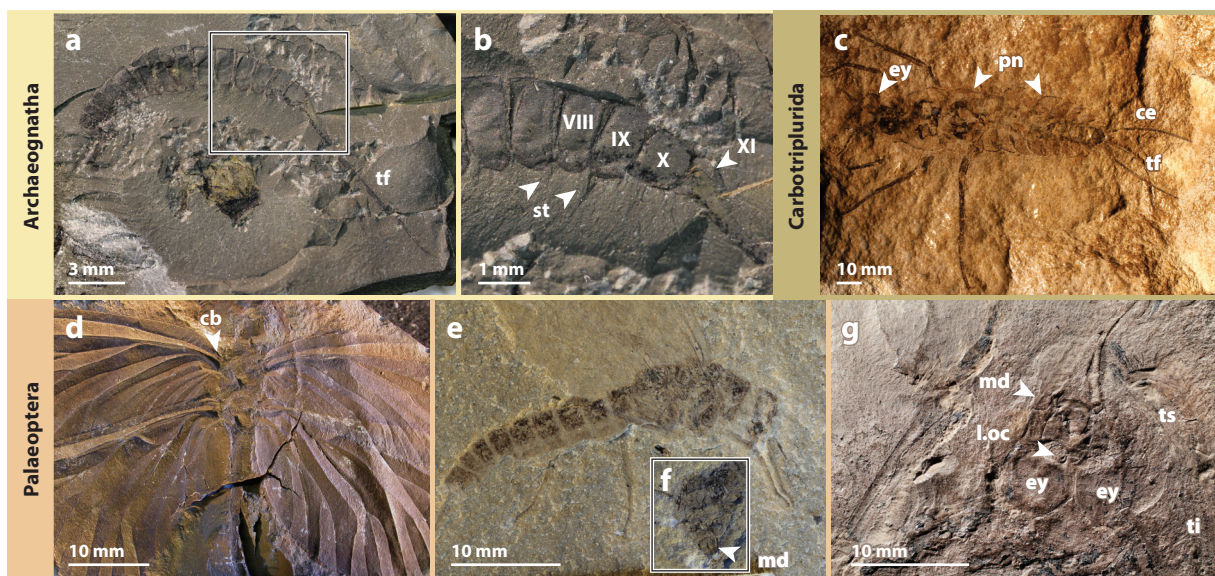
**Figure 3**

Exceptionally preserved Late Paleozoic hexapods depicting crucial characteristics. (*a,b*) *Dasyleptus brongniarti* (Archaeognatha: Dasyleptidae). (*c*) *Carbotriplura kukalovae* (Carbotriplurida). (*d*) *Lithoneura lameerei* (Syntonopteroidea: Syntonopteridae). (*e,f*) *Misthodotes sharovi* (Permoplectoptera: Misthodotidae). (*g*) *Meganeurites gracilipes* (Meganisoptera: Meganeuridae) head and prothoracic legs. Abbreviations: cb, costal brace; ce, cerci; ey, compound eyes; l.oc, lateral ocelli; md, mandibles; pn, paranotal lobes; st, styli; tf, terminal filum; ti, tibia; ts, tarsus. Panels *e* and *f* adapted from Reference 162; CC BY-SA 4.0. Panel *g* adapted from Reference 100; CC BY-SA 4.0.

Primary wingless insects are known from a few Paleozoic species and quite often from species of the bristletail genus *Dasyleptus*, a group earlier classified as the extinct order Monura and as sister to Ectognatha (50, 173). Many dasyleptids were eventually discovered to be neotenic bristletails, with the same pedomorphic characteristics found in late embryos of Machilidae, such as short antennae, undivided tarsi with a single pretarsal claw, suppressed cerci, and a well-developed abdominal segment XI (136) (**Figure 3*a,b***). Subsequent studies indicated that the Dasyleptidae were likely sister to all other Archaeognatha, representing either a suborder of Monura or a distinct order alongside archaeognaths (7, 18). The group was eventually revised as a lineage of Archaeognatha and a key developed (37). Dasyleptidae were hypothesized to have lived near seashores or the edges of freshwater bodies and swamps (136). The discovery of *Dasyleptus* in the Middle Triassic of Switzerland demonstrated that these early archaeognaths survived the End Permian mass extinction (7), likely owing to a cryptic biology similar to that of modern Archaeognatha.

Other early groups are less clearly identifiable than *Dasyleptus*. A putative dipluran, *Testajapyx thomasi* (72), from the Pennsylvanian of Mazon Creek was tentatively considered to be related to stem-Dermaptera (165); some characters, such as the abdominal leglets, eversible vesicles, number of abdominal segments, and putatively entognathous mouthparts, were in doubt (66). Similarly, *Ramsdelepidion schusteri* from the Pennsylvanian of Mazon Creek was originally attributed to Zygentoma (72) but has been reconsidered as a stem group of Hexapoda (7, 18, 173).

The difficulties with the placement of some Paleozoic wingless insects is demonstrated by *Carbotriplura kukalovae* from the Pennsylvanian of the Czech Republic (**Figure 3*c***), which was originally identified as a larva of Palaeoptera (Ephemerida) but later as a new suborder within

"Thysanura" and ultimately attributed as belonging within Zygentoma or as a potential sister group to Pterygota (18, 63, 71, 165, 173) (**Figure 2**), a stunning range of phylogenetic placements. Quite critically, this fossil has been used as an outgroup to resolve phylogenetic relationships among palaeopteran insects, purportedly to improve the rooting of topologies (163). Given the uncertainty of its proper placement, such a calibration point for rooting or dating lacks credibility.

## 3.2. Palaeopteran Insects (Panephemeroptera, Odonatoptera)

The best-known examples of Paleozoic palaeopteran insects are giant predators such as griffenflies (Meganisoptera), which reached wingspans of approximately 70 cm; however, the majority of Carboniferous and Permian species had dimensions comparable to those of their modern relatives. A recent analysis incorporating fossil species of major palaeopteran groups recovered a monophyletic Hydropalaeoptera, including Bojophlebiidae + (Odonatoptera + Panephemeroptera), as well as supporting Palaeoptera as a clade (163), corroborating estimates based on morphological and genomic analyses (19, 77, 92, 157). The Late Paleozoic Palaeodictyopterida was resolved as monophyletic and recognized as a sister group to Neoptera.

Panephemeroptera comprises crown-group mayflies (Ephemeroptera) and their stem group, the latter of which first appears in the Late Carboniferous. Paleozoic representatives had strongly corrugated venation with an ancestrally formed costal brace remote from the anterior wing margin, along with fully developed fore- and hind wings, in contrast to modern relatives (71, 164). The controversial *Lithoneura lameerei* from Mazon Creek was determined to be an early mayfly (172) (**Figure 3d**), and phylogenetic relationships have been established for Ephemeroptera and its stem group (174). Similarly, the record of Syntonopteroidea was reviewed and new synapomorphies proposed for their monophyly and placement among Panephemeroptera (121). A reexamination of imagoes of *Misthodotes sharovi* and *Misthodotes zalesskyi* (Permoplectoptera) from the Early Permian of Tshekarda (Russia) demonstrated the presence of functional chewing mouthparts and inflexible wing axilla similar to those found in modern mayflies (162) (**Figure 3e,f**). Permoplectopteran larvae from the same locality cannot be unambiguously associated with the adults, but they do exhibit some morphological specializations, such as nine pairs of abdominal tracheal gills, supporting the conclusion that at least immature Misthodotidae were benthic, with legs specialized for burrowing. One of the most controversial Carboniferous species is *Triplosoba pulchella* from Commentry, France. The placement of this species among stem-Ephemeroptera was questioned (118, 171), and instead, a position among Palaeodictyopterida was established owing to many wing venational characters incompatible with mayflies, including the basally fused veins RA, RP, and MA and the lack of a costal brace. Nonetheless, another reexamination argued for a return to Ephemeroptera sensu lato on the basis of the presence of a forked RP2 in one hind wing but not the other (11), and therefore an ambiguous character, as it is not possible to determine which wing venation is aberrant for this species.

Odonatoptera are among the most ancient and morphologically conservative groups of insects, comprising crown-group Odonata (dragon- and damselflies) and their extensive stem group, with their earliest relatives documented since the mid-Carboniferous. Our evidence confirms that the specialized structure of the synthorax with mostly direct flight musculature, and therefore uncoupled wings, is already present in Paleozoic Odonatoptera. These were certainly among the first aerial predators, with impressive flight skills (180). Compared to Panephemeroptera, there has been greater phylogenetic exploration within this group (5, 6), with the general pattern recovered as Geroptera + [Eomeganisoptera + (Meganisoptera + Odonatoclada)], the last including Odonata (**Figure 2**). Three new representatives of early branching Geroptera were described from the mid-Carboniferous of Argentina that preserve the morphology of various body parts including

small prothoracic lobes (112); together with earlier work, these findings provide a robust picture of these earliest Odonatoptera (140). In particular, the wing base of *Kirchnerala treintamil* was interpreted, using the scheme of Kukalová-Peck (70), as having parallel columns of sclerites linked to the costa (112). Perhaps the most iconic of the Paleozoic insects are the diverse griffenflies (Meganisoptera), with some giants reaching wingspans up to 71 cm (44, 96). These insects lacked a developed nodus and pterostigma, in contrast to Odonata, and coexisted in early ecosystems with quite small protozygopteran species. A reexamination of the large griffenfly *Meganeurites gracilipes* from Commentry revealed it to have hawker specializations, like greatly enlarged compound eyes, sturdy mandibles with acute teeth (**Figure 3f**), strong spines on the tibiae and tarsi, and a pronounced thoracic skewness allowing for prey capture while in flight, like modern Odonata (100). The male postabdomen of *Namurotypus sippeli* from Hagen-Vorhalle, Germany preserved genital appendages with paired penes, a pair of lateral parameres, and a pair of leaf-like gonopods of segment IX, otherwise unknown in Meganisoptera (6). The grade of Paleozoic and Mesozoic Protozygoptera consisted of the superfamily Permagrionoidea and the Archizygoptera (95). The larger species of the permagrionoid lineage apparently did not survive the Permian–Triassic extinction, while the more gracile Archizygoptera demonstrated a remarkable longevity from the Late Carboniferous to the Early Cretaceous. Small damselfly-like Odonatoptera with subpetiolate or petiolate wings appeared during the Carboniferous convergently in several lineages, such as Enigmapteridae, Bechlyidae, or even the meganisopteran Bechalidae (98). Fossil larvae are rare, but evidence from the early instar meganisopteran *Dragonympha srokai* from Mazon Creek shows the presence of a labial mask and filamentous lateral gill-like appendage on abdominal segments I–VII comparable to the extant Euphaeidae and Polythoridae (77). These lateral gill-like projections are considered to be possible homologs of tergalia in mayflies and presumably also abdominal lateral outgrowths (flaps) in palaeodictyopterans (129, 168).

### 3.3. The One That Got Away: The Superorder Palaeodictyopterida

Palaeodictyopterida is one of the most diversified and common groups of insects during the Late Carboniferous and Permian periods, with characteristic piercing and sucking mouthparts in the form of a stylate rostrum, a distinctive synapomorphy for the clade. These archaic insects were most probably specialized herbivores, feeding presumably on spores, phloem tissue, or even pollination drops of early seed plants like medullosans or *Cordaites*, based on indirect evidence of feeding traces and punctures on various plant organs (83, 110, 156). The superorder consisted of three orders with permanently outstretched wings, Palaeodictyoptera, Dicliptera, and Megasecoptera, and one order with the ability to fold their wings roof-like over the abdomen at rest, Diaphanopterodea (**Figure 4**). Megasecoptera and Diaphanopterodea share a similar pattern of wing venation and body structures (22), which seems to suggest shared ancestry, although functional convergence has yet to be ruled out. The phylogeny of palaeopteran insects (163) resolved monophyly of Palaeodictyopterida, Megasecoptera, Diaphanopterodea, and Dicliptera (=Permothemistida), while Palaeodictyoptera was paraphyletic (**Figure 2**). Alternative, and somewhat radical, reclassifications do exist for the group (159) but are by no means cladistically founded. Certainly, more morphological data beyond just data related to the wings are needed to truly resolve intraordinal relationships of Palaeodictyopterida and elucidate the early divergences among pterygotes.

Wing characters are principally used for the classification of Palaeodictyopterida, as structural details of other body parts are infrequently recovered. A few species have been documented from a series of specimens comprising both sexes and even different ontogenetic stages. One of these is the diaphanopterodean *Permuralia maculata* from the Early Permian of Tshekarda, which
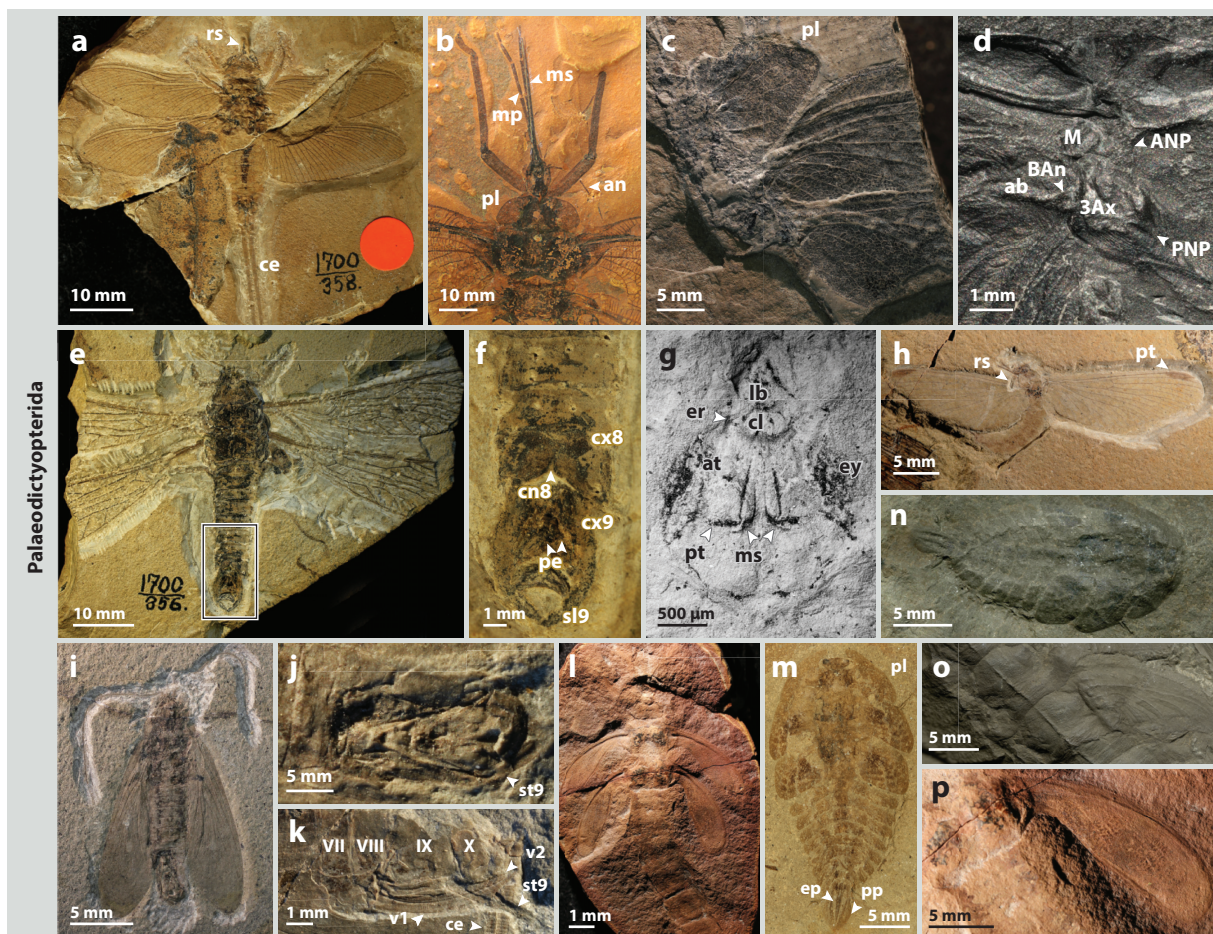
**Figure 4**

Exceptionally preserved Paleozoic Palaeodictyopterida depicting crucial larval and imaginal characters. (*a*) *Paradunbaria pectinata* (Palaeodictyoptera: Spilapteridae). (*b*) *Eugereon boeckingi* (Palaeodictyoptera: Eugereonidae) head and thorax. (*c*) *Stenodictya pygmaea* (Palaeodictyoptera: Dictyoneuridae) thoracic segments with prothoracic lobes and wings. (*d*) *Dunbaria quinquefasciata* (Palaeodictyoptera: Spilapteridae) wing base. (*e,f*) *Sylvohymen* cf. *sibiricus* (Megasecoptera: Bardohymenidae), detail of male external genitalia. (*g*) *Protohymen novokshonovi* (Megasecoptera: Protohymenidae) head under SEM. (*h*) *Diathemidia monstruosa* (Dicliptera: Diathemidae). (*i–k*) *Permuralia maculata* (Diaphanopterodea: Permuralidae) habitus and male and female external genitalia. (*l,p*) *Lameereites* sp. (Megasecoptera: Brodiidae) larva and detail of metathoracic wing pad. (*m,n*) *Idoptilus* sp. (Palaeodictyoptera) nymphal exuvia. (*o*) *Idoptilus onisciformis* (Palaeodictyoptera), detail of thoracic nota and metathoracic wing pad. Abbreviations: 3Ax, third axillary sclerite; ab, anal brace; an, antennae; ANP/PNP, anterior/posterior notal wing process; at/pt, anterior/posterior tentorial arms; BAn, basianale; cl, clypeus; cn, median membrane separating coxal lobes; ce, cerci; cx, coxal lobes; ep, epiproct; er, epistomal ridge; ey, compound eyes; lb, labrum; M, median plate; mp, maxilary palpi; ms, mandibulary stylets; pe, penial lobes; pl, prothoracic lobes; pp, paraprocts; pt, pterostigma; rs, rostrum; st, styli; v, valvulae. Panel *c* adapted from Reference 38; copyright 2013 Springer-Verlag. Panels *e* and *f* adapted from Reference 128; copyright 2020 Elsevier Ltd. Panel *g* adapted from Reference 109; copyright 2017 Elsevier Ltd. Panel *i* adapted from Reference 114; copyright 2019 Elsevier Ltd. Panels *l*, *o*, and *p* adapted from Reference 116; copyright 2019 by the Royal Society CC BY-SA 4.0. Panels *m* and *n* adapted from Reference 123; copyright 2018 The Royal Society of Edinburgh.

permitted a study of the mouthparts, including the labium with apical endites; the thorax from different aspects; leg details; and the abdomen with external genitalia of both sexes (74). Naturally, the interpretation of observations is critical; one study concluded that the species had unusual structures for insects or even hexapods, such as legs with more than six podomeres, maxillary palpi with apically paired claws, or male claspers fully homologized with thoracic legs including paired pretarsal claws. Such interpretations are fully in line with the controversial model of the pterygote groundplan (73), although these conclusions have been vigorously debated and are considered dubious (e.g., 67, 171). A reexamination of the same material concluded that leg podites and male external genitalia had been overinterpreted and confirmed other plesiomorphies such as pregenital styli (138). The megasecopteran *Brodioptera sinensis* from Xiaheyan, China and the palaeodictyopteran *Dunbaria fascipennis* from Elmo, United States are other examples of exceptional preservation of structural details in a series of specimens allowing for the study of intraspecific variability and sexual dimorphism (8, 68, 108, 125, 127).

The palaeodictyopterid head, where it is known, was usually hypognathous, but in some extremely long rostrate taxa, it could be slightly prognathous, be inclined, and have mouthparts directed ahead, as in *Eugereon boeckingi* or *B. sinensis* (83, 93, 108) (**Figure 4b**). The structure of the cephalic endoskeleton (tentorium), with anterior and posterior tentorial arms, was reconstructed in the megasecopteran *Protohymen novokshonovi* and partly in *P. maculata*, and it was possible to discern the proximal parts of stylets (109, 138). The morphology of mouthparts across Palaeodictyoptera shows a spectacular variety of rostra in terms of lengths and shapes of the mandibular stylets, probably reflecting specializations for piercing and sucking on various parts of Paleozoic plants, such as cordaite seeds (83, 154). Where known, the maxillary palpi were markedly elongate, while the labial palpi were completely absent (108, 127, 138, 159).

The prothorax of some species of Palaeodictyoptera had developed characteristic membranous, subtriangular, lateral lobes. The lobes of *Stenodictya lobata* possessed the full set of main veins comparable to the meso- and metathoracic wings and even separate axillary sclerites (80). However, this interpretation cannot be accepted without reservation (125). The meso- and metathoracic wings bear a full set of distinctly pleated longitudinal veins and a diversely developed pattern of crossveins, including a dense network of irregular cells, called an archedictyon (22, 179). In some palaeodictyopterid species, such as *Namuroningxia elegans*, the forewing had proximally well-differentiated costal and subcostal veins, with a structure comparable to some Odonatoptera, such as *Zygophlebia tongchuanensis* (54, 81, 127). The well-separated subcosta anterior was also developed in two species of megasecopteran Brodiidae (124) and seem to be homologous to the first primary antenodal crossvein, Ax0, thus representing a putative synapomorphy of Odonatoptera, Ephemeroptera, and at least some Palaeodictyopterida (5, 54, 140). The forelegs probably helped to manipulate the elongate mouthparts during feeding, as their lengths, where known, correspond among different groups of Palaeodictyopterida (108, 127, 156). The prothoracic tarsi had five tarsomeres, corresponding to the plesiomorphic condition for Pterygota.

The abdomen was 11-segmented in Palaeodictyopterida, with the terminal segment in the form of long, paired, and multijointed cerci in adults. The cerci were often covered with prominent long setae arranged in rings and most probably served a tactile function (127). The presence of archaic characters such as styli on the pregenital abdominal segments, resembling those of primary wingless Archaeognatha and Zygentoma, has been a controversial topic for decades (74, 171). Nonsegmented styli, sometimes called leglets, were present on pregenital segments III–VII of the diaphanopterodean *P. maculata* and were considered to be plesiomorphic characters shared with primary wingless insects (74, 138). Evidence of external genitalia from both sexes of Palaeodictyopterida is exceptionally rare (22, 108, 109, 138) (**Figure 4i–k**). The female genitalia formed as an endophytic valvular ovipositor, with two pairs of cutting valvulae (gonapophyses VIII and

IX) and a pair of sheathing valvulae (gonoplacs of segment IX); is known among representatives of all palaeodictyopteridan orders; and resembles the genitalia of modern zygopteran Odonata. These ovipositors differ in relative lengths and microstructural details, reflecting various oviposition specializations and substrates (74, 108, 127, 138). The male external genitalia generally consist of incompletely fused (gono)coxal lobes of segment IX, long multijointed (gono)styli known as claspers for grasping the female during copulation, and a pair of penial lobes. Surprisingly, in the two megasecopteran families Bardohymenidae and Brodiopteridae, the structure of the genital segments reveals the presence of separated coxal plates VIII and ventral expansions of coxal lobes IX, which demonstrates that early pterygotes like Megasecoptera had quite archaic traits; these traits are otherwise found in most extant Archaeognatha and in some Zygentoma (62, 128) (**Figure 4***e,f*).

The larvae of palaeodictyopterids are known only for Palaeodictyoptera and Megasecoptera. They show a remarkable morphological disparity reflecting various ecomorphological strategies, from the trilobite-like onisciform larvae of some Palaeodictyoptera to elongate forms with spined thoraces in Megasecoptera (116) (**Figure 4***l–p*). While an exclusively aquatic lifestyle was suggested by early scholars, most authors during the twentieth century concluded that they were terrestrial due to a lack of distinctive aquatic specializations (22, 177). A recent reexamination of early larval exuvia of the palaeodictyopteran *Idoptilus* sp. revealed the presence of three triangular caudal appendages bearing prominent lateral lamellae. These were modified caudal appendages made up of paired paraprocts and epiproct that are formed as tracheal gills in Zygoptera (123). Thus, the latest hypothesis is that some species were amphibious or aquatic in early instars, possibly transitioning to a semiaquatic mode in more mature larvae (much like in petalurid dragonflies) and even an amphibious lifestyle in some adults where rudimentary or even functional lateral abdominal tracheal gills were seemingly retained (116). However, it cannot be assumed that such biology was fixed across all orders given the extreme morphological variety, and it is likely that both terrestrial and aquatic lineages of Palaeodictyopterida coexisted.

Ultimately, Palaeodictyopterida, despite their considerable diversity and biological breadth, succumbed to the End Permian extinction. Their passing marked them as the only superordinal clade of insects to have gone wholly extinct in the over 400-million-year history of hexapods. Their loss was likely due to a combination of factors linked to the geological turmoil of the time, along with the changing global climate and the disappearance of the floral lineages upon which many had apparently specialized.

### 3.4. Polyneopteran Insects (Polyneoptera)

While the monophyly of Polyneoptera has been well established, the understanding of the placement and relationships among the Paleozoic polyneopteran groups remains largely unresolved, albeit with some notable exceptions, such as the orthopteroid clade Archaeorthoptera, Dictyoptera with its sister group Paoliida, stem group of Plecoptera, stem group of Embiodea, and Protelytroptera as a stem group to Dermaptera (16, 17, 117, 153) (**Figures 2** and **5***a–e*). Unfortunately, the vast majority of described taxa are categorized based on wing characters, sometimes modified as protective tegmina, and lack other obvious body characters. An extreme situation with considerable intraspecific variability of forewing venation is the case of the Paleozoic roachoids (stem-Blattodea or stem-Dictyoptera); the same variability has been recently demonstrated in alleged "grylloblattidan" insects of the Sinonamuropteridae (30). The postabdominal morphology of some Jurassic grylloblattid Bajanzhargalanidae demonstrates that the classification of fully winged Paleozoic and Mesozoic stem-Grylloblattida (167) as united with crown-group Grylloblattidae, which comprise only wingless species, remains uncertain due to a lack of clear homologies (29). A reexamination of clypeal structures by ESEM in *Gerarus* spp.
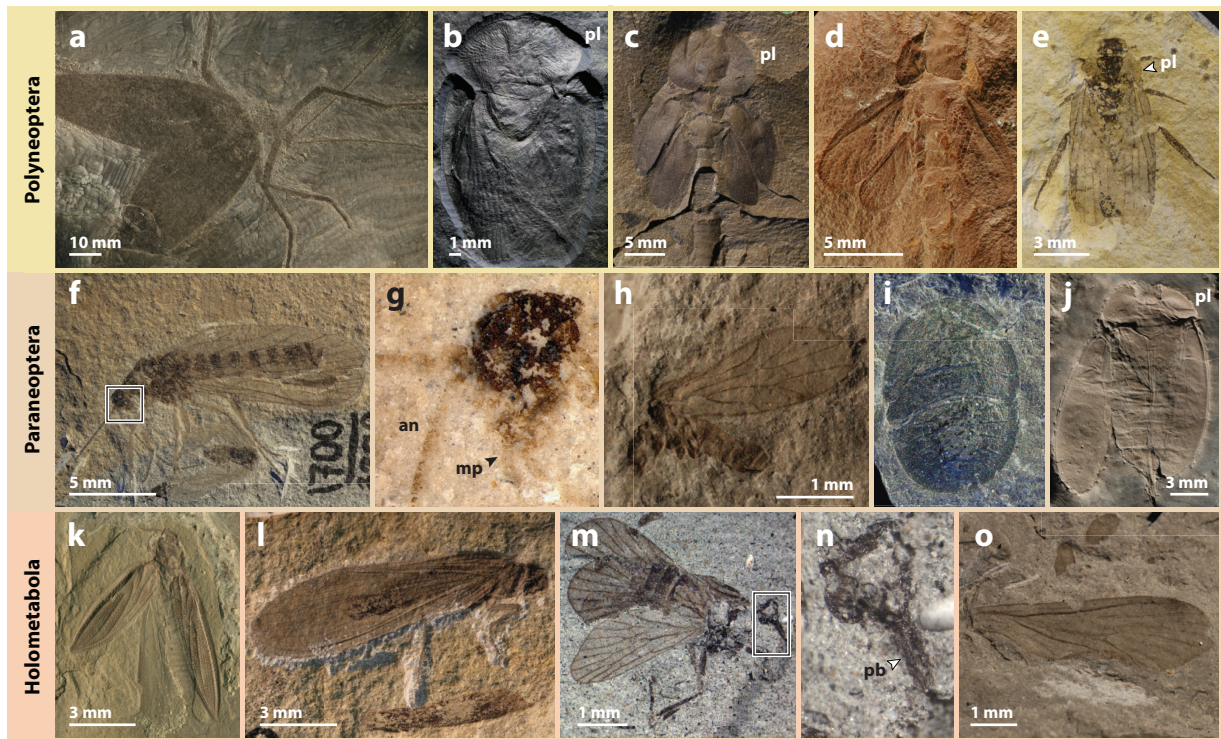
**Figure 5**

Exceptionally preserved Paleozoic Neoptera depicting crucial larval and imaginal characters. (*a*) *Kemperala hagensis* (Paoliida: Paoliidae). (*b–c*) Imago and larva of roachoids (Dictyoptera: stem Blattodea). (*d*) *Herdina mirificus* (order uncertain: Herdinidae) brachypterous imago. (*e*) *Lemmatophora typa* (Grylloblattida: Lemmatophoridae). (*f,g*) *Idelopsocus* cf. *splendens* (Hypoperlida: Hypoperlidae) habitus and detail of head. (*h*) *Lophiocypha permiana* (Lophioneurida: Lophioneuridae). (*i*) Disc-shaped larva (Hemiptera). (*j*) *Paraknightia magnifica* (Hemiptera: Paraknightiidae). (*k*) *Moravocoleus permianus* (stem Coleoptera: Tshekardocoleidae). (*l*) *Glossopterum martynovae* (Glosselytrodea: Glossopteridae). (*m,n*) *Nedubrovia shcherbakovi* (Mecoptera: Nedubroviidae) habitus and detail of head. (*o*) *Permotipula patricia* (stem Diptera: Permotipulidae). Abbreviation: pl, prothoracic lobes. Panels *f* and *g* adapted from Reference 122; copyright 2020 Elsevier Ltd. Panels *m* and *n* adapted with permission from Reference 3; copyright 2011 Magnolia Press.

(Geraridae) combined with wing characters corroborated its placement within the stem-group of Orthoptera, in stark contrast to previous assertions that these species belonged to Paraneoptera (12, 79). *Gerarus* did not have leg exites like *P. maculata* (Diaphanopterodea), and thus, the existence of these structures among Paleozoic pterygotes remains hypothetical (66, 138).

Diverse polyneopteran insects discovered from the Pennsylvanian locality Xiaheyan comprise stem groups of Orthoptera, Plecoptera, and Dictyoptera, occasionally with well-preserved body structures (14, 45). A study describing details of body parts, including mouthparts, wings, and female external genitalia, of the Carboniferous archaeorthopteran *Ctenoptilus frequens* from this locality was based on a series of rather complete specimens (26). The results of a morphometric analysis of mandibular shape indicated possible omnivorous feeding habits in *C. frequens*. The comparative analysis of characters of their needle-shaped ovipositors suggested that these insects were likely laying their eggs in the ground.

Insect primary ovipositors have been organized into four principal types: (*a*) Odonatoptera, (*b*) Diaphanopterodea, (*c*) Paraneoptera and Hymenoptera, and (*d*) Orthoptera (36). This hypothesized functional arrangement was based on homologies of the gonangulum in the female genitalia,

which is interpreted as half of sternite IX lateral of the midline plus the paratergite of the same segment. The ovipositors of roachoid larvae and adults from various Late Paleozoic localities were divided into two different morphotypes on the basis of relative length and shape of the ovipositor valvulae (52). These results supported the notion that these ovipositing species could be classified as either Dictyoptera sensu lato (total group of Dictyoptera) or Dictyoptera sensu stricto.

Polyneoptera were certainly a considerable component of the Paleozoic fauna, with the early roachoids and many relatives of early Orthoptera and other groups being most prevalent among their members. While some groups are currently unknown after the End Permian event (e.g., Caloneurodea), some minor lineages of the time survived and then flourished during the early Mesozoic, transforming the composition of the polyneopteran fauna.

## 3.5. Paraneopteran Insects (Paraneoptera)

Like Polyneoptera, paraneopteran insects were certainly present in the Paleozoic, with stem-group representatives of Psocodea, Thripida, and Hemiptera all recorded from the Late Carboniferous (Pennsylvanian) alongside extinct lineages like Permopsocida, Miomoptera, and Hypoperlida (122) (**Figure 5f–j**). Phylogenetic analyses have resolved Permopsocida as the sister group to Hemiptera + Thripida, while Miomoptera + Hypoperlida was recovered as a sister group of Acercaria (**Figure 2**). The structure of the mouthparts in Permopsocida represented an evolutionary step documenting the transition from chewing to piercing in relation to suction feeding, a position corroborated by the structure of the wing base (53, 183). In the early history of Thripida, the Permian Lophioneurida were a critical group, already possessing mouthparts with an asymmetrical mouth cone and reduction or loss of the right mandible (83, 103), like modern Thysanoptera. The earliest evidence of a piercing-sucking proboscis in Hemiptera is recorded in the psyllid-like Archescytinidae attributed to Paleorrhyncha as a stem group of Sternorrhyncha from the Early Permian of Russia (155) (**Figure 2**). While the diversification and geographical distribution of homopteran families during the Permian, including their supposed host-plant associations and the impact of the End Permian mass extinction, have been reviewed (150), a comprehensive exploration of Paleozoic Hemiptera from a critical phylogenetic perspective has yet to be performed.

## 3.6. Holometabolous Insects (Endopterygota)

The earliest representatives of Holometabola were discovered in the Pennsylvanian and display body miniaturization similar to that of many paraneopterans (101, 102, 130, 152). However, these Carboniferous taxa cannot be attributed to contemporary insect orders and represent stem groups. Moreover, the assignment of certain taxa, such as that of *Avioxyela* as the earliest stem-Hymenoptera, has been questioned (152). The difficulty with the systematic placement of certain Permian endopterygotes, particularly based on wing venation, has been repeatedly demonstrated, and all such fossils need to be carefully evaluated (78, 91, 171). The first species of Coleoptera and Mecoptera appeared during the Permian, while for many other orders, the earliest evidence of species comes after the Permian–Triassic boundary. Stem groups of these orders or their superordinal clades existed prior to the extinction, but recognizing them as such has been a challenge (**Figure 5k–o**).

The early radiation of Coleoptera is well documented from at least the Early Permian and from several localities worldwide. Indeed, fossils attributed to the adephagan Gyrinidae are known from the Late Permian, while families of less-confident subordinal assignment, like Permocupedidae, Ponomarenkiidae, Rhombocoleidae, Triadocupedidae, and Tshekardocoleidae, are well documented throughout the Permian (61, 181, 182). Nonetheless, the results of Bayesian analyses

imply that the Tshekardocoleidae and Permocupedidae form a transition series from relatively soft-bodied to hard-bodied and desiccation-resistant stem Coleoptera (20). Deforestation caused by climate and ecosystem changes in the Late Permian was probably instrumental in the extinction of the largely xylophagous Permian beetle fauna by the Permian–Triassic boundary (185). The related superorder Neuropterida evolved early and developed recognizable elements during the Permian; specifically, the Permithonidae and Permoberothidae had a similar wing morphology and either both represent stem group of Eidoneuroptera (Megaloptera + Neuroptera), or the Permithonidae could be more closely related to Neuroptera (40, 115). The Parasialidae and Nanosialidae are putatively members of stem-Raphidioptera (40, 152).

The clade Mecopterida (= Amphiesmenoptera + Antliophora) is recorded from the Late Carboniferous onward (102, 130). The problematic Permian families Microptysmatidae and Protomeropidae were considered to be either early trichopteran lineages or members of the stem-group to Amphiesmenoptera (4, 91), although at least one study suggested that Microptysmatidae belonged to a separate order, Permotrichoptera, Mecopterida, and belonged neither to Amphiesmenoptera nor to Antliophora (91). The first radiation of holometabolous long-proboscid nectar feeders appeared in the Permian (58), with the earliest evidence of a long siphonate proboscis suitable for nectar feeding present in *Marimerobius* and other protomeropids with an ability to gather sugary fluids from gymnosperm ovulate organs discovered in the Early Permian of Tshekarda (59). Suctorial mouthparts were also discovered in Late Permian mecopterans of the families Permochoristidae and Permotanyderidae, putatively specialized on nectarivory (58). In Mecoptera, a siphonate mouthpart form evolved convergent with the earliest evidence of a proboscis in Nedubroviidae, the latter recorded from the Late Permian of Russia (3) (**Figure 5*m,n***).

The extinct order Glosselytrodea is problematic and of uncertain systematic position, although the group was widely distributed across Pangea from the early Permian and perhaps into the Middle Jurassic. The group has, at one time or another, been placed among the orthopteroids, stem-Holometabola, or stem-Neuropterida, reflective of the lack of critical data available for the group. Nonetheless, a reexamination of *Permoberotha villosa* and *Sylvaelytron latipennatum*, both of Permoberothidae, has uncovered structural details of male and female external genitalia and a possible relationship of this group to the antliophoran clade (106, 111).

These studies have confirmed that holometabolous insects were a significant part of Paleozoic fauna and were surprisingly diversified (59, 101, 105). However, the sampling from many Carboniferous localities was probably biased due to common body miniaturization of endopterygotes and difficulty with their attribution based solely on wing venation.

## 4. POSTEMBRYONIC DEVELOPMENT IN DEEP TIME

The immature stages of Paleozoic insects are rarely preserved as complete body fossils and often lack the morphological details, like the structure of developing wings, crucial for systematic assignment. Thus, precise determinations of these immatures to species, genus, or sometimes even family remain commonly tentative. The extreme case are larvae of holometabolous insects, which are morphologically and ecologically different from their imagoes. Accordingly, finding successive series of different instars attributable to single species is rare among Paleozoic fossils (e.g., 143, 158). Hypotheses regarding the postembryonic development of Paleozoic hexapods and particularly of winged insects (Pterygota) were greatly influenced during the past 40 years by the studies of Kukalová-Peck (69, 70, 73, 75, 76), which were partially based on earlier works by Sharov (148, 149). These were later either adopted without critical revision of examined specimens or partly disputed on the grounds of unconvincing evidence (10, 15, 47, 65, 126, 139, 146). Given this state of affairs, our view of postembryonic development in Paleozoic hexapods relative to that of extant

## PRZIBRAM'S RULE

Przibram's rule states that the average ratio of the mean weights for successive instars of hemimetabolous insects is 2.09 and that the average ratio of the mean lengths for successive instars is 1.29. It is derived from weight and length measurements of successive larval instars and adults of a mantid, *Sphodromantis bioculata* (Mantidae) (133).

species remains blurred and somewhat controversial. To avoid any confusion with the variety of terms for immature stages of insects (e.g., naiads, nymphs, larvae), we follow precedent and treat all juveniles of Pterygota as larvae (146).

Ametabolous development, whereby molting continues past maturity, is known in the primary wingless groups of insects lacking a predetermined final instar (146). In contrast, the appearance of the final molt in hemimetabolous and later holometabolous insects represented a key innovation in the origin of insect metamorphosis (9). The ontogeny of the Carboniferous archaeognathan *Dasyleptus bronghniarti* had six instars and a general body growth pattern following Przibram's rule (see the sidebar titled Przibram's Rule), comparable to modern Archaeognatha and Zygentoma (141). Surprisingly, winged ametabolous insects (alate ametaboly) have been asserted for some groups of Paleozoic pterygotes, such as Panephemeroptera, Palaeodictyopterida, and even some early groups of Neoptera (73); however, the evidence for several subimaginal stages prior to the imago in fossils of these groups is exceedingly tenuous (143).

A substantial part of the evidence for the development of wings in Paleozoic insects is revealed in fossils of Panephemeroptera, Odonatoptera, and Palaeodictyopterida (except Diaphanopterodea), the adults of all of which were unable to fold their wings over the abdomen at rest. Many authors considered the wing development of these lineages to be quite gradual (archemetaboly), with numerous larval and several subimaginal instars, although with the exception of Odonatoptera (47, 73, 75, 158). However, tangible evidence is lacking for such numerous series of larvae and particularly subimagoes of a single species (143). The developing wings in all of these groups were sometimes formed as and referred to as winglets with true venation, which were purported to be fully articulated and even allow for larvae to produce simple flapping flight (47, 75). Such hypothesized flying larvae are entirely speculative, and it remains to be demonstrated whether functional articulations were present or whether putatively moveable winglets were capable of producing sufficient lift to permit flight of any kind.

There has been an effort to critically evaluate newly discovered and original source material of larvae from Palaeodictyoptera, Megasecoptera, Panephemeroptera, and Odonatoptera, with a focus on wing pads (124, 126, 143, 162). Evidence for articulation of such wing pads is not widespread (177), and as is documented in palaeodictyopteran larvae, the wing bases show anterior and particularly broad posterior fusion with the tergum above the area of articulation. Accordingly, the wings were not fully articulated along the base (126, 135), and the insects were likely unable to fly given that wing loading would be absurdly high and their joints probably allowed only limited divergence. Whether these structures had functions beyond the simple necessities of developing the wings of adults remains to be resolved.

Several marked differences can be observed between the larvae of Palaeodictyoptera and those of Megasecoptera (**Figure 4***l–p*). The costal area in the forewings of Palaeodictyoptera have a noticeably broad keel, usually as a continuation of the enlarged prothoracic winglets, while the larvae of Megasecoptera lack such an extension, and their wing pads are usually more expanded along the body axis (22, 116). The prothorax of Palaeodictyoptera often has prominent prothoracic lobes (what some authors call winglets), while some species of Megasecoptera had

long, laterally protruding spines, most likely serving a protective function. Interestingly, expanded pronotal lobes occur in some extant mayfly larvae of *Cincticostella* spp. (Ephemerellidae) and resemble the supposed winglets of palaeodictyopteran larvae (2).

Some authors presumed that winglets were curved backward in younger larvae and that, during successive larval and subimaginal stages, these would gradually straighten until reaching their final, nearly perpendicular position relative to the body axis in the adult (47, 73, 75). Although partial growth of wing pads between successive instars is natural, there is no evidence in the larval stages of species of Palaeodictyoptera for any straightening of the orientation of wing pads into a final perpendicular position. Interestingly, the partial lateral spread of wing pads from approximately 15° to approximately 20°, documented in later larval stages of the extant damselfly *Calopteryx splendens*, is a response to a lack of oxygen (28). A series of palaeodictyopteran larvae tentatively attributed to *Rochdalia* sp. from Piesberg (Germany) was compared to *Rochdalia parkeri* described from Lancashire, United Kingdom; this comparison allegedly demonstrated a partial straightening of the wing pads (as extrapolated from 18°) during development, despite the fact that some researchers have indicated that the larvae are quite probably not conspecific (60). By contrast, several palaeodictyopteran specimens tentatively assigned to Breyeriidae possessed small wing pads beginning earlier in development that were nearly perpendicular to the thorax; these specimens can hardly be considered to be subimagoes (132). In fact, the series of ontogenetic stages illustrated and discussed by Kukalová-Peck (73) mainly correspond to different taxa, and the putative multiple subimaginal stages are more likely only teneral adults, as they do not show other supportive characters such as long setae along the posterior wing margin or shortened appendages (143). The thickness of the wing membrane in larval and subimaginal instars of palaeodictyopterans and its transparency were among the clues demonstrating the retention of hypodermal tissue in the subimago, which is essential for the wing molt, in contrast to adult wings (139, 158). However, such evidence is difficult to discern from compressed fossils, particularly those of teneral adults. In this context, it is relevant to note that some extant oligoneuriine mayflies shed the exuvia from the body when molting to the adult but retain subimaginal cuticle on the wings. In addition, in representatives of Leptophlebiidae, apolysis of the subimago to the imago occurs, while ecdysis does not (10, 35). The functional role of the subimago in development has been broadly discussed, including its evolutionary context (35). Maiorana (90) considered the subimago to be an adult stage and suggested that its functional significance lies in growth and rapid elongation of appendages, such as the forelegs and cerci, between the last larval instar and the final imago. These outcomes are corroborated by a study of the ephemeropteran *Cloeon dipterum*, which found that its metamorphosis is regulated as in neopteran insects and is determined prior to the formation of the subimago (57).

The recently discovered palaeodictyopteran larva *Bizzarea obscura* possessed a well-developed ovipositor, while the wing pads remained relatively small. The same situation has been found in larval exuvia of *Paimbia* cf. *fenestrata* (120, 143). Putative teneral adults or potential subimagoes were also identified in the megasecopteran *Brodioptera sinensis*, exhibiting wings with more densely clustered setae that possibly served a hydrophobic function; however, evidence that these are truly subimagoes is uncertain (108, 127). Even in the case of the Permian stem mayflies, *Misthodotes* spp. (Permoplectoptera), there was no recognizable subimaginal stage among a large series of specimens, despite the fact that it is likely that such a stage exists in this lineage (162). Finally, the position of lateroposteriorly directed wing pads in larvae of Permoplectoptera and Palaedictyopterida, in contrast to crown groups of Ephemeroptera and Odonata, seems to be a plesiomorphic condition and corresponds to the situation found in neopterous larvae of polyneopteran and paraneopteran groups (e.g., Plecoptera or Hemiptera); thus, their mode of growth reflects ecomorphological demand (49).

These examples demonstrate an inconsistency with the gradual growth and particularly the straightening of developing wings for at least some members of Megasecoptera and Palaeodictyoptera. The tissue of the wings in all of these groups developed inside the wing sheaths as wing pads. While some species of Megasecoptera and Palaeodictyoptera held these wing pads nearly perpendicular to the body axis, others retained wing pads in an oblique position until the late instars and for unknown functions (perhaps thermoregulation). Straightened developing wings also occur in some prepupae and pupae stages of Neuroptera and Coleoptera (184). The evidence for motility of these wing pads in Paleozoic insects is uncertain due to their position and prominent fusion with the tergum in some groups, but certain divergence is admitted, particularly if we compare the developing joints to the extant groups known for their wing rotation (anastrepsiptery) during postembryonic development, in Odonata and Orthoptera. The evidence for a subimago among Palaeodictyopterida is tenuous at best.

In general, Paleozoic evidence of immature stages of Polyneoptera demonstrates development of wings inside the cuticular sheath as wing pads (or pterothecae), numerous larval instars, and only one winged stage as the imago. Nevertheless, some authors have reported in certain groups, such as Archaeorthoptera, evidence for a gradual development of wings with the presence of subimaginal stages and thus several winged stages during ontogeny (73, 134, 139). This evidence has been questioned or ignored by other researchers (22, 65), yet imaginal and subimaginal wings were found in the orthopterid *Narkemina angustata* from the Pennsylvanian of Chunya, Siberia (139), demonstrating that the structure of wings was thick and diffuse in the subimago and thin and clear-cut in the imago. Similar differences were found for the grylloblattid *Atactophlebia termitoides* from the Late Permian of Tikhiye Gory and for alleged subimaginal wings of *Evenka archaica* (Archaeorthoptera) from the Chunya (134).

Controversial evidence regarding wing development comes from the neopteran *Herdina mirificus*, originally described as a brachypterous polyneopteran adult from Mazon Creek, which has well-sclerotized wings with thick veins in an oblique position relative to the body axis (22, 24). However, an alternative view, based on additional material, considered that these actually represent flight-capable larvae and even suggested that these pterygotes did not undergo metamorphosis (75). Moreover, the same study posited that *Herdina* is an early paraneopteran with close relationships to Psocoptera, based on traits in venation and the reduced hind wings (75), a conclusion that is quite unlikely given *Herdina*'s broad cubito-anal area with numerous veins. Some of this evidence has been reexamined (47), and this study supported the view that these fossils were larval stages but questioned the presence of an articulation to the winglets and considered them to have minimal motility. While these wings, as present on the holotype, are neither in an outstretched position nor folded over the abdomen, they have a clearly developed corrugate venation including numerous crossveins, as well as likely having an originally hyaline membrane typical of an imago (**Figure 5d**). In other groups, such as Paoliidae, adult wings are in an oblique position at rest (117); thus, there is no reasonable argument to consider that the development of larval stages in *H. mirificus* material is unusual (22).

Paraneopterans are largely phytophagous insects recorded first in the Late Carboniferous but more clearly diversified during the Permian, when the Paleophytic flora was replaced by the Mesophytic (22). Our knowledge of the body structures of larvae and adults is poorly documented, although we do have examples of early radiations in small hemipterans (Archescytinidae and Aphidomorpha) that probably lived on the reproductive organs or plant surface of early gymnosperms. Disc-shaped larvae tentatively attributed to these hemipterans were described from several Late Permian deposits (151) (**Figure 5i**).

Adults classified as holometabous insects are recorded from the Late Carboniferous, particularly of clades allied or belonging to the Coleopterida and Mecopterida (61, 101, 102), but their

larvae are virtually unknown. This could be due to their low abundance in Late Paleozoic ecosystems or to poor sclerotization of their exoskeletons and a general lack of distinctive diagnostic features owing to the fact that their wings develop beneath the cuticle. There are only four isolated fossils from the Paleozoic considered to be holometabolan larvae: a coleopteran aquatic larva of *Kargalarva permosialis* (Archostemata) from the Lower Permian of Kargala, which was originally interpreted as a megalopteran, *Permosialis* sp. (113); the neuropterid larva *Srokalarva berthei* from Mazon Creek (48, 73); and two fossils with uncertain systematic positions but including the campodeiform larva *Cavalarva caudata*, with long caudal filaments described from the Tshekarda, and the eruciform larva *Metabolarva bella* from the Pennsylvanian of Piesberg (1, 101). Obviously, our knowledge of the postembryonic development of holometabolous lineages during the Paleozoic remains incomplete, to say the least.

## SUMMARY POINTS

1. While Mesozoic, Paleogene, and Neogene insect faunas generally resemble our modern fauna, the Paleozoic fauna was dramatically different. This fauna provides clues to key questions ranging from the origin of wings to the evolution of cephalic structures such as mouthparts, male and female external genitalia, and modifications of postembryonic development including holometaboly. Studying Paleozoic fauna is critical to understanding the origin of innovations originating after the Permian–Triassic mass extinction.

2. Deep-divergence estimates suggest that the majority of contemporary insect orders originated in the Late Paleozoic, but do these reflect divergences between stem groups of each lineage, rather than the later appearance of the crown groups? Fossil evidence and the simple reality that divergences are speciation events indicate the former.

3. Larvae of Paleozoic Palaeodictyopterida, Panephemeroptera, and Odonatoptera had wings developing inside the cuticular sheath with a markedly enlarged outer margin, characteristic of the wing pads of other hemimetabolous insects.

4. Evidence is lacking for a gradual straightening of wing pads during postembryonic development in Palaeodictyopterida.

5. Evidence from Paleozoic insects for multiple subimaginal stages in Panephemeroptera, Palaeodictyopterida, and Neoptera prior to the imago is tenuous.

6. The current evidence for the insect groundplan, morphology of different body parts, and postembryonic development from Paleozoic fossils is not as unusual, relative to modern insects, as was suggested by earlier researchers, and instead largely matches with neontology. The Paleozoic was certainly unique in many ways, but it was perhaps not that fundamentally different from the modern era after all.

## FUTURE ISSUES

1. Careful evaluation of morphological traits of larvae and adults of Paleozoic insects using various microscopic and imaging techniques in comparison to close relatives from the Mesozoic and Cenozoic is essential.

2. Application of new techniques on well-preserved historical material, such as micro-computed tomography for 3D visualization to reveal otherwise hidden structures and

environmental scanning electron microscopy to reveal integumental details, should be more widely used.

3. Reconstructions of crucial insect body parts of Paleozoic insects, such as mouthparts, wing venation and axillae, and external genitalia, and exploration of their morphology in relation to their function, are needed, as these body parts represent the sole evidence from the deep past.

4. Exploration of accessible terrestrial deposits in Roemer's Gap [Late Devonian to Early Carboniferous (Mississippian)], as well as the search for the early stem hexapods in the Late Silurian, has the potential for new and revolutionary discoveries.

5. Can Paleozoic resins be found in greater quantities and with either whole, albeit minute, insects or fragments of larger insects, such that these insects can be studied with life-like fidelity?

## DISCLOSURE STATEMENT

## ACKNOWLEDGMENTS

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