
1.3.9 Rise and Diversification of Insects

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Introduction

Insects are the most speciose group of macroscopic organisms ever to inhabit the planet. They are the major player in generating associations with microorganisms, fungi, and especially vascular plants; collectively these interacting groups contribute overwhelmingly to the bulk of community structure in land and freshwater ecosystems. The ecological dominance of insects also extends to estimates of biomass, abundance of individuals, and complexity of trophic webs, a condition probably present since the late Palaeozoic when global diversity estimates, as well as site-specific tabulations, indicate that insects were taxonomically the dominant terrestrial group (Labandeira and Sepkoski 1993), at least in lowland vegetated environments.

Origin and earliest fossil records of hexapods

The sparse fossil record of mid-Palaeozoic hexapods, the pattern of colonization of land by Palaeozoic plant and arthropod groups, and temporal constraints on hexapod origins imposed by hypotheses of arthropod phylogeny on hexapod origins all suggest that the earliest hexapods probably appeared during the Late Silurian. Although often used as a synonym for 'Insecta', the term 'Hexapoda' designates the more inclusive clade that consists of the Collembola (springtails) and Protura (proturans), collectively termed the Parainsecta, as well as its sister-group, the Insecta, which encompasses all other hexapods.

Early hexapod phylogeny

Phylogenetic evidence for the derivation of hexapods from another arthropod clade is still in an exploratory phase. Currently there are five major hypotheses of the origin of the Hexapoda (Fig. 1.3.9.1), but each is sufficiently unstable that differences in methodological approach, changes in included taxa or characters, and consideration of the fossil record can result in significant topological shifts within cladograms. This field is rapidly changing, and evidence linking the genetics and developmental biology of major arthropod clades is being used to test major phylogenetic schemes.

One of the oldest views of arthropod phylogeny is diphyly, with two superclades: the Schizoramia, consist-

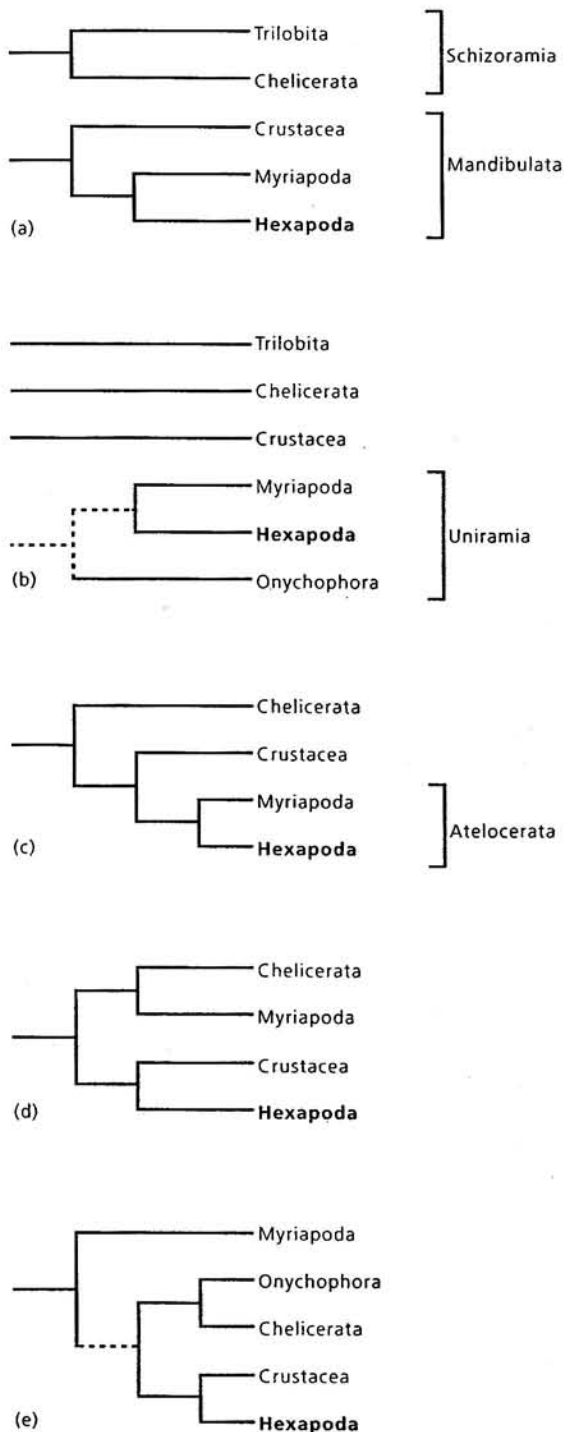


Fig. 1.3.9.1 Summaries of five hypotheses indicating the relationships of hexapods (in **bold**) to other major arthropod groups. (a) The hypothesis of arthropod diphyly, with Schizoramia and Mandibulata as distinct clades. (b) The hypothesis of extensive arthropod polyphyly, showing the traditional Uniramia as a distinct clade. (c) The hypothesis of arthropod monophyly, featuring the Mandibulata and its subgroup, the Atelocerata, as distinct clades. (d) One hypothesis of arthropod monophyly and a Crustacea + Hexapoda clade. (e) Another hypothesis of arthropod monophyly and a Crustacea + Hexapoda clade, with Onychophora included as arthropods. Branch lengths are arbitrary; dashed lines indicate nodes that are either theoretically inferred or not statistically valid. This is not an exhaustive list; see Fortey and Thomas (1997) for additional details.

Hexapoda + Myriapoda (Fig. 1.3.9.1b). Since her thesis was presented, arthropod polyphyly and the concept of the 'Uniramia' has largely been abandoned. Variations of two other major hypotheses receive most support from recent biomolecular and morphological studies. The first is the mandibulate/atelocerate hypothesis, consisting of a Crustacea and Hexapoda + Myriapoda clade that is a sister group to the Chelicerata, with or without inclusion of the Trilobita (Fig. 1.3.9.1c). The second, most recent, hypothesis posits a monophyletic Crustacea + Hexapoda clade that is a sister-group to other major arthropod clades, namely the Chelicerata + Myriapoda (Fig. 1.3.9.1d) or the Chelicerata + Onychophora with Myriapoda occurring as a basalmost clade (Fig. 1.3.9.1e). (See contributions in Fortey and Thomas (1997) for differing perspectives regarding the position of the Hexapoda within the Arthropoda.)

Within the Hexapoda, the position of the Parainsecta has always been controversial, particularly as the unique entognathous mouthparts and head sensory organs of the Collembola + Protura have frequently been cited as distinct from the Insecta. There is limited evidence that the Parainsecta may be separately derived from branchiopod crustaceans, a result that may explain why internal analyses of hexapods frequently result in an unresolved trichotomy involving the Parainsecta, the Diplura (which has variously been considered as parainsectan or insectan), and the Insecta. Nevertheless, the Insecta is generally regarded as monophyletic, and is united by several secure apomorphies. The most important evolutionary developments within the Insecta (Kukalová-Peck 1991; Fig. 1.3.9.2) were: (1) the transformation of the monocondylous mandible of the Archaeognatha into a robust mandible articulating with the head capsule by two condyles (Dicondylia); (2) the acquisition of wings (Pterygota); (3) the origin of holometabolous development (Holometabola), in which a larval stage became separated from its morpho-

ing of Chelicerata + Trilobita; and its sister-group, the Mandibulata, comprising the Crustacea and Hexapoda + Myriapoda (Fig. 1.3.9.1a). By contrast, Sydney Manton did not recognize these relationships, arguing instead for separate origins of the Trilobita, Crustacea, Chelicerata, and a Uniramia clade defined as Onychophora and

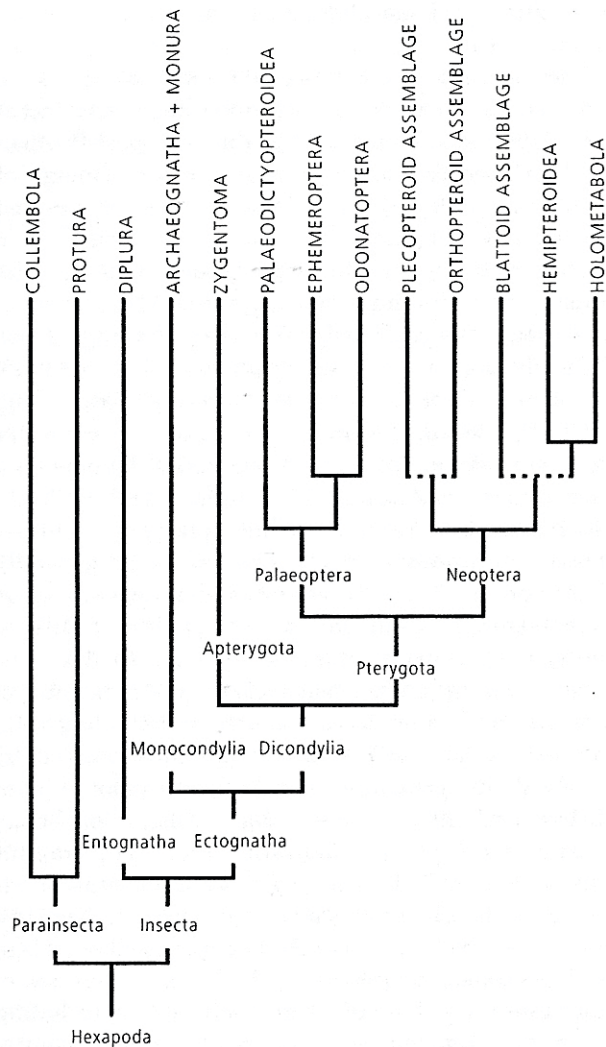


Fig. 1.3.9.2 Phylogeny of the major groups of hexapods, proposed by Kukalová-Peck (1991). Dashed lines indicate less secure relationships.

gically and ecologically distinct adult stage by a resting and non-feeding stage called the pupa; and (4) the invention of eusociality.

Devonian hexapods

The earliest known hexapod is the springtail *Rhyniella* from the Rhynie chert of Scotland, of Early Devonian age, which occurs within a biota that includes primitive vascular plants and other arthropods, such as trigonotarbids, spiders, mites, crustaceans, and myriapods (see Section 3.4.5). The earliest fossil insects are bristletails, known from a somewhat younger Early Devonian deposit from the Gaspé region of Quebec, Canada, and from the Middle Devonian of Gilboa, New York State. These earliest hexapod occurrences are unimpressive in

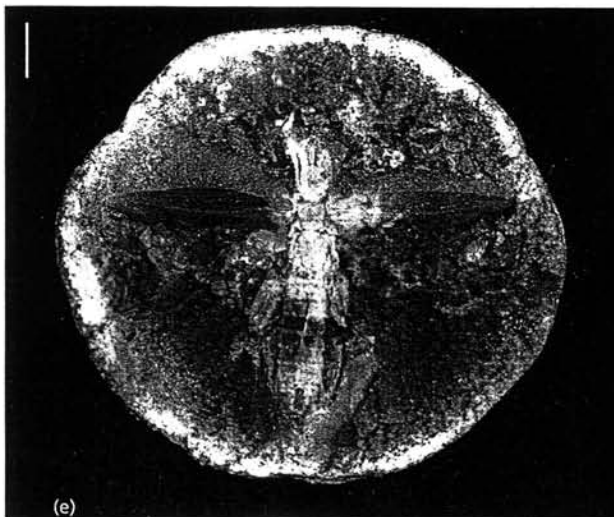
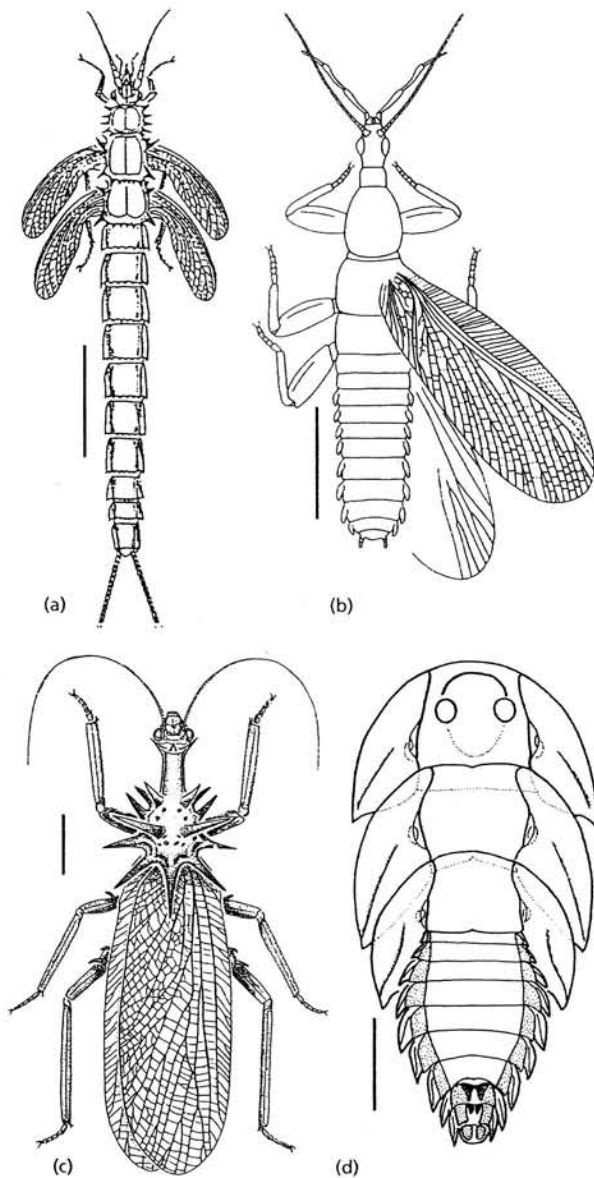
diversity and abundance, presenting more questions than answers (Shear and Kukalová-Peck 1990). Hexapods are absent as fossils during a 55 million year interval from the Middle Devonian to the latest Early Carboniferous, during which time the major features of winged insects (Pterygota) must have evolved, based on the spectacular diversity of approximately 10 pterygote insect orders that appear suddenly at an interval straddling the Early to Late Carboniferous boundary (Brauckmann *et al.* 1995).

Insects in late Palaeozoic environments

During the early Late Carboniferous there was a dramatic appearance of diverse insect faunas at several major localities across equatorial Euramerica. A few middle Late Carboniferous to Early Permian localities yield faunas that are sufficiently diverse, abundant, and well preserved to have attracted considerable attention from palaeoentomologists. Two of the more notable insect fossil localities are in Illinois, USA. The first, Mazon Creek, is a celebrated body-fossil site in the north-central part of the state, of middle Late Carboniferous age. The second is the Calhoun Coal, a later Late Carboniferous trace-fossil deposit in the east-central region that provides a rare window into the associations of coal-swamp plants and their insects.

Late Carboniferous insects from an equatorial lowland

A relatively abundant assemblage of insects from Mazon Creek has been known for over 120 years (Carpenter 1997), consisting of approximately 175 known species, allocated to 38 families and 15 orders. This assemblage provides the earliest, well-documented glimpse of Palaeozoic insect life—inhabiting an emergent, equatorial landscape on a clastic delta that prograded south-westerly into a shallow epeiric sea. Insects from this deposit also originated from the ‘uplands’ surrounding this deltaic sedimentary wedge. Mazon Creek insects are preserved as moulds within flattened ovoidal concretions that are composed dominantly of siderite matrix, although the mineralized surfaces coating the entombed insects contain calcite, sphalerite, pyrite, kaolinite, and reduced iron oxides (Fig. 1.3.9.3e). These minerals were presumably formed in an anaerobic aquatic environment as insect carcasses were degraded by saprobic organisms that produced alkaline by-products resulting in early diagenetic mineralization. When carefully prepared, Mazon Creek insect fossils reveal considerable anatomical structure, such as minute venules and dark/light membrane patterns on wings. Other, typically preserved, features include sutures separating external body sclerites, cuticular ornamentation, spination, and the presence of delicate appendages such as



ovipositors, genitalia, abdominal exites, maxillary palpi, and antennae.

The major insect taxa recovered from Mazon Creek are typical of the Palaeozoic Insect Fauna, and are distinct at the highest taxonomic levels from the post-Permian Modern Insect Fauna, which consists overwhelmingly of familiar hemipteroid and holometabolous lineages that occur today. The fauna at Mazon Creek consists of the apterygote lineages Diplura (telsontails), Archaeognatha (bristletails), Monura, and Zygentoma (silverfish), as well as the pterygote lineages Protodonata (dragonflies), Palaeodictyoptera, Megasecoptera (Fig. 1.3.9.3a), Diaphanopteroidea, Blattodea (cockroaches) (Fig. 1.3.9.3d), 'Protorthoptera' (Fig. 1.3.9.3b,c), Orthoptera (grasshopper-like insects), Caloneuroidea, Hypoperlida (ancestral hemipteroids), Miomoptera, and probably Holometabola. Presumably the apterygote clades—those taxa primitively lacking wings—were generally detritivorous (Archaeognatha, Monura, Zygentoma) or probably predatory on other insects (Diplura). Clades of Pterygota that were primitively unable to flex their wings over their abdomen were large to gigantic in size, and were either top aerial predators (Protodonata) or had stylate mouthparts (Palaeodictyopteroidea) involved in piercing-and-sucking of plant tissues (Labandeira 1997). Mandibulate orthopteroid taxa, mostly the polyphyletic and varied 'Protorthoptera', but also oedischiid Orthoptera, may have been either detritivores or herbivorous consumers of plant foliage. By contrast, early members of the hemipteroid assemblage (Caloneuroidea, Hypoperlida) bore mouthpart structures presaging those of Permian Hemiptera, including styliform mouthpart elements and a domed clypeal pump indicating imbibation of plant fluids or small particles such as spores. The enigmatic Miomoptera are considered holometabolous by some, although there is stronger evidence for the presence of early Holometabola with the recent discovery of a caterpillar-like larva (Kukalová-Peck 1991). If this assignment is true—and there is additional evidence for the presence of Holometabola from plant damage in a slightly

Fig. 1.3.9.3 A representative sample of Mazon Creek insects, from the middle Late Carboniferous of Illinois, USA. (a) Nymph of *Mischoptera douglassi* (Megasecoptera: Mischopteridae). (b) Adult of *Eucaenus ovalis* ('Protorthoptera': Eucaenidae). (c) Adult of *Gerarus danielsi* ('Protorthoptera': Geraridae). (d) Undetermined cockroach nymph, ventral view. (e) Siderite concretion of an unnamed eucaenid protorthopteran. Scale bars = 1 cm. (b, From Carpenter 1997, reproduced with permission of Northeastern Illinois University Press; a,c,d, from Kukalová-Peck 1991, reproduced with permission of Cornell University Press.)

younger Late Carboniferous deposit (Labandeira 1998)—then this diverse assemblage embodies three major evolutionary events that characterized the history of the Insecta (see above), with the exception of the origin of eusociality during the Early Cretaceous.

A Late Carboniferous community of insects on a tree fern

Virtually all understanding of Palaeozoic insects is based on their external morphologies and intragroup and intergroup taxonomic relationships. The ecological associations of Palaeozoic insects with other organisms, and their trophic roles in terrestrial ecosystems, are a more recent focus of research. The best-studied deposit for assessing Palaeozoic insect palaeoecology is the Calhoun Coal of the Mattoon Formation. Within this coal unit there are permineralized nodular structures that preserve swamp plants in exceptional anatomical detail, including cellular detail of tissues and the histological structure of organs, principally from the marattialean tree fern *Psaronius* and the seed fern *Medullosa*. Tissue damage patterns in these two arborescent plants provide a clear picture of how insect herbivores and detritivores trophically partitioned plant organs and reveal the spectrum of insect functional feeding groups that was present during the Late Carboniferous (Labandeira 1998).

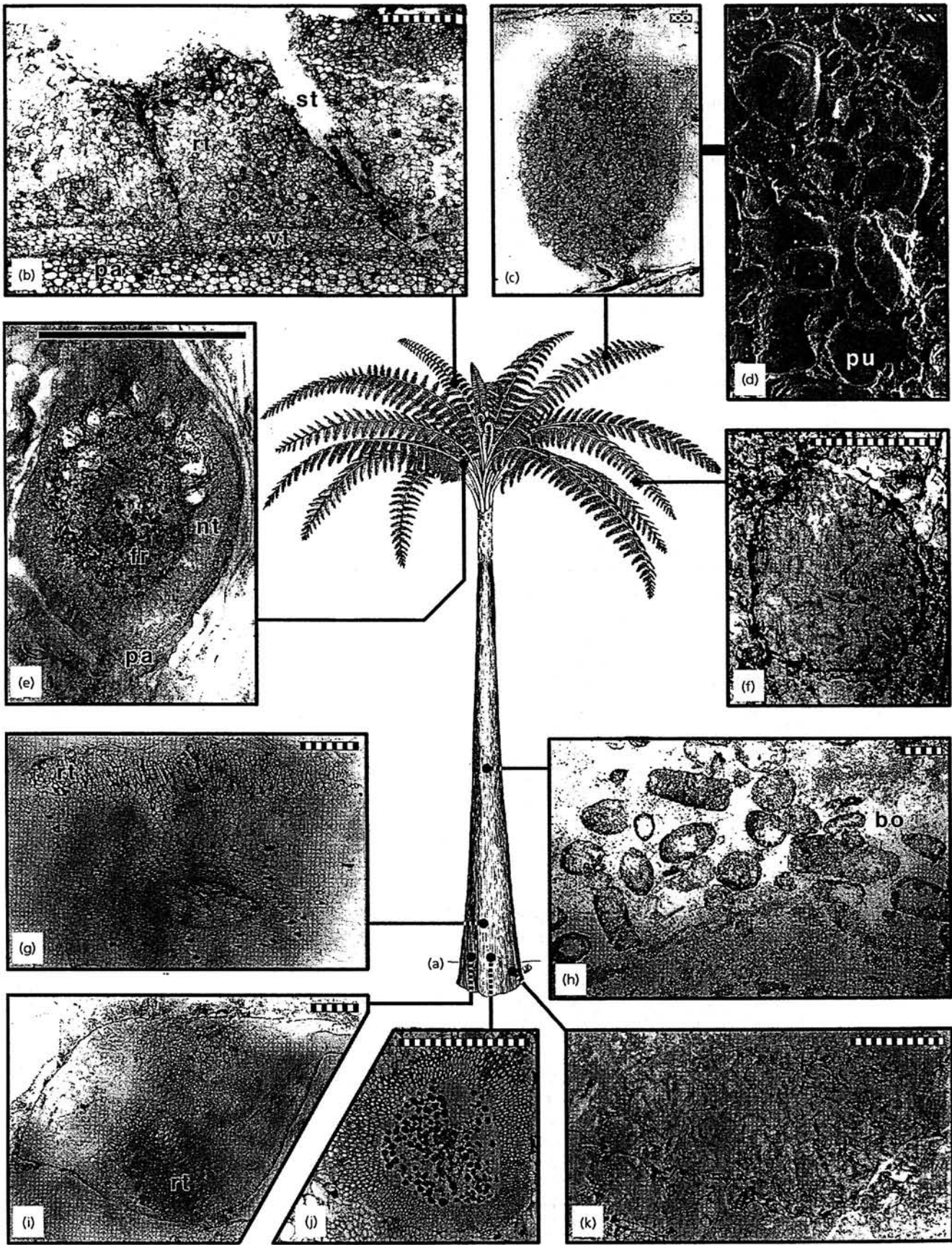
At least seven distinctive insect functional feeding groups have been documented for *Psaronius* (Fig. 1.3.9.4a), collectively representing a community of consumers trophically dependent on a plant host, each using a stereotyped mode of feeding to target a particular tissue (Labandeira 1998). Mandibulate insects representing canopy herbivores fed externally on most foliar tissues (Fig. 1.3.9.4f); other mandibulate insects tapped sporangia collectively or spores individually for selective ingestion (Fig. 1.3.9.4c,d); a palaeodictyopteran insect with stylet mouthparts consumed xylem and phloem of petiolar vascular tissue by piercing and sucking (Fig. 1.3.9.4b); and a holometabolous larva encapsulated in petiolar inner parenchyma elicited a reciprocal host-plant response through galling (Fig. 1.3.9.4e). Evidence also indicates that this insect galler induced proliferation of a distinctive response tissue from *Psaronius* (Fig. 1.3.9.4e) and was targeting the basal frond petioles of only this species, indicating an intimate and host-specific association. Within the trunk and root system of *Psaronius*, three types of endophytic borers are known: an unknown herbivorous insect borer of parenchyma within exposed roots (Fig. 1.3.9.4i,k), and two detritivorous borers—a stem borer of soft parenchyma located between more indurated trunk tissues (ecologically analogous to certain modern cockroaches) (Fig. 1.3.9.4h), and a mite on the hard supportive tissue of the root mantle (Fig. 1.3.9.4j). Lastly there

was an external grazer on root epidermis (Fig. 1.3.9.4g). With the exception of leaf mining, the earliest occurrence of which is Middle Triassic, the coarse spectrum of herbivore and detritivore functional feeding groups in this Carboniferous community is remarkably complete and modern, although the post-Palaeozoic counterparts of these feeding types were occupied by entirely different taxa.

Post-Palaeozoic developments

During the Permian there was gradual supplementation of typical Late Carboniferous insect taxa by basal

Fig. 1.3.9.4 (Facing page) The community of insect herbivores and detritivores on their late Pennsylvanian (300 Ma) host plant, *Psaronius*, a tree fern that dominated peat-substrate swamp forests of the Illinois Basin. Members of the *Psaronius* component community are inferred from patterns of host-plant tissue damage and associated coprolite contents. All interactions are from insects, except (j) which is a mite. Most of these associations indicate feeding on live plant tissue (herbivory) and are confined to the canopy or exposed roots at ground level; however, interactions indicated by (h), (j), and probably (k) are examples of detritivory. (a) Reconstruction of *Psaronius chasei* Morgan, a marattialean tree fern approximately 10 m tall, from the Mattoon Formation (Calhoun Coal) of the Illinois Basin. (b) Stylet tracks in a frond-bearing petiole, showing that vascular tissue (xylem and phloem) was being targeted by a piercing-and-sucking palaeodictyopteran insect. (c) Insect coprolite occurring in peat litter, consisting almost entirely of *Punctatisporites* spores from a *Psaronius* source plant. (d) SEM enlargement of section in (c) showing crushed and relatively intact spores that have passed through an insect's gut. (e) Gall from a frond petiole, showing a tunnelled centre replaced by insect frass, surrounded by a zone of nutritive tissue proliferation and normal outer parenchyma; the galler is a holometabolous insect. (f) Another coprolite from peat litter, containing leaf cuticle and trichomes borne by *Psaronius* foliage. (g) Surface grazing on a ground-level root, characterized by files of abnormally produced cells of reaction tissue. (h) An insect boring of stem tissue within the central trunk, displaying consumption of softer parenchyma but avoidance of more indurated root mantle, sclerenchyma, and vascular strands (outer root mantle is toward the bottom; inner stem tissues are at the top). (i) A boring of a surface root, showing a chamber filled with coprolites, surrounded by tufts of reaction tissue. (j) An example of mite consumption of woody tissue along the outer root mantle, indicated by very small coprolites occurring in the lumen of a mantle root. (k) An elongate coprolite wedged in peat litter, showing a distinctive texture of collapsed root epidermis, indicating consumption of a ground-level root. Abbreviations: bo, stem boring; fr, insect-associated frass; nt, gall-produced nutritive tissue; pa, parenchyma; pu, *Punctatisporites* spores as gut contents; rt, reaction tissue; st, stylet trace piercing outer parenchyma tissue; vt, vascular tissue (xylem). Scale bars: solid = 1.0 cm; striped = 0.1 cm; dotted = 0.01 cm; backslashed = 0.001 m.



lineages of hemipteroid and holometabolous insects. Although Late Permian insect faunas are poorly known, it is clear that the terminal Permian extinction had a profound effect on the course of insect evolution by extirpating most of the major Palaeozoic lineages. Those that survived into the Triassic were preferentially enriched in hemipteroid and holometabolous taxa. The spectrum of insect taxa from Late Triassic faunas is fundamentally modern in composition, containing few Palaeozoic lineages (Labandeira and Sepkoski 1993; Anderson *et al.* 1998). Importantly, this Modern Insect Fauna represents a separate macroevolutionary radiation into the same ecological roles previously occupied by the Palaeozoic Insect Fauna (Labandeira 1997).

During the preangiospermous Mesozoic, freshwater habitats were invaded by several insect clades, particularly Diptera (flies) and Trichoptera (caddisflies). Meanwhile, the diversification of many seed-plant lineages on land, such as conifers, seed ferns, cycads, bennettitaleans, and ephedrales, resulted in a proliferation of associations with insects, including external feeders such as chrysomelid beetles, endophytic gallers, and leaf miners, in addition to pollination mutualisms such as those between cycads and weevils that persist today. The appearance of angiosperms during the Early Cretaceous offered new and diverse substrates for dietary partitioning (Labandeira 1997; Wilf *et al.* 2000), even though major feeding adaptations had occurred earlier on other seed-plant lineages. Later events of importance for insect evolution included the extensive diversification of placental mammals during the early Cenozoic, which offered new opportunities for colonization by endoparasitic and ectoparasitic insects, and the geographical spread of the grassland biome during the mid-Cenozoic, which induced specialization by numerous herbivorous insect lineages.

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