# INSECTS AND OTHER HEXAPODS

Hexapods are a distinctive group of six-legged arthropods that possess tracheae (branching tubes) as breathing organs and bodies that are subdivided into an identifiable head, thorax, and abdomen. They are differentiated from other arthropods by the presence on the head of a single pair of antennae, three pairs of externally visible, mouthpart appendages, a three-segmented thorax, an abdomen of 12 or fewer evident segments, and an elongate terminal filament originating from the last abdominal segment. Hexapods inhabit virtually all terrestrial and freshwater environments and have been the most species-rich and ecologically wide-ranging group of macroscopic life since the spread of Carboniferous forests. The origin and early evolution of hexapods is poorly understood, principally because of uncertain relationships to other major clades of arthropods, and a poorly documented Devonian and Early Carboniferous record shrouded by the absence of forms connecting ancestral marine and subsequent terrestrial lineages. Traditionally thought to be closely related to myriapods such as centipedes and millipedes (Snodgrass 1935; Boudreaux 1987), recent biomolecular studies indicate that hexapods are derived from an unspecified lineage of crustaceans (Wägele 1993). This proposed placement reestablishes an older view of a close Crustacea + Hexapoda relationship and the erection of a broader clade, the Mandibulata, perhaps with inclusion of the Myriapoda as an early evolutionary lineage. Fossil evidence indicates that myriapods are an older mandibulate group whose similarities to hexapods may have arisen in parallel by convergent evolution resulting from the similar functional demands of a land existence. Nevertheless, the issue of hexapod origins remains unsettled; several basic features of the head are shared by myriapods and hexapods, providing evidence for descent from a non-crustacean ancestor.

## Hexapod Structure

Hexapods primitively consist of probably 21 or 22 segments. These segments are organized during early development into three body regions, or tagmata: the head, responsible for sensory perception of the environment and procurement and ingestion of food; the thorax, bearing the organs of locomotion; and the abdomen, housing the reproductive organs and much of the digestive tract (Figure 1). These regions have been externally altered in diverse ways, principally by embryonic rearrangement of the fundamental exoskeletal elements, the sclerites, into a shifted, secondary segmentation (Gillott 1995). Because hexapod internal anatomy is rarely preserved as fossils, this discussion will emphasize external structure.

### Head

The hexapod head is a sclerotized, or stiffened, spheroidal capsule whose anatomically ventral aspect houses the mouthparts (Figure 2). The head capsule typically has an internal skeleton, the tentorium, possessing rigid processes that attach to numerous muscles involved in movement of mouthparts and other structures. These tentorial processes originate on the head capsule at important anatomic landmarks—the anterior and posterior tentorial pits. In a generalized mandibulate (chewing) insect such as the grasshopper, compound eyes occur dorsolaterally on the top and to the side of the head, and three ocelli face anteriorly and frontally, two between the compound eyes and a median ocellus located on an anterior triangular sclerite, the frons. The single pair of segmented sensory antennae are inserted typically below the ocelli, adjacent to the compound eyes. The area between the compound eye and the mouthparts is the gena. The head capsule is often divided by posterior, dorsal, and frontal sutures, which are lines of juncture between sclerites. The
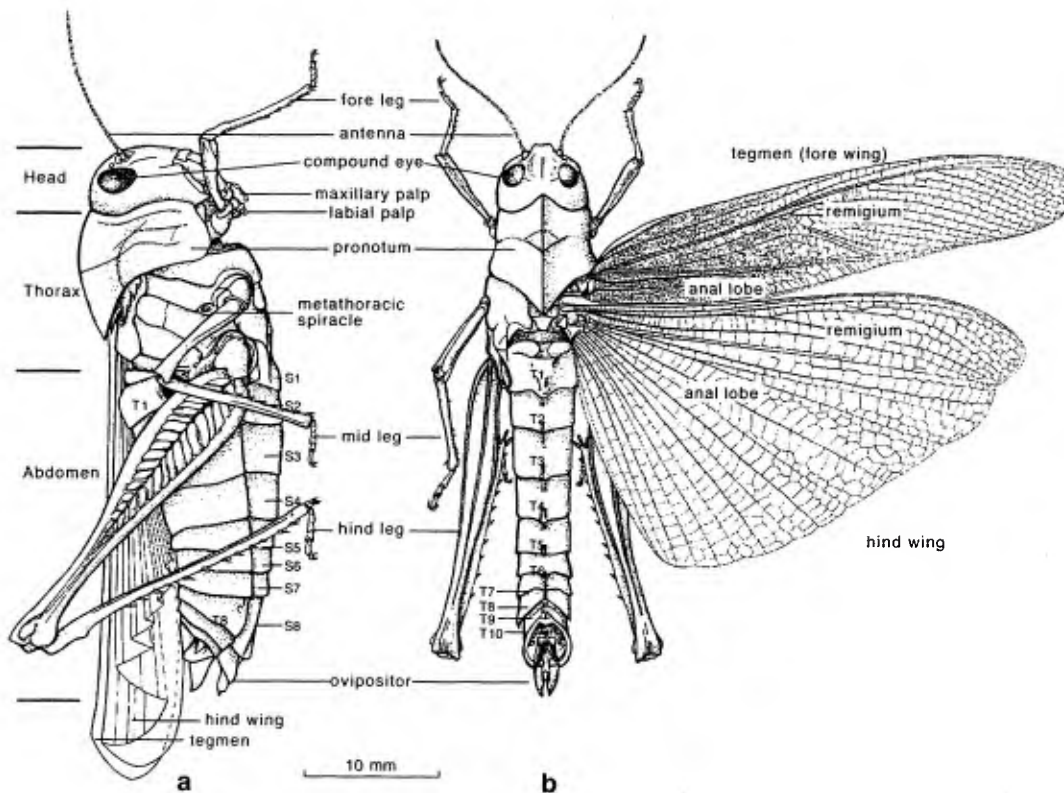
**Figure 1.** Major structural divisions and landmarks of a generalized female insect, the common locust. Key: S, sternum; T, tergum, Modified from Lawrence et al. (1991). Copyright © Commonwealth Scientific and Industrial Research Organization 1991. Used by permission of the American Publisher, Cornell University Press.

medial epicranial suture, which splits during molting, may bifurcate anteriorly and terminate at the transverse clypeal suture. The grasshopper has mouthparts that are ventrally attached, whereas insects such as cicadas have mouthparts angulated posteriorly; other insects such as ground beetles have mouthparts that are forwardly directed.

Hexapods have five major mouthpart regions, the posterior three of which correspond to primitive segment divisions (Snodgrass 1935). The anterior-most labrum, or "upper lip" (Figure 2a), is a medially located, movable, and enclosing flap that bears gustatory (taste) and other sensory receptors on its inner surface, the epipharynx. The hypopharynx (Figure 2d) is a typically fleshy, medially positioned (mesal) lobe that divides the preoral cavity into a dorsal mouth and a ventral salivarium; it usually bears a complement of sclerites in primitive lineages. The mandibles are paired, generally triangular, and highly sclerotized jaws that generally contact the clypeus anteriorly by an articulatory hinge, and the gena posteriorly by an exoskeletal process (condyle) and associated head cavity (Figure 2b, d). Posterior and ventral to the mandibles are the paired maxillae that consist of medial and lateral elements (Figure 2b, c). A basal sclerite attaches each maxilla to a head cavity, whereas a longer, distal segment bears all the appendages. These include a mesal, often spinose (spiny) or toothed lobe, the lacinia, and a generally fleshy lateral galea, in addition to a one- to seven-segmented palp. The labium, or "lower lip," is a medial structure representing fusion of two maxilla-like structures membranously connected to the posterior and ventral margin of

the head capsule. This structure is divided into proximal and a distal sclerites, the latter which supports two pairs of lobes—mesal glossae and lateral paraglossae—and a pair of lateral, one- to four-segmented palps.

Mouthparts are modified into major, diverse, multielement organs used for consuming fluid and particulate food (Snodgrass 1935). Piercing-and-sucking mouthparts are formed by transformation of various combinations of mandibles, maxillary laciniae, hypopharynx, and other mouthpart elements into stylets, often housed in a closed sheath or an open channel. Feeding on surface fluids is accomplished by modification of mouthparts into various mechanisms such as a siphon formed by conjoined galeae, or a sponging organ resulting from expansion of the labium into a fleshy structure. Relatively minor modifications of individual mouthpart elements can result in pronounced mouthpart asymmetry, co-optation of adjacent regions such as the labium and hypopharynx in the formation of silk-producing spinneret organs in certain larvae such as caterpillars, and transformation of mandibles and maxillary lobes into rakes and brushes as filtering or sieving devices for consumption of water-suspended detritus.

### Thorax

The thorax consists of three segments: an anterior prothorax, middle mesothorax, and posterior metathorax. Each thoracic segment is divided into a dorsal tergum, two lateral pleura, and a ventral
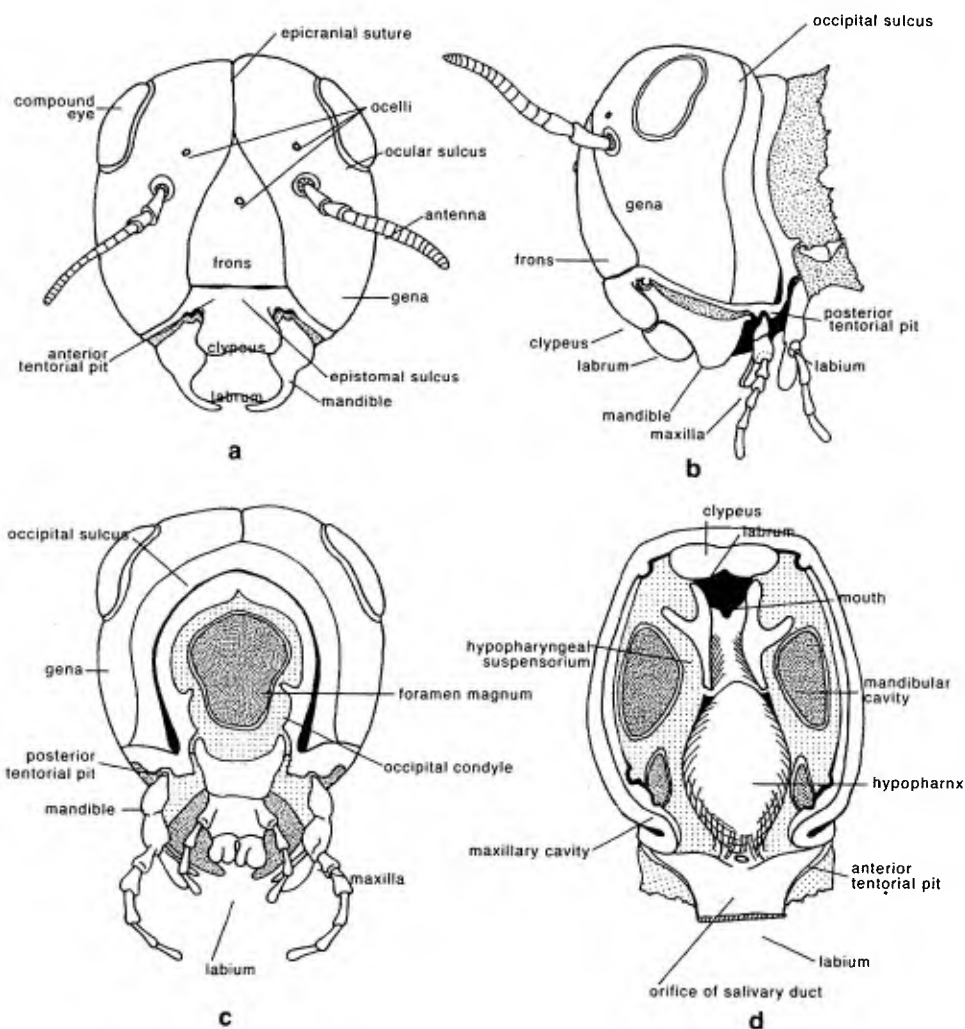
**Figure 2.** Head and mouthpart structures of a generalized pterygotan insect. *a*, anterior; *b*, lateral; *c*, posterior; *d*, ventral. Modified from Gillott (1995).

sternum, which respectively bear tergites, pleurites, and sternites. These sclerites are arranged in a complex series of exoskeletal plates of varying sizes and shapes, connected by intersegmental membranes (Figure 1). In winged insects thoracic segments are structured to meet the biomechanical forces induced by wings, and the segments can accommodate a significant volume of flight muscle. The anchoring and movement of legs also determine sclerite size, shape, and robustness. Although the archetypal hexapodan leg is used for walking or climbing, specializations include jumping, swimming, and impaling prey. The number of fundamental segments in the hexapod leg is debated, but it is likely that Paleozoic insects bore additional free segments that later became fused in more modern formal taxonomic groups, or taxa (Kukalová-Peck 1991). Modern taxa have, from proximal to distal, the following segments: a coxa, the functional leg base articulating with the thoracic pleurite; a trochanter that is often rigidly attached to the

femur; a femur that is the most conspicuous part of the leg; a generally elongate tibia; a slender tarsus, which is subdivided into a musculated basitarsus and two to four nonmusculated subsegments known as the eutarsus, and the pretarsus, which in most forms bears one to three lobes and a pair of lateral claws.

Apterygote hexapods are defined as primitively lacking wings, whereas modern pterygotes bear two pairs of lateral wings that articulate to the meso- and metathoracic segments by a complex system of articular sclerites (Gillott 1995). The prothoracic segment of some Paleozoic insects bore movable, lateral lobes with veins that indicate a parallel developmental path (serial homology) with functional wings. In other insects the prothorax elongated as a feeding specialization, or became spinose to deter predation. Both pairs of wings are primitively similar in general form and construction, and they are fluted into a system of alternating convex and concave veins to impart structural rigidity to the wing

membrane. Often there is a distinctive, often pigmented spot, the pterostigma, on the distal end of the anterior margin of both wing pairs. In many lineages the anterior pair became modified into leathery or rigid wing covers such as tegmina in grasshoppers or the elytra of beetles, whereas the hind wing remained membranous, stored in a pleatlike fashion over the abdomen by a system of wing folds (Figure 3). Some insects, such as true flies (Diptera) and adult male scale insects, have modified one of the pairs of metathoracic wings into small, spoon-shaped balance organs, or halteres. Similar structures, arising through the modification of wing covers, occur on the mesothorax of adult male twisted-wing parasites (Strepsiptera). Some parasitic insect groups have lost all external evidence of wings, such as the Phthiraptera (lice) and Siphonaptera (fleas).

The primitive insect wing is a double-walled membrane supported by a network of radiating, bifurcating veins that commonly connect by short crossveins that define enclosed areas called cells (Figure 3). From the anterior to the posterior wing margin, the principal veins and their abbreviations are the following, with raised convex veins designated as (+) and depressed concave veins as (–): costa, C (+); subcosta, Sc (–); radius, R (+); media, M (–); cubitus, Cu (–); first anal, 1A (+); second anal, 2A (– or +); third anal, 3A (+) (nomenclature after Kukalová-Peck 1991). Each of these veins, with the exception of the costa, bifurcate once to several times and support increasing surface area toward the distal wing membrane. In the case of plecopteroid and orthopteroid insects, the hind wing anal veins are arranged into an anal fan that is distinguished from the wing proper (remigium) by a characteristic claval fold; for blattoid, hemipteroid, and holometabolous insects, the anal lobe starts with the anal fold. The nomenclature of these veinal branches has been standardized, although there are difficulties in applying these names homologously across some insect orders. A few important primary branches are the anterior branch of the radius, designated as RA, and the posterior branch, designated as RP (also known as the radial sector); the anterior media, MA, and the posterior media, MP; and the anterior and posterior branches of the cubitus, which are CuA and CuP, respectively (Figure 3). Modification of this fundamental venation has occurred principally by reduction of veins, especially in hemipteroid and holometabolous lineages. In forms possessing generalized venation, especially primitive palaeodictyopteroids, orthopteroids, and blattoids, a characteristic archedictyon occurs between major veins, consisting of an intricate meshwork of venules. Derived from a few selected veins of this archedictyon are major crossveins (Figure 3), which are diagnostic features, particularly among holometabolous insects. Primitively the fore- and hind wing pairs moved independently, although in derived lineages there were parallel tendencies to couple adjacent fore- and hind wings for synchronized motion during flight (Brodsky 1994). Various wing-coupling devices included mutual overlap of interdigitating lobes and interconnecting bristles or hooks.

## Abdomen

Evidence from developmental genetics indicates that the hexapod abdomen primitively consists of 12 segments (Raff 1996). Unlike
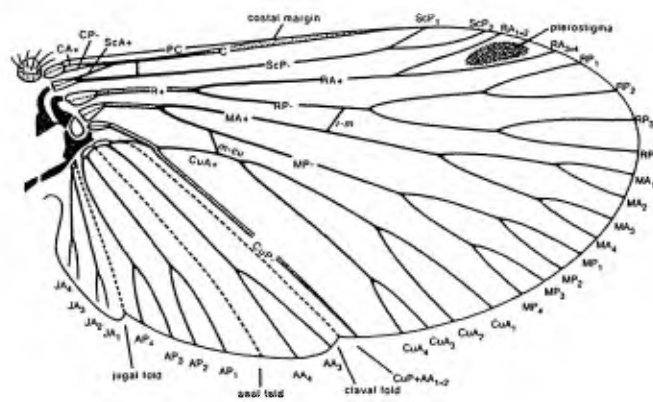


**Figure 3.** Nomenclature of wing venation in a hypothetical generalized insect. Crossveins: *r-m*, radio-medial; *m-cu*, medio-cubitus; see text for key to other abbreviations. From Lawrence et al. (1991). Copyright © Commonwealth Scientific and Industrial Research Organization 1991. Used by permission of the American Publisher, Cornell University Press.

the thorax, which has been extensively remodeled to accommodate the demands of locomotion, the abdomen consists of series of segments with relatively simple, mostly undivided terga and sterna. The anatomically dorsal terga are connected to anatomically ventral sterna either by a rigid pleuron or by a pleural membrane. Major changes have occurred anteriorly, where the first abdominal segment has been reduced or incorporated with the metathorax in some insects, and in the eighth to tenth segments, which have been significantly modified for appendicular genitalia. The 11th segment almost always occurs in the embryonic stage, and its appendages are externally evident as the cerci of many basal insect groups, transformed into forceps in diplurans and earwigs. Primitive insects bear abdominal appendages known as styli, which are developmentally equivalent, or homologous, to walking limbs (Raff 1996). Additional evidence from studies of early insect development (Raff 1996) indicate that appendages positioned above the styli, such as gills in mayfly naiads and prolegs of some holometabolous caterpillars, are homologous to wings.

There is considerable confusion regarding homologies of external hexapod genitalia across the taxonomic orders. However, a generalized description of basic structures is useful for male genitalia and the female ovipositor. The male genitalia originate from the ninth segment, are highly variable structurally, and frequently are comprised of a pair of claspers, originating from modified styles to grasp the female during copulation, and a median intromittent organ. The claspers are well developed on modern mayflies, although Paleozoic mayflies displayed more generalized and larger structures. The intromittent organ consists of a penis, sometimes paired as hemipenes, and lateral structures variously termed parameres or gonapophyses. In the female the leg appendages of the eighth and ninth segments provide the first (ventral) and second (dorsal) valves of a compound organ, the ovipositor (Figure 4), which deposits eggs through an egg canal on or into various substrates. A third valve or sheath occurs in many insects as a posterior process originating from the gono-

coxite of the ninth segment (Gullan and Cranston 1994). The ovipositor can range from a barely protruding stub to an impressively long organ that is used to insert eggs into substrates as diverse as soil, wood, plant tissues, or other animals such as insects and vertebrates. In paleodictyopteroids, grasshoppers, and sawflies, ovipositor valve cuticle is often modified into sawtooth structures and is primarily involved in piercing fleshy plant tissues. In some ichneumonid wasps a terminal "drill" bores through wood for oviposition in wood-boring larvae. Departures from typical egg-laying include formation of egg cases known as oöthecae in cockroaches and mantids, egg retention and live birth in aphids and some parasitic flies, and indiscriminate ejection by walkingsticks.

## Characterization and Fossil History of Major Hexapod Groups

Recently, anatomic and morphologic features have been used to differentiate the most basal (primitive) lineages from "typical" insects (Figure 5). With this fundamental distinction, the term "Hexapoda" is now used to characterize all terrestrial arthropods with three independent tagmata and three walking legs. The Hexapoda, in turn, are formally subdivided by some into the Parainsecta and Insecta (Figure 5). (In the following discussion, Table 1 lists the geochronological duration of major insect clades.)

### Parainsecta

The Parainsecta are defined by several major features, principally entognathy, or an overgrowth of the lateral head wall to form an oral cavity that surrounds often attenuated mouthparts. Degenerate to absent compound eyes and unpaired pretarsal claws are also diagnostic features. The Parainsecta consists of two taxa: the Collembola (springtails), which have a fossil record extending to the Early Devonian; and the rarely encountered Protura (proturans), lacking a fossil record. The Insecta comprise all other hexapods and are characterized by a transverse bar in the posterior part of tentorium, leg-articulating coxae that do not include the sternum, and an ovipositor formed by limb-base endites on segments eight and nine. Although the position of the Diplura was previously unresolved (Kristensen 1991), several lines of evidence indicate that they are true insects (Kukalová-Peck 1987; Raff 1996).

### Archaeognatha and Zygentoma

Within the Insecta, the primary subdivision is between the Archaeognatha (bristletails) and all other insects. Archaeognatha possess the derived characteristics of medially abutting compound eyes and the absence of spiracles on the first thoracic segment. They are the only true insect clade that primitively bear mandibles that articulate with the head capsule by a single condyle. The fossil Monura are now known to be a Late Paleozoic subgroup of the Archaeognatha. The more-derived Zygentoma by contrast evolved mandibles with a secondary, anterior condyle (Kukalová-Peck 1991) and thus define the insect clade Dicondylia. Fossil archaeognathans first appear during the Early Devonian, whereas
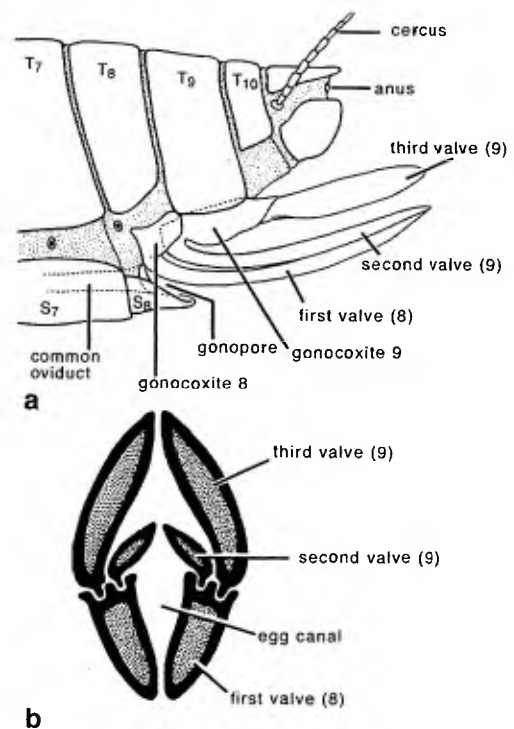


**Figure 4.** Terminal aspect of a female insect abdomen and associated ovipositor. a, Lateral view of a generalized orthopteroid ovipositor; b, Transverse section of a katydid (Orthoptera) ovipositor. Parenthetical insertions refer to segment number origin. Key: S, sternum; T, tergum. From Gullan and Cranston (1994).

zygentomans are known from the Late Carboniferous; both have a sporadic fossil record to the Recent.

### Pterygota

Within the Dicondylia, the vast clade Pterygota, or winged insects, is defined primarily by the presence of two pairs of wings on the second (mesothoracic) and third (metathoracic) segments and by a remodeled thorax associated with flight. The Pterygota also is characterized by fusion of major elements of the head endoskeleton and by suppression of eversible sacs, which are small and ventral abdominal structures that presumably absorb water. The Pterygota consists of two major clades, the Neoptera and probably the Palaeoptera. Fossils of these taxa first appear at the Early to Late Carboniferous boundary and are represented by ten orders of insects. This suggests that the Pterygota had an appreciably earlier origin.

*PALAEOPTERA.* With one Paleozoic exception, the Palaeoptera is characterized by wings that are held outstretched from the body, incapable of being folded over the abdomen. Additionally the Paleoptera bear homonomous wings, in which fore- and hind wings appear similar and have identical wing venation. The Palaeoptera is comprised of the extant Ephemeroptera (mayflies) and Odonatoptera (dragonflies), and the Paleozoic Palaeodicty-
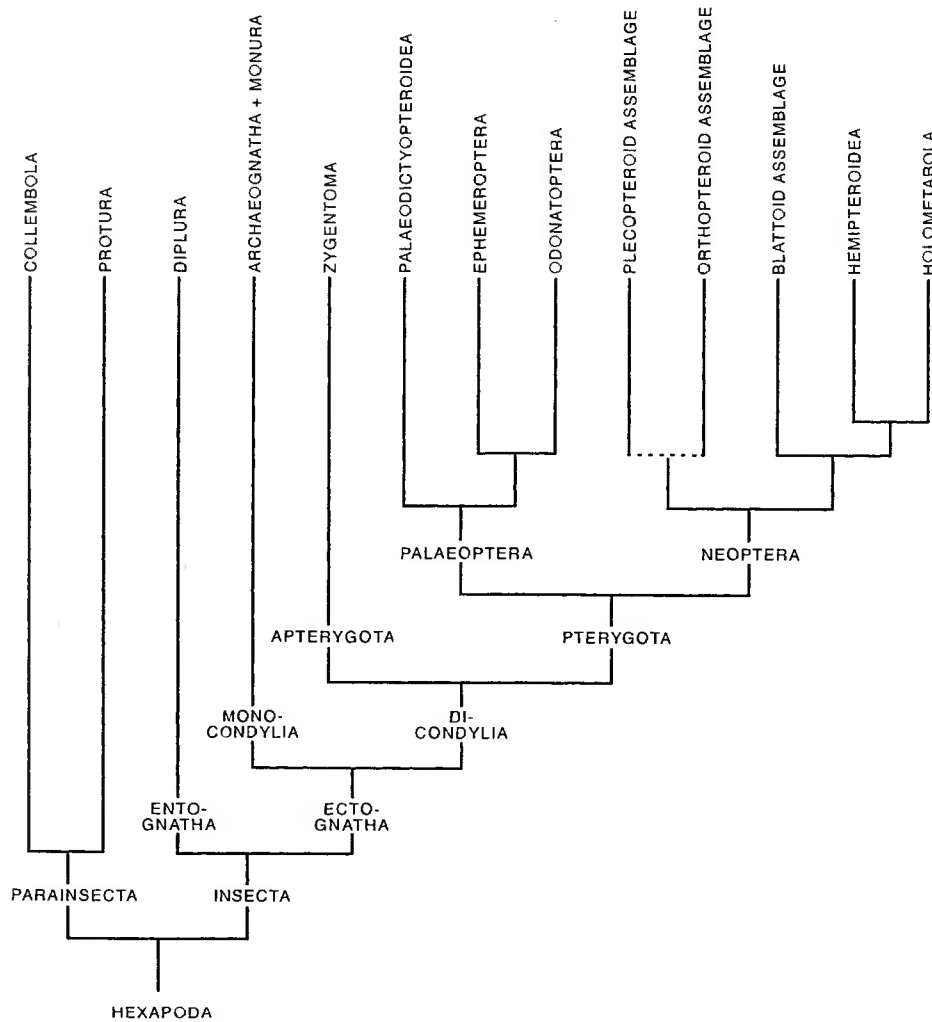
**Figure 5.** Phylogeny of major groups of hexapods, as proposed by Kukalová-Peck (1991). Symbols: *dashed lines,* less assured relationships.

opteroidea. The Palaeoptera is considered by many as a monophyletic group, in which all lineages originate from a common ancestor. For modern taxa, features, particularly wing venation and articulation structures, convincingly indicate that the Odonatoptera + Ephemeroptera jointly have a sister-group relationship with the Neoptera. Other features, such as loss of certain muscles in the thorax and absence of the molt in the fully winged stage, have been used to suggest that the Odonata alone may bear a sister-group relationship with the remaining Neoptera (Kristensen 1991). The third possible combination—a sister-group relationship between the Ephemeroptera and Neoptera—has been supported by the presence of direct sperm transfer during copulation in the two groups, contrasting with the indirect and external mode used by the Odonata.

*Palaeodictyopteroidea.* The Palaeodictyopteroidea constituted a majority of Late Carboniferous taxa and is distinguished from other paleopterous insects by the presence of unique stylate-nonhaustellate mouthparts characterized by exposed piercing stylets lacking an encompassing sheath. The Palaeodictyopteroidea is subdivided into four orders, the Diaphanopterodea, Palaeodictyoptera, Megasecoptera, and Permothemistida (Kukalová-Peck 1991). The Palaeodictyopteroidea, the only extinct supraordinal taxon of insects, was a structurally diverse clade; wingspans, for example, ranged by more than an order of magnitude, from mosquito-like permothemistids at 0.9 centimeters to giant paleodictyopterids at 56 centimeters. The strongly fluted, stiff, archedictyon-rich wings of large paleodictyopteroids were modified into the streamlined, petiolate shapes of the Megasecoptera, or they were significantly reduced as hind wings in the Permothemistida. The Diaphanopterodea independently evolved a non-neopteran mechanism of abdominal wing folding. Major differences in beak shape also occurred among these orders.

*Odonatoptera.* The shared ancestry of the Protodonata and Odonata is indicated by the presence of distinctive intercalary

## Table 1. Geochronologic distribution of hexapod orders

| Order[2] | Common name | First occurrence[3] | Last occurrence[3] |
| --- | --- | --- | --- |
| Collembola | springtails | Devonian (Lochkovian) | Recent |
| Diplura | telsontails | Carboniferous (Moscovian) | Recent |
| Archaeognatha | bristletails | Devonian (Pragian) | Recent |
| Monura | monurans | Carboniferous (Bashkirian) | Permian (Artinskian) |
| Zygentoma | silverfish, firebrats | Carboniferous (Moscovian) | Recent |
| Ephemeroptera | mayflies | Carboniferous (Moscovian) | Recent |
| Odonata | dragonflies, damselflies | Carboniferous (Bashkirian) | Recent |
| Palaeodictyoptera | paleodictyopterans | Carboniferous (Serpukhovian) | Permian (Wordian) |
| Diaphanopterodea | diaphanopterodeans | Carboniferous (Bashkirian) | Permian (Capitanian) |
| Megasecoptera | megasecopterans | Carboniferous (Bashkirian) | Permian (Longtanian) |
| Permothemistida | permothemistidans | Carboniferous (Bashkirian) | Permian (Wordian) |
| "Protorthoptera"[4] | protorthopterans | Carboniferous (Bashkirian) | Triassic (Anisian) |
| Blattodea | cockroaches | Carboniferous (Bashkirian) | Recent |
| Mantodea | mantids | Cretaceous (Hauterivian) | Recent |
| Isoptera | termites | Cretaceous (Valanginian) | Recent |
| Protelytroptera | protelytropterans | Carboniferous (Kasimovian) | Recent |
| Dermaptera | earwigs | Jurassic (Sinemurian) | Recent |
| Orthoptera | grasshoppers, katydids, crickets | Carboniferous (Moscovian) | Recent |
| Phasmatoptera[5] | walkingsticks, leaf insects | Triassic (Ladinian) | Recent |
| Titanoptera | titanopterans | Triassic (Anisian) | Jurassic (Hettangian) |
| Embioptera | webspinners | Permian (Wordian) | Recent |
| Grylloblattodea | rock crawlers | Carboniferous (Gzelian) | Recent |
| Plecoptera | stoneflies | Carboniferous (Gzelian) | Recent |
| Caloneurodea | caloneurids | Carboniferous (Moscovian) | Permian (Capitanian) |
| Hypoperlida | ancestral hemipteroids | Carboniferous (Bashkirian) | Triassic (Anisian) |
| Zoraptera | angel insects | Paleogene (Chattian) | Recent |
| Psocoptera | booklice, psocids | Permian (Sakmarian) | Recent |
| Phthiraptera | lice | Paleogene (Priabonian) | Recent |
| Thysanoptera | thrips | Permian (Sakmarian) | Recent |
| Hemiptera | bugs, cicadas, hoppers, aphids, whiteflies, scales | Carboniferous (Moscovian) | Recent |
| Miomoptera | miomopterans | Carboniferous (Bashkirian) | Recent |
| Glosselytrodea | glosselytrodeans | Carboniferous (Bashkirian) | Jurassic (Sinemurian) |
| Megaloptera | alderflies, dobsonflies | Permian (Kungurian) | Recent |
| Raphidioidea | snakeflies | Permian (Wordian) | Recent |

| Order[2] | Common name | First occurrence[3] | Last occurrence[3] |
|---|---|---|---|
| Planipennia[6] | lacewings, antlions, owlflies | Permian (Sakmarian) | Recent |
| Coleoptera[7] | beetles | Permian (Sakmarian) | Recent |
| Strepsiptera | twisted-wing parasites | Paleogene (Lutetian) | Recent |
| "Paratrichoptera"[4] | paratrichopterans | Permian (Sakmarian) | Cretaceous (Berriasian) |
| Mecoptera | scorpionflies | Permian (Asselian) | Recent |
| Siphonaptera | fleas | ?Cretaceous (Aptian) | Recent |
| Diptera | flies | ?Permian (Ufimian) | Recent |
| Trichoptera | caddisflies | Triassic (Ladinian) | Recent |
| Lepidoptera | moths, butterflies | Jurassic (Sinemurian) | Recent |
| Hymenoptera | sawflies, wasps, ants, bees | Triassic (Ladinian) | Recent |

Notes 1. This list is modified slightly from Labandeira (1994).
2. The Protura lack a fossil record.
3. Epoch and stage names from Harland et al. (1990).
4. An informal, paraphyletic designation.
5. Includes the Early Mesozoic Chresmodidae, Aeroplanidae, and related families.
6. Also known as Neuroptera *sensu stricto*.
7. Includes the Protocoleoptera of several authors.

wing veins, the oblique orientation of thoracic segments (Hennig 1981), and a raptorial and protractile labial mask in the aquatic nymph (Kukalová-Peck 1991). The Protodonata, including the gigantic Meganeuridae, are distinguished from the Odonata by absence of or an incomplete nodus, costal triangle, and pterostigma on the wing, and by serrate anterior wing margins, a sinuous CuP vein, and unreduced male genitalia. The Protodonata and Odonata generally have often been considered distinctive at the ordinal level; however, there now is evidence for a third order, the Paleozoic Geroptera (Bechley 1996). The Protodonata and Odonata have a rich fossil record, attributable to their large size and sturdy wing construction. Late Carboniferous members of the Meganeuridae that achieved wingspans of 70 centimeters are the largest known insects.

*Ephemeroptera.* The most compelling derived feature (autapomorphy) of the Ephemeroptera is a vein known as the "subcostal brace." The Paleozoic Syntonopterodea resembled protodonatan dragonflies and palaeodictyopteroids, with hind wings broader than forewings and a shorter subcostal brace—as opposed to modern mayflies, which possess reduced hind wings and elongate male forelegs (Kristensen 1991). Paleozoic adult mayflies had robust, functional mouthparts and probably were active feeders (Shear and Kukalová-Peck 1990); by contrast, post-Paleozoic adults had strongly reduced, nonfunctional mouthparts. Ephemeropteran nymphs, however, were aquatic detritus feeders that had a mandibular articulation with the head capsule unique among extant insects. Some Paleozoic ephemeropterans were frequently large, one species reaching 45 centimeters in wingspan.

*NEOPTERA.* The fundamental defining feature of the Neoptera is a distinctive wing-articulation mechanism resulting in rotation, flexing, and locking of the wings over the abdomen. Of the five major neopteran assemblages that encompasses 33 conventional orders, the best-circumscribed is the Holometabola. The Hemipteroidea is less well defined, but their unity is widely accepted. The Hemipteroidea and the Holometabola together have been termed the "higher" Neoptera, and probably are sister groups, constituting the Eumetabola (Kristensen 1991). The three assemblages of "lower" Neoptera are broadly termed the plecopteroid, orthopteroid, and blattoid assemblages. Collectively these taxa have been placed in the presumably polyphyletic lower Neoptera, in which descent has proceeded from multiple unrelated ancestors (Kristensen 1994).

*Plecopteroid Assemblage.* Autapomorphies of the Plecoptera include males lacking gonostyli, intromittent organs on the ninth abdominal segment, and presence of a common medial stem to the MA and MP veins (Kristensen 1991; Kukalová-Peck 1991). Recognition of plecopteran vein characters in some members of the extinct "Prororthoptera" has resulted in extension of stem-group plecopteroids into the Late Carboniferous (Kukalová-Peck 1991). Most of these taxa are woefully incomplete and are based principally on wings, although near-complete bodies are known for many. The nymphs of Permian plecopteroids were aquatic, although A.G. Sharov (1966) indicated that some were probably terrestrial and capable of flight. Modern Plecoptera are among the least derived of Neoptera and may be the sister group to all other Neoptera (Hennig 1981). The presently relict Grylloblattida (rock crawlers) also may be members (Rohdendorf and Rasnitsyn 1980).

*Orthopteroid Assemblage.* The most taxonomically confusing of all lower Neoptera is the orthopteroid assemblage. Orthopteroids have generalized mandibulate mouthparts and an enlarged anal fan in the hind wing. Members of this group are the Orthoptera (grasshoppers and crickets), Phasmatoptera (stick insects), the extinct Titanoptera, probably the Embioptera (webspinners), and possibly the Zoraptera (angel insects). Orthopterans with leathery, rooflike folded forewings (tegmina) and jumping hind legs are known from the Middle Pennsylvanian; forms with stridulatory organs are documented for the Lower Permian, although the earliest members of the cricket lineage are Late Triassic to Early Jurassic (Hennig 1981). Phasmatopterans have a poor fossil record, although modern-aspect taxa are known from the Late Jurassic. The Titanoptera are exclusively a Mid-Mesozoic clade of structurally derived and apparently predaceous insects with raptorial forelegs, incisiform mandibles, and wings ·with spans up to 36 centimeters that were folded flat over their abdomen. Embiopterans, characterized by absence of a hind wing anal fan, are reported from the Late Permian of Russia. Modern Zoraptera are poorly known anatomically and have a single occurrence in the Mid-Cenozoic (Poinar 1992).

A vexing issue in insect paleobiology is taxonomic characterization and phylogenetic relationships of the diverse, abundant, and undoubtedly polyphyletic "Protorthoptera" (Hennig 1981). Because of the very generalized structure and the consequent absence of identifiable, derived features in this Paleozoic group, paleoentomologists have found definition of this group difficult. Many protorthopterans exhibit features of primitive hemipteroids, whereas others are taxonomically isolated because of very incomplete knowledge regarding head, mouthpart, and reproductive structures. As knowledge of these features and interpretation of wing venation advances, definable groups will be segregated and allocated to other neopteran clades (Kukalová-Peck 1991).

*Blattoid Assemblage.* As in the plecopteroid and orthopteroid assemblages, debate surrounds whether the blattoid assemblage is separable from the rest of the lower Neoptera as an identifiable clade. Nevertheless, an intact group of Mantodea + (Blattodea + Isoptera) has been established, and other, more distant members of this group probably include the extinct Protelytroptera and its modern descendants, the Dermaptera (earwigs). As a major clade, the Blattodea (cockroaches) is a ubiquitous and persistent element in equatorial Paleozoic localities (Wootton 1981). Numerically they are the most frequently encountered insect and occur overwhelmingly as isolated tegmina or hind wings in many deposits. During the Paleozoic, as now, cockroaches were dorsoventrally flattened, had an inconspicuous head that bore ventrally deployed mouthparts, and were covered dorsally by a pronotal shield. At least some Paleozoic and Mesozoic cockroaches possessed prominent, external ovipositors capable of penetrating firm substrates (see Hennig 1981 for an alternative view). Modern cockroaches lack external ovipositors and produce eggs that occur in an oötheca, a leathery egg case that is dropped from the body. Although most studies cite a sister-group relationship between the Blattodea and the Isoptera, there is recent evidence that termites may be derived from within the cockroach clade. Supporting the view that termites are modified cockroaches is the absence of pre-Cretaceous
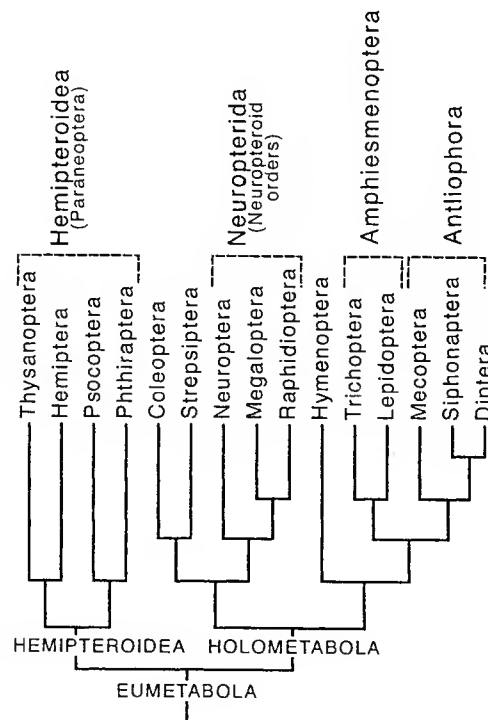


**Figure 6.** Possible phylogeny of the Hemipteroidea and Holometabola. Modified from Gullan and Cranston (1994).

termite body-fossils and trace-fossils, suggesting a Mid-Mesozoic origin. Mantids have a sporadic and poor fossil record that begins during the Early Cretaceous.

*Hemipteroidea (Paraneoptera).* The Hemipteroidea (Figure 6) are principally characterized by head and mouthpart specializations, such as an enlarged segment of the clypeus, the postclypeus, with mouth-cavity dilator muscles, and a detached and slender maxillary lacinia (Kukalová-Peck 1991). They also bear six or fewer Malpighian excretory tubules and have abdominal ganglia consolidated into one mass. Included in this group are certain Paleozoic taxa, long considered as "Protorthoptera" and taxonomically segregated by Russian paleoentomologists, that bore head and mouthpart modifications similar to modern Psocoptera (psocids) and Hemiptera (cicadas, aphids, scale insects, and bugs). Modern Hemipteroidea is divisible into four clades, the Psocoptera (booklice) + Phthiraptera (lice), and the Thysanoptera (thrips) + Hemiptera (aphids, bugs, and relatives). The relationship of the Phthiraptera to the Psocoptera is contentious; the two major proposals are either a sister-group relationship or gradual paraphyletic branching of multiple phthirapteran lineages from within the Psocoptera. By contrast the sister-group relationship of the Thysanoptera and Hemiptera is better established. Ancestral hemipteroids were common in Late Paleozoic insect faunas; all modern hemipteroid lineages except the Phthiraptera are known from the Early Permian (Labandeira 1994).

The evolution of mouthparts in the Hemipteroidea parallels that of the Palaeodictyopteroidea. In both clades there was a transformation of mandibulate mouthparts associated with solid-food

feeding into highly integrated, multielement structures capable of piercing tissue and imbibing deep-seated fluid food. The Permian demise of paleodictyopteroids was probably a consequence of extinction of their food plants and competition from the hemipteroid diversification that resulted in occupation of earlier paleodictyopteroid feeding niches (Labandeira and Phillips 1996). This radiation produced early, plant-feeding, homopterous hemipterans that included taxa superficially resembling modern cicadas and jumping lice. During the Late Permian, heteropterous hemipterans were established, although the earliest modern lineages are recorded from Late Triassic strata.

*Holometabola (Endopterygota).* The Holometabola consists of 11 orders united by the well-accepted feature of holometabolous development (Figure 6). The holometabolous life cycle is characterized by an egg→larva→pupa→adult sequence rather than the nonholometabolous egg→nymph→adult sequence. Holometabolous insects have an active juvenile stage, termed a larva, that is separated from a morphologically and ecologically differentiated adult stage by a typically quiescent pupal stage. Related to this unique life cycle are several other distinctive features of the eyes, genitalia, and wings. Larvae lack true ocelli and instead have lateral stemmata, whereas adults have structurally different compound eyes. Wings and genitalia occur as rudiments in larvae, namely inpocketings under the body wall, which subsequently become everted externally during the pupal stage.

The Holometabola, comprising 90 percent of hexapod species, is probably divisible into two major assemblages (Kristensen 1991). One is the Coleoptera + the neuropteroid orders, consisting of the Coleoptera (beetles) and their sister group, the three neuropteroid orders of Planipennia (lacewings, antlions, owlflies), Raphidioidea (snakeflies), and Megaloptera (dobsonflies and alderflies). The second assemblage is the Hymenoptera (sawflies, wasps, ants, and bees) and the five orders of the panorpoid complex—the Mecoptera (scorpionflies), Diptera (flies), Siphonaptera (fleas), collectively designated as the Antliophora, and the Trichoptera (caddisflies) and Lepidoptera (moths, butterflies) which form the Amphiesmenoptera.

The Coleoptera + neuropteroid assemblage is poorly defined, but it is based on valvular modifications of the ovipositor and reduction of terminal abdominal cerci to short and nonarticulated structures, among other features (Kristensen 1994). While true beetles do not appear until the Late Permian, their stem group, known as the Protocoleoptera, occur in earliest Permian deposits from Europe. The distinction between these two groups is that the Protocoleoptera bore a unique elytral locking mechanism, a significantly long external ovipositor rather than one retracted internally, 13- rather than 11-segmented antennae, and wing venation with primitive cross-veins that are lacking in true beetles. Within the neuropteroid orders, several structures provide links among taxa, including a medially divided dorsal thoracic sclerite, the metapostnotum, and fused third valves of the ovipositor. Basal lineages of Coleoptera, Planipennia and Mecoptera, are the earliest documented fossil holometabolous insects, occurring in earliest Permian riparian (river) and lacustrine (lake) environments.

Features linking the Hymenoptera to the Mecopterida are larval silk production from a labial spinneret and unpaired pretar-sal claws, among others (Kristensen 1991). The Hymenoptera is defined by several derived characters, including considerable reduction of the hind wing, coupling of the hind wing to the forewing by hooks, major flight musculature located in the mesothorax rather than metathorax, and haplodiploid sex determination. The Hymenoptera undoubtedly originated considerably earlier than their Middle Triassic fossil appearance would indicate, but it is noteworthy that the earliest fossil representatives of Hymenoptera are closely related to the Xyelidae, considered to be the most basal extant hymenopteran lineage.

The Mecopterida is an ecologically varied and taxonomically diverse clade, united by loss or extreme reduction of the ovipositor and certain mouthpart losses. Within this clade, two groupings are evident: the Antliophora consisting of Mecoptera + (Diptera + Siphonaptera), and the Amphiesmenoptera comprising the well-corroborated Trichoptera + Lepidoptera. The Antliophora are defined by structures such as larval mouthparts. The Nannochoristidae, a basal mecopteran lineage with a Late Permian record, have been considered by some as ordinally distinct and perhaps the most primitive extant antliophoran. Adult nannochoristids, unlike other mecopterans, possess a few mouthpart specializations similar to some basal Diptera and have a unique, aquatic larva. Nannochoristids notwithstanding, the earliest body-fossil representatives of the Mecopterida are Early Permian stem-group lineages historically designated as "Paramecoptera" (Hennig 1981). The enigmatic Miomoptera, including Late Carboniferous taxa that bear mecopterid wing venation, may be such a lineage. True Mecoptera and the earliest Diptera, the latter with vestigial but veined hind wings, appear during the Late Permian. The Mecoptera experienced a major taxonomic radiation during the Early Mesozoic and achieved a diversity considerably greater than its collective modern descendants, many of which now have relict geographical distributions. The earliest documented Siphonaptera are Late Eocene, although Early Cretaceous specimens from Australia may be primitive fleas. Some recent molecular studies, however, have relegated fleas to a clade within the Mecoptera.

Approximately 20 discrete characters unite the Trichoptera and Lepidoptera into the Amphiesmenoptera, of which the most prominent are looped anal veins in the forewing and fusion of the prelabium with the hypopharynx to form a projecting silk gland with an apical aperture (Kristensen 1991). The Amphiesmenoptera are probably represented in the Permian, and by the Middle Triassic the Trichoptera and Lepidoptera probably had emerged as distinct lineages. The earliest fossil trichopterans are from the Middle Triassic of Asia and include the extant family Philopotamidae. Many Recent trichopteran families can be recognized as body fossils in Jurassic deposits. There also is a parallel trace-fossil record in later Mesozoic strata of distinctive caddisfly cases, though they are not associated with respective body fossils.

Unlike aquatic trichopteran larvae, lepidopteran larvae are terrestrial, with primitive lineages inhabiting bryophyte foliage or commonly are endophytic herbivores as miners, borers, or gallers. Even though the Lepidoptera are characterized by approximately 25 derived characters, much debate has surrounded the age of the oldest Lepidoptera (Hennig 1981). Spec-
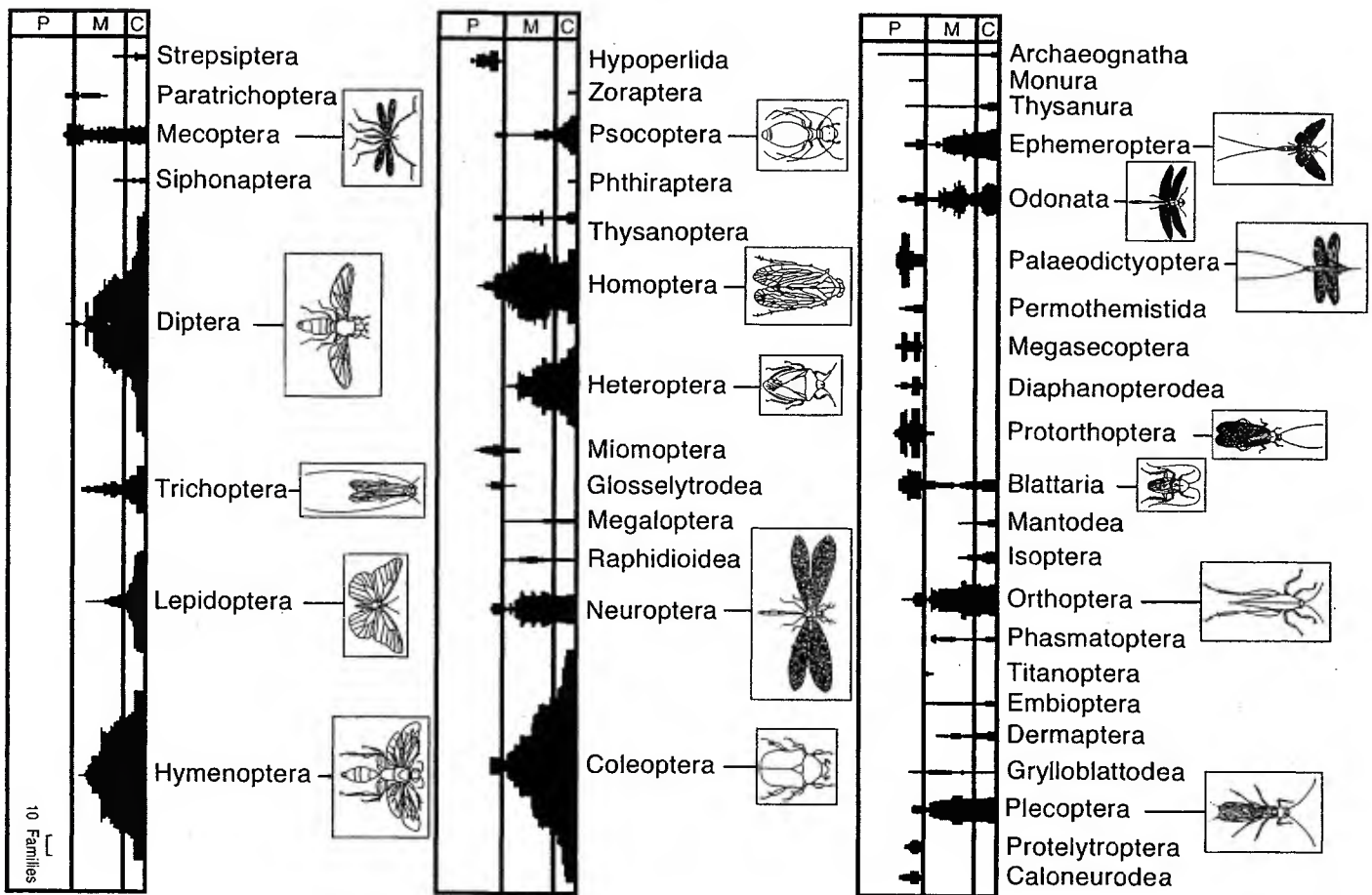
**Figure 7.** Family-level diversity of major insect clades through time. (Homoptera, an apparently paraphyletic assemblage, and Heteroptera are now combined into a composite clade, the Hemiptera.) Reprinted from Labandeira and Sepkoski (1993). Copyright © 1993 American Association for the Advancement of Science.

imens from the Middle and Upper Triassic were initially described as lepidopterans, although they subsequently have been reassigned to early trichopteran lineages or to the undifferentiated Amphiesmenoptera. The earliest lepidopteran is a Lower Jurassic moth. By the Mid-Cretaceous, there was a radiation of primitive phytophagous lineages (Labandeira et al. 1994). More derived, externally feeding clades, such as butterflies, are present during the earliest Cenozoic.

## Diversity

Hexapod diversity can be gauged by three measures. "Taxonomic diversity" documents the breadth of unique and cumulative speciation events produced by the evolutionary process. "Morphoecologic diversity" refers to the modes by which hexapods interact with their environment, as determined by associated structural adaptations evolved to meet ecologic demand. "Behavioral diversity" reveals the repertoire of sexual, social, parental, feeding, and defensive strategies of a particular life history. All three assessments express the different ways that hexapods have subdi-

vided their environment and achieved dominance on land and in fresh water.

### Taxonomic

Estimates of modern insect taxonomic diversity range from a low of approximately 5 million to a high of 80 million species, although there is much uncertainty. Regardless, only 876,000 extant species are taxonomically named or otherwise known, compared to approximately 20,000 identified insect fossil species, relegating the insect fossil record to less than 1 percent of inferred modern species diversity (Carpenter 1992). At the genus level, the record is better, with the fossil record representing 11 percent of extant generic diversity. However, because of the omnipresence of insect species and the prevalence of well-preserved fossil insect deposits, the family-level representation of insects is high: 63 percent of the approximately 1,000 extant families of insects are represented as fossils (Labandeira 1994). Additionally, many of these families have long geologic durations. These features show that gross aspects of the insect fossil record are well documented (Fig-
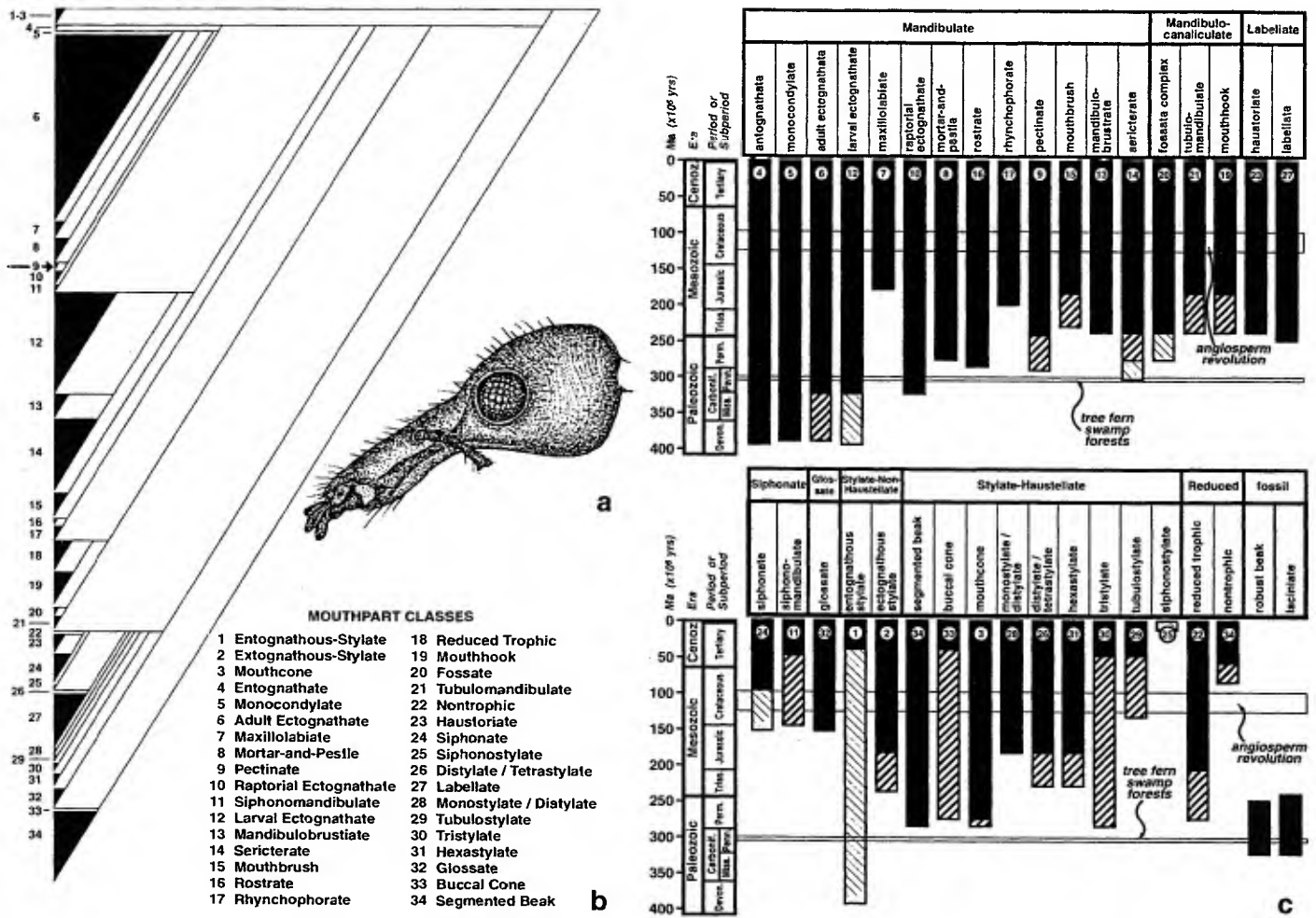
**MOUTHPART CLASSES**

| | |
|---|---|
| 1 Entognathous-Stylate | 18 Reduced Trophic |
| 2 Extognathous-Stylate | 19 Mouthhook |
| 3 Mouthcone | 20 Fossate |
| 4 Entognathate | 21 Tubulomandibulate |
| 5 Monocondylate | 22 Nontrophic |
| 6 Adult Ectognathate | 23 Haustoriate |
| 7 Maxillolabiate | 24 Siphonate |
| 8 Mortar-and-Pestle | 25 Siphonostylate |
| 9 Pectinate | 26 Distylate / Tetrastylate |
| 10 Raptorial Ectognathate | 27 Labellate |
| 11 Siphonomandibulate | 28 Monostylate / Distylate |
| 12 Larval Ectognathate | 29 Tubulostylate |
| 13 Mandibulobrustiate | 30 Tristylate |
| 14 Sericterate | 31 Hexastylate |
| 15 Mouthbrush | 32 Glossate |
| 16 Rostrate | 33 Buccal Cone |
| 17 Rhynchophorate | 34 Segmented Beak |

**Figure 8.** The geochronological extension of modern mouthpart classes for an assessment of mouthpart diversity through time. a, Head and mouthparts of a weevil, corresponding to dendrogram cluster 9 in b (indicated by arrow). b, Dendrogram resulting from a cluster analysis of recent hexapod mouthparts; for details of dataset structure and methods of analysis, see Labandeira (1997). c, Extension of basic mouthpart types in b into the fossil record. Symbols: solid black segments, solid evidence; heavy slashed segments, based on sister-group relationships; lightly slashed segments, more indirect evidence, based on trace fossils or presence of conspecific but alternate life stage of the life stage pertaining to the mouthpart class under consideration. Abbreviations: Devon., Devonian; Carbonif., Carboniferous; Miss., Mississippian; Penn., Pennsylvanian; Perm., Permian; Trias., Triassic; Cenoz., Cenozoic. From Labandeira (1997). With permission from the Annual Review of Ecology and Systematics, volume 28, © 1997, by Annual Reviews, Inc.

ure 7), driven principally by exceptional fossil deposits (Labandeira and Sepkoski 1993).

### Morphoecologic

Since securing and consuming food is central to an insect's existence, an evaluation of mouthpart structure (Figures 2, 8a) is an important measure of morphoecologic diversity. In a recent study it was found that there are 34 fundamental mouthpart classes among extant hexapods and two additional classes that are extinct (Figure 8b), of which all but three can be tracked with some certainty in the fossil record (Labandeira 1997). When the geochronologic ranges of these mouthpart classes are integrated over

geologic time (Figure 8c), there is a characteristic pattern of logistic increase with a rapid rise during the Late Carboniferous to Late Triassic, followed by an essentially modern level after the Mid-Jurassic (Figure 9). Superimposed on this pattern are five discrete episodes of mouthpart class origination (Labandeira 1997), the first consisting of approximately five mandibulate (chewing) and stylate (piercing-and-sucking) types for penetrating dead and live plant tissue by early hexapod colonists of land. The second expansion of mouthpart types is evident during the Late Carboniferous, perhaps earlier, with additions to existing mandibulate and stylate classes. A third phase during the Early Permian is associated with the early radiation of stylate-haustellate mouthpart types—piercing mouthparts surrounded by a labial sheath—in
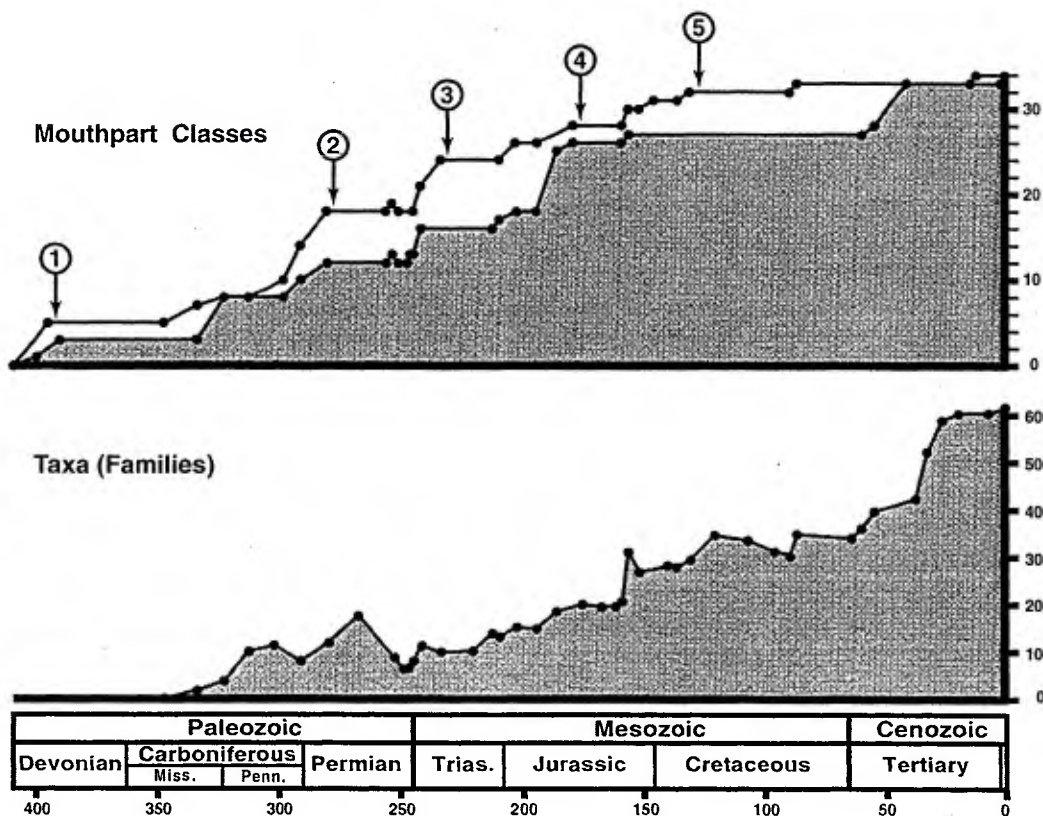
**Figure 9.** A comparison of mouthpart class diversity *(top)* and family-level taxonomic diversity *(bottom)* for the past 400 million years. Data is resolved to stage level. Key: *light grey*, less reliable evidence (as indicated by the slashed segments in Figure 8c). Abbreviations: *Miss.*, Mississippian; *Penn.*, Pennsylvanian; *Trias.*, Triassic. From Labandeira (1997). See Labandeira and Sepkoski (1993) and Labandeira (1997) for additional details.

basal hemipteroids and modified mandibulate mouthpart types associated with early holometabolous lineages. During the Late Triassic to Early Jurassic the radiation of several holometabolous clades, especially Diptera, resulted in a major addition of stylate-haustellate mouthpart types for extracting tissue-embedded and surface-exposed fluid, including blood and nectar. Contemporaneously in freshwater habitats there was exploitation of the thin neuston zone just below the water surface, the water column itself, and the benthos by immatures of dipteran, trichopteran, and coleopteran lineages. The last phase, during the Late Jurassic to Early Cretaceous, documents further partitioning of vascular-plant resources by the addition of the labellate (sponging), glossate (lapping), and siphonate (siphoning) mouthpart classes. These surface-fluid-feeding mouthparts subsequently became highly integrated with angiosperms as pollinators.

Several conclusions are obvious from an ecomorphic analysis of mouthpart design through geologic time. A major trend has been the conversion of primitive mandibulate mouthparts from the coordination of structurally independent elements borne on separate mouthpart regions, to mouthpart types consisting of functionally integrated ensembles of fused elements. The evolution of these derived mouthpart types was directed into three broad directions: (1) transformation into stylate-nonhaustellate and stylate-haustellate mouthparts during the Late Carboniferous and Early Permian, followed by an additional wave of stylate-haustellate mouthparts during the Late Triassic to Early Jurassic; (2) modifications for capturing fine particulate matter, both in the water by sieving and filtering devices and on land by investing mouthpart element surfaces with hairs or spines to form brushes or rakes; and (3) integration of elements within and between the maxilla and labium for siphoning, lapping, and sponging exposed surface fluids. A relevant feature of these patterns is that there has been considerable convergence on particular mouthpart designs by unrelated lineages of insects; in some cases a particular mouthpart class originated independently at least seven times (Labandeira 1997). Evidently there was significant early dietary partitioning of ecologic resources, judging from the comparatively early occurrence of major mouthpart types when compared to subsequent rises in hexapod taxonomic diversity (Figure 9).

## Behavioral

The behavioral diversity of hexapods is difficult to characterize. This is because, unlike most morphological characters, behavioral

traits are difficult to define, have been neglected historically in classification and phylogeny, and exhibit considerably more rampant and independent origination than most structural features. However, five types of behavior—sexual, egg-laying, defensive, parental care, and feeding (Preston-Mafham and Preston-Mafham 1993)—categorize most of hexapod behavioral diversity. Diversity in sexual behavior includes courtship and prenuptial offerings and displays, notably sound and light emission, and secretions of various volatile chemicals that promote eventual copulation. Particular egg-laying behaviors determine the location and microhabitat for developing eggs, although insects with ovipositors accurately insert eggs into substrates that are otherwise behaviorally inaccessible. With the exception of feeding, perhaps the most studied insect behavior has been parental care, particularly the role of nest construction and provisioning among social insects. A variety of insect-fashioned substrates are used for housing immatures, including subterranean chambers, brood balls constructed of dung, and nests fabricated from resin, wax, mud, and carton. Some of these nest types have a fossil record; subterranean chambers are known from the Mid-Mesozoic, and bee nests have been identified in Late Cretaceous and Cenozoic deposits.

There are several hard-wired behaviors associated with the securing, processing, and consumption of food that extend what is only physically possible with mouthparts. Foraging patterns can occur as a solitary or a colonial effort, as passive or active pursuit of food, or the seeking of a species-specific host substrate. Behavioral preludes to feeding can employ latex vein cutting, mowing of trichomes, or avoidance of tissues that are difficult to process. During feeding, the use of noxious pheromones, silk shelters, mimicry, frightening displays, or disruptive coloration effectively deters predation. Of these attributes, the fossil record is best for various patterns of coloration to protect insect herbivores. Examples of Batesian mimicry, where a mimic resembles a conspicuous but less palatable model to evade a predator, is known for a Late Eocene solder fly bearing a conspicuous color-barred abdomen mimicking an aculeate wasp. Similarly, crypsis—where there is confusion to a potential predator based on disruptive coloration—occurs in Paleozoic Paleoptera (Carpenter 1971). The wings of some Carboniferous protorthopterans and Jurassic kalligrammatid planipennians record the presence of large, "frightening" eyespots that were predator deterrents, based on identical patterns in modern insects.

## Geographic Distribution

Known fossil insect deposits have an uneven distribution on modern continents (Figure 10). Major reasons for this concentration of fossil insect sites are the vagaries of sediment preservation and the elevated intensity of paleoentomological effort in Europe and to a lesser degree in North America. These deposits record a 400-million-year interval that began as several major Late Paleozoic continents were separated by major deep-ocean barriers, namely Laurussia and the North China and South China terranes at low latitudes, Siberia and Kazakhstania to the north, and Gondwanaland to the south. With the possible exception of China, consolidation of these major continents into a major land mass, Pangaea,

occurred during the Late Permian and resulted in a pole-to-pole supercontinent that persisted into the Early Jurassic. During the Jurassic, Pangaea fragmented into a northern Laurasia and a southern Gondwanaland, followed by renewed fragmentation within Laurasia and Gondwanaland during the Early Cretaceous into the dispersed continental configuration of today.

### Paleozoic Continents

The earliest evidence for hexapod fossils occurs in Lower Devonian environments adjacent marine deposits approximately 30° south of the paleoequator of Laurussia, a paleocontinent consisting of most of Europe and North America. After a 50-million-year hiatus, relatively diverse assemblages of earliest Late Carboniferous insects are known from Laurussia and, to a much lesser extent, Siberia, the North China and South China terranes, and southern Gondwanaland. Overwhelmingly, knowledge of Paleozoic insect faunas originates from the broad, warm, and humid equatorial belt of Laurussia typically consisting of lowland, wetland environments during the Late Carboniferous (Wootton 1981), incorporating some better-drained, riparian, and lacustrine environments of the Early Permian. Although insect faunas from these paleocontinents have not been analyzed biogeographically, they appear distinctive at the highest taxonomic levels. This regional intercontinental endemism probably persisted until the end-Permian mass extinction. Martynov recognized lower-level taxonomic similarities between Lower Permian insect taxa from Kansas and the central Urals, widely separated localities within Laurussia. This distinctive, Late Paleozoic insect fauna suffered a major extinction at the end of the Permian. It was replaced during the Triassic by a modern insect fauna characterized by taxonomic orders and many families that occur today (Figure 7).

### Gondwanan Distributions

Many insect clades that occurred on Gondwanaland during the Early to Middle Mesozoic currently have distributions, relict or otherwise, on some of the Southern Hemisphere continents (Briggs 1995). The earliest separation event was probably South America plus Africa from the rest of Gondwanaland, both of which contain unique subfamilies of earwigs, vespid wasps, and fideliid bees, among others. South America and Australia, but occasionally New Zealand and presumably interconnecting Antarctica in the past, harbor many insect groups that indicate a more recent, Mesozoic connection. These include belid and nemonychid weevils occurring in South America and Australia, most which are associated with the primitive seed-plant families Araucariaceae and Podocarpaceae. Similarly, although the beetle family Boganiidae incorporates one subfamily feeding on angiosperms in South Africa and Australia, a second cycad-feeding subfamily also occurs in these two regions. These associations of basal lineages of insects that are coevolved with nonangiospermous seed plants probably represent ancient associations that extend to the Middle Mesozoic (Labandeira 1997). Ancient nonphytophagous lineages with extant Gondwanan distributions include nannochoristid scorpionflies, the corydalid megalopteran *Archichauliodes,* and stilbopterygine antlions (Briggs 1995). One analysis of Gondwanan
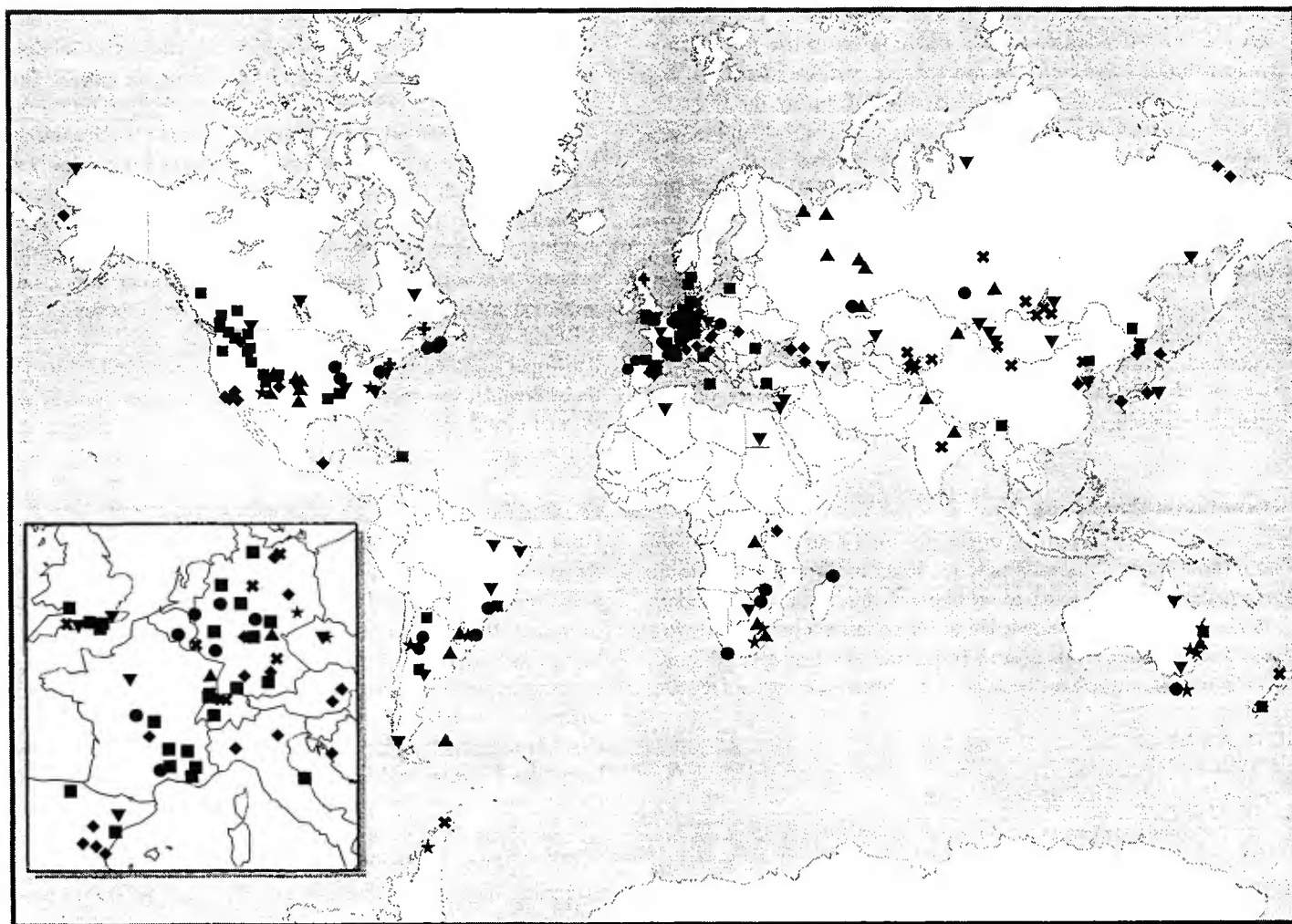
**Figure 10.** Geographic distribution of major fossil insect deposits from which taxa have been documented in the primary literature. Inset at lower left depicts an enlarged western Europe to resolve site overlap. Symbols: **+** = Devonian, ● = Carboniferous, ▲ = Permian, ✳ = Triassic, ✕ = Jurassic, ▼ = Cretaceous, ■ = Paleogene, ◆ = Neogene. This map does not depict all known localities, and Quaternary and extreme polar localities are not recorded (see Elias 1994); it is representative of the pre-Quaternary fossil insect record.

insect distributions is Brundin's biogeographic study of midges, which demonstrates that several Gondwanan landmasses were colonized successively in a vicariant fashion. Brundin's conclusions subsequently have been supplemented by studies of other Early Mesozoic aquatic clades, including leptophlebiid and siphlonurid mayflies, petalurid dragonflies, and anarctoperlian stoneflies.

Some modern, primitive Gondwanan taxa occur as fossils only in Laurasia (Grimaldi 1990). For example, the primitive, cycad-feeding chrysomelid beetle *Aulacoscelis* of Central America and Andean South America is virtually identical to the Upper Jurassic *Protoscelis* of Kazakhstan. Early Cretaceous examples are the snakefly *Baissoptera*, known as a fossil from northeastern Brazil but congeneric with penecontemporaneous specimens from northern Asia, and the termite *Meiatermes*, also from the same deposit in Brazil but congeneric with similarly aged specimens from northern

Spain. The extant primitive termite from Australia, *Mastotermes*, occurs in the fossil record of only northern continents, and the primitive Australian moth-lacewing family Ithonidae has its closest relatives in southwestern North America. These distributions indicate that some modern relict occurrences are the result of significant extinction in regions formerly occupied, rather than past vicariant events separating continental faunas.

### Subsequent Events

Important biogeographic events during the Cenozoic include faunal movements promoted by filter bridges such as island arcs and intercontinental isthmuses, and colonization of oceanic islands followed by often spectacular radiations of taxa. For the former, the Bering island arc has been invoked to explain the Asian origins

of North American ground beetles and certain ichneumonid wasps. The intercontinental dispersal of insects across the Panamanian isthmus has resulted in more direct, two-way traffic since a permanent land connection was established during the Pliocene. One of the most spectacular radiations on an island chain has been pomace flies on Hawai'i, which comprise approximately 700 species from two north-subtropical introductions within the last 5 to 6 million years. Other examples are several groups of insects, particularly cryptorhynchine weevils and sphinx moths, that have colonized the southeastern Pacific from sources in Indonesia, New Guinea, and northern Australia through a series of island archipelagos that extend as far west as Samoa. A modest radiation has occurred on Rapa, a small south-central Pacific island, where 67 species of *Miocalles* weevils have radiated on a variety of host plants, including many ferns.

## Functional Morphology

Two of the most important organs for insects are wings for flight and mouthparts for obtaining food. Tentative inferences regarding the origin of flight are based on biomechanical models of modern primitive insects and knowledge of the wing structure in early fossils. For mouthparts, there are a few instances where specific structures and function have been used to determine ancient feeding habits.

### The Origin of Insect Wings and Flight

Perhaps the most controversial topic in paleoentomology is the origin of insect wings and flight. Several theories have been proposed (Gillott 1995), only two of which retain currency. The paranotal theory historically is the older view. It proposes that wings originated from rigid, lateral projections of thoracic terga that became enlarged, flattened, supplied with a regularized system of veins, and eventually articulated with the thorax to produce flapping flight. However, the paranotal theory suffers from several deficits, including absence of evidence for an articulatory wing hinge characterizing the attachment of paranotal lobes to an associated thorax, thus disallowing flapping flight. Nevertheless, the use of paranotal lobes as airfoils to guide takeoff from elevated perches onto horizontal air currents has been experimentally modeled (Brodsky 1994).

An alternative to the paranotal theory is Kukalová-Peck's epicoxal exite theory. Accordingly, serially homologous protowings originated in semiaquatic insects from small appendages located above the leg bases, known as epicoxal exites, initially for purposes other than aerial flight. Subsequently protowings developed laterally on thoracic and abdominal segments from these exites, which were initially articulated to the pleurae, a condition different from the initially rigid attachment proposed by the paranotal theory. This theory is consistent with much embryological, genetic, and fossil evidence, although these structures initially may have functioned on the abdomen as coverlets for tracheal openings to retard water loss in terrestrial insects or to prevent water entry in aquatic forms. Nevertheless, an intermediate stage by which gills or other homologous lateral structures could have been converted to functional aerial wings has always been challenging. One plausible proposal involves an insect dwelling on the water surface in which its winglike gills flapped to provide forward thrust and modest lift while its abdomen was supported by water surface tension. Such a locomotory mechanism has been documented in modern primitive stoneflies (Marden and Kramer 1994) as the surface skimming hypothesis and may represent a modern analog for how fully aerial flight originated. Another proposal potentially linking gills or its homologues to fully developed wings is the thermoregulatory hypothesis proposed by Kingsolver and Koehl (1985) and others. Initially envisaged as pertaining to paranotal lobes, wings increased in size and changed their angle to intercept incident solar radiation; such a function could have occurred on any lateral, flat organ supplied by blood, such as abdominal gills. Later, such thermoregulatory structures could have been functionally transformed into flight organs.

### Feeding Habits of Some Late Cretaceous Flies

From Late Cretaceous amber deposits of Alberta, Canada, certain dipterans with piercing-and-sucking mouthparts—biting midges—are commonly preserved with good resolution of external body structures. In many specimens, structures such as antennae, maxillary palps, mouthpart stylets, and other head-associated structures are exquisitely preserved and include detail of trichomes, sensillae, and surface ornamentation (Borkent 1995). Depending on the species, biting midges imbibe the internal fluids of other insects, vertebrate blood, nectar, and rarely other substances. In modern female biting midges, there is a strong correlation between serrated mandibular stylets and the blood-sucking habit. Within blood-sucking species, females that imbibe vertebrate blood have coarsely toothed mandibles, recurved-toothed lacinial stylets, and generally a toothed labrum and hypopharyngeal stylet (Figure 11a, b), as opposed to species not feeding on blood that lack these features. Additionally, patterns of sensilla number, size, and placement on the antennae, and the third maxillary palp segment are important for distinguishing between species feeding on small birds or large mammals. Modern *Culicoides* species feeding on large mammals bear from 9 to 24 capitate palpal sensilla, whereas those feeding on birds have 29 to 75 such sensilla (Borkent 1995). Species feeding on larger vertebrates need considerably fewer sensillae to detect elevated $CO_2$ levels in the downwind plume of large hosts. Isolated exceptions to these robust associations are species that possess other mouthpart and antennal features that identify them as nonblood feeders.

Two, perhaps three, Canadian amber species of *Culicoides* fit the mouthpart morphological criteria for feeding on large vertebrates. Both birds and mammals were relatively small during the Late Cretaceous. The likely candidate hosts for these *Culicoides* species were hadrosaurian dinosaurs (Figure 11c), which are recorded in the same deposits. The site of host attack was probably exposed, blood-filled membranes such as eyelids (Figure 11d) or membranous zones between much thicker dermal scales or scutes.

## Relationships to Other Organisms

Hexapods interact with virtually all terrestrial and freshwater organisms in some way. For many, these interactions provide reciprocal

benefit, such as the mutually beneficial gut symbioses of termites or the pollination mutualisms between butterflies and flowering plants. Others result in an advantage provided to the insect at the expense of its live host, which may be a herbivorized plant or an insect attacked by a parasitoid larva. Such associations are the result of adaptive and other reciprocal processes occurring on large numbers of individuals and populations at geologically long intervals.

## Microorganisms

Insects interact with five major types of organisms, generally with negative consequences to the plant and animal world. They are viruses, rikettsias, bacteria, protozoans, and fungi. Additionally macroscopic internal parasites, principally nematodes and cestodes, are transmitted to plants, fungi, and animals by insect vectors. Many bacteria are important as gut symbionts in rendering wood digestively available for wood-consuming insects, but other interactions are expressed as diseases that are debilitating to crop plants, livestock, and humans. A few examples are known where insect vector species have been tracked in the fossil record. One involves a bark beetle species responsible for Dutch elm disease, which apparently experienced a dieback in northern Europe during the Holocene. More ancient examples are particular mosquito and tsetse taxa with Cenozoic fossil records that are highly associated with diseases such as malaria and sleeping sickness (both protozoans), yellow fever (a virus), and filiariasis (a worm). These diseases probably originated on mammals and birds during the Early Cenozoic and colonized early hominid populations during the Pliocene.

## Fungi

Hexapods interact with fungi in diverse ways. Beetles and flies dietarily partition ephemeral fruiting bodies such as polypores and gilled mushrooms in an intricate fashion. Other insects such as leaf-cutting ants and macrotermitine termites culture fungi in underground galleries that contain decomposing plant substrates. Nonmutualistic consumption of macrofungi, in which one participant does not benefit, is accomplished principally by specialists on spores and hyphae. This feeding mode is known extensively for beetles and flies, and to a lesser extent for thrips, bugs, moths, and wasps. Nonmutualistic interactions of hexapods and fungi probably extends to the Devonian, supported by two occurrences of unattributed arthropod borings with reaction tissue in a large, enigmatic, Devonian fungus. Limited occurrences in anatomically preserved coprolites of the Late Carboniferous of Laurussia also hint at fungivory, although it is not until the Lower Jurassic that insectan wood-borings are known with fungal contents. Several modern lineages of fungus-associated insects are known from the Early Cretaceous, including bark beetles, which have their borings preserved in conifer wood.

## Plants

Plants contribute the most intensively examined and wide-ranging spectrum of interactions that insects have with any major organismic group. These myriad associations include seed preda-
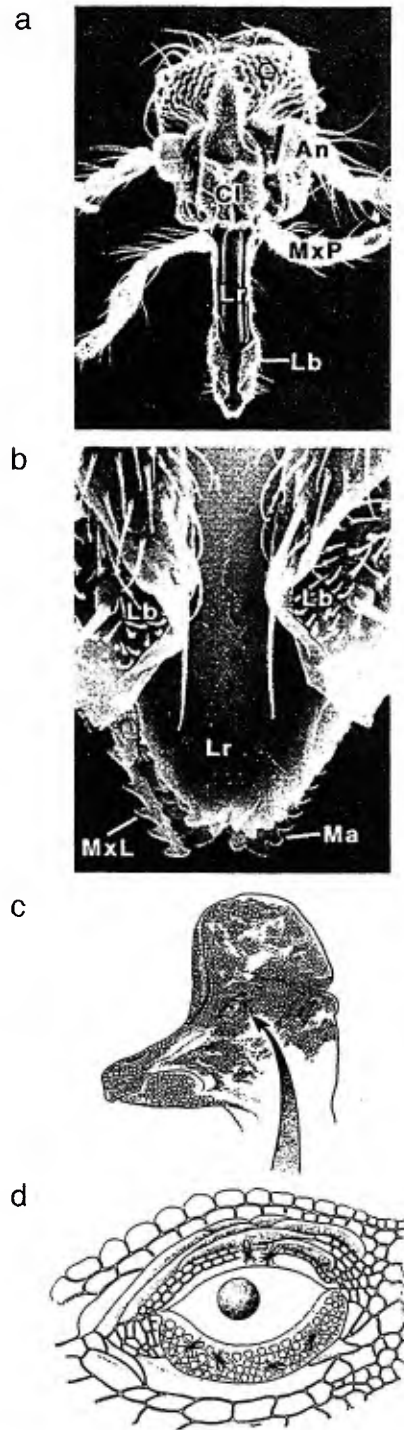


**Figure 11.** Female ceratopogonid midge mouthpart structure and blood-feeding on Late Cretaceous hadrosaurs. a, extant blood-feeding species of *Culicoides*; frontal (dorsal) view of head and mouthparts; b, dorsal, distal view of labrum, mandibular and lacinial stylets, and labellum, with serrated teeth; c, the Late Cretaceous hadrosaur *Corythosaurus*; with d, *Culicoides* blood-feeding on eye membrane tissue. See Borkent (1995) for additional details. a, b, reprinted by permission of the Entomological Society of America; c, d, from Borkent (1995), permission to reproduce kindly granted by Backhuys Publishers, Leiden, The Netherlands.

tion, pollinator mutualisms, and consumption of externally and internally accessible tissues by modes as distinctive as external foliage feeding, leaf-mining, galling, stem boring, and piercing-and-sucking. Many of these interactions are performed by more eclectic-feeding generalists; others are host specific and represent intricate and intimate codependence through long stretches of geologic time (Labandeira et al. 1994). Examination of insect-mediated plant damage from well-preserved plant deposits indicates that significant insect herbivory began during the Late Carboniferous to Early Permian, providing evidence for a distinctive Paleozoic herbivore fauna preceding the post-Paleozoic herbivore fauna of today.

A trace-fossil record, parallel to and independent of the body-fossil record, exists for the varied effects of hexapods on plants, notably damage resulting from herbivory (Labandeira 1997). The earliest documented examples of hexapod-mediated plant damage are rare Early Devonian herbivory, principally external feeding and stylet penetration of stem tissues. By the Late Carboniferous, leaf margins were consumed by external feeders, internal petiolar parenchyma was galled (Figure 12b), petiolar vascular tissue was targeted by piercer-and-suckers, and pith borers were tunneling through softer stem tissues. During the Early Permian, external foliage feeders expanded their repertoire to include hole-feeding, skeletonization, and consumption of near-entire leaves. Pollinivory is first documented from the Late Carboniferous but expanded during the Early Permian. The earliest evidence for leaf mining is on a Late Triassic seed fern, although this herbivory type was well established on another seed-fern lineage by the latest Jurassic. Leaf mining subsequently diversified during the Mid-Cretaceous on basal angiosperm clades (Figure 12d, e; Labandeira et al. 1994). Recently, galls have been identified from Triassic conifers, especially on the terminal branchlets and reproductive organs. Although earlier Permian borings are known from glossopterid wood, there are beetle borings in heartwood, developing cambial tissue, and reproductive organs of conifers and cycadeoids that occur throughout the Late Triassic to Early Cretaceous. By the Late Jurassic, beetles were pollinating cycadophytes; some of these associations persist today. As angiosperms expanded ecologically during the Middle to Late Cretaceous, some major pollination syndromes became fine-tuned mutualisms.

## Animals

Hexapod consumption of dead animal tissue, together with plant and fungal detritivory, is an ancient feeding habit that undoubtedly extends to the Early Devonian. Predation upon live insect tissue was present during the Late Carboniferous, evidenced by protodonatan dragonflies with robust, incisiform mandibles and raptorial forelegs. It is unclear whether any fluid-feeding paleodictyopteroid consumed other insects or vertebrate blood, but the exceptionally small size of some dipterous Permian taxa suggest functional comparisons to mosquitos (Shear and Kukalová-Peck 1990). During the Late Triassic to Early Jurassic, the radiation of lower Diptera resulted in a significant expansion of piercing-and-sucking mouthpart types that included blood- and insect-feeding (Labandeira 1997). In the Jurassic there was a significant radiation

of the hymenopteran parasitoid guild. More modern lineages of insects feeding on vertebrate blood, integument, hair, lymph, and other substances expanded during the Late Cretaceous and Early Cenozoic, principally fleas, several clades of brachycerous flies and lice, but also bugs and earwigs. Contemporaneously there was expansion of carnivorous and predatory insect clades, possibly responding to increases in phytophagous insect diversity associated with the ecological expansion of seed plants.

## The Fossil Record and Paleoentomology

The common perception is that the insect fossil record is poor when compared to other fossil groups such as vascular plants and vertebrates. However, it is well represented at the family level (Labandeira 1994). Additionally, a strong association exists between those orders that are currently the most diverse (Hemiptera, Coleoptera, Diptera, and Hymenoptera) and their diversities in the fossil record (Figure 7). The greatest deficit of the insect fossil record is representation of the lowest taxonomic levels and the Lepidoptera. Figure 12 illustrates several typical occurrences of fossil insects in commonly encountered deposits.

### Types of Deposits

The hexapod fossil record is characterized by ten major deposit types (Figure 13), ranging in age from Early Devonian to Quaternary. Some of these deposits are restricted paleolatitudinally and reveal the vagaries of sediment cover preservation during the past 400 million years. Others are restricted spatiotemporally and document unique, often geologically unusual environments for entombing insects.

The earliest hexapods are from the Early to Middle Devonian of equatorial Laurussia. The Rhynie Chert in Scotland, Gaspé in Québec, and Gilboa in New York share a common feature of being deposited marginally above sea level adjacent to major ocean basins, rather than by lithological uniformity. Similar earlier deposits containing myriapods and land plants extend to the Late Silurian. From the Carboniferous, characteristic ironstone concretions are known for several sites in clastic-dominated swamps in the interior of Laurussia. Occurring at about the same time but extending into the Early Permian at some localities are coal-ball deposits that represent three-dimensional permineralizations of plant tissue that reveal considerable evidence for vascular plant/insect interactions. These deposits are best developed in equatorial, peat-dominated swamps of Laurussia and China. Succeeding typically black, Late Carboniferous strata are Early Permian redbed deposits that represent better-drained, higher elevated, and riparian habitats. Redbed deposits occur in extratropical latitudes in Laurussia and Gondwanaland, extending to the Triassic in many stratigraphic sequences.

Distinct from previous and succeeding deposit types, fine-grained lacustrine deposits represent the persistence of a sediment type for the past 280 million years. Lake basin sediments and associated fine-grained deposits provide the single most important source for the fossil insect record. A variant of lacustrine deposits, but lithologically distinctive and confined to basins with some
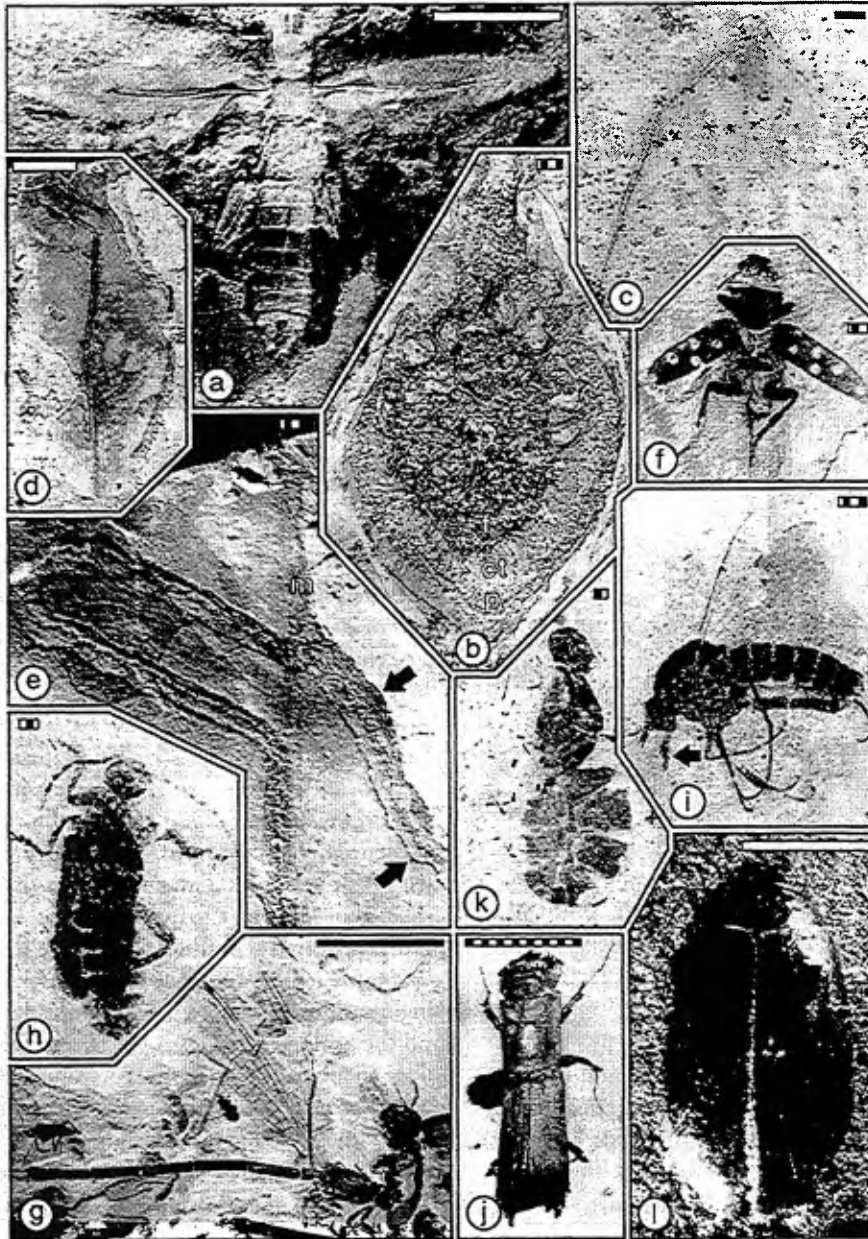
**Figure 12.** Fossil insects occurring in several commonly encountered depositional environments (see also Figure 13). a, a protorthopteran insect (Family Eucaenidae) in an ironstone concretion (Middle Pennsylvanian; Carbondale Formation, Mazon Creek, north-central Illinois) (FMNH-PE967). b, a primitive gall of an early holometabolous insect in the frond rhachis of the tree fern *Psaronius;* from a coal-ball permineralization (Late Pennsylvanian, Mattoon Formation of east-central Illinois) (NMNH-483990); key: p, normal parenchyma; ct, callus tissue created as a response to insect-induced trauma; f, insect frass. c, member of an extinct clade of aquatic, surface-dwelling insects (Order Phasmatoptera) in lithographic limestone (Late Jurassic Solnhofen Formation, southern Germany) (USNM-33067). d, a leaf mine of a moth larva (Lepidoptera) and external foliage feeding by a mandibulate insect on a primitive angiosperm leaf (Middle Cretaceous Dakota Formation of Kansas) (UF-14881). e, Enlargement of leaf mine in D, showing central frass trail of mine *(lower arrow)*, avoidance of leaf midrib *(m)*, and chewed leaf edge *(upper arrow)*. f, Longhorn beetle (Coleoptera: Cerambycidae) from a lacustrine shale (Middle Eocene Green River Formation, Colorado) (USNM-497410). g, A narrowwing damselfly (Odonata: Coenagrionidae) (Green River Formation) (USNM-497411). h, Beetle (Coleoptera: ?Meloidae) from a lacustrine shale (Early Oligocene Antero Formation, Florissant, Colorado) (USNM-90535). i, bee fly (Diptera: Bombyliidae) (Antero Formation) (USNM-127677); key: arrow, elongate mouthparts for imbibing floral nectar. j, pinhole borer (Coleoptera: Platypodidae) entombed in amber (Early Miocene, Dominican Republic) (USNM-497409). k, A giant ant (Hymenoptera: Formicidae) (Late Miocene lacustrine shales at Oeningen, northern Switzerland) (USNM-38549). Body length, excluding appendages: 2.2 centimeters. l, a predaceous diving beetle (Coleoptera: Dytiscidae) (Late Pleistocene, McKittrick asphalt deposit, south-central California) (USNM-33879). Scale bars: solid, 1 centimeters; striped, 0.1 centimeters. Repository abbreviations: A, Field Museum of Natural History (FMNH); B, C, F, G, H, I, J, K, L, National Museum of Natural History (USNM); D, E, University of Florida (UF).
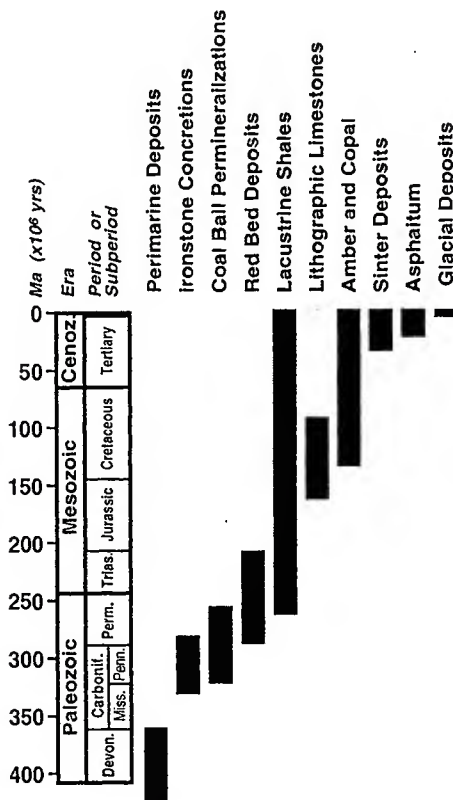
**Figure 13.** Geochronologic distribution of major types of insect-bearing deposits. Abbreviations: *Devon.*, Devonian; *Carbonif.*, Carboniferous; *Miss.*, Mississippian; *Penn.*, Pennsylvanian; *Perm.*, Permian; *Trias.*, Triassic; *Cenoz.* Cenozoic.

marine input, are Mid-Mesozoic lithographic limestones. By contrast, amber represents the accumulation of tree resins generally in forested habitats (Poinar 1992). Although Late Triassic amber is known, insect inclusions are traceable only to the Early Cretaceous. Subsequently, more geologically ephemeral, insect-bearing deposits are those confined to sites of minimal areal extent, namely sinter and asphaltum traps. These Late Cenozoic deposits trap insects, respectively, in pools of highly mineralized water and viscous tar. The most geologically fleeting of all deposits are Quaternary glacial deposits. These deposits document the advances and retreats of the most recent glacial episodes and are confined to high latitudes of the Northern and Southern Hemispheres and to higher elevations at lower latitudes (Elias 1994).

## History of Paleoentomology

Twentieth-century paleoentomology has been dominated by two countries, Russia and Germany. Both countries have had strong academic traditions and institutions capable of supporting several to as many as 20 paleoentomologists simultaneously in various academic institutions. Unlike other national traditions, a strong tendency of the Russian school of paleoentomology is investigator specialization on particular taxonomic groups, usually at the ordi-

nal level, during the course of a career (Rohdendorf 1973). Less well-established traditions occur in France, the United Kingdom, the United States, and more recently Poland and China, where a few to several full-time researchers simultaneously have devoted major responsibilities to paleoentomology. Beyond this second tier, several other countries periodically have supported one or a few paleoentomologists, including Australia, Brazil, Canada, South Africa, and Spain. The paleoentomological histories of Russia and Germany will be emphasized in this brief sketch; the reader is referred to Rohdendorf's (1973) comprehensive, albeit dated, article on this topic.

The most coordinated and extensive enterprise in the study of fossil insects has been the paleoentomology group at the Paleontological Institute of the Soviet (now Russian) Academy of Sciences (Rohdendorf 1973). A.V. Martynov provided the major impetus to the Soviet school during the mid-1920s with description of Upper Jurassic material from Karatau in Kazakhstan, followed by discovery and documentation of Mid-Permian insects at Chekarda and other localities in the central Urals, and eventual investigation of Lower Jurassic material from Fergana in Kirghizstan. During the mid-1920s to 1950s, additional taxa from the central Urals and new Late Carboniferous to Mid-Permian material from the Kaltan locality of the Kuznetsk Basin was extensively studied. After Martynov's death in 1938 and particularly after World War II, O.M. Martynova continued paleoentomological investigations in these deposits. During the 1950s additional paleoentomologists joined the Paleontological Institute. Their first major work was a monograph on the insects of the Kuznetsk Basin, published in 1961. Approximately 20 major monographic studies appeared from the 1960s to the late 1990s, either focusing on comprehensive and systematic accounts of major insect taxa by single authors or multiauthored works describing fossil insect taxa and the geological context of a diverse, well-preserved, and intensively collected fossil deposit. An important volume was *Historical Development of the Class Insecta*, a comprehensive survey of the evolutionary biology and ecology of all well-documented fossil insect lineages, edited by B.B. Rohdendorf and A.P. Rasnitsyn in 1980. During this flowering of paleoentomology in the Soviet Union, paleoentomologists representing a broad spectrum of specialities were added to the Paleontological Institute and other academic institutions. Recently, the direction of research has included examination of extensive Baltic Amber collections, although several important sites in central Asia are still being intensively explored.

In Germany the earliest major monographer of fossil insects was O. Heer, who described from the mid-1840s to mid-1860s insect faunas from the Early Miocene of Radaboj in Croatia and Late Miocene of Oeningen in Switzerland. Although subsequent German and British researchers described additional European insect faunas and occasional specimens, it was A. Handlirsch who, from 1906 to 1908, provided a comprehensive taxonomic synthesis of all known fossil insect material in his classic *Die Fossilien Insekten*, which remained the only major taxonomic compendium of the fossil insect record until B.B. Rohdendorf's (1962; English translation, 1991) and F.M. Carpenter's (1992) treatises. From the 1930s to 1960s, P. Guthörl described in a series of articles Upper

Carboniferous to Lower Permian Rothliegende strata in Thuringia. A. Bode in 1953 monographed Early Jurassic insects from the Posidionschiefer of Dobbertin and O. Kuhn did likewise in 1961 for the Late Jurassic Solnhofen Limestone in Bavaria. Meanwhile W. Hennig had established a research program at Stuttgart, focusing on examination of fossil Diptera, particularly material from Baltic and Lebanese amber. Hennig also provided an extensive treatise on the phylogenetic systematics and fossil history of insects that culminated in his much-cited work, *Die Stammesgeschichte der Insekten* (English translation, 1981). Recently, C. Brauckmann, W. Zessin, J. Schneider, and others have explored intensively Paleozoic insect faunas in northern Europe, including description of the earliest known pterygote insects.

J. Kukalová-Peck of Canada and F.M. Carpenter of the United States have provided significant perspectives in interpreting the fossil insect record, invigorating recent biological interest in Paleozoic insects (e.g., Brodsky 1994; Bechley 1996; Raff 1996). Both have documented extensive structural detail in Paleozoic insects that was previously unexplored. Kukalová-Peck's notable contributions to paleoentomology include the development of a homologizable, universal system of veinal nomenclature and in particular the assembly of multidisciplinary evidence—including the fossil record, developmental genetics, embryology, and the morphology of modern forms—for inferring patterns of early insect evolution.

### Recent Discoveries

From 1980 to 1990, newly reported insect deposits enlarged considerably the stratigraphic, geographic, and taxonomic scope of the fossil insect record. Most notable are six mostly Lower Cretaceous compression deposits from widely scattered regions. They are, approximately from oldest to youngest, Montsec in Spain, Baissa in Transbaikalian Russia, Gurvan and associated sites in northwestern Mongolia, Santana in Brazil (Grimaldi 1990), Koonwarra in Australia, and Orapa in Botswana. These deposits have extended the stratigraphic ranges of many Cenozoic taxa to the Lower Cretaceous, enlarged our knowledge of the past and present biogeographic distributions of Gondwanan taxa, and have provided data for paleoenvironmental settings that contrast with amber deposits of the Late Cretaceous.

There are other recently discovered but important deposits. The documentation of paleodictyopteroid, protodonatan, and "protorthopteran" insects at Hagen-Vorhalle in Germany now contains some of the earliest known winged insects. Initially described in 1978, the Newark Basin insect fauna of Virginia has confirmed the earliest occurrences of several modern insect families, supporting the unusually long family durations documented by Labandeira and Sepkoski (1993). Although the Middle Eocene Messel deposits have been known since the earlier 1900s, recent discoveries have revealed exquisitely preserved insects that have retained external color patterns and internal gut contents. A flurry of recently described taxa from the Early Miocene Dominican amber now ranks this deposit as the second most abundant amber fauna, revealing examples of arthropod parasitism on insects rarely preserved in the fossil record.

## Works Cited

Bechley, G. 1996. Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata). *Petalura* Special volume, 2:1–402.

Boudreaux, H.B. 1987. *Arthropod Phylogeny with Special Reference to Insects*. Malabar, Florida: Krieger.

Borkent, A. 1995. *Biting Midges in the Cretaceous Amber of North America (Diptera: Ceratopogonidae)*. Leiden: Backhuys.

Briggs, J.C. 1995. *Global Biogeography*. Amsterdam and New York: Elsevier.

Brodsky, A.K. 1994. *The Evolution of Insect Flight*. Oxford and New York: Oxford University Press.

Carpenter, F.M. 1971. Adaptations among Paleozoic insects. *In* E.L. Yochelson (ed.), *Proceedings of the First North American Paleontological Convention*. Lawrence, Kansas: Allen Press.

———. 1992. *Superclass Insecta*. In R.C. Moore, R.L. Kaesler, E. Brosius, J. Kiem, and J. Priesner (eds.), *Treatise on Invertebrate Paleontology*, vol. 3, part R, *Arthropoda 4*. Boulder, Colorado, and Lawrence, Kansas: Geological Society of America and University of Kansas.

Elias, S.A. 1994. *Quaternary Insects and Their Environments*. Washington, D.C.: Smithsonian Institution Press.

Gillott, C. 1995. *Entomology*. 2nd ed., New York: Plenum.

Grimaldi, D.A. (ed.). 1990. Insects from the Santana Formation, Lower Cretaceous, of Brazil. *Bulletin of the American Museum of Natural History* 195:1–191.

Gullan, P.J., and P.S. Cranston. 1994. *The Insects: An Outline of Entomology*. London and New York: Chapman and Hall.

Harland, W.B., R.L. Armstrong, A.V. Cox, L.E. Craig, A.G. Smith, and D.G. Smith. 1990. *A Geologic Time Scale: 1989*. Cambridge and New York: Cambridge University Press.

Hennig, W. 1981. *Insect Phylogeny*. New York and Chichester: Wiley.

Kingsolver, J.G., and M.A.R. Koehl. 1985. Aerodynamics, thermoregulation, and the evolution of insect wings: Differential scaling and evolutionary change. *Evolution* 39:488–504.

Kristensen, N.P. 1991. Phylogeny of extant hexapods. *In* I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, R.W. Taylor, M.J. Whitten, and M.J. Littlejohn (eds.), *The Insects of Australia: A Textbook for Students and Research Workers*. 2 vols. 2nd ed., Ithaca, New York: Cornell University Press; Carlton, Victoria: Melbourne University Press.

———. 1994. Forty years' insect phylogenetic systematics. Hennig's "Kritische Bemerkungen. . . ," and subsequent developments. *Zoologische Beiträge* 36:83–124.

Kukalová-Peck, J. 1987. New Carboniferous Diplura, Monura, Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta). *Canadian Journal of Zoology* 65:2327–45.

————. 1991. Fossil history and the evolution of hexapod structures. *In* I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, R.W. Taylor, M.J. Whitten, and M.J. Littlejohn (eds.), *The Insects of Australia: A Textbook for Students and Research Workers.* 2 vols. 2nd ed., Ithaca, New York: Cornell University Press; Carlton, Victoria: Melbourne University Press.

Labandeira, C.C. 1994. A compendium of fossil insect families. *Milwaukee Public Museum Contributions in Biology and Geology* 88:1–71.

————. 1997. Insect mouthparts: Ascertaining the paleobiology of insect feeding strategies. *Annual Review of Ecology and Systematics* 28:153–93.

Labandeira, C.C., D.L. Dilcher, D.R. Davis, and D.L. Wagner. 1994. Ninety-seven million years of angiosperm-insect association: Paleobiological insights into the meaning of coevolution. *Proceedings of the National Academy of Sciences USA* 91 (12):278–82.

Labandeira, C.C., and T.L. Phillips. 1996. Insect fluid-feeding on Upper Pennsylvanian tree ferns (Palaeodictyoptera, Marattiales) and the early history of the piercing-and-sucking functional feeding group. *Annals of the Entomological Society of America* 89:157–83.

Labandeira, C.C., and J.J. Sepkoski Jr. 1993. Insect diversity in the fossil record. *Science* 261:310–15.

Lawrence, J.F., E.S. Nielsen, and I.M. Mackerras. 1991. Skeletal anatomy and key to orders. *In* I.D. Naumann, P.B. Carne, J.F. Lawrence, E.S. Nielsen, J.P. Spradbery, R.W. Taylor, M.J. Whitten, and M.J. Littlejohn (eds.), *The Insects of Australia: A Textbook for Students and Research Workers.* 2 vols. 2nd ed., Ithaca, New York: Cornell University Press; Carlton, Victoria: Melbourne University Press.

Marden, J.H., and M.G. Kramer. 1994. Surface-skimming stoneflies: A possible intermediate stage in insect flight evolution. *Science* 266:427–30.

Poinar Jr., G.L. 1992. *Life in Amber.* Stanford, California: Stanford University Press.

Preston-Mafham, R., and K. Preston-Mafham. 1993. *Encyclopedia of Land Invertebrate Behavior.* Cambridge, Massachusetts: MIT Press; London: Blandford.

Raff, R.A. 1996. *The Shape of Life.* Chicago: University of Chicago Press.

Rohdendorf, B.B. (ed.). 1973. The history of paleoentomology. *In* R.F. Smith, T.E. Mittler, and C.N. Smith (eds.), *History of Entomology.* Palo Alto, California: Annual Reviews.

————. 1991. Arthropoda, Tracheata, Chelicerata. *In* Y.A. Orlov (ed.), *Fundamentals of Paleontology.* S. Viswanathan (trans.) 9:1–894.

Rohdendorf, B.B., E.E. Becker-Migdisova, O.M. Martynova, and A.G. Sharov. 1961. Paleozoic insects from the Kuznetsk Basin. *Transactions of the Paleontological Institute* 85:1–705. [in Russian]

Rohdendorf, B.B., and A.P. Rasnitsyn. 1980. Historical development of the class Insecta. *Transactions of the Paleontological Institute* 175:1–270. [in Russian]

Sharov, A.G. 1966. *Basic Arthropodan Stock, with Special Reference to Insects.* Oxford and New York: Pergamon.

Shear, W.A., and J. Kukalová-Peck. 1990. The ecology of Paleozoic terrestrial arthropods: The fossil evidence. *Canadian Journal of Zoology* 68:1807–34.

Snodgrass, R.E. 1935. *Principles of Insect Morphology.* New York and London: McGraw-Hill.

Wägele, J.W. 1993. Rejection of the "Uniramia" hypothesis and implications of the Mandibulata concept. *Zoologisches Jahrbuch, Systematik* 120:253–88.

Wootton, R.J. 1981. Palaeozoic insects. *Annual Review of Entomology* 26:319–44.

## Further Reading

Boudreaux, H.B. 1987. *Arthropod Phylogeny with Special Reference to Insects.* Malabar, Florida: Krieger.

Brodsky, A.K. 1994. *The Evolution of Insect Flight.* Oxford and New York: Oxford University Press.

Carpenter, F.M. 1992. *Superclass Insecta.* *In* R.C. Moore, R.L. Kaesler, E. Brosius, J. Kiem, and J. Priesner (eds.), *Treatise on Invertebrate Paleontology,* vol. 3, part R, *Arthropoda 4.* Boulder, Colorado, and Lawrence, Kansas: Geological Society of America and University of Kansas.

Gillott, C. 1980. *Entomology.* New York: Plenum; 2nd ed., 1995.

Gullan, P.J., and P.S. Cranston. 1994. *The Insects: An Outline of Entomology.* London and New York: Chapman and Hall.

Hennig, W. 1981. *Insect Phylogeny.* New York and Chichester: Wiley.