

# PALEOBIOLOGY OF PREDATORS, PARASITOIDS, AND PARASITES: DEATH AND ACCOMODATION IN THE FOSSIL RECORD OF CONTINENTAL INVERTEBRATES

CONRAD C. LABANDEIRA

Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0121 and Department of Entomology, University of Maryland, College Park, Maryland 20742 USA

**ABSTRACT**—Carnivory is the consumption of one animal by another animal; among invertebrates in terrestrial and freshwater ecosystems this type of feeding can take three forms: predation, parasitoidism, and parasitism. Differences among these three functional modes involve (i) whether the duration of feeding on the prey item is quick or there is an accommodation, coevolutionary or otherwise, between the carnivore and the host prey; (ii) whether the prey or host is killed; (iii) whether single or multiple prey or host items are consumed during the carnivore's lifespan, and (iv) the relative sizes of the carnivore and its prey or host. Uniformitarian and nonuniformitarian evidence directly relating to the history of carnivory can be found in exceptionally preserved deposits from the mid-Paleozoic to the Recent, but such evidence is relatively rare because carnivores are the least represented trophic group in ecosystems. Six types of paleobiological data provide evidence for carnivory: taxonomic affiliation, fossil structural and functional attributes, organismic damage, gut contents, coprolites, and indications of mechanisms for predator avoidance.

Only 12 invertebrate phyla have become carnivorous in the continental realm. Six are lophotrochozoans (Acanthocephala, Rotifera, Platyhelminthes, Nemertinea, Mollusca, and Annelida) and six are ecdysozoans (Nematoda, Nematomorpha, Tardigrada, Onychophora, Pentastoma, and Arthropoda). Most of these groups have poor continental fossil records, but the two most diverse—nematodes and arthropods—have comparatively good representation. The record of arthropods documents (i) the presence of predators among primary producers, herbivores, and decomposers in early terrestrial ecosystems; (ii) the addition later in the fossil record of the more accommodationist strategies of parasitoids and parasites interacting with animal hosts; (iii) the occurrence of simpler food-web structures in terrestrial ecosystems prior to parasitoid and parasite diversification; and (iv) a role for mass extinction in the degradation of food-web structure that ultimately affected carnivory. Future research should explore how different modes of carnivory have brought about changes in ecosystem structure through time. Despite numerous caveats and uncertainties, trace fossils left by predators on skeletons of their prey remain one of the most promising research directions in paleoecology and evolutionary paleobiology.

## INTRODUCTION

"The distinctive element is that in many, but not all, of the predaceous forms the female eats the male while mating is in progress, by piercing the cuticle and dissolving and sucking out the body contents as with any other small insect prey [Fig. 1a]..."

"...The female [of *Probazzia concinna*] attacks the male through the head, the only part of the body the proboscis can reach, and the whole process of injection of the lytic saliva and intake of the liquefied tissues takes place at this one site. [T]he male ... was reduced to an empty and dry cuticle

only. When the female moved away however, the [male's] cuticle broke at the membrane between the 6th and 7th abdominal segments, leaving the torn off terminalia attached to the female in the mating position [Fig. 1b].

"...In the male of the predaceous midges destruction of the head by the saliva of the female, soon after mating is established, appears to result in a sustained copulatory position maintained until the tissues of the male have been entirely consumed, and even longer."

—J. A. Downes (1971a, p. 38–39)  
(Brackets added.)

THE POET TENNYSON described nature as "red in tooth and claw," a metaphoric and seemingly apt description of predation. His image of vertebrates dispatching other vertebrates by the use of carnassials and talons, however, is clearly exceptional, considering where the preponderance of terrestrial carnivory resides; this picture should be replaced by the equally grisly image of hemolymph-encrusted mouthparts and tarsi—for it is among the invertebrates, and particularly the arthropods, where the overwhelming bulk of carnivory occurs in terrestrial settings. The above quotation from Downes (1971a) about predation in the biting midge *Probezzia* is emblematic of the invertebrate world, which forms an important part of the trophic capstone in terrestrial food webs. In this contribution, the fossil history of terrestrial invertebrate carnivory is explored, with a focus on arthropods and especially insects. The discussion includes examples from both freshwater and terrestrial environments, both of which belong to the continental realm. This paper begins with a definition of carnivory and its subcategories, then addresses the nature of the fossil evidence, enters into a discussion of the historical pattern of carnivory, delves into four salient issues regarding its evolution, and ends in a summary. The brevity of this review does not allow for adequate coverage of all relevant issues, and it is hoped that the interested will consult the cited references for additional information and insight.

## THE NATURE OF CARNIVORY

There are three basic types of carnivory: predation, parasitoidism, and parasitism (Vinson and Barbosa, 1987). All three comprise the third trophic level characterized by the consumption of organisms, especially of herbivores and other carnivores. The ultimate basis of carnivory is in primary producers whose energy originates either from the sun (photoautotrophs) or the chemical bonds of oxidized compounds (chemoautotrophs). Primary producers provide food, via herbivores and eventually carnivores, for the sustenance of food webs. This trophic pyramid, together with a crucial side-loop for organisms that degrade all types of

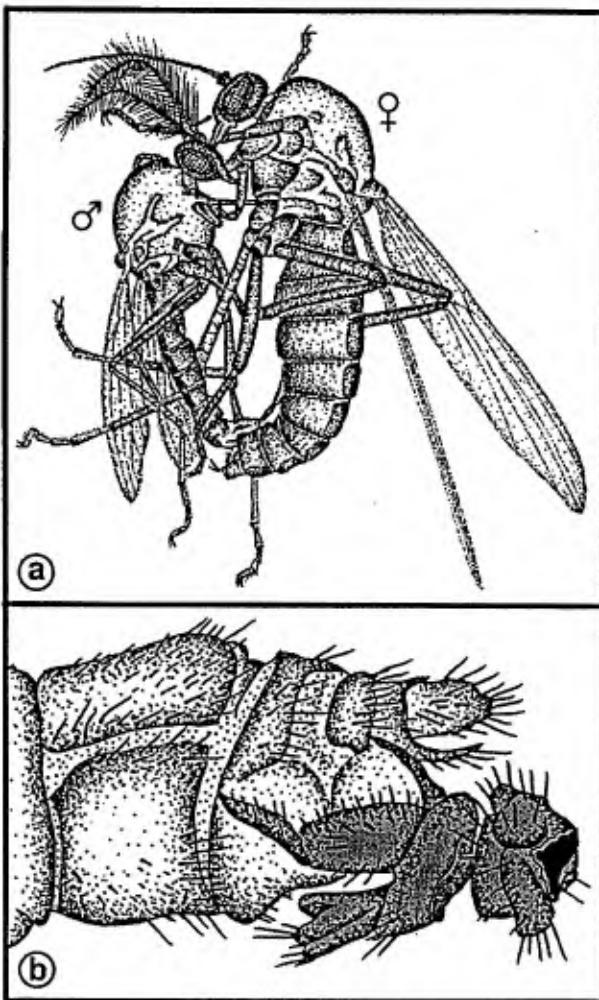


FIGURE 1—A, Two biting midges of *Probezzia concinna* (Diptera: Ceratopogonidae), *in copulo* with the female simultaneously feeding on the male through a single puncture of his head capsule. B, Posterior female abdomen of a closely related genus, *Palpomyia*, after mating, with attached, torn-off male genitalia in light-grey shading. Both redrawn from Downes (1971a).

dead tissues (sapropes), is characterized by a typical 90 percent loss in biomass and energy assimilated at each interface between levels (DeAngelis, 1992). Interestingly, this decrease in mass and energy transferred between adjacent levels is also evident for each trophic type in the fossil record. Records of carnivory are much scarcer than records of plant-herbivore associations (Labandeira, 2002a).

Invertebrates in general, and insects in particular, dominate continental food webs; among insects, approximately 50 percent of all species are herbivorous and 25 percent are predaceous (Hagen, 1987; Wilson, 1992). Site-specific studies provide similar values (Erwin and Scott, 1980). Nevertheless, the comparative scarcity of evidence for carnivory in fossil assemblages should not belie the intricate, diverse, and fascinating roles played by predation, parasitoidism, and parasitism in continental ecology during the past 420 million years. It is for this reason that an understanding of these three types of feeding strategies, subsumed under “carnivory,” is important.

The common conception of predation involves a consumption of prey resulting in the victim’s death. Predation is defined as the total or near-total consumption of a live organism (Price, 1980), but also includes suspended zooplankton in aquatic systems (Merritt and Cummins, 1984), plant organisms such as seeds (Janzen, 1978), and pollen or spores (Fuchs, 1975). Both seed predation and palynivory are nutritionally important for many continental arthropods (Proctor et al., 1996), and represent feeding strategies that are distinct from typical herbivory, which is characterized by survival of the host plant. Conventional continental predators are animals that directly and immediately consume other animals (Hagen, 1987; Sih, 1987), although trophically equivalent modes are seen in fungi (Evans, 1989) and even plants (Juniper, 1986) that slowly dispatch their animal prey. Organisms that feed on invertebrate prey more slowly and incompletely are known as parasitoids (Godfray, 1994); in parasitoidism, a relatively long-lived host is eventually consumed and dies. A third type of carnivory is parasitism (Schmid-Hempel, 1998), characterized by multiple hosts that survive and are only partially consumed. Consumption of vegetative tissues which does not result in the death of the host plant has also been termed parasitism (Schoonhoven et al., 1998), but is excluded here because of its equation with herbivory in the literature and its status as the contrasting trophic mode to carnivory. Additionally, the consumption of suspended plankton and benthic films in aquatic

systems by microvorous filter feeders, sievers, and scrapers includes the consumption of minute animals, but is often ecologically equated with herbivory and will not be treated here further (see Merritt and Cummins, 1984).

The life histories of parasitoids are ecologically transitional between predators—which rapidly consume multiple and often unrelated individuals during a lifetime—and parasites, which feed through several generations on a near-infinite food resource from mostly single, generally surviving individuals (Price, 1980; Vinson and Barbosa, 1987). Thus, parasitoids pursue an ecologically intermediate strategy of feeding generally on a predictable and finite food resource consisting of a single host that is eventually killed; moreover, they are characterized by a life cycle that includes a free-living reproductive stage whose habitat is separate from that of the developing larva (Yeates and Greathead, 1997). Additional distinctions between predators and parasites help to define the role of parasitoids. Whereas predators are similar in size to their prey, parasites are quite small compared to their hosts. Also, predators typically are generalized feeders that acquire and dispatch their prey by force; but parasites generally are tissue specialists that are often coevolved with their hosts. Lastly, predators are characterized by fewer and broader ecological niches than are specialist parasites, which typically partition monospecific hosts into multiple microhabitats. The host-accommodation exhibited by parasites and parasitoids, in contrast to the rapid consumption of prey by predators, is a major theme in the evolutionary history of invertebrate carnivory in continental ecosystems.

## **TYPES OF EVIDENCE**

Much of our understanding of the paleobiology of carnivory is inferential, relying on imperfect preservation, circumstantial evidence, and rare insights gleaned by way of unique and spectacular modes of preservation. These data are principally derived from Fossil-Lagerstätten such as silicified hot-spring deposits, sideritic nodules within organic shales, ambers, and lacustrine oil shales that have particular spatiotemporal distributions in

the 420-million-year continental invertebrate record. These and more typical deposits (Figs. 1, 2) provide six types of evidence for carnivory: taxonomic affiliation, structural and functional attributes, organismic damage, gut contents, coprolites, and mechanisms of predation avoidance—all but the last of which are analogous to those cited for recognition of arthropod herbivory (Labandeira, 1998b, 2002a). Of these types of evidence, taxonomic affiliation is most often used, whereas coprolites from vertebrate or insect carnivores are rarely reported (Thulborn, 1999). Functional and structural attributes as well as damage to organisms are more frequent in the fossil record, but have been underused for inferring diets and life habits. Gut contents provide a “smoking gun” by establishing both the carnivore and its prey, but are rarely preserved. Mechanisms of carnivore avoidance, such as mimicry, spines, large size, larval cases, and the presence of auditory tymbals for avoiding aerial predators are recognizable from analogous patterns in the modern world, but become more problematic deeper in the fossil record (Labandeira, 2002a). In fact, the applicability of taxonomic uniformitarianism for understanding carnivory decreases into the geologic past, and must be supplemented or supplanted by other, intrinsic approaches such as structural and functional attributes or gut contents.

*Taxonomic Affiliation.*—Obvious invertebrate clades that are pre-eminent carnivores are the Chilopoda (centipedes), Araneida (spiders), Odonatoptera (dragonflies and damselflies), Mantodea (mantises), the Raphidioptera, Megaloptera, and Planipennia (snakeflies, alderflies, lacewings, and relatives), the Carabidae (ground beetles), Dytiscidae (predaceous diving beetles), and Asilidae (robber flies) (Fig. 2J), among many others. For these taxa, which have phylogenetic continuity to the present day, a taxonomic uniformitarian approach is valid. An extensive literature has documented the obligate dependence of these extant groups on live prey (Withycombe, 1922; Clausen, 1940; Brues, 1972; Sih, 1987; Hagen, 1987; Foelix, 1996; Corbet, 1999). A uniformitarian approach is also applicable to fossil representatives of animal

endoparasites such as tylenchid and mermithid nematodes, which consume live internal tissues (Poinar, 1991; Weitschat and Wichard, 1998); and ectoparasitic lice (Fig. 2H) and fleas (Fig. 2L), which feed on dermal and subcutaneous tissues. Much discussion of extant carnivory is centered on mouthpart structures and their association with diet (reviewed in Labandeira, 1990) and behavior, drawing inferences from functional morphology. In diverse taxa that encompass multiple diets and feeding strategies and larval stages—for example, leiodid and meloid beetles, and ants—a finer taxonomic resolution is necessary for certitude in dietary assignments.

There are instances in which prey and carnivore are preserved in conjunction, especially in single pieces of amber (Weitschat and Wichard, 1998; Kutscher and Koteja, 2000a), and frequently involving ants as predators. Many of these examples represent predator-prey interactions that occur today. Perhaps the ultimate direct demonstrations of carnivory are those samples of Baltic amber in which a predatory ant is grasping a scale insect with its mandibles (Kutscher and Koteja, 2000b), or a spider is grasping a captured ant (Weitschat and Wichard, 1998). Other samples preserve parasites or parasitoids exiting the body cavity immediately after envelopment by resin (Weitschat and Wichard, 1998; Poinar and Poinar, 1999). Lastly, there are amber specimens where ectoparasites such as mites or nematodes are entombed with mouthparts firmly attached to their host's intersegmental membrane (Poinar et al., 1994a, 1997; Weitschat and Wichard, 1998), or displaying body distension due to engorgement of host hemolymph (Poinar et al., 1991).

*Structural and Functional Attributes.*—Continental invertebrates possess several structures that indicate carnivorous habits. Prominent among these are mouthparts. Also included are body shape, the presence of attachment suckers, auditory tympanal organs, spider spinnerets, specializations of the legs, ovipositor type, and cerci. Among mandibulate hexapods, head mobility and forwardly positioned mouthparts are associated with predation (Walker, 1932), as are mandibles

characterized by incisiform and shearing teeth rather than broad molar shelves for grinding (Samways et al., 1997). In insects with stylate mouthparts, such as flies with piercing-and-sucking beaks, serrate or barbed mandibular stylets or blades indicate hematophagy (blood feeding) (Borkent, 1995; McKeever et al., 1991). Additionally, elongate and falcate mandibles that are distally curved are almost always borne by predators, some of which display a complicated “trap jaw” mechanism such as larval antlions and many adult ants (Korn, 1943; Gronenberg, 1996). Other types of mouthparts are fashioned as co-coordinated multielement structures that can be hurled at prey immediately anterior of the head, such as the labial mask of aquatic odonatopterans (Pritchard, 1976) or the adhesive labial sling of some terrestrial rove beetles (Betz, 1996), both of which demonstrate obligate predation. Although it is the mouthparts of invertebrates that most directly interact with prey, other external appendicular structures are used to subdue potential victims, including raptorial prothoracic legs armed with spines in Mantodea, cerci modified into forceps in japygid Diplura (telson tails), ovipositors designed to penetrate arthropod hosts for insertion of parasitoid eggs (Fig. 2F), or chelate tarsi used for grasping hair among ectoparasites of warm-blooded tetrapods (Askew, 1979; Godfray, 1994) (Fig. 2E). Additionally, extrasomatic structures may reveal carnivory, such as nits, or eggs glued to hair shafts, that are deposited by ectoparasitic lice (Weitschat and Wichard, 1998) (Fig. 2K). Other fossilizable structures produced by carnivores are silk webs that ensnare potential prey (Bachofen-Echt, 1934; Gerhard and Rietschel, 1968; Weitschat and Wichard, 1998). The body structures responsible for spider silk have a record extending back to the Middle Devonian (Shear et al., 1989a) (Fig. 2B).

**Organismic Damage.**—Carnivory can result in many kinds of damage to continental invertebrates. This damage can occur on the prey or host or alternatively on the carnivore itself, and includes teratologies (abnormal growths) (Poinar and Poinar, 1999), amputated appendages or broken body processes (Petrunkewitch, 1942; Rolfe, 1985;

Hannibal and Feldman, 1988), small exit holes of parasitoids from cocoons (Houston, 1987; Bown et al., 1997) (Fig. 2N), prey items wrapped by spider silk (Weitschat and Wichard, 1998), excavated soft tissue of arthropods consistent with predation (Poinar, 1999a), and refuse accumulations of discarded victim carcasses (Abel, 1935; Weitschat and Wichard, 1998). These examples involve unusual removal or alteration of tissue that results from both unsuccessful and successful predation attempts; and they indicate the behavior of a predator located at a stationary site for an extended time. Although plant rather than animal individuals are killed, there is a fossil history of seed predation extending to the Late Paleozoic (Zherikhin, 1989; Labandeira, 2002a), characterized by various modes of removal of endosperm or its nutritive equivalent in plants (Sharov, 1973; Genise, 1995; Mikulas et al., 1998) (Fig. 2M). An analogous situation is that of palynivory (Fig. 2A) (Labandeira, 1998b, 2000).

**Gut Contents.**—Instances of terrestrial invertebrates preserved in the digestive tracts of predators are extremely rare in the fossil record. Regurgitated gut contents have been identified in macerated material from the Middle Devonian Gilboa deposit in New York State and are attributed to trigonotarbid arachnids (Gray and Shear, 1992). Large carnivorous insects such as protodonatan dragonflies should reveal boluses of insect-bearing material, but due to the rarity of preserved and intact soft tissues, only one specimen is known: a terminal abdomen with a dark, oval mass within the last segment (Durden, 1988). The best examples of gut contents in the fossil record come from mammals of the middle Eocene Messel oil shale of Germany. This diverse assemblage contains gut contents from several archaic antecedents of extant mammalian orders. They include the bat *Palaeochiropteryx* that preyed on beetles and especially primitive moths and butterflies active at night, dawn, or sunset (Franzen, 1985) (Fig. 2I); the hedgehog *Pholidocercus*, whose stomach contents include beetles and other types of insects (Von Koenigswald et al., 1992); and the anteater *Eotamandua*, an avid consumer of termites, among other insects (Storch and Richter, 1992). It

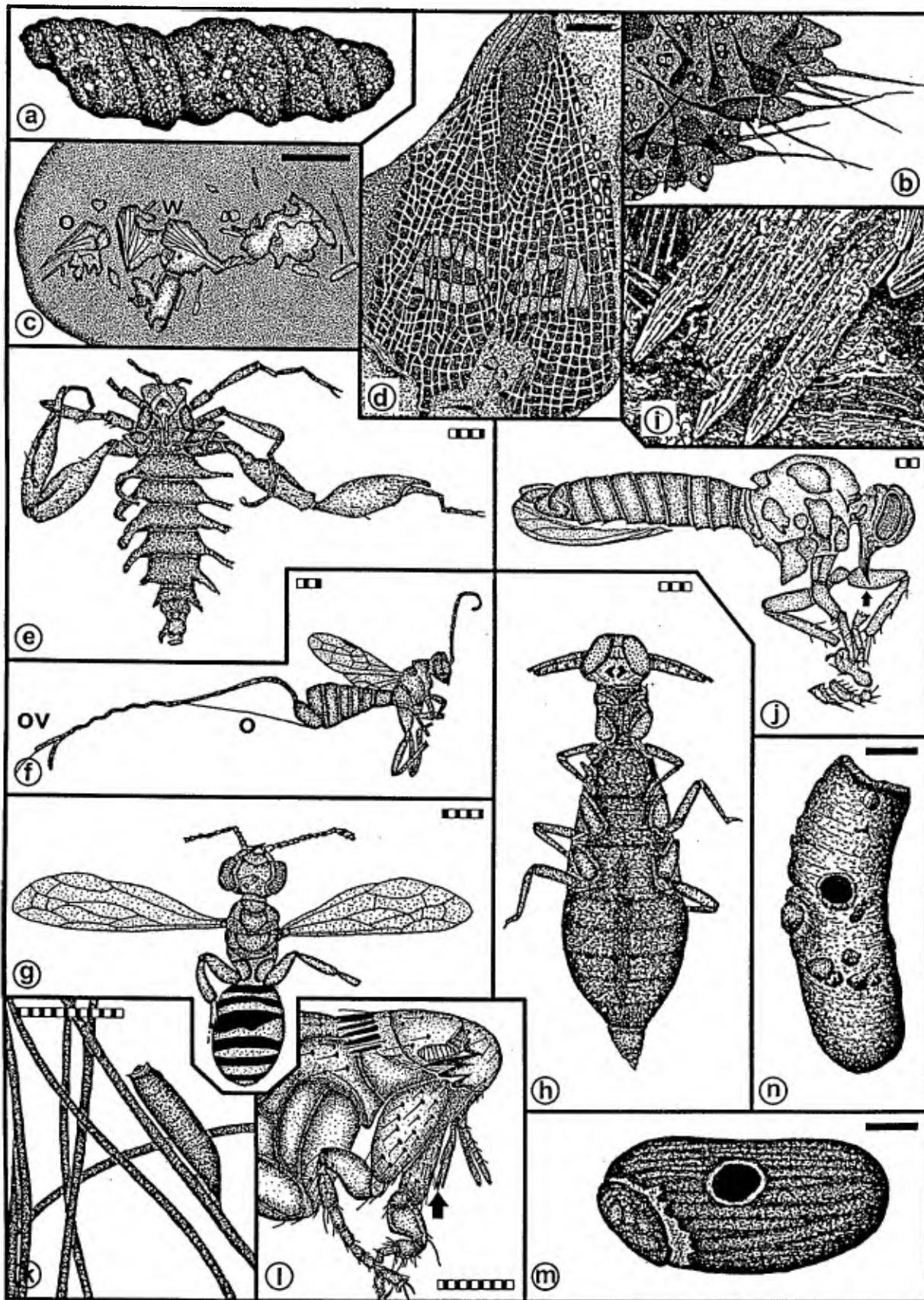


FIGURE 2

is clear that anaerobic sealing of these carcasses resulted in exceptional preservation and promoted in particular the preservation of chitin, thus providing rare dietary data on early insectivorous mammals (Richter, 1992).

**Coprolites.**—Vertebrate-produced coprolites that contain identifiable terrestrial invertebrates are, like gut contents, rare in the fossil record. The best examples come from the Late Paleozoic. For example, from the Upper Carboniferous (Moscovian) Mazon Creek site in north-central Illinois, Fischer (1979) reported coprolites that

contained disarticulated sclerites of scorpions, millipedes, and cockroaches, indicating a terrestrial but unknown predator. Occasionally, coprolites with fragmented insect material contain dismembered elements that reveal morphological structures otherwise difficult to observe in insect body fossils (Fig. 2C). For example, from lowermost Permian deposits in central Kansas, coprolites laden with euphorberiid millipede sclerites, some still articulated, have been described by Hannibal and Feldman (1988). A more recent occurrence of carnivore coprolites is described in Richter and



FIGURE 2—Evidence from taxonomic affiliation (F,H,J–L), structural and functional attributes (B,E,F,H,J,L), organismic damage (M,N), gut contents (I), coprolites (A,C), and predation avoidance (D,G) for insect carnivory in the fossil record. Examples of carnivory are predation (A–D,G,I,J,M), parasitoidism (F,N), and parasitism (E,H,K,L). A, A coprolite containing early land-plant spores from the Lower Devonian (Lochovian) of Wales; from Edwards et al. (1995). Approximate coprolite length: 1.5 to 2.0 mm. B, A fossil spider spinneret, showing a cluster of attached and detached spigots, from the Middle Devonian (Givetian) of Gilboa, New York; from Shear et al. (1989a). Horizontal length (excluding spigots): 0.24 mm. C, Vertebrate coprolite containing remains of a cockroach, including wings (w), legs (l) and ovipositor (o) from the middle Pennsylvanian Mazon Creek locality of Illinois (FMNH PE 54114). D, From the same locality as (C), the insect *Protodiamphipnoa woodwardi* Brongniart (Protorthoptera: Cnemidolestidae), with prominent eyespot on forewing; from Carpenter (1971). E, The enigmatic mecopteroid insect, *Strashila incredibilis* Rasnitsyn (Mecopteroidea: Strashilidae), from the Upper Jurassic (?Oxfordian) of Transbaikalia, Russia, showing ectoparasitic structures such as a chelate hind tarsus, suctorial beak, and absence of wings; from Rasnitsyn (1992). F, The parasitoid wasp *Leptephialtites caudatus* Rasnitsyn (Hymenoptera: Ephialtidae) from the Upper Jurassic (Kimmeridgian) of Karatau, Kazakhstan, with elongate ovipositor (o) and ovipositor valves (ov); from Rasnitsyn (1975). G, The digger wasp *Palaeapis beiboziensis* Hong (Hymenoptera: Sphecidae) from the Jurassic-Cretaceous boundary of China, bearing an abdomen with contrasting color-banding and typical of a Batesian model; from Hong (1984). H, The chewing louse *Sauvadectes vrsanskyi* Rasnitsyn and Zherikhin (Phthiraptera: Mallophaga: Sauvadectidae), from the Early Cretaceous (Berriasian) of Baissa, Transbaikalia, Russia; from Rasnitsyn and Zherikhin (1999). I, Gut contents of the middle Eocene bat *Palaeochiropteryx tupaiodon* Revilliod (Chiroptera: Palaeochiropterygidae) from Messel, Germany, exhibiting butterfly scales and other insect fragments; from Richter and Storch (1980). Approximate length of scale at right: 90 µm. J, Robber fly (Diptera: Asilidae) from the Piceance Creek Basin of the Green River Formation of Colorado (USNM 501477), showing raptorial forelegs and mouthparts of a single, dagger-like stylet (arrow). K, The nit (egg) of an undetermined sucking louse (Phthiraptera: Anoplura) on a shaft of mammalian hair, from late Eocene Baltic amber of Germany; from Voigt (1952). L, The mammal-parasitizing flea, *Palaeopsylla klebsiana* Dampf (Siphonaptera: Hystrichopsyllidae) from the same deposit as (K), showing the socketed antennae, head comb, and maxillary lever/stylet fascicle (arrow) typical of many ectoparasitic insects; from Dampf (1910). M, Seed of *Tectocarya rhenana* (Cornaceae), with exit hole of a seed predator, from the Miocene (Aquitanian) Braunkohle of Germany; from Schmidt et al. (1958). N, A bee cell (Hymenoptera: Stenotritidae) from the Pleistocene of South Australia, displaying a small exit hole of a probable parasitoid; from Houston (1987). All subfigures are redrawn from original photographs or line drawings, or are from camera-lucida sketches of specimens. Scale bars: solid = 1.0 cm, striped = 0.1 cm. FMNH = Field Museum of Natural History; USNM = National Museum of Natural History.

Baszio's (2001) report of fish coprolites with terrestrial arthropod remains, including insects, from the middle Eocene Messel Deposit of Germany.

*Mechanisms of Predation Avoidance.*—There are two broad classes of defense strategies by means of which terrestrial invertebrates avoid predation. First, there are those that involve resemblance of a potential prey's external body to another organism or aspect of its ambient environment. Second, there is physical deterrence based on increasing the level of difficulty for predation, exemplified by the presence of spines. Instances of the resemblance of one organism to another in color, overall form, or behavior are well documented among modern insects, and are likewise represented in the fossil record. The three basic types of protection are mimicry (both Batesian and Müllerian versions), warning coloration, and crypsis (Price, 1997). For mimicry, the fossil record provides few clues to distinguish the Batesian type, where a palatable mimic resembles an unpalatable model, from the Müllerian type, where both the mimic and the model are distasteful or otherwise negatively affect the predator. However, in some fossil examples, determination of mimicry can be approached by modern analogy (Jarzembski, 1989). One example is the distinctive color banding on the digger wasp *Palaeapis* from the Jurassic-Cretaceous boundary of China (Hong, 1984) (Fig. 2G), which probably was a model. Another example, the soldier fly "Stratiomys" from the late Eocene of southern England (Jarzembski, 1976), likely was a mimic. Other instructive examples of the use of color and pattern for protection include the disruptive coloration—with light and countershaded dark patterns—on the wings of canopy-inhabiting paleodictyopteroid insects, presumably to enhance concealment when viewed from below, or perhaps representing an example of aposematic (warning) coloration for potential dragonfly predators from above (Shear and Kukalová-Peck, 1990). Additionally, there is a fossil record of distinctive wing eyespots, which function in extant insects to inflate apparent size and to startle predators (Preston-Mafham and Preston-Mafham, 1993). Such warning coloration occurs in a protorthopteran from the Late

Carboniferous at Mazon Creek (Carpenter, 1971) (Fig. 2D), as well as throughout the later Mesozoic in the planipennian family Kalligrammatidae, a butterfly-like lineage in which some species bore prominent eyespots (Panfilov, 1968; Jarzembski, 1984). Unlike mimicry and warning coloration, crypsis (camouflage) in the fossil record has faced a more checkered interpretation: one of the best examples is the resemblance of Late Carboniferous cockroach wings to seed-fern pinnules, first noted by Scudder (1895). Subsequent observers such as Pruvost (1919) and North (1931) expanded the taxonomic scope of this pinnule similarity by extending it to orthopteroid insects. The resemblance of cockroach forewings to seed-fern pinnules, however, is more likely attributable to structural convergence—based on biomechanical principles for the support of planated structures—than to protective camouflage (Shear and Kukalová-Peck, 1990; Jarzembski, 1994). A similar criticism can be applied to Fischer's (1979) argument regarding the subaerial occurrence of the horseshoe crab *Euproops* and its proposed concealment amid leafy *Lepidodendron* shoots, whose elongate leaves resemble the animal's carapace spines. The most perplexing possible occurrence of crypsis is the leaf-like color patterns on the tegmina of the Middle Triassic grasshopper *Triassophyllum* (Papier, et al., 1997), which resembles certain fern leaves with angiosperm-like venation.

Evidence of defenses against predators involving spines, large size, and protective domiciles occurs sporadically throughout the fossil record. From the Upper Carboniferous, the herbivorous Mazon Creek form *Gerarus* bore robust and radiating prothoracic spines that evidently functioned for predation deterrence (Shear and Kukalová-Peck, 1990), a feature found in modern tropical grasshoppers and other insects. In the same deposit and throughout the Late Carboniferous, many terrestrial arthropods achieved great size, including arthropleurid myriapods, the arachnid *Megarachne*, paleodictyopteroids, protodonatan dragonflies, and even Diplura and Zygentoma (silverfish) (Dudley, 1998). Although this gigantism is ultimately attributable to atmospheric oxygen

levels (Dudley, 1998), a predator-prey arms race could have developed in which not only insect predators approached the physiological upper limits of arthropod size, but so did their prey (Vermeij, 1987; Graham et al., 1995). A third mechanism of physical defense is the construction of larval cases, which may be used to shield against carnivores. This mode of larval living is standard in fossil and extant caddisflies (Sukacheva, 1982), bagworms (Weitschat and Wichard, 1998), coleophorid moths (Labandeira, 2002b), and certain chrysomelid beetles (Poinar, 1999a). Nevertheless, one of the most intriguing recent investigations focuses on the geochronology of nocturnal bat predation on large moths, based on these insects' ultrasound-detecting tympanal structures, or "ears," that are located on their metathoraces, legs, and mouthparts (Göpfert and Wasserthal, 1999; Fullard and Napoleone, 2001). These ultrasound-perceiving tympanal organs, which alert the moth to the presence of echolocating insectivorous bats, are prime evidence for predator avoidance strategies. Although other evidence suggests that this system existed by the middle Eocene (Richter and Storch, 1980), pre-Eocene bats are unknown, as is the structure of fossil moth tympanal ears.

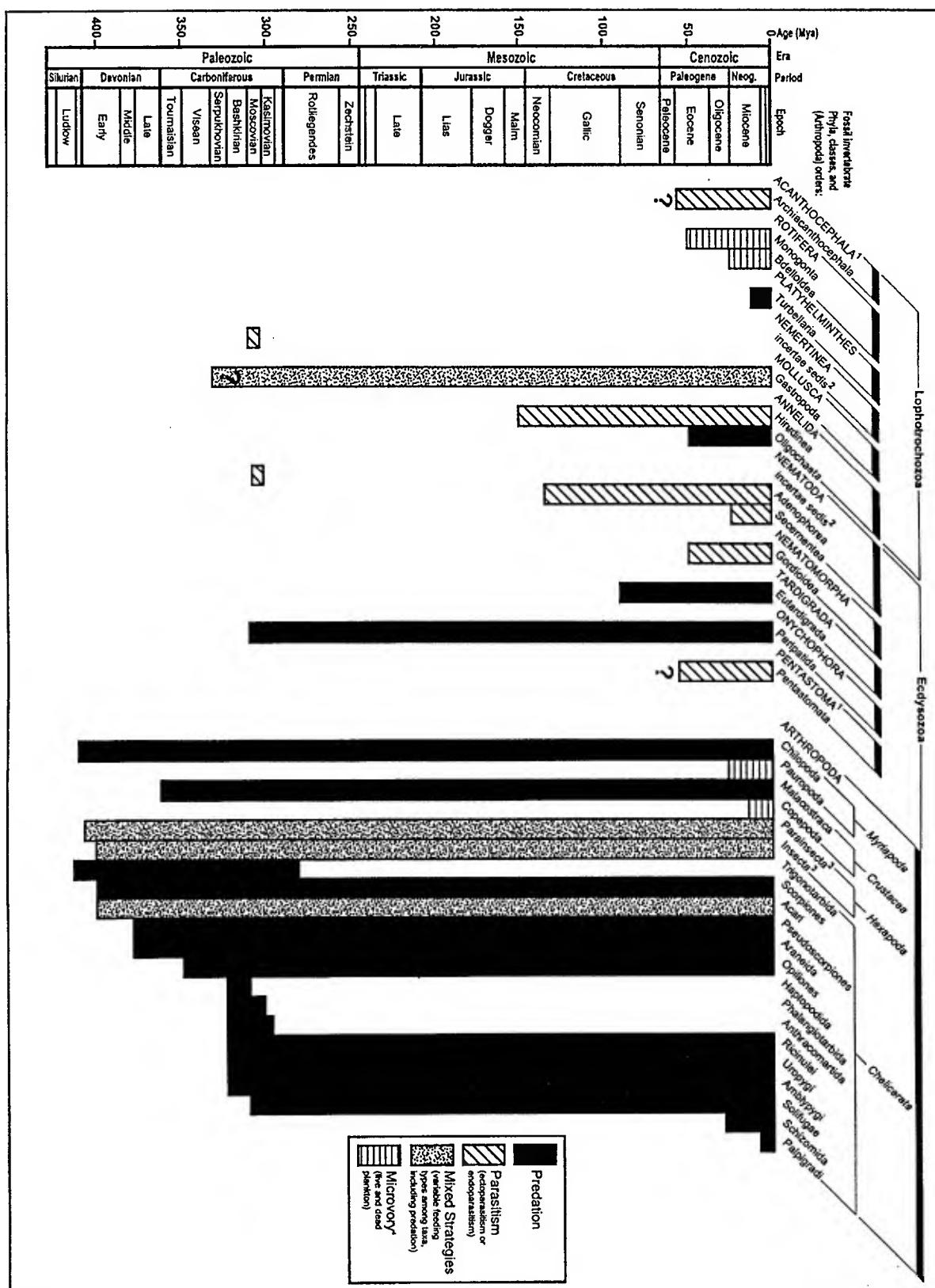
## PATTERNS OF CARNIVORY AMONG CONTINENTAL PHYLA

Of the approximately 40 extant and extinct phyla, only 12 have invaded the continental realm of freshwater and land habitats, and of these only a few have any significant species-level diversity—principally nematodes, molluscs, annelids, and, spectacularly, arthropods. These invertebrates have excelled at life on land (Fig. 3), although all have a marine origin, based on physiological, paleontological, or phylogenetic data (Conway Morris, 1981; Little, 1990; Gordon and Olson, 1995; Fortey and Thomas, 1998). These twelve phyla are assigned to two superphyla (Aguinaldo et al., 1997; Ruiz-Trillo et al., 1999): the Lophotrochozoa, characterized by the presence or a derivative of the trochophore larva; and the Ecdysozoa, characterized by the key developmental innovation of molting. The origin of

terrestrial carnivory is represented in all twelve phyla, but there are in fact multiple independent origins within subclades of these phyla. For example, within the Crustacea alone—conventionally ranked as a subphylum of the Arthropoda—the Ostracoda, Branchiopoda, Amphipoda, Isopoda, and several lineages within the Decapoda have each developed carnivory and either a facultative or obligate continental existence (Little, 1983).

With the exception of the arthropods and probably nematodes, all invertebrate continental phyla have poor fossil records. Intriguingly, the Acanthocephala and Pentostoma, extant members of which are endoparasitic on mammals, do not occur in the fossil record, but are thought to have originated in marine habitats during the earlier Cambrian, based on sister-group relationships (Conway Morris and Crompton, 1982) and a remarkable early Paleozoic record (Andres, 1989; Walossek and Müller, 1994; Walossek et al., 1994). Similarly, the Tardigrada and Onychophora, though today free-living and carnivorous, have their earliest occurrences in the Cambrian marine realm (Müller et al., 1995; Conway Morris, 1998), but appear, respectively, in Late Paleozoic compression deposits (Thompson and Jones, 1980; Rolfe et al., 1982) and Late Mesozoic amber (Cooper, 1964; Bertolani and Grimaldi, 2000). For other nonarthropodan phyla, early fossil documentation is limited to either systematically unassignable or questionably attributed Late Paleozoic finds (Nemertinea, Nematoda, Mollusca) or to mid-Mesozoic earliest occurrences of modern classes (Annelida). The phyla with the poorest and most recent (Cenozoic) fossil records are the Platyhelminthes, Rotifera, and Nematomorpha, and their fossil representatives are referable to extant families and even genera (Fig. 3) (Wills, 1993).

Structural specializations related to feeding on other animals are varied and have evolved multiple times in both the Lophotrochozoa and Ecdysozoa. Predation and parasitism were common during the early terrestrialization of these twelve phyla, as there is no evidence for the direct transfer of aquatic filter feeding and epibenthic or infaunal detritivory into terrestrial habitats (Little, 1990). In this realm, the



**FIGURE 3**

## LABANDEIRA—PREDATORS, PARASITOIDS, AND PARASITES

Lophotrochozoa display the most varied strategies for predation: two phyla use cutaneous absorption through the body wall (platyhelminth flukes and tapeworms, acanthocephalans); one group uses modifications of a distinctive oral device, the radula (pulmonate gastropods); another group produces copious amounts of pharyngeal mucus to ensnare prey, with or without an oral circlet of buccal cilia or hooks (oligochaete annelids); hirudinean annelids (leeches) use their distinctive oral armature of slicing jaws in conjunction with a suction apparatus; and a last group (other leeches, nemertineans) houses stylets within an eversible proboscis. By contrast, the Ecdysozoa displays a more uniform pattern of predation and parasitism. Proboscides with protractile chitinous stylets involved in fluid feeding are found in some nematodes (one stylet), tardigrades (two stylets), and larval pentastomes and nematomorphs (three stylets), housed in a mouthcone or tubular rostrum (Brusca and Brusca, 1990). Other ecdysozoan feeding apparatuses include the three or more radially symmetrical jaw-like structures in some nematodes; the two pairs of slicing, chitinous jaws in onychophorans; the chelicerae and pedipalps of arachnids; and especially the primitively adducting/abducting mandibles of crustaceans, myriapods, and hexapods. The mouthparts of basal mandibulate hexapods have been transformed into a bewildering array of

particulate and invasive or noninvasive system of fluid feeding, including filter-feeding, sponging, siphoning, rasping, lapping, and boring (Schram, 1986; Labandeira, 1997a; Walter and Proctor, 1999).

*Lophotrochozoans.*—The Lophotrochozoa—represented by the Rotifera, Acanthocephala, Platyhelminthes, Nemertinea, Mollusca, and Annelida—have not successfully entered the continental realm, and remain overwhelmingly marine. The only significant continental clades are the gastropod molluscs, and annelids (earthworms and leeches), many of which occur in fresh water rather than on land. Extant and extinct speciose clades include bivalve molluscs, cephalopods, and nonpulmonate gastropods, some of which have only marginally invaded fresh water. Terrestrialized lophotrochozoan phyla range in species diversity from about 750 species for the Acanthocephala to about 20,000 for pulmonate gastropods.

Unlike the Ecdysozoa, the Lophotrochozoa lack a unifying synapomorphous or otherwise obvious feature that could account for their prevalence in terrestrial habitats. Rather, they have become terrestrial and subsequently carnivorous via four basic strategies, each of which has originated multiple times within and among phyla. The first pathway is via endoparasitism—as in cestode and trematode platyhelminths (flukes and tapeworms) and acanthocephalans, all of which



FIGURE 3—The fossil history of carnivory by terrestrial invertebrates, expressed as predation, parasitism, mixed strategies, and microvory. Major sources are Conway Morris (1981), Little (1983), Eisenbeis and Wichard (1988), Gray (1988), Brusca and Brusca (1990), Wills (1993), Foelix (1996), Selden (1996), and Poinar and Poinar (1999). Phyla are capitalized; classes or approximately equivalent ranks are in lowercase and standard font; and supraphyletic ranks are in lower case and bold. Geochronology is resolved to stage level and is modified from Gradstein and Ogg (1996); abbreviation: Neog., Neogene. A question mark indicates a questionable geochronologic assignment. Missing epoch designations, from bottom to top: Wenlock and Pridoli (Silurian); Gzelian (Carboniferous), Early and Middle (Triassic); and Pliocene and Pleistocene (Neogene).

*Notes:* (1) The Pentostoma and Acanthocephala lack a body-fossil terrestrial fossil record, though both are internal parasites of mammals and other vertebrate lineages that extend to the Paleogene. (2) The Nemertinea and Nematoda have earliest terrestrial occurrences in the Paleozoic that cannot be assigned to a higher-level clade (Schram, 1973). (3) See Figure 4 for delimitation of lower taxonomic ranks. (4) Microvory is defined as the consumption of live or dead small particulate food and includes unicellular organisms.

lack a significant fossil record—or by the ectoparasitism of leeches. A second route is through small size and inconspicuousness in free-living forms, exemplified by rotifers, turbellarian flatworms, and some nemerteans that occur as soil and litter meiofauna. Third, there has been the development of an external, mineralized, protective shell, as in the vast majority of pulmonate gastropods. Fourth, terrestrialization has been accompanied by infaunalization within soils and other moist habitats, as typified by relatively large animals such as oligochaetes and some nemerteans. The only large, free-living exceptions to the above options are the shellless pulmonates, or slugs, which are rarely predaceous, exude copious amounts of slime, and probably are defended by noxious compounds in their tissues (Greene, 1975).

1. *Acanthocephalans*. Acanthocephalans are obligate endoparasites of the alimentary tract of vertebrates, especially teleost fish, although a minority of species infect arthropods such as terrestrial crustaceans and insects as intermediate hosts (Conway Morris and Crompton 1982). Historically, acanthocephalans have been considered to have their origin among the pseudocoelomate “aschelminth” phyla, although it has been suggested that they are closely related to the Priapulida; both of these groups were diverse during the Cambrian (Conway Morris, 1981; but see Barnes et al., 1993). Unlike the arthropod-like onychophorans, tardigrades, and pentastomes (see below), acanthocephalans lack a continental or pre-Cenozoic fossil record. It has been speculated (Brusca and Brusca, 1990) that they may have had an evolutionary trajectory similar to the pentastomes—endoparasitism of primitive marine vertebrates and subsequent evolution paralleling vertebrate phylogeny, including terrestrialization along with an early, land-based, tetrapod stock (Brusca and Brusca, 1990).

2. *Rotifers*. Of the continental phyla, the one with the smallest individuals is the Rotifera, most of which are less than a millimeter long. Rotifers frequently occur in marine and especially freshwater habitats, as well as in moist soils and on the wet surfaces of mosses. Approximately 1,800 species

have been described, distinguished by the structure of their oral corona—the metrachronally beating band of cilia encircling the mouth—and the type of their mouthpart-like mastax. They are variously detritivorous filter feeders, raptorial predators that ingest small animals, or piercers-and-suckers that fluid-feed on larger prey. A few are parasitic on other meiofauna, whereas others have entered into mutualistic associations with crustaceans (Brusca and Brusca, 1990). With regard to the evolution of various carnivorous feeding strategies, the fossil record is uninformative, except inasmuch as it can document the presence of particular clades, such as the Monogonta in the Eocene (Lutetian) of South Australia (Southcott and Lange, 1971), and the Bdelloidea in the Miocene (Aquitanian) of Dominican amber (Poinar and Ricci, 1992).

3. *Platyhelminths*. The Platyhelminthes, or flatworms, include approximately 20,000 named species and constitute one of the simplest morphological grades of bilaterian metazoans; they are triploblastic, acoelomate, and dorsoventrally flattened. The class Turbellaria is free living and generally predaceous, although some species are symbiotic with other invertebrates; by contrast, the classes Monogenea (single-host flukes), Trematoda (multiple-host flukes), and Cestoda (tapeworms) are all ecto- or endoparasitic on vertebrates and, to a lesser extent, cephalopods and crustaceans (Brusca and Brusca, 1990). One group of flatworms, the Acoela, were once included in the Turbellaria, but now are considered to be very basal bilaterians unrelated to the lophotrochozoic Platyhelminthes (Ruiz-Trillo et al., 1999). Feeding among turbellarians is diverse and involves structural variations of a well-muscled pharynx for suction, release of mucus for external prey entrapment, capture of small prey by adoral ciliary action, or use of a copulatory stylet or oral hooks for impalement of victims. The fossil record of flukes and tapeworms is nonexistent, and that of turbellarians is confined to the Neogene, with their earliest occurrence in the late Miocene of California (Pierce, 1960). Resistant egg capsules and cocoons have been documented from the European Pleistocene (Frey, 1964). A putative turbellarian from the late

Precambrian of Alaska (Allison, 1975) is not reliably assignable to the phylum (Conway-Morris, 1981).

4. *Nemertineans*. Nemertineans, or ribbonworms, include about 900 species that range in length from less than 1 cm to nearly 60 m, some of which occur in terrestrial habitats. Nemertineans superficially resemble flatworms but are clearly differentiated from them by their feeding specializations, including a complete digestive tract and an unique, eversible proboscis housed separately in a hydrostatically-controlled rhynchocoel. This proboscis may possess a single large stylet or many smaller stylets for lancing prey. Nemertineans generally prey on small invertebrates, wrapping their everted proboscis around a prey item, sometimes also introducing toxic exudates into the victim by repeated styletal punctures (Brusca and Brusca, 1990). The proboscis draws the subdued or nearly dead prey to the region of the mouth and into the rhynchocoel. The history of this distinctive mode of feeding, as documented by nemertinean fossils, is represented only by the Late Carboniferous (Moscovian) *Archisymplectes rhothon*, discovered by Schram (1973), which probably lived in brackish or fresh water. There are no other fossil occurrences, although with their distinctive morphology (Stricker, 1983), mineralized nemertinean stylets should be identifiable in the fossil record.

5. *Molluscs*. Of the molluscs, only pulmonate gastropods (land snails and slugs) have expanded their ecological range to fresh water and land. Pulmonate gastropods display a variety of feeding strategies, including detritivory, carnivory, and, most commonly, herbivory; but they are united by possession of a unique and variously modified radula (Brusca and Brusca, 1990). The radula is a bulbous organ, on the surface of which are several or more rows of rasp-like, chitinous teeth that scrape, tear, peel, or otherwise remove tissue for ingestion. Carnivorous pulmonates have evolved multiple times and include forms with unmodified radulae that use slime to entangle prey for eventual consumption; forms with radular teeth modified into lance-like structures; and others with a radula fashioned into a barbed harpoon functionally similar to that of marine cone snails (Vermeij,

1987). Pulmonates have a significant fossil record (Gray, 1988; Tracey et al., 1993) and occur in Cenozoic fluvial deposits and in amber (Larsson, 1978; Roth, 1986), but are particularly abundant in Neogene lake deposits (Cohen, 1989). However, the oldest pulmonate fossils come from several Late Carboniferous localities in North America (Solem and Yochelson, 1979). The taxonomic assignment of these early specimens has been challenged (Tillier et al., 1996) based on taphonomic arguments and the presence of an unacceptably long temporal gap before the next occurrences in the late Mesozoic. Without explicit taxonomic consideration of the fossil material, however, the Late Carboniferous date is accepted.

6. *Annelids*. Both predaceous and parasitic lifestyles occur in the two continental classes of annelids, Oligochaeta (earthworms) and Hirudinea (leeches). Oligochaetes are commonly associated with detritivory, although many—especially freshwater—species are predaceous; leeches, on the other hand, are typically identified with ectoparasitism on tetrapods, even though many tropical species are predaceous (Brusca and Brusca, 1990). Oligochaete trace fossils have been mentioned in the literature (Buatois et al., 1998), but predaceous forms are known from body fossils in Baltic amber (Menge, 1866; Schlee and Glöckner, 1978), and later from the Pleistocene of the same region (Frey, 1964). Interestingly, the fossil record of leech-like forms may extend to the Early Silurian, with a specimen reported from an obviously marine biota in Wisconsin (Mikulic et al., 1985). However, the taxonomic assignment of this specimen is tentative (Mikulic et al., 1985), and a more reliable representative of the group occurs in a late Jurassic compression: *Hirudella angusta* Münster, from the Solnhofen lithographic limestone of Germany (Kozur, 1970). This latter form may not have been parasitic according to Conway Morris (1981), and was probably predaceous.

*Ecdysozoans*.—The Ecdysozoa are considerably more diverse than the Lophotrochozoa, probably as a result of their success in terrestrial environments (Figs. 3, 4). This success is probably attributable to their very namesake: ecdysis was an

exaptation for life in a subaerial environment where water conservation and osmotic regulation of body tissues were critically important. Almost all phyla of Ecdysozoa have terrestrial members, namely the Nematoda, Nematomorpha, Tardigrada, Onychophora, Pentastoma, and Arthropoda, the latter synonymous with the Euarthropoda of some workers. The exception is the more removed and exclusively marine Kinorhyncha + Priapulida subgroup which was more diverse in the Cambrian than it is today (Conway Morris, 1998). In terms of present speciosity, most of Ecdysozoan phyla are not very diverse—there are approximately 90 species of Onychophora, 110 species of Pentastoma, and 450 species of Tardigrada—particularly considering that all three have their origins in Cambrian marine ecosystems older than 500 Ma. These conservative, basal lineages to the Arthropoda have been interpreted by Gould (1995) as exhibiting prolonged stasis. Alternatively, drastic habitat changes in the history of these groups suggests the continuous evolution of a durable body plan: free-living onychophorans and tardigrades have shifted from the marine to the continental realm; parasitic pentastomes have undergone profound shifts in hosts from unspecified marine fish or perhaps arthropods to terrestrial vertebrates (Walossek and Müller, 1994; Müller et al., 1995; Poinar, 1996). Interestingly, three of these phyla were present in the Cambrian, occupying an epibenthic habitat (Müller et al., 1995); and together with the lophotrochozoan Acanthocephala, they subsequently produced lineages that became continental parasites or predators. The Nematomorpha may have had a similar history, but lack an adequate fossil record (Poinar, pers. comm., 2002).

Two phyla, nematodes and arthropods, dominate continental ecosystems today in terms of abundance and diversity. Both phyla have invaded every possible continental habitat, including the interiors and exteriors of virtually all other organisms. About 15,000 species of nematodes have been described, although an estimated one million species probably exist. Arthropods in particular represent the ultimate success story of life on land in terms of the breadth of their feeding strategies, their numerical and

taxonomic dominance in ecosystems, and estimates of biomass (Wheeler, 1990; Wilson, 1992; Brusca, 2000). Arthropods comprise about one million described species (Brusca, 2000), and estimates of the number of undescribed species range from several million to 80 million species (Erwin and Scott, 1980; Gaston and Hudson, 1994).

1. *Nematodes*. Of the twelve continental invertebrate phyla, the Nematoda, or roundworms, are second only to the Arthropoda in number of carnivorous taxa documented in the fossil record. Most specimens occur in amber from the Early Cretaceous of Lebanon, the middle Eocene of the Baltic region, and the early Miocene of the Dominican Republic (Poinar, 1977; Poinar et al., 1994a, 1994b; Poinar and Poinar, 1999). The earliest description of these organisms cites elongate bodies on appendage exocuticle of the large Early Mississippian scorpion, *Gigantoscorpio willsi* (Størmer, 1963). These minuscule structures were preserved in a process akin to permineralization and retain some micromorphology. However, these structures are probably not nematodes (Wills, 1993; Poinar et al., 1994a). The earliest credible occurrence is from the Late Carboniferous (Schram, 1973), and is followed by a long absence of specimens from the Permian to Early Cretaceous. During the Early Cretaceous, the nematode fossil record resumes with several amber occurrences (Poinar and Poinar, 1999) and a few reports from compression deposits (Voigt, 1957; Dubinina, 1972). The Cretaceous and Cenozoic occurrences provide examples of parasitism on known arthropod hosts, principally insects, by members of two most speciose nematode clades: the order Tylenchida of the Class Secernentea and the order Mermithida of the class Adenophorea (Poinar, 1984a, 1993). These two clades of nematodes represent two of the four independent originations of continental arthropod parasitism by nematodes (Blaxter et al., 1998). Individuals are excellently preserved in conjunction with infected beetles and flies trapped in amber, whose ruptured bodies have allowed release of nematodes into adjacent resin (Schlee and Glöckner, 1978; Larsson, 1978; Poinar 1984a). Among the several recorded families of

Tylenchida, insect hosts include the Staphylinidae (rove beetles; Poinar and Brodzhinsky, 1985), Mycetophilidae (fungus gnats; Poinar 1991a), and Drosophilidae (pomace flies; Poinar 1984a, 1984b). In the Mermithida, reported insect hosts are the Cerambycidae (longhorn beetles; Heyden, 1860, 1862), Chrysomelidae (leaf beetles; Voigt, 1957), Limoniidae (crane flies; Poinar, 1984c), Culicidae (mosquitoes; Poinar, 1984c; Poinar et al., 1994a), and Chironomidae (aquatic midges; Menge, 1866; Schlee and Glöckner, 1978; Poinar et al., 1994b; Poinar and Milki, 2001). Nematode trails have been found in the Middle Eocene Green River Formation in Utah (Moussa, 1970); and the parasites have been found in association with spiders from Baltic amber (Poinar, 2000), and in Pleistocene mammals, including a horse from the Balkans (Dubinina, 1972) and a ground squirrel and a mammoth from Russia (Dubinin, 1948).

2. *Nematomorphs*. Nematomorphs, or hair worms, are thin endoparasitic worms that may reach a meter in length. In the juvenile phase they inhabit particular species-specific tissues or organs in arthropods, particularly orthopteroid insects (Brusca and Brusca, 1990). As adults they are aquatic and free-living. The obligately parasitic phylum Nematomorpha includes about 250 extant species, and has a sparser historical record than nematodes, with only two known fossil occurrences. Members of the Gordidae are preserved in middle Eocene compression deposits in Germany and Italy (Voigt, 1938; Sciacchitano, 1955), although this assignment has been questioned by Poinar (1999b). By contrast, a member of the Chorododidae has been found extruding from the anus of a member of the cockroach family Blattellidae in younger Dominican amber (Poinar, 1999b).

3. *Tardigrades*. Water bears, or tardigrades, are a poorly known phylum of arthropod-like invertebrates that occur in the oceans, fresh water, and humid terrestrial environments (Dewel and Dewel, 1998). They have a fossil record beginning in Middle Cambrian deposits of northern Siberia (Müller et al., 1995). These specimens, however, are demonstrably marine, cannot be assigned to any post-Jurassic clade, and have been considered to

belong to a stem-group lineage (Müller et al., 1995). The next and only post-Paleozoic fossil tardigrades are members of the Class Eutardigrada found in Late Cretaceous ambers of North America—specifically the Turonian of New Jersey (Bertolani and Grimaldi, 2000) and the Campanian of Manitoba (Cooper, 1964)—as well as in the Pleistocene of Italy (Durante and Maucci, 1972). Continental, free-living tardigrades are herbivores or predatory carnivores. They are significantly different from their Cambrian marine progenitors, as they possess a fourth, hind-pair of legs that are positioned laterally rather than ventrally. However, there are similarities between extant marine parasitic Tardigrades and the Cambrian forms, such as dorsoventral flattening, the presence of anterior cephalic (suction) discs, an involated mouth, and laterally deployed, robustly clawed legs (Müller et al., 1995). The Cambrian forms most likely are ancestors of extant marine tardigrades—namely the mostly parasitic arthrotardigrades of the Class Heterotardigrada, which are basal within the phylum and exhibit the greatest range of morphology (Dewel and Dewel, 1998). They represent the stock from which the continental lineages evolved, especially the comparatively diverse Eutardigrada.

4. *Onychophorans*. Velvet worms, or onychophorans, are predaceous, terrestrial, caterpillar-like relatives of arthropods with lobopodous limbs. Their head region has hidden mouthparts consisting of two pairs of cutting blades that serve as jaws and slice tissue in a fore-and-aft motion (Manton, 1977). Onychophorans currently have a Gondwanan distribution and typically prey on terrestrial invertebrates in tropical to subtropical environments. The fossil record of the phylum extends to the primitive form *Aysheaia* from the Middle Cambrian Burgess Shale of Alberta (Gould, 1995). A hiatus of approximately 225 million years separates these early marine forms from the next fossil occurrences, the Late Carboniferous and terrestrial Mazon Creek *Helenodora* in Illinois (Thompson and Jones, 1980), and an undescribed form from Montceau-les-Mines in France (Rolle et al., 1982). No Mesozoic specimens are known. Two demonstrably terrestrial taxa, however, are

known from mid-Cenozoic Baltic and Dominican ambers (Poinar, 1996); they exhibit features, such as the absence of foot portions with claws, which show a closer link to the Paleozoic forms than to extant taxa. There is no evidence to indicate that this evolutionarily conservative lineage was ever diverse; and it may have been trophically outcompeted by the ecologically equivalent and predaceous centipedes.

**4. Pentastomids.** As structurally distinctive endoparasites of tetrapod respiratory systems, pentastomids are a unique phylum with resemblances to lobopods, crustacean nauplius larvae, and annelids (Brusca and Brusca, 1990). Although recent molecular-based studies indicate crustacean affinities with a divergence date of 350 to 225 Ma (Abele et al., 1989), an alternative interpretation that suggests an independent, higher-ranking origin is supported by the occurrence of marine pentastomids 510-Ma deposits (Gould, 1995). Currently, their typical host is a terrestrial tetrapod, often a reptile, but they are also known to make use of bird and mammal hosts. Some species display a larval stage that temporarily parasitizes an intermediate vertebrate host. In these instances the intermediate host with its pentastomid parasites is, in turn, consumed by the ultimate host, a predaceous tetrapod, completing the cycle. Adults attach themselves securely to the tissues of the lungs and nasal passageways of their host, sucking blood with a simple mouth and a powerful pharyngeal pump. Given their current obligate parasitism of terrestrial tetrapods, three occurrences of pentastomids in upper Cambrian and lowermost Ordovician marine deposits (Andres, 1989; Walossek and Müller, 1994; Walossek et al., 1994) are intriguing, particularly as there are no subsequent fossil specimens. Considering their marine origins during the early Paleozoic and their presence among abundant conodont faunas, it has been speculated that they were parasites in the gill chambers of marine chordates or basal vertebrates (Walossek and Müller, 1994). This association then continued through the terrestrialization of tetrapods during the late Paleozoic, and is manifested today in their amniote descendants.

**6. Arthropods.** The four arthropod subphyla with carnivorous representatives—Chelicerata, Myriapoda, Crustacea, and Hexapoda—occur among the earliest of continental deposits, from the uppermost Silurian of northwestern Europe to the Middle Devonian of northeastern North America (Labandeira et al., 1988; Shear and Selden, 2001). This pattern is quite unlike the terrestrial record of the other eleven phyla, which occur more sporadically later in the Paleozoic (Nemertinea, Mollusca, Onychophora), or are confined to the late Mesozoic or Cenozoic (Rotifera, Annelida, Nematoda, Tardigrada), or have a very poor or absent fossil record (Platyhelminthes, Acanthocephala, Nematomorpha, Pentastoma). One explanation for this is the greater preservability of cursorial, megascopic, and structurally distinctive arthropods that bear a chitinous or otherwise mineralized exoskeleton and could be buried in mid-Paleozoic paralic and continental basinal environments. Several factors, in addition to incumbency (Wilson, 1992), indicate that arthropods have always been diverse and abundant in marine and particularly in continental ecosystems during the Phanerozoic (Brusca, 2000); and thus their taxonomic dominance in modern ecosystems has a longstanding history.

The chelicerates, with the exception of the many detritivorous and parasitic mites, are predaceous; one apomorphic feature that has arisen in the group is the specialized use of silk by spiders (Araneida) to trap prey. Chelicerates use a pair of claw-bearing mouthparts, the chelicerae, for predation (Snodgrass, 1952). In spiders, the chelicerae are modified into horizontally or vertically oriented structures with terminally articulating fangs; ducts in these fangs connect to poison glands (Foelix, 1996). A second, posterior pair of typically grasping mouthparts, the pedipalps, are used to manipulate prey in Scorpionida (scorpions), Amblypygi (tailless whipscorpions), and Opiliones (harvestmen). The continental fossil record of chelicerates (Størmer, 1969; Selden, 1996) begins in the latest Silurian, and by the mid-Early Carboniferous six orders are represented, including spinneret-bearing spiders (Shear et al., 1989a, 1989b). From the middle to

## LABANDEIRA—PREDATORS, PARASITOIDS, AND PARASITES

late Carboniferous an additional seven orders appear in the record, the best known of which is the Trigonotarbida (Dunlop, 1994). Only the Schizomida (short-tailed whipscorpions) and Palpigradi (whipscorpions) have their known first appearances in the Cenozoic (Selden, 1996), although they undoubtedly originated during the Paleozoic based on phylogenetic position.

One of the most interesting phenomena in the record of chelicerate interactions with other animals is the preservation of phoretic or parasitic associations in amber—particularly mites and ticks on arthropods and vertebrates. For example, mites are known to occur ectoparasitically on Chironomidae in Late Cretaceous Canadian amber and middle Eocene Baltic amber (Schlee and Glöckner, 1978; Poinar, 1985, 1997); these associations have no present-day counterparts. An older fossil, however—an erythraeid mite on a biting midge (*Ceratopogonidae*) in Early Cretaceous Lebanese amber (Poinar et al., 1994)—represents an association that is still extant. More recent associations involving modern taxa are documented in lower Miocene Dominican amber, such as erythraeid mites on gracillariid and tineid moths (Poinar et al., 1991), and macrochelid and other mites phoretically attached to drosophilid flies and leiodid beetles (Poinar and Grimaldi, 1990; Poinar, 1993). Parasitic interactions between chelicerates and vertebrates can support particular biogeographic hypotheses: for instance, a flightless host-unassociated argasid tick with Neotropical affinities in New Jersey amber suggests dispersal by birds or pterosaurs (Klompen and Grimaldi, 2001); and listrophorid mites on probable rodent hair in Dominican amber suggest vicariant mammalian colonization of the Antilles during the Cenozoic (Poinar, 1988).

In addition to chelicerates, continental predaceous representatives of the Myriapoda, Crustacea, and Hexapoda also appear during the latest Silurian to Middle Devonian interval (Tasch, 1957; Shear and Bonamo, 1988; Greenslade and Whalley, 1986; Labandeira et al., 1988)—although early members of diplopods and scorpions have been interpreted to be aquatic (Almond, 1985;

Jeram, 1990). The continental Crustacean taxa include the Phyllopoda (Scourfield, 1926) and Malacostraca (Schram, et al., 1978); continental myriapods are represented by the Chilopoda (Shear and Bonamo, 1988); and continental hexapods by the Parainsecta (Greenslade and Whalley, 1986) and Insecta (Labandeira et al., 1988). Unlike the overwhelmingly carnivorous Chelicerata and the Chilopoda, the crustaceans and hexapods represent an eclectic mix of feeding strategies, including aquatic filter feeding, detritivory, fungivory, and herbivory, as well as carnivory (Schram, 1986; Labandeira, 1997a).

### PATTERNS OF CARNIVORY AMONG HEXAPOD ARTHROPODS

The Hexapoda comprises two clades, the Parainsecta—consisting of the Collembola (springtails) + Protura (proturans) and probably the more distantly related Diplura—and the Insecta, sister-group to the Parainsecta. The Insecta include the basal Archaeognatha (bristletails), the more derived Zygentoma, and the yet more derived Pterygota, or winged insects, which represents 99 percent of extant hexapod diversity (Kukalová-Peck, 1990). There are two major lineages within the Pterygota; one lineage, the Palaeoptera, is characterized by the inability to fold the wings over the abdomen, and includes the Odonatoptera, Ephemeroptera (mayflies), and the highly diverse Palaeodictyopteroidea of the Paleozoic, nominally divided into four orders. The other pterygote lineage, the Neoptera, is represented by five major supraordinal clades: the Plecoptera, consisting largely of the Plecoptera (stoneflies); its sister-group, the Orthoneoptera, comprised of various orthopteroid lineages such as the Orthoptera (grasshoppers and crickets); the Blattoneoptera containing the Blattodea (cockroaches), Mantodea, and Dermaptera (earwigs); the Hemineoptera, sister-group to the Blattodea, representing the hemipteroid orders Psocoptera (booklice), Phthiraptera (lice), Thysanoptera (thrips), and Hemiptera (bugs, aphids and relatives); and the very successful

Endoneoptera, or Holometabola (Haas and Kukalová-Peck, 2001). This latter group is characterized by a four-phase metamorphosis—egg, to larva, to pupa, to adult—and includes all the orders from Megaloptera (alderflies and dobsonflies) to Hymenoptera (sawflies, wasps, ants, and bees) in Figure 4. Holometabolous insects represent about 90% of all insect species, and insects represent 86–92% of all known metazoan species (Wheeler, 1990; Brusca, 2000). They have been the most taxonomically, if not numerically dominant animal clade since the earliest Pennsylvanian.

Continental carnivorous hexapods have two key structures: mouthparts and ovipositors. The generalized mandibulate mouthparts of the primitive hexapod (Kukalová-Peck, 1990) have been modified into 34 major types, all extant, each of which represents considerable to subtle variations on a basic plan (Labandeira, 1997a). For example, the broader category of mandibulo-canaliculate mouthparts comprises three of the 34 mouthpart classes; each of these three is characterized by unique features associated with scythe-shaped mandibles and/or associated maxillae that are used by larval holometabolans for pursuit or entrapment of prey (Labandeira, 1997a). Other examples include the structurally diverse stylate mouthparts of fluid-feeding ectoparasites (Smith, 1985), and the analogous concealed nectar extraction apparatus used by parasitoid adults at a certain stage in their life cycle (Jervis and Kidd, 1986). Similarly, the ovipositor has been used by parasitoids, especially hymenopterans, to insert eggs into hosts such as wood-boring larvae.

The record of hexapod carnivory (Fig. 4) shows three basic trends, each corresponding to the rise of family-level lineages representing the three functional feeding groups: predation, parasitoidism, and parasitism. The first trend is the expansion of insect predators during the Late Paleozoic. The second is the spectacular diversification of parasitoid groups during the Middle Jurassic to mid-Cretaceous. And the third trend is the radiation of parasitic groups during the Late Jurassic to mid-Cretaceous, lasting into the Paleogene. Two ancillary patterns should also be noted. One is the

beginning of heavy seed predation during the middle Cretaceous to Paleogene—although the ichnofossil and functional morphological evidence for seed endosperm consumption extends back to the Late Carboniferous and Early Permian (Sharov, 1973; Scott and Taylor, 1983). Post-Paleozoic seed predators and parasitoids include stylate piercing-and-sucking and mandibulate chewing forms, and are concentrated in three clades: pentatomorph Hemiptera, “phytophagan” Coleoptera, and chalcidoid Hymenoptera. A few families of Lepidoptera are notable larval consumers of endosperm (Janzen, 1971), but lack fossil records. The other secondary trend is reflected in the ancient record of palynivory (sporivory and pollinivory; Taylor, 1981), which is analogous to predation on gametophytic seeds, representing consumption of the sporophyte phase of a vascular plant. There are four specific pollinivorous evolutionary assemblages, defined by plant taxa consumed and associated consuming insects (Labandeira, 1998b, 2000). Palynivory and predation and parasitoidism on seeds will not be considered further.

**Predators.**—The earliest terrestrial predators were chilopods and several major chelicerate taxa, with first occurrences during the latest Silurian to Middle Devonian; several additional lineages appear during the earlier Pennsylvanian (Fig. 3). Among the hexapods, the Odonatoptera—with approximately 20 family-level taxa—were the dominant airborne predators, including some members of the Meganeuridae with wingspans up to 71 cm (Durden, 1988). These large forms were probably the ecological equivalent of birds, and caught their victims on the wing, judging by their well-developed raptorial mandibles, leg baskets for securing prey, and canted thoracic segments (Rohdendorf and Rasnitsyn, 1980; Brauckmann and Zessin, 1989). Ground-dwelling, Late Paleozoic hexapod predators included several families of protorthopterans, as revealed by taxa with spinose and raptorial forelegs, and robust and incisiform mandibles. Early holometabolous lineages of the neuropteroid complex—Megaloptera, Raphidioptera, and Planipennia—originated during the earliest Permian (Asselian); virtually all of their

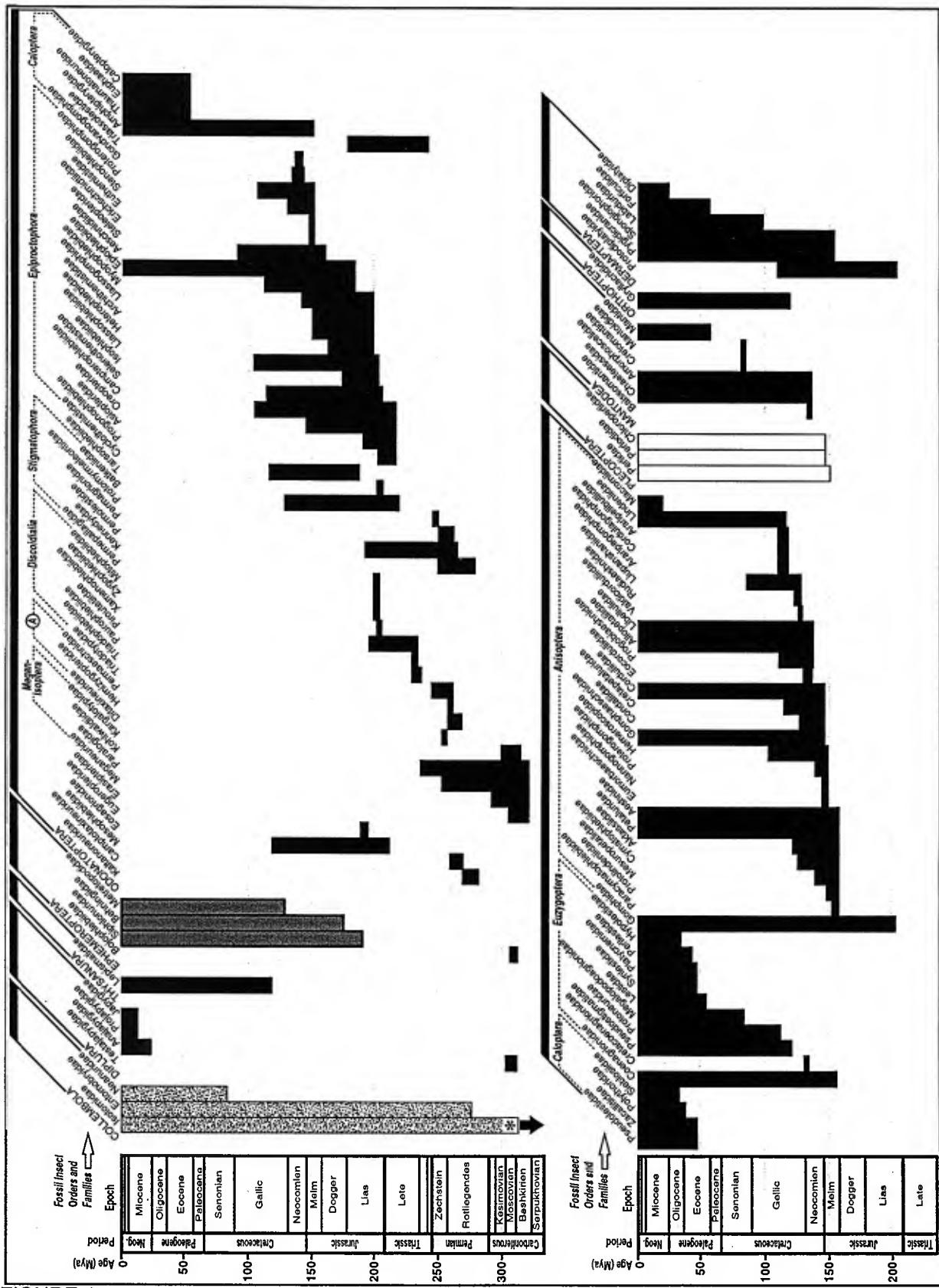
## LABANDEIRA—PREDATORS, PARASITOIDS, AND PARASITES

larvae are assumed to have been predaceous, based on descendant taxa. There is little direct evidence for freshwater predation, though the immatures of Odonatoptera and Ephemeroptera, if aquatic in the Paleozoic (Rohdendorf and Rasnitsyn, 1980), were likely predaceous.

During the Mesozoic, more derived odonatopteran lineages—representing about 80 families and subsumed within the extant high-ranked subgroup, Odonata—replaced the Late Paleozoic and Early Mesozoic lineages (Bechley, 1996; Bechley et al., 2001). This diverse fauna is preserved in the Solnhofen Limestone of southern Germany (Barthel et al., 1994) and similar Mesozoic deposits. Additionally, insectivorous brachyceran Diptera—such as Rhagionidae (snipe flies), Asilidae, Empididae (dance flies), and others—became aerial predators during the later Mesozoic. This expansion accompanied the diversification of dipteran mouthpart types, which involved modifications of the mandibular, maxillary, and hypopharyngeal styles, as well as the tracheation and dentition of the labellum. These changes provided several new ways to secure, process, and consume prey. At the same time, Mesozoic hexapod predators dwelling on the ground were dominated by the Mantodea, neuropteroids, and the superfamilies Caraboidea, Staphylinoidea, and Elateroidea among the Coleoptera. Later, during the Cretaceous, vespid wasps and ants became important ground predators. Among the first well-substantiated predators in freshwater ecosystems were nepomorph Hemiptera and caraboid Coleoptera during the latest Triassic to early Jurassic; these clades undoubtedly subsisted on a trophic base of other, perhaps herbivorous, arthropods (Ponomarenko, 1996). This Mesozoic array of freshwater and terrestrial predators essentially persisted into the Cenozoic, judging by the geochronologic ranges of major family-level taxa (Labandeira, 1994). Recent evidence, however, indicates a significant diminution of herbivorous taxa at taxonomically lower levels at the Cretaceous-Paleocene boundary in the Western Interior (Labandeira et al., 2002; cf. Labandeira and Sepkoski, 1993). This would have significantly impacted the herbivore component of food web

structure; and based on theoretical (Dunne et al., 2002) and empirical (Godfray et al., 1999) data, should translate to significant decreases in taxonomic diversity. This impoverishment probably cascaded upward to trophically dependent predators, parasitoids, and parasites.

**Parasitoids.**—One of the biggest transitions in continental carnivory was the rather rapid appearance of major parasitoid taxa during the Middle Jurassic to mid-Cretaceous. Of the 74 parasitoid families recorded in Figure 4, 57 (or 77 percent) are Hymenoptera, 12 (16 percent) are Diptera, and the remaining 5 (7 percent) represent Planipennia, Coleoptera, and Lepidoptera. In the Hymenoptera, the overwhelming presence of sawflies (Symphyta) plus seven superfamilies of apocritan and aculeate lineages (Gauld and Boulton, 1988), as well as the superfamilies Tabanoidea, Asiloidea, Empidoidea, Muscoidea, and a few other lineages in the brachyceran Diptera, truly records a major shift in the mode of carnivory within terrestrial ecosystems (Fig. 4). In the post-Triassic fossil record, evidence for parasitism comes from taxonomic assignments (Rasnitsyn, 1988), the presence of small parasitoid emergence holes in fossil pupae (Bown et al., 1997) (Fig. 2N), or teratologies of adult insects in amber (Poinar and Poinar, 1999), such as an exceptional case of a braconid larva preserved in the act of emerging from an adult ant (Poinar and Miller, 2002). The transition to parasitoidism was accomplished by modifications in the reproductive biology of numerous holometabolous lineages (Godfray, 1994). For the Hymenoptera, an important structural change was the transformation of a laterally compressed, sawtooth ovipositor—designed for slicing plant tissues—into a needle-like piercing or drilling mechanism with a circular cross-section. This structure, initially used for inserting eggs into wood, was transformed into a device for puncturing endophytic larvae—a key innovation for basal parasitoid taxa (Rasnitsyn, 1988). An analogous structure is the highly telescoped posterior abdomen of the Diptera. The second important development in early parasitoids was a shift in larval food source, from less nutritious plant tissues



---

**FIGURE 4**

to more proteinaceous animal tissues, which were often supplied by the adult (Malyshev, 1968). A part of this general shift was the appearance of the larval cleptoparasitoid habit, in which an insect develops at the expense of another (host) insect by consuming its food supply and depriving the host of nutrition, thus assuring its eventual death (Eggleton and Belshaw, 1992).

Several trophic pathways leading to the evolution of the parasitoid life-habit have been identified (Eggleton and Belshaw, 1992). Within the Hymenoptera, parasitoidism apparently originated only once, and most likely grew out of mycophagy in an earlier Mesozoic symphytan lineage, such as the siricoid sawflies (Whitfield, 1998). Siricoid larvae generally inhabit dead wood

and feed on symbiotic fungi in tunnels, but some constituent taxa, lacking such a food supply, deposit their eggs on other insects that occur in the same habitat. Thus the initial step toward parasitoidism could be the usurpation of another species' fungal food supply, resulting in the death of the starved larval host. Subsequently, there would be a shift from the introduced larva feeding on symbiotic fungi to consumption of the host itself. A modification of this scenario has been proposed by Crowson (1981) to account for the origin of parasitoids in wood-associated beetle lineages. On the other hand, in multiple independent lineages of Diptera, vertebrate parasitoidism has originated by step-wise conversion from carrion saprophagy. The sequence of this transition would have been (i)

---

←

FIGURE 4—At left and on the following two pages is represented the fossil history of carnivory for 359 hexapod families, expressed as predation, parasitoidism, parasitism, and mixed strategies. Taxonomic ranks are orders (capitalized), suborders or superfamilies (italicized, lower-case), and families (regular font, lower-case). A conservative approach is taken whereby assignments to predator, parasitoid, or parasite categories in extant families are based on a plurality of carnivorous relative to non-carnivorous member species. Trophic assignments of fossil families were inferred from multiple criteria, including relatedness to or inclusion within modern clades with known ecologies, functional morphology, ecological evidence such as gut contents, or trace-fossil context (see Fig. 2). Many family-level taxa with sporadic or otherwise limited occurrences of carnivory among overwhelmingly herbivorous, fungivorous, or detritivorous confamilials were excluded. Sporivory and pollinivory were not included. Only carnivorous taxa with fossil records are included. Geochronology is resolved to stage level and is modified from Gradstein and Ogg (1996), with updated Lagerstätten ages such as Baltic amber (Ritzkowski, 1997), the Florissant biota (Evanoff et al., 2001), and Dominican amber (Iturralde-Vinent, 2001). Major sources for feeding-type assignments are Clausen (1940, carnivorous insects), Janzen (1971, seed predators), Carpenter (1971, 1992, fossil groups), Askew (1979, parasites), Richards and Davies (1977, all insects), Crowson (1981, Coleoptera), Merritt and Cummings (1984, aquatic insects), Hagen (1987, insect predators), Gauld and Bolton (1988, Hymenoptera), Lehane (1991, hematophagous insects), Eggleton and Belshaw (1992, parasitoids), Godfray (1994, parasitoids), Schuh and Slater (1995, heteropterous Hemiptera), and Arnett (2000, all insects). Fossil occurrences are from Bechley (1996), Bechley et al. (2001), Labandeira (1994) and subsequent updates, Poinar and Poinar (1999), and Rasnitsyn (2000; 2002, pers. comm.). Taxonomic classification follows Bechley (1996) and Bechley et al. (2001) for Odonatoptera, Schuh and Slater (1995) for heteropteran Hemiptera, and Naumann et al. (1990) for all other insect orders. Missing epoch designations, from bottom to top: Gzelian (Carboniferous), Early and Middle (Triassic), and Pliocene and Pleistocene (Neogene). Suprafamilial or subordinal designations are: A, Prostanisoptera; B, Leptopodomorpha; C, Mantispoidae; D, Tenebrionoidea; E, "Phytophaga"; F, Empidoidea; G, Sciomyzoidea; H, Tephritoidea; I, Ichneumonoidea; and J, Cynipoidea. Asterisks at the bottom of the ranges of the Isotomidae (Collembola) indicate an earliest occurrence in the Lochkovian Stage of the Devonian; for the Osmylidae and Nymphidae (Planipennia), first appearances in the Ladinian Stage of the Triassic; and for the Staphylinidae (Coleoptera) the oldest is from the Carnian Stage of the Triassic. A question mark indicates a questionable trophic assignment for the interval indicated.

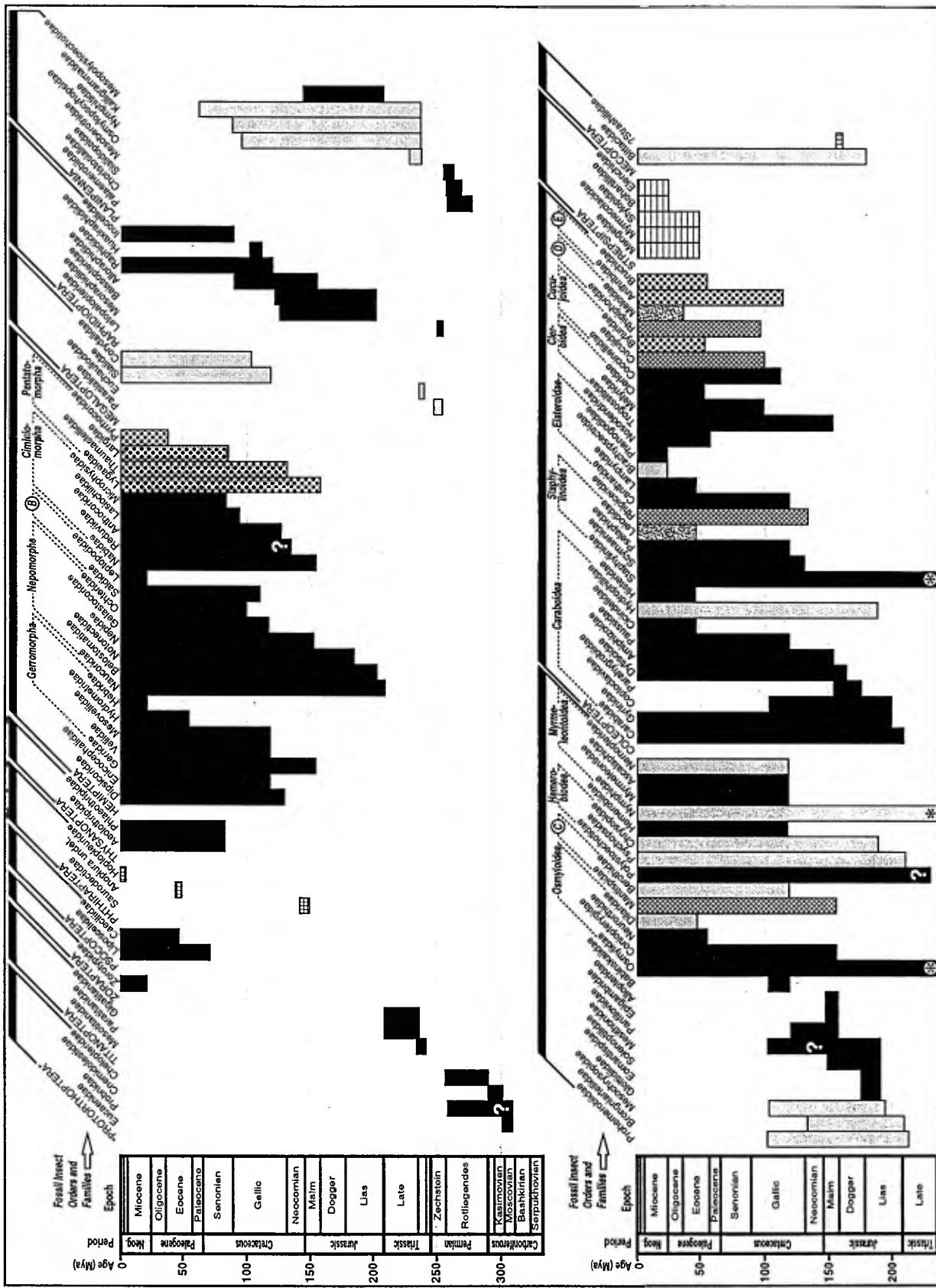
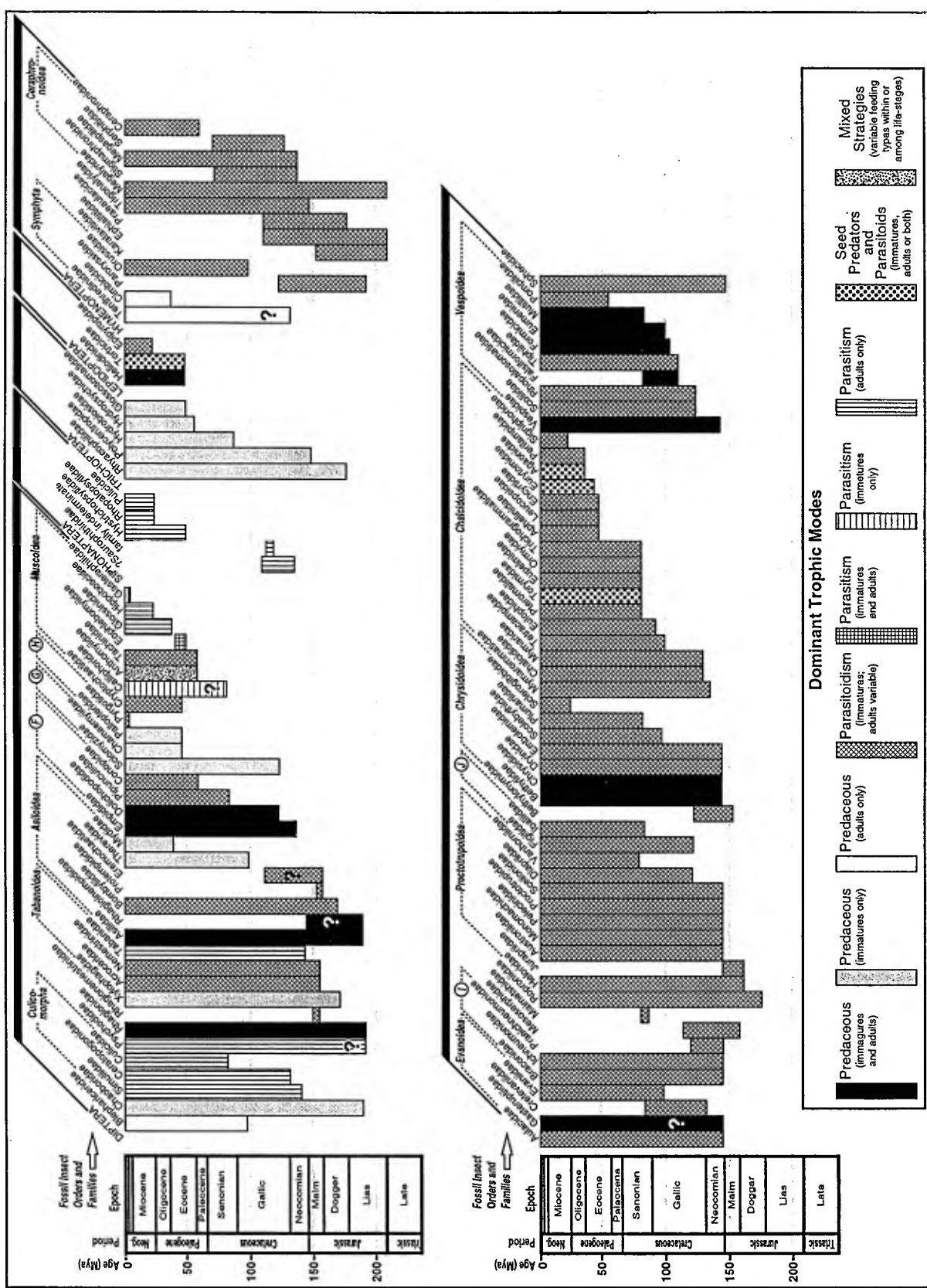


FIGURE 4 (cont.)

LABANDEIRA—PREDATORS, PARASITOIDS, AND PARASITES



**FIGURE 4 (cont.)**

initially attacking live but dying animals, or subsisting on their wounds (facultative ectoparasitism), followed by (ii) initiating wounds (obligate ectoparasitism), and finally (iii) invading the host itself and causing its death (parasitoidism) (Zumpt, 1965). In lineages such as carabid beetles, parasitoidism may have developed from predation. Erwin and Erwin (1976) proposed a sequence in which an ancestral ground beetle species was a polyphagous predator on insects; it was characterized by an active larva that emerged from eggs deposited in the general habitat of its eventual victims, and it pupated in an area removed from its prey. The spatial confinement of a particular prey species resulted in monophagy of the beetle larval predator, and the reduction of prey seeking resulted in metabolic savings. This in turn favored consumption of fewer prey items and pupation within the immediate host environment. Any environmental change that provoked host dispersal would favor a shift from a larval predator to a small, immobile, parasitoid living within a single host. This explanation works best for spatially confined hosts, such as wood-boring or gall-inhabiting larvae. There are at least 100 known originations of parasitoidism in insects, most by way of mycophagy, then saprophagy, and the fewest through predation and herbivory (Eggleton and Belshaw, 1992). Parasitoidism itself has in turn evolved into other trophic modes such as provisioning polyphagy and predation in some coleopteran, dipteran, and hymenopteran lineages (Eggleton and Belshaw, 1992).

*Parasites.*—When compared to the relatively good fossil record of parasitoids, the record of insect parasitism is poor: only about 30 percent of parasite families have fossil occurrences. The reason for this deficiency is that, whereas the adult forms of parasitoids are overwhelmingly free-living and so can enter the fossil record through a variety of environments (many are small wasps), the adults of most parasitic organisms are attached to their vertebrate hosts and are destroyed by the processes of carcass decomposition. Consequently, only in exceptional environments, such as resin flows, are insect parasites preserved (Lewis and Grimaldi,

1997). Fine-grained compression deposits occasionally contain fossil parasites, such as the enigmatic mecopteroid *Strashila* from the Upper Jurassic of the Siberia (Rasnitsyn, 1992), the possible flea *Saurophthirus* from the Lower Cretaceous of Transbaikalia (Ponomarenko, 1976; but see Lakshminarayana et al., 1984), and the flea *Tarwinia* from the Lower Cretaceous of New South Wales, Australia (Riek, 1970; Jell and Duncan, 1986; but see Smit, 1972). All three taxa display ectoparasitic features, including hypognathous, piercing-and sucking mouthparts, compact antennae, long legs with grasping claws, and distensible abdomens (Rasnitsyn, 1992). Both *Strashila* and *Saurophthirus* are dorsoventrally flattened and morphologically convergent on bat parasites such as the hemipteran Polycenidae, the dipteran Nycteribiidae, and even the dermopteran Arixeniidae (Popham, 1962; Ponomarenko, 1976), which feed on bat wing membranes and occupy sparse to tomentose hair; the resemblance suggests a similar feeding style for the Mesozoic fossils, possibly on pterosaurs. In the Australian flea, of indeterminate family assignment, lateral body compression indicates life in dense fur near the body core, rather than on the wing membrane; and they likely inhabited mammalian hosts such as monotremes, triconodonts, or multituberculates. Perplexingly, a literal reading of this evidence points to an apparently missing fossil record, judging from the relationship of these parasitic clades to their free-living (and so represented by more fossils) sister clades (Lyal, 1985; Kristensen, 1999). These phylogenetic relationships, in conjunction with the fossil records of the better-preserved clade, indicate splitting events ranging from the Early Permian to the Late Jurassic (Downes, 1971b; Lyal, 1985; Kinzelbach and Pohl, 1994; Fang et al., 1999). The conflicting data suggest either that the parasite clades are good examples of fossil ghost taxa, or that they originated much later within the crown groups of their sister-clades (e.g., Chalwatzis et al., 1996).

The origins of hematophagy during the Mesozoic, and the likely initial hosts for several major parasitic insect clades, have generated considerable discussion. The best evidence comes

from the record of dipteran parasites, particularly the Culicomorpha, whose adults are free-ranging and not bound to particular host individuals. Within the Culicomorpha, the Ceratopogonidae are well known to feed on vertebrate blood and hemolymph; this feeding behavior is considered a plesiomorphic feature within the family (Downes, 1971a; Borkent, 1995). The ceratopogonid fossil record extends back to the Early Cretaceous and, notably, includes several extant genera that feed on reptilian blood (Desportes, 1942; Wirth and Hubert, 1989). In light of this feeding capacity of ceratopogonids, Borkent (1995) examined the correlations between palpal and antennal sensillae, stylet dentition, and whether the host organisms were invertebrates, birds, or large tetrapods—the latter determined by downwind plumes of host-generated carbon dioxide and heat (Rowley and Cornford, 1972; McKeever et al., 1991; Blackwell et al., 1992). He concluded that two or three species of biting midges from Canadian Upper Cretaceous amber were parasitizing large vertebrates, most likely co-occurring hadrosaurs (but see Szadziewski, 1996). Two of the three ceratopogonid genera he identified are extant and suck blood from large vertebrates, including reptiles and mammals. This plesiomorphic feature of the Ceratopogonidae may extend to the rest of the superfamily Culicomorpha, appearing in the form of functional piercing mouthparts in females, subsequently lost in lineages such as the Chaoboridae (phantom midges), Chironomidae, and Dixidae. The Tanyderidae (primitive crane flies), one of the oldest dipteran lineages, had stylate mouthparts during the Late Triassic and probably fed on blood (Kalugina, 1991; Borkent, 1995). Based on this evidence, some authors suggest that stylate mouthparts consisting of a fascicle of 3 to 5 stylets may be plesiomorphic for the Culicomorpha, with a modest expansion of the labellar pad as a later development (Downes and Colless, 1967; Downes, 1971b; Fang et al., 1999). According to these authors it is unlikely that there was repeated evolution of the same mouthpart type. However, Pawlowski et al. (1996) provide a molecular phylogenetic analysis indicating at least two independent derivations of blood feeding within the Culicomorpha; they

conclude that nectarivory is the primitive feeding strategy. Similarly, Glukhova (1989) proposed that the basal Culicomorpha and related taxa initially were saprophagous on carrion, and then, through the production of salivary proteolytic enzymes, were able to feed on the external secretions of living vertebrates, followed by subsistence on blood. Such an evolutionary shift, however, seems more appropriate for the origin of advanced blood feeding in (muscoid) flies (Szadziewski, 1996), and certain Southeast Asian blood-sucking moths (Bänziger, 1975). Another hypothesis is that insect hematophagy originated from inquiline associations in vertebrate nests by a shift from nest detritivory of epidermis, feces, sebum, and other exudates to blood feeding (Balashov, 1999). This hypothesis is most relevant to the origin of ectoparasitism in the Phthiraptera, since many members of the closely related Psocoptera are nest associates of vertebrate hosts (Waage, 1979).

There are two ecologically different approaches to blood feeding. The first is solenophagy—found in the Culicidae (mosquitoes), Reduviidae (assassin bugs), Cimicidae (bed bugs), and anopluran Phthiraptera (sucking lice)—in which blood vessels such as capillaries are punctured with needle-like stylets (Brown, 1989). In contrast, telmophagy—found in the Ceratopogonidae, Tabanidae (horseflies), Muscidae (house flies), and ticks—is characterized by the creation of pockets of lacerated tissue that has been slashed by stylets, which in these organisms are often modified into serrated blades and used in opposition by scissor-like movements. The insect then drinks the resulting pool of blood and lymph (Brown, 1989). Members of the Glossinidae (tsetse flies) have unique piercing-and-sucking mouthparts and an intermediate strategy for obtaining blood. Although glossinid fossils occur in the North American late Eocene (Cockerell, 1917; Grimaldi, 1992), glossinids today are biogeographically restricted today to sub-Saharan Africa. They are currently major vectors for infectious trypanosomiases that affect ungulates (nagana) and humans (sleeping sickness) (Lehane, 1991). It has been suggested that nagana-like diseases may have been vectored by

North American glossinids feeding on titanotheres (Tasnádi-Kubacska, 1962) or on nonhominid primates (Lambrecht, 1993) during the mid Cenozoic, and subsequently transferred to hominids in eastern Africa. Similarly, certain fossil species in the North American Paleogene belong to the hematophagous culicid genus *Culex* (a mosquito), and a parallel argument has been advanced for the Neogene transferral of plasmodia, filariae, and arborviruses such as malaria to early hominids in Africa (Capasso, 1993).

## THE ROLE OF CARNIVORY IN ECOSYSTEM EVOLUTION

In the preceding overview of the fossil record of continental invertebrate carnivory, six classes of evidence were discussed (Fig. 2), and distinctive patterns of trophic evolution were cited among the 12 invertebrate phyla (Fig. 3) and 359 insect families (Fig. 4) that occur in freshwater and terrestrial ecosystems. Equally important to address, however, are the effects that these patterns had on terrestrial ecosystems. The data cited here, in conjunction with other features of the terrestrial fossil record, generate four questions that are central to the role of arthropod carnivory in terrestrial and freshwater ecosystem evolution.

*Which came first: herbivory or carnivory?*—There are two hypotheses regarding the trophic structure of the earliest well-preserved terrestrial ecosystems from the latest Silurian to the mid-Devonian. One view holds that these early communities were dominated almost exclusively by detritivorous and predatory animals, similar to modern litter communities (Gray and Shear, 1992). An alternative is that herbivores are as old as carnivores and detritivores, and all three trophic modes were present a system analogous to extant depauperate communities on grass. In addition to cryptogams, bryophytes, early land plants, and the fungus *Prototaxites*, the animal component of these early communities consisted of trigonotarbids, pseudoscorpions, spiders, mites, chilopods, arthropleurids, collembolans, and archaeognathans. Among these arthropods, piercing-and-sucking

pachygnathoid mites from the Rhynie Chert have been associated with feeding on live algal protoplasts (Shear and Selden, 2001). Collembolans from the same deposit have been identified as members of the Isotomidae (Greenslade and Whalley, 1986), and possibly the Neanuridae (Hopkin, 1997), modern representatives of which subsist on live fungal spores and hyphae, dead vascular plant tissue, and detritus. As evidence regarding plant-insect associations there are spore-rich coprolites, typically containing multiple spore taxa and exhibiting stereotyped fecal shapes and sizes, from latest Silurian and Early Devonian deposits of the Welsh Borderland (Edwards, et al., 1995). Coprolites containing vascular tissues are also known from the Lower Devonian of Gaspé, Canada (Banks and Colthart, 1993). These associations, as well as those documented in the Rhynie Chert (Kevan et al., 1975), indicate an important role for palynivores, exploiting highly nutritious, land-plant spore protoplasts. Additionally, evidence for surface feeding on plant axes—complete with proliferation of anomalous reaction tissue (Kevan et al., 1975; Banks and Colthart, 1993)—and the occurrence of stylate punctures surrounded by conical regions of histolytic tissue (Banks and Colthart, 1993)—similar to damage produced by modern piercing-and-sucking microarthropods—indicate a diverse herbivore community of both chewing and piercing-and-sucking forms. Thus the balance of evidence supports that the earliest terrestrial communities consisted of herbivores, as well as detritivores and predators—a pattern unlike the delayed herbivory hypothesis of Vermeij and Lindberg (2000) for the marine realm.

*Is prey death or host accommodation the dominant mode in arthropod carnivory?*—The introduction to this chapter presents the canonical view of carnivory at all times and places: predators dispatch and consume prey in the manner of lionesses and antelope. This view has been the dominant research paradigm in marine invertebrate paleobiology (Vermeij, 1987; Kelley and Hansen, 1996), and justifiably so. Such an approach to marine invertebrate predation probably reflects actual differences in the marine versus continental

versions of carnivory—though there is a small literature on the more poorly known associations of marine invertebrate parasites. By contrast, research on the history of terrestrial invertebrate carnivory has been dominated by studies of parasitoids and parasites, and far fewer of predators, particularly during the past 40 years (Askew, 1979; Price, 1980; Godfray, 1994; Schmid-Hempel, 1998). The work on parasites and especially parasitoids has been a primary source of data for ecological theories of community structure, particularly valuable for studies of tritrophic interactions (Abrahamson and Weis, 1997), for instance, and for food-web analyses (Godfray et al., 1999). In fact, many investigations center around whether the parasitic habit promotes diversification (Wiegmann et al., 1993; Cronin and Abrahamson, 2001), and if individual phylogenies of hosts and their parasites reflect coevolved associations (Lyal, 1987; Kim, 1988; Hafner and Nadler, 1988). Recent biological work and the fossil history of parasitoids and parasites supports the conclusion that more accommodationist mechanisms, typified by the coexistence of host and consumer, characterize the post-Triassic history of carnivory in freshwater and terrestrial ecosystems.

*What was trophic structure like before parasites and parasitoids?*—There is no direct fossil evidence for insect parasitism or parasitoidism on arthropods in continental ecosystems before the Early Jurassic. Evidence from the phylogenetic relationships of noninsectan parasites and parasitoids would strongly support the presence during this interval of freshwater or terrestrial members of the phyla Acanthocephala, Platyhelminthes, Annelida, Nematoda, Nematomorpha, and Pentastoma, whose hosts presumably were vertebrates, arachnids, or insects. The absence of direct evidence for parasitic insects is countered by phylogenetic relationships indicating that some of these life-habits originated during the Permian to Late Jurassic (Waage, 1979), in, for example, the Phthiraptera (Kim, 1988), Siphonaptera (Traub and Starcke, 1980), and Strepsiptera (Kinzelbach and Pohl, 1994). These orders could have existed for all that time as ghost lineages alongside their earlier occurring, free-

living sister groups, but this is unlikely. In other clades dominated by parasitoids, which have a considerably better fossil record than parasites, the record reveals explosive diversification for the Hymenoptera and to a lesser extent the Diptera during the Middle Jurassic to mid-Cretaceous. Thus continental invertebrate carnivory from the latest Silurian to Early Jurassic can be characterized as entirely or near-entirely predaceous in nature. The fossil record indicates that predators were the sole or overwhelmingly dominant carnivores during the earliest Pennsylvanian to the mid-Cretaceous, as evidenced by the dominance of Odonatoptera, some protorthopteran lineages, Titanoptera, gerromorph Hemiptera, Raphidoptera, Megaloptera, Planipennia, and caraboid and staphylinoid Coleoptera (Fig. 4). The presence of only predator guilds of carnivores in continental ecosystems must have had a profound effect on the regulation of herbivorous and other heterotrophic organisms (see Eggleton and Belshaw, 1992), particularly since considerable evidence shows that modern trophic webs are strongly regulated by parasites and parasitoids (DeAngelis, 1992; Godfray et al., 1999). Accordingly, in a world without these two key carnivore guilds, one would expect simpler food webs with linear trophic pathways (Dunne et al., 2002), and the absence of lineages with typical defensive strategies to ward off parasites and parasitoids, such as small size, concealment, exoskeletal or other types of mechanical isolation, and behaviors to reduce the risk of attack such as parental or group care and protection. The latter would include the caste-based, regulated societies seen today in social insects—and this may explain the rise of sociality in termites, ants, wasps, and bees (Wilson, 1992) during the Mesozoic diversification of parasitoids.

*Is there trophic-level selectivity at mass extinctions?*—Among terrestrial carnivorous invertebrates, insects have the best fossil record. The insect fossil record is characterized by two important extinction events. The first is deduced from the geochronologic distributions of order-rank clades. This was a catastrophic extinction at the

end of the Permian Period, in which the Paleozoic Insect Fauna was replaced by the Modern Insect Fauna through the loss of a high percentage of high-ranked clades (Labandeira and Sepkoski, 1993). Among carnivores, this event affected only predators, as the other carnivore guilds presumably were absent. The second event, at the Cretaceous-Paleogene boundary, is more surprising, given previous studies that failed to detect any family-level signal beyond background rates (Ponomarenko, 1988; Jarzemowski, 1989; Labandeira and Sepkoski, 1993). A recent examination, however, has taken the explicitly ecological approach of evaluating insect-mediated leaf damage patterns in well-preserved and diverse floras across the K-T boundary in North Dakota (Labandeira et al., 2002). This study demonstrated a pronounced qualitative and quantitative diminution of insect herbivory (especially among specialists) at the boundary, indicating a significant deterioration of the herbivore portion of terrestrial food webs. Such a major trophic alteration would have induced extinctions, based on our present knowledge of food-web perturbation from both theoretical modeling and empirical field observations (DeAngelis, 1992; Dunne et al., 2002). After the expansion of parasitoidism and parasitism during the later Mesozoic, this sudden reduction in host resource probably trophically affected major carnivore guilds in continental food chains.

## SUMMARY

The transfer of energy in terrestrial ecosystems, both in fresh water and on land, culminates in the process of carnivory or the consumption of animals by animals. This consumption may be rapid as in the case of predators and their prey, or it may be prolonged as in the case of parasitoids with their relatively small hosts, and parasites with their comparatively large hosts. While these three types of carnivory are essential to the structure of food webs in modern ecosystems, their detection in the fossil record presents challenges. Six types of paleobiological evidence can reveal the presence of carnivory: taxonomic affiliation, structural and functional attributes (especially mouthparts and

ovipositors), organismic damage, gut contents, coprolites, and mechanisms of predation avoidance. This evidence typically occurs in well-preserved deposits.

Twelve invertebrate phyla have adopted a continental carnivorous existence, representing predatory, parasitoid, and parasitic life-habits. Of these phyla, the most speciose, ecologically varied, and abundant are nematodes and arthropods, both of which have representative members practicing each of the three modes of carnivory. This hyperdiversity is related, particularly in arthropods, to such features as small size, ecdysis, ovipositors, and mouthpart morphology. This latter can involve either a buccal stylet apparatus or the varied, often co-opted multielement mouthpart structures that have been modified into several functional modes for obtaining nutrition—including chewing, piercing-and-sucking, and boring. In the terrestrial invertebrate world, accommodationist strategies such as forms of carnivory that result in the prolonged survival of a host, are probably more common than the rapid dispatching of prey.

Members of all twelve continental invertebrate phyla are documented in the fossil record, and arthropods are first represented by predators coexisting with detritivores and herbivores. They have their first appearances in the earliest terrestrial biotas from the latest Silurian to Middle Devonian, but it is not until the Middle Jurassic to mid-Cretaceous, approximately 250 million years later, that parasitoids and parasites are recorded as fossils, even though their phylogenetic relationships may indicate greater antiquity. The diversification of these two functional groups of carnivores added considerable complexity to food webs and may have been associated with the origin of insect sociality as a means of warding off attack. Although insect mass extinctions at the end of the Permian had a profound effect on terrestrial invertebrate predation, recent evidence indicates that an end-Cretaceous extinction may have had less profound but more integrative consequences on food webs by affecting dependent predators, parasitoids, and parasites. Thus an intriguing aim for further study is to understand the

fabric of terrestrial food webs in a world in which predators were the only carnivores, preceding the emergence of parasitoids and parasites.

## ACKNOWLEDGMENTS

Appreciation is extended to Finnegan Marsh, who formatted the figures. I thank the following people for reviews: Steven Hasiotis, Ed Jarzembowski, Elena Lukashevich, Mihail

Mostovski, George Poinar, Jr., Alex Rasnitsyn, and Dena Smith. This is contribution 92 of the Evolution of Terrestrial Ecosystems consortium at the National Museum of Natural History. This article is dedicated to the deceased paleoentomologist Vladimir Zherikhin of the Paleontological Institute of the Russian Academy of Sciences (Moscow), a systematist and a pioneer in the use of phylogenetic, taxic, and associational data in insect paleoecology.

## REFERENCES

- ABEL, O. 1935. Vorzeitliche Lebensspuren. Gustav Fischer, Jena, 644 p.
- ABELE, L. G., W. KIM, AND B. E. FELGENHAUER. 1989. Molecular evidence for inclusion of the phylum Pentastomida in the Crustacea. *Molecular Biology and Evolution*, 6:685–691.
- ABRAHAMSON, W. G., AND A. E. WEIS. 1997. The Evolutionary Ecology of a Tritrophic-level Interaction: Goldenrod, the Stem Gall maker and its Natural Enemies. Princeton University Press, Princeton, NJ.
- AGUINALDO, A. M. A., J. M. TURBEVILLE, L. S. LINFORD, M. C. RIVERA, J. R. GAREY, R. A. RAFF, AND J. A. LAKE. 1997. Evidence for a clade of nematodes, arthropods and other moulting animals. *Nature*, 387:489–493.
- ALLISON, C. W. 1975. Primitive fossil flatworm from Alaska: new evidence bearing on ancestry of the Metazoa. *Geology*, 3:649–652.
- ALMOND, J. E. 1985. The Silurian-Devonian fossil record of the Myriapoda. *Philosophical Transactions of the Royal Society of London*, B, 309:227–237.
- ANDRES, D. 1989. Phosphatisierte Fossilien aus dem unteren Ordoviz von Südschweden. *Berliner Geowissenschaftliche Abhandlungen* A, 106:9–19.
- ARNETT, R. H., JR. 2000. American Insects, Second Edition. CRC Press, Boca Raton, FL, 1003 p.
- ASKEW, R. W. 1979. Parasitic Insects. Heinemann, London, 316 p.
- BACHOFEN-ECHT, A. 1934. Beobachtungen über im Bernstein vorkommende Spinnengewebe. *Biologia Generalis*, 10:179–184.
- BALASHOV, Y. S. 1999. Evolution of haematophagy in insects and ticks. *Entomological Review*, 79:943–954.
- BANKS, H. P., AND B. J. COLTHART. 1993. Plant-animal-fungal interactions in Early Devonian trimerophytes from Gaspé, Canada. *American Journal of Botany*, 80:992–1001.
- BÄNZIGER, H. 1975. Skin-piercing blood-sucking moths I: ecological and ethological studies on *Calpe eustrigata* (Lepid., Noctuidae). *Acta Tropica*, 32:125–144.
- BARNES, R. S. K., P. CALOW, AND P. J. W. OLIVE. 1993. The Invertebrates: A New Synthesis, Second Edition. Blackwell, London, 488 p.
- BARTHÉL, K. W., N. H. M. SWINBURNE, AND S. CONWAY MORRIS. 1994. Solnhofen: A Study in Mesozoic Palaeontology. Cambridge University Press, Cambridge, UK, 236 p.
- BECHLEY, G. 1996. Morphologische Untersuchungen am Flügelgeäder der Rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata). *Petalura*, 2:1–402.
- BECHLEY, G., A. NEL, X. MARTÍNEZ-DELCLÒS, E. JARZEMBOWSKI, R. CORAM, D. MARTILL, G. FLECK, F. ESCUILLET, M. M. WISSHA, AND M. MAISCH. 2001. A revision and phylogenetic study of Mesozoic Aeschnoptera, with description of numerous new taxa (Insecta: Odonata: Anisoptera). *Neue Paläontologische Abhandlungen*, 4:1–219.
- BERTOLANI, R., AND D. GRIMALDI. 2000. A new eutardigrade (Tardigrada: Milnesiidae) in amber from the Upper Cretaceous (Turonian) of New Jersey, p. 103–110. *In* D. A. Grimaldi (ed.), Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey. Backhuys, Leiden.

- BETZ, O. 1996. Function and evolution of the adhesion-capture apparatus of *Stenus* species (Coleoptera, Staphylinidae). *Zoomorphology*, 116:15–34.
- BLACKWELL, A., A. J. MORDUE, M. R. YOUNG, AND W. MORDUE. 1992. Morphology of the antennae of two species of biting midge: *Culicoides impunctatus* (Goetghebuer) and *Culicoides nubeculosus* (Meigen) (Diptera, Ceratopogonidae). *Journal of Morphology*, 213:85–103.
- BLAXTER, M. L., P. DE LEY, J. R. GAREY, L. X. LIU, P. SCHELDEMAN, A. VIERSTRAETE, J. R. VANFLETEREN, L. Y. MACKAY, M. DORRIS, L. M. FRISSE, J. T. VIDA, AND W. K. THOMAS. 1998. A molecular framework for the phylum Nematoda. *Nature*, 392:71–75.
- BORKENT, A. 1995. Biting Midges in the Cretaceous Amber of North America (Diptera: Ceratopogonidae). Backhuys, Leiden, 237 p.
- BOWN, T. M., S. T. HASIOTIS, J. F. GENISE, F. MALDONADO, AND E. M. BROUWERS. 1997. Trace fossils of Hymenoptera and other insects and paleoenvironments of the Claron Formation (Paleocene and Eocene), southwestern Utah. United States Geological Survey Bulletin, 2153-C:41–58.
- BRAUCKMANN, C., AND W. ZESSIN. 1989. Neue Meganeuridae aus dem Namurium von Hagen-Vorhalle (BRD) und die Phylogenie der Meganisoptera (Insecta, Odonata). *Deutsche Entomologische Zeitschrift*, N.F., 36:177–215.
- BROWN, S. J. 1989. Pathological consequences of feeding by hematophagous arthropods: comparison of feeding strategies, p. 4–15. In C. J. Jones and R. E. Williams (eds.), *Physiological Interactions between Hematophagous Arthropods and Their Vertebrate Hosts*. Entomological Society of America, Lanham, MD.
- BRUES, C. T. 1972. *Insects, Food and Ecology*. Dover Publications, New York, 466 p.
- BRUSCA, R. C. 2000. Unraveling the history of arthropod biodiversification. *Annals of the Missouri Botanical Garden*, 87:13–25.
- BRUSCA, R. C., AND G. J. BRUSCA. 1990. *Invertebrates*. Sinauer, Sunderland, MA, 922 p.
- BUATOIS, L., M. G MÁNGANO, J. F. GENISE, AND T. N. TAYLOR. 1998. The ichnologic record of the continental invertebrate invasion: evolutionary trends in environmental expansion, ecospace utilization, and behavioral complexity. *Palaios*, 13:217–240.
- CAPASSO, L. 1993. Fossil mosquitoes and the spread of infectious diseases in man's ancestors. *Journal of Paleopathology*, 3:171–201.
- CARPENTER, F. M. 1971. Adaptations among Paleozoic insects, p. 1236–1251. In E. Yochelson (ed.), *Proceedings of the First North American Paleontological Convention*. Allen Press, Lawrence, KS.
- CARPENTER, F. M. 1992. Volume 3: Superclass Hexapoda. In R. L. Kaesler, E. Brosius, J. Keim, and J. Priesner (eds.), *Treatise on Invertebrate Paleontology*, Part R, Arthropoda 4. Geological Society of America and University of Kansas, Lawrence, KS, 655 p.
- CHALWATZIS, N., J. HAUF, P. Y. VAN DER PEER, R. KINZELBACH, AND F. K. ZIMMERMANN. 1996. 18S ribosomal RNA genes of insects: primary structure of the genes and molecular phylogeny of the Holometabola. *Annals of the Entomological Society of America*, 89:789–803.
- CLAUSEN, C. P. 1940. *Entomophagous Insects*. McGraw-Hill, New York, 688 p.
- COCKERELL, T. D. A. 1917. *Glossina* and the extinction of Tertiary mammals. *Nature*, 103:265.
- COHEN, A. S. 1989. The taphonomy of gastropod shell accumulations in large lakes: an example from Lake Tanganyika, Africa. *Paleobiology*, 15:26–45.
- CONWAY MORRIS, S. 1981. Parasites and the fossil record. *Parasitology*, 82:489–509.
- CONWAY MORRIS, S. 1998. *The Crucible of Creation: The Burgess Shale and the Rise of Animals*. Oxford University Press, Oxford, UK, 242 p.
- CONWAY MORRIS, S., AND D. W. T. CROMPTON. 1982. The origins and evolution of the Acanthocephala. *Biological Reviews*, 57:85–115.
- COOPER, K. W. 1964. The first fossil tardigrade: *Beorn leggi* Cooper, from Cretaceous amber. *Psyche*, 71:41–48.
- CORBET, P. S. 1999. Dragonflies—Behaviour and Ecology of Odonata. Harley, Colchester, UK, 829 p.
- CRONIN, J. T., AND W. G. ABRAHAMSON. 2001. Do parasitoids diversify in response to host-plant shifts by herbivorous insects? *Ecological Entomology*, 26:347–355.
- CROWSON, R. A. 1981. *The Biology of the Coleoptera*. Academic Press, New York, 802 p.
- DAMPF, A. 1910. *Palaeopsylla klebsiana* n. sp., ein fossiler Flöh aus dem baltischen Bernstein. *Schriften der Physikalisch-ökonomischen Gesellschaft zu Königsberg in Prussia*, 51:248–259.

## LABANDEIRA—PREDATORS, PARASITOIDS, AND PARASITES

- DEANGELIS, D. L. 1992. Dynamics of Nutrient Cycling and Food Webs. Chapman & Hall, London, 270 p.
- DESPORTES, C. 1942. *Forcipomyia velox* Winn. et *Sycorax silacea* Curtis, vecteurs d'*Icosiella neglecta* (Diesing): filaire commune de la grenouille verte. Annales de Parasitologie, 19:53–68.
- DEWEL, R. A., AND W. C. DEWEL. 1998. The place of tardigrades in arthropod evolution, p. 109–123. In R. A. Fortey and R. H. Thomas (eds.), Arthropod Relationships. Chapman and Hall, London.
- DOWNES, J. A. 1971a. Feeding and mating in the insectivorous Ceratopogoninae (Diptera). Memoirs of the Entomological Society of Canada, 104:1–62.
- DOWNES, J. A. 1971b. The ecology of blood-sucking Diptera: an evolutionary perspective, p. 232–258. In A. M. Fallis (ed.), Ecology and Physiology of Parasites. University of Toronto Press, Toronto.
- DOWNES, J. A., AND D. H. COLLESS. 1967. Mouthparts of the biting and blood-sucking type in Tanyderidae and Chironomidae (Diptera). Nature, 214:1355–1356.
- DUBININ, B. V. 1948. Discovery of a Pleistocene louse (Anoplura) and nematodes during the study of corpses of Indigirsk fossil gophers. Doklady Akademii Nauk SSSR, N.S., 62:417–420 [in Russian].
- DUBININA, M. N. 1972. Nematoda *Alfortia edentatus* (Looss, 1900) iz Kischechinka Verkhne pleistotsenovoi loshadi. Parasitologiya, 6:441–443 [in Russian].
- DUDLEY, R. 1998. Atmospheric oxygen, giant Paleozoic insects and the evolution of aerial locomotor performance. Journal of Experimental Biology, 201:1043–1050.
- DUNLOP, J. A. 1994. The palaeobiology of the Writhlington trigontarbid arachnid. Proceedings of the Geologists' Association, 105:287–296.
- DUNNE, J. A., R. J. WILLIAMS, AND N. D. MARTINEZ. 2002. Network topology and species loss in food webs: robustness increases with connectance. Santa Fe Institute Working Paper, 02-03-013:1–17.
- DURANTE, M. V., AND W. MAUCCI. 1972. Descrizione di *Hybisibius (Isohyp.) basalovoi* sp. nov. e altre notizie su tardigradi del Veronese. Memorie del Museo Civico di Storia Naturale di Verona, 20:275–281.
- DURDEN, C. J. 1988. Hamilton insect fauna, p. 117–124. In G. Mapes and R. H. Mapes (eds.), Regional Geology and Paleontology of Upper Paleozoic Hamilton Quarry Area in Southeastern Kansas. Geological Society of America, Lawrence, KS.
- EDWARDS, D., P. A. SELDEN, J. B. RICHARDSON, AND L. AXE. 1995. Coprolites as evidence for plant-animal interaction in Siluro-Devonian terrestrial ecosystems. Nature, 377:329–331.
- EGGLETON, P., AND R. BELSHAW. 1992. Insect parasitoids: an evolutionary overview. Proceedings of the Royal Society of London, B, 337:1–20.
- EISENBEIS, G., AND W. WICHARD. 1988. An Atlas on the Biology of Soil Arthropods. Springer Verlag, Berlin, 437 p.
- ERWIN, T. L., AND L. J. M. ERWIN. 1976. Relationships of predaceous beetles to tropical forest wood decay, Part II: The natural history of Neotropical *Eurycoleus macularis* Chevrolat (Carabidae: Lebiini) and its implications in the evolution of ectoparasitoidism. Biotropica, 8:215–224.
- ERWIN, T. L., AND J. C. SCOTT. 1980. Seasonal and size patterns, trophic structure and richness of Coleoptera in the tropical arboreal ecosystem: the fauna of the tree *Luehea seemannii* Triana and Planch in the Canal Zone of Panama. Coleopterists Bulletin, 34:305–322.
- EVANOFF, E., W. C. MCINTOSH, AND P. C. MORPHEY. 2001. Stratigraphic summary and  $^{40}\text{Ar}/^{39}\text{Ar}$  geochronology of the Florissant Formation, Colorado, p. 1–16. In E. Evanoff, K. M. Gregory-Wodzicki, and K. R. Johnson (eds.), Fossil Flora and Stratigraphy of the Florissant Formation, Colorado. Proceedings of the Denver Museum of Nature and Science, 4.
- EVANS, H. C. 1989. Mycopathogens of insects of epigeal and aerial habitats, p. 205–238. In N. Wilding, N. M. Collins, P. M. Hammond, and J. F. Webber (eds.), Insect-Fungus Interactions. Academic Press, London.
- FANG, Q. Q., S. MCKEEVER, AND F. E. FRENCH. 1999. Cladistic analysis of tabanids (Diptera: Tabanidae) using microscopic characters of the mouthparts. Memoirs on Entomology International, 14:355–366.
- FISCHER, D. C. 1979. Evidence for subaerial activity of *Euproops danae* (Merostomata, Xiphosurida), p. 379–447. In M. H. Nitecki (ed.), Mazon Creek Fossils. Academic Press, New York.
- FOELIX, R. F. 1996. Biology of Spiders, Second Edition. Oxford University Press, New York, 330 p.
- FORTEY, R. A., AND R. H. THOMAS. 1998. Arthropod Relationships. Chapman & Hall, London, 383 p.
- FRANZEN, J. L. 1985. Exceptional preservation of Eocene vertebrates in the lake deposit at Grube Messel (West Germany). Philosophical Transactions of the Royal Society of London, B, 311:181–186.

- FREY, D. G. 1964. Remains of animals in Quaternary lake and bog sediments and their interpretation. *Archiv für Hydrobiologie, Beihefte*, 2:1–114.
- FUCHS, G.-V. 1975. Die Gewinnung von Pollen und Nektar bei Käfern. *Natur und Museum*, 104:45–54.
- FULLARD, J. H., AND N. NAPEOLEONE. 2001. Diel flight periodicity and the evolution of auditory defences in the Macrolepidoptera. *Animal Behaviour*, 62:349–368.
- GASTON, K. J., AND E. HUDSON. 1994. Regional patterns of diversity and estimates of global insect species richness. *Biodiversity and Conservation*, 3:493–500.
- GAULD, I., AND B. BOLTON. 1988. The Hymenoptera. Oxford University Press, Oxford, UK, 332 p.
- GENISE, J. F. 1995. Upper Cretaceous trace fossils in permineralized plant remains from Patagonia, Argentina. *Ichnos*, 3:287–299.
- GERHARD, S., AND W. RIETSCHEL. 1968. Ein Stück Bernstein und seine Einschlüsse. *Natur und Museum*, 98:515–520.
- GLUKHOVA, V. M. 1989. Blood-sucking midges of the genera *Culicoides* and *Forcipomyia* (Ceratopogonidae). Fauna of the USSR, 139,3,5a, 408. Nauka, Leningrad.
- GODFRAY, H. C. J. 1994. Parasitoids: Behavioral and Evolutionary Ecology. Princeton University Press, Princeton, NJ, 473 p.
- GODFRAY, H. C. J., O. T. LEWIS, AND J. MEMMOTT. 1999. Studying insect diversity in the tropics. *Philosophical Transactions of the Royal Society of London*, B, 354:1811–1824.
- GÖPFERT, M. C., AND L. T. WASSERTHAL. 1999. Hearing with the mouthparts: behavioural response and the structural basis of ultrasound perception in acherontiine hawkmoths. *Journal of Experimental Biology*, 202:909–918.
- GORDON, M. S., AND E. C. OLSON. 1995. Invasions of the Land: The Transitions of Organisms from Aquatic to Terrestrial Life. Columbia University Press, New York, 312 p.
- GOULD, S. J. 1995. Of tongue worms, velvet worms, and water bears. *Natural History*, 103:1–15.
- GRADSTEIN, F., AND J. OGG. 1996. A Phanerozoic time scale. *Episodes*, 19:3–5.
- GRAHAM, J. B., R. DUDLEY, N. AGUILAR, AND C. GANS. 1995. Implications of the late Palaeozoic oxygen pulse for physiology and evolution. *Nature*, 375:117–120.
- GRAY, J. 1988. Evolution of the freshwater ecosystem: the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 61:1–214.
- GRAY, J., AND W. SHEAR. 1992. Early life on land. *American Scientist*, 80:444–456.
- GREENE, A. 1975. Biology of the five species of Cychrini (Coleoptera: Carabidae) in the steppe region of southeastern Washington. *Melanderia*, 19:1–43.
- GREENSLADE, P. J. M., AND P. E. S. WHALLEY. 1986. The systematic position of *Rhyniella praecursor* Hirst & Maulik (Collembola), the earliest known hexapod, p. 319–323. In R. Dallai (ed.), Second International Seminar on Apterygota. University of Siena, Italy.
- GRIMALDI, D. A. 1992. Vicariance biogeography, geographic extinctions, and the North American tsetse flies, p. 178–204. In M. J. Novacek and Q. D. Wheeler (eds.), *Extinction and Phylogeny*. Columbia University Press, New York.
- GRONENBERG, W. 1996. The trap-jaw mechanism in the dacetine ants *Daceton armigerum* and *Strumigenys* sp. *Journal of Experimental Biology*, 99:2021–2033.
- HAFNER, M. S., AND S. A. NADLER. 1988. Phylogenetic trees support the coevolution of parasites and their hosts. *Nature*, 332:258–259.
- HAAS, F., AND J. KUKALOVÁ-PECK. 2001. Dermaptera hindwing structure and folding: new evidence for familial, ordinal and superordinal relationships within the Neoptera (Insecta). *European Journal of Entomology*, 98:445–509.
- HAGEN, K. S. 1987. Nutritional ecology of terrestrial insect predators, p. 533–577. In F. Slansky, Jr., and J. G. Rodriguez (eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*. John Wiley & Sons, New York.
- HANNIBAL, J. T., AND R. M. FELDMANN. 1988. Millipedes from late Paleozoic limestones at Hamilton, Kansas, p. 125–131. In G. Mapes and R. H. Mapes (eds.), *Regional Geology and Paleontology of Upper Paleozoic Hamilton Quarry Area in Southeastern Kansas*. Geological Society of America, Lawrence, KS.
- VON HEYDEN, C. 1860. *Mermis antiqua*, ein fossiler Eingeweidewurm. *Entomologische Zeitung*, 21:38.
- VON HEYDEN, C. 1862. Gliederthiere aus der Braunkohle des Niederrhein's der Wetterau und der Rohn. *Palaeontographica*, 10:62–82.
- HONG, Y.-C. 1984. New fossil insects of Laiyang Group from Laiyang Basin, Shandong Province. *Professional Papers in Stratigraphy and Palaeontology*, 11:31–41 [in Chinese with English abstract].

## LABANDEIRA—PREDATORS, PARASITOIDS, AND PARASITES

- HOPKIN, S. P. 1997. The Biology of the Springtails (Insecta: Collembola). Oxford University Press, Oxford, UK, 330 p.
- HOUSTON, T. F. 1987. Fossil brood cells of stenotritid bees (Hymenoptera: Apoidea) from the Pleistocene of South Australia. *Transactions of the Royal Society of South Australia*, 3:93–97.
- ITURRALDE-VINENT, M. A. 2001. Geology of the amber-bearing deposits of the Greater Antilles. *Caribbean Journal of Science*, 37:141–167.
- JANZEN, D. H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics*, 2:465–492.
- JANZEN, D. H. 1978. The ecology and evolutionary biology of seed chemistry as related to seed predation. In J. B. Harborne (ed.), *Biochemical Aspects of Plant and Animal Coevolution*. Annals and Proceedings of the Phytochemical Society of Europe, 15:163–206.
- JARZEMBOWSKI, E. A. 1976. Report of Easter Field Meeting: the Lower Tertiaries of the Isle of Wight, 27–31.III.1975. *Tertiary Research*, 1:11–16.
- JARZEMBOWSKI, E. A. 1984. Early Cretaceous insects from southern England. *Modern Geology*, 9:71–93.
- JARZEMBOWSKI, E. A. 1989. Cretaceous insect extinction. *Mesozoic Research*, 2:25–28.
- JARZEMBOWSKI, E. A. 1994. Fossil cockroaches or pinnule insects? *Proceedings of the Geologists' Association*, 105:305–311.
- JELL, P. A., AND P. M. DUNCAN. 1986. Invertebrates, mainly insects, from the freshwater Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. *Memoir of the Association of Australasian Palaeontologists*, 3:111–205.
- JUNIPER, B. E. 1986. The path to plant carnivory, p. 195–218. In B. E. Juniper and T. R. E. Southwood (eds.), *Insects and the Plant Surface*. Edward Arnold, London.
- JERAM, A. J. 1990. Book-lungs in a Lower Carboniferous scorpion. *Nature*, 343:360–361.
- JERVIS, M. A., AND N. A. C. KIDD. 1986. Host-feeding strategies in hymenopteran parasitoids. *Biological Reviews*, 61:395–434.
- KALUGINA, N. S. 1991. New Mesozoic Simuliidae and Leptoconopidae and blood-sucking origin in lower dipterans. *Paleontologicheskii Zhurnal*, 1991:69–70 [in Russian].
- KELLEY, P. H., AND T. A. HANSEN. 1996. Naticid gastropod prey selectivity through time and the hypothesis of escalation. *Palaios*, 11:437–445.
- KEVAN P. G., W. G. CHALONER, AND D. B. O. SAVILE. 1975. Interrelationships of early terrestrial arthropods and plants. *Palaeontology*, 18:391–417.
- KIM, K. C. 1988. Evolutionary parallelism in Anoplura and eutherian mammals. In M. W. Service (ed.), *Biosystematics of Haematophagous Insects*. Systematics Association Special Volume, 37:91–114. Oxford University Press, Oxford, UK.
- KINZELBACH, R. K., AND H. POHL. 1994. The fossil Strepsiptera (Insecta: Strepsiptera). *Annals of the Entomological Society of America*, 87:59–70.
- KLOMPEN, H., AND D. A. GRIMALDI. 2001. First Mesozoic record of a parasitiform mite: a larval argasid tick in Cretaceous amber (Acari: Ixodida: Argasidae). *Annals of the Entomological Society of America*, 94:10–15.
- KORN, W. 1943. Die Muskulatur des Kopfes und des Thorax von *Myrmeleon europaeus* und ihre Metamorphose. *Zoologischer Jahrbücher (Anatomie)*, 68:273–330.
- KOZUR, H. 1970. Fossile Hirudinea aus dem Oberjura von Bayern. *Lethaia*, 3:225–232.
- KRISTENSEN, N. P. 1999. Phylogeny of endopterygote insects, the most successful lineage of living organisms. *European Journal of Entomology*, 96:237–253.
- KUKALOVÁ-PECK, J. 1990. Fossil history and the evolution of hexapod structures, p. 141–179. In I. D. Naumann, P. B. Carne, J. U. F. Lawrence, E. S. Nielsen, J. P. Spradbery, R. W. Taylor, M. J. Whitten, and M. J. Littlejohn (eds.), *The Insects of Australia*, Second Edition, 1. Cornell University Press, Ithaca, NY.
- KUTSCHER, M., AND J. KOTEJA. 2000a. Trace fossils in Bitterfeld amber: excrements or detritus? *Polskie Pismo Entomologiczne*, 69:175–178.
- KUTSCHER, M., AND J. KOTEJA. 2000b. Coccids and aphids (Hemiptera: Coccoidea, Aphidoidea), prey of ants (Hymenoptera: Formicidae): evidence from Bitterfeld amber. *Polskie Pismo Entomologiczne*, 69:179–185.
- LABANDEIRA, C. C. 1990. Use of a Phenetic Analysis of Recent hexapod Mouthparts for the Distribution of Hexapod Food Resource Guilds in the Fossil Record. Ph.D. Dissertation, University of Chicago, 1186 p.
- LABANDEIRA, C. C. 1994. A compendium of fossil insect families. *Milwaukee Public Museum Contributions in Biology and Geology*, 88:1–71.

- LABANDEIRA, C. C. 1997a. Insect mouthparts: ascertaining the paleobiology of insect feeding strategies. *Annual Review of Ecology and Systematics*, 28:153–193.
- LABANDEIRA, C. C. 1997b. Permian pollen eating. *Science*, 277:1422–1423.
- LABANDEIRA, C. C. 1998a. The role of insects in Late Jurassic to middle Cretaceous ecosystems, p. 105–124. *In* S. G. Lucas, J. I. Kirkland, and J. W. Estep (eds.), *Lower and Middle Cretaceous Terrestrial Ecosystems*. New Mexico Museum of Natural History and Science Bulletin, 14.
- LABANDEIRA, C. C. 1998b. Early history of arthropod and vascular plant associations. *Annual Review of Earth and Planetary Sciences*, 26:329–377.
- LABANDEIRA, C. C. 2000. The paleobiology of pollination and its precursors, p. 233–269. *In* R. Gastaldo and W. DiMichele (eds.), *Phanerozoic Terrestrial Ecosystems*. Paleontological Society Papers, 6.
- LABANDEIRA, C. C. 2002a. The history of associations between plants and animals, p. 26–74, 248–261. *In* C. Herrera and O. Pellmyr (eds.), *Plant-Animal Interactions*. Blackwell Science, Oxford, UK.
- LABANDEIRA, C. C. 2002b. The paleobiology of middle Eocene plant-insect associations from the Pacific Northwest: a preliminary report. *Rocky Mountain Geology*, 37 (in press).
- LABANDEIRA, C. C., AND J. J. SEPkoski, JR. 1993. Insect diversity in the fossil record. *Science*, 261:310–315.
- LABANDEIRA, C. C., B. S. BEALL, AND F. M. HUEBER. 1988. Early insect diversification: evidence from a Lower Devonian bristletail from Québec. *Science*, 242:913–916.
- LABANDEIRA, C. C., K. R. JOHNSON, AND P. WILF. 2002. Impact of the terminal Cretaceous event on plant-insect associations. *Proceedings of the National Academy of Sciences, USA*, 99:2061–2066.
- LAKSHMINARAYANA, K. V., M. S. MANI, AND W. D. EICHLER. 1984. On the relationship of the fossil flea *Saurophthirus longipes* Ponomarenko (Siphonaptera: Insecta). *Records of the Zoological Survey of India*, 81:43–48.
- LAMBRECHT, F. L. 1993. Tsetse flies and trypanosomiasis during the American Tertiary. *National Geographic Society Research Reports*, 21:241–249.
- LARSSON, S. G. 1978. Baltic amber—a palaeobiological study. *Entomonograph*, 1:1–192.
- LEHANE, M. J. 1991. *Biology of Blood-Sucking Insects*. Harper-Collins, London, 288 p.
- LEWIS, R. E., AND D. A. GRIMALDI. 1997. A pulicid flea in Miocene amber from the Dominican Republic (Insecta: Siphonaptera: Pulicidae). *American Museum Novitates*, 3205:1–9.
- LITTLE, C. 1983. *The Colonisation of Land: Origins and Adaptations of Terrestrial Animals*. Cambridge University Press, Cambridge, UK, 290 p.
- LITTLE, C. 1990. *The Terrestrial Invasion: An Ecophysiological Approach to the Origins of Land Animals*. Cambridge University Press, Cambridge, UK, 304 p.
- LYAL, C. H. C. 1985. Phylogeny and classification of the Psocodea, with special reference to the lice (Psocodea: Phthiraptera). *Systematic Entomology*, 10:145–165.
- LYAL, C. H. C. 1987. Co-evolution of trichodectid lice (Insecta: Phthiraptera) and their mammalian hosts. *Journal of Natural History*, 21:1–28.
- MALYSHEV, S. I. 1968. *Genesis of the Hymenoptera and the Phases of their Evolution*. Methuen, London, 319 p.
- MANTON, S. M. 1977. *The Arthropoda: Habits, Functional Morphology and Evolution*. Oxford University Press, Oxford UK, 527 p.
- MCKEEVER, S., D. V. HAGAN, AND W. L. GROGAN. 1991. Comparative study of mouthparts of ten species of predaceous midges of the tribe Ceratopogonini (Diptera: Ceratopogonidae). *Annals of the Entomological Society of America*, 84:93–106.
- MENGE, A. 1866. Ueber ein Rhipidipteron und einiger andere im Bernstein eingeschlossene Tiere. *Schriften der Naturforschenden Gesellschaft in Danzig*, N.F., 1:1–8.
- MERRITT, R. W., AND K. W. CUMMINS (eds.). 1984. *An Introduction to the Aquatic Insects*. Second edition. Kendall/Hunt, Dubuque, IA, 722 p.
- MIKUILÁS, R., Z. DVORAK, AND I. PEK. 1998. *Lamniporichnus vulgaris* igen. et isp. nov.: traces of insect larvae in stone fruits of hackberry (*Celtis*) from the Miocene and Pliocene of the Czech Republic. *Journal of the Czech Geological Society*, 43:277–280.
- MIKULIC, D. G., D. E. G. BRIGGS, AND J. E. KLUESSENDORF. 1985. A Silurian soft-bodied biota. *Science*, 228:715–717.
- MOUSSA, M. T. 1970. Nematode fossil trails from the Green River Formation (Eocene) in the Uinta Basin, Utah. *Journal of Paleontology*, 44:304–307.

## LABANDEIRA—PREDATORS, PARASITOIDS, AND PARASITES

- MÜLLER, K. J., D. WALOSSEK, AND A. ZAKHAROV. 1995. "Orsten" type phosphatized soft-integument preservation and a new record from the Middle Cambrian Kuonamka Formation in Siberia. *Neues Jahrbüch für Geologie und Paläontologie Abhandlungen*, 197:101–118.
- NAUMANN, I. D., P. B. CARNE, J. F. LAWRENCE, E. S. NIELSEN, J. P. SPRADBERRY, R. W. TAYLOR, M. J. WHITTEN, AND M. J. LITTLEJOHN (eds.). 1990. *The Insects of Australia: A Textbook for Students and Research Workers*, Second Edition. Cornell University Press, Ithaca, NY, 1137 p.
- NORTH, F. J. 1931. Insect-life in the coal forests, with special reference to South Wales. *Transactions of the Cardiff Naturalists Society*, 62:16–44.
- PANFILOV, D. V. 1968. Kalligrammatids (Neuroptera, Kalligrammatidae) in Jurassic deposits of Karatau, p. 166–175. In B. B. Rohdendorf (ed.), *Jurassic Insects of Karatau*. Izdatel'stvo Nauka, Moscow [in Russian].
- PAPIER, F., A. NEL, L. GRAUVOGEL-STAMM, AND J.-C. GALL. 1997. La plus ancienne sauterelle Tettigoniidae, Orthoptera (Trias, NE France): Mimétisme ou exaptation? *Paläontologische Zeitschrift*, 71:71–77.
- PAWLOWSKI, J., R. SZADZIEWSKI, D. KMIECIAK, J. FAHRNI, AND G. BITTAR. 1996. Phylogeny of the infraorder Culicomorpha (Diptera: Nematocera) based on 28S RNA gene sequences. *Systematic Entomology*, 21:167–178.
- PETRUNKEVITCH, A. 1942. A study of amber spiders. *Transactions of the Connecticut Academy of Arts and Sciences*, 34:119–464.
- PIERCE, W. D. 1960. Silicified Turbellaria from Calico Mountains nodules. *Bulletin of the South California Academy of Sciences*, 59:138–143.
- POINAR, G. O., JR. 1977. Fossil nematodes from Mexican amber. *Nematologica*, 23:232–238.
- POINAR, G. O., JR. 1984a. Fossil evidence of nematode parasitism. *Revue de Nématologie*, 7:201–203.
- POINAR, G. O., JR. 1984b. First fossil record of parasitism by insect parasitic Tylenchida (Allantonematidae: Nematoda). *Journal of Parasitology*, 70:306–308.
- POINAR, G. O., JR. 1984c. *Heydenius dominicus* n. sp. (Nematoda: Mermithidae), a fossil parasite from the Dominican amber. *Journal of Nematology*, 16:371–375.
- POINAR, G. O., JR. 1985. Fossil evidence of insect parasitism by mites. *International Journal of Acarology*, 11:37–38.
- POINAR, G. O., JR. 1987. Fossil evidence of spider parasitism by Ichneumonidae. *Journal of Arachnology*, 14:399–400.
- POINAR, G. O., JR. 1988. Hair in Dominican amber: evidence for Tertiary land mammals in the Antilles. *Experientia*, 44:88–89.
- POINAR, G. O., JR. 1991. The mycetophagous and entomophagous stages of *Iotonchium californicum* n. sp. (Iotonchiidae: Tylenchida). *Revue de Nématologie*, 14:565–580.
- POINAR, G. O., JR. 1993. Insects in amber. *Annual Review of Entomology*, 46:145–159.
- POINAR, G. O., JR. 1996. Fossil velvet worms in Baltic and Dominican amber: onychophoran evolution and biogeography. *Science*, 273:1370–1371.
- POINAR, G. O., JR. 1999a. Chrysomelidae in fossil resin: behavioural inferences, p. 1–16. In M. L. Cox (ed.), *Advances in Chrysomelidae Biology* 1. Backhuys, Leiden.
- POINAR, G. O., JR. 1999b. *Paleochordodes protus* n. g., n. sp. (Nematomorpha, Chordodidae), parasites of a fossil cockroach, with a critical examination of other fossil hairworms and helminthes of extant cockroaches (Insecta: Blattaria). *Invertebrate Biology*, 118:109–115.
- POINAR, G. O., JR. 2000. *Heydenius araneus* n. sp. (Nematoda: Mermithidae), a parasite of a fossil spider, with an examination of fossil helminths from extant spiders. *Invertebrate Biology*, 119:388–393.
- POINAR, G. O., JR., AND J. BRODZHINSKY. 1985. Fossil evidence of nematode (Tylenchida) parasitism in Staphylinidae (Coleoptera). *Nematologica*, 32:353–355.
- POINAR, G. O., JR., AND D. A. GRIMALDI. 1990. Fossil and extant macrochelid mites (Acari: Macrochelidae) phoretic on drosophilid flies (Diptera: Drosophilidae). *Journal of the New York Entomological Society*, 98:88–92.
- POINAR, G. O., JR., AND R. MILKI. 2001. *Lebanese Amber: The Oldest Insect Ecosystem in Fossilized Resin*. Oregon State University Press, Corvallis, OR, 96 p.
- POINAR, G. O., JR., AND J. C. MILLER. 2002. First fossil record of endoparasitism of adult ants (Formicidae: Hymenoptera) by Braconidae (Hymenoptera). *Annals of the Entomological Society of America*, 95:41–43.
- POINAR, G. O., JR., AND R. POINAR. 1999. *The Amber Forest: A Reconstruction of a Vanished World*. Princeton University Press, Princeton, NJ, 239 p.

- POINAR, G. O., JR., AND C. RICCI. 1992. Bdelloid rotifers in Dominican amber: evidence for parthenogenetic continuity. *Experientia*, 48:408–410.
- POINAR, G. O., JR., A. ACRA, AND F. ACRA. 1994a. Animal-animal parasitism in Lebanese amber. *Medical Science Research*, 22:159.
- POINAR, G. O., JR., A. ACRA, AND F. ACRA. 1994b. Earliest fossil nematode (Mermithidae) in Cretaceous Lebanese amber. *Fundamental and Applied Nematology*, 17:475–477.
- POINAR, G. O., JR., A. E. TREAT, AND R. V. SOUTHCOTT. 1991. Mite parasitism of moths: examples of paleosymbiosis in Dominican amber. *Experientia*, 47:210–212.
- PONOMARENKO, A. G. 1976. A new insect from the Cretaceous of Transbaikalia, a possible parasite of pterosaurians. *Paleontological Journal*, 1976:339–343.
- PONOMARENKO, A. G. (ed.). 1988. *The Cretaceous Biocoenotic Crisis in the Evolution of Insects*. USSR Academy of Sciences, Moscow, 230 p. [in Russian].
- PONOMARENKO, A. G. 1996. Evolution of continental aquatic ecosystems. *Paleontological Journal*, 30:705–709.
- POPHAM, E. J. 1962. The anatomy related to the feeding habits of *Arixenia* and *Hemimerus* (Dermaptera). *Proceedings of the Zoological Society of London*, 139:429–450.
- PRESTON-MAFHAM, R., AND K. PRESTON-MAFHAM. 1993. *The Encyclopedia of Land Invertebrate Behaviour*. Massachusetts Institute of Technology Press, Cambridge, MA, 320 p.
- PRICE, P. W. 1980. *Evolutionary Biology of Parasites*. Princeton University Press, Princeton, NJ.
- PRICE, P. W. 1997. *Insect Ecology*, Third Edition. Wiley, New York, 874 p.
- PROCTOR, M., P. YEO, AND A. LACK. 1996. *The Natural History of Pollination*. Timber Press, Portland, OR, 479 p.
- PRUVOST, P. 1919. Le faune continentale du terrain houiller du Nord de la France. *Mémoire pour Servir à l'Explication de la Carte Géologique Détailée de la France*. Imprimerie Nationale, Paris, 584 p.
- PRITCHARD G. 1976. Further observations on the functional morphology of the head and mouthparts of dragonfly larvae (Odonata). *Quaestiones Entomologicae*, 12:89–114.
- RASNITSYN, A. P. 1975. Hymenoptera Apocrita of the Mesozoic. *Transactions of the Paleontological Institute*, 147:1–134 [in Russian].
- RASNITSYN, A. P. 1988. An outline of evolution of the hymenopterous insects (order Vespoidea). *Oriental Insects*, 22:115–145.
- RASNITSYN, A. P. 1992. *Strashila incredibilis*, a new enigmatic mecopteroid insect with possible siphonapteran affinities from the Upper Jurassic of Siberia. *Psyche*, 99:323–333.
- RASNITSYN, A. P., AND V. V. ZHERIKHIN. 1999. First fossil chewing louse from the Lower Cretaceous of Baissa, Transbaikalia (Insecta, Pediculida = Phthiraptera, Saurodectidae fam. n.). *Russian Entomological Journal*, 8:253–255.
- RICHARDS, O. W., AND R. G. DAVIES. 1977. *Imms' General Textbook of Entomology*, Tenth Edition. Chapman and Hall, London, 1354 p.
- RICHTER, G. 1992. Fossilized gut contents: analysis and interpretation, p. 285–289. In S. Schaal and W. Ziegler (eds.), *Messel—An Insight into the History of Life and of the Earth*. Oxford University Press, Oxford, UK.
- RICHTER, G., AND S. BASZIO. 2001. First proof of planctivory/insectivory in a fossil fish: *Thaumaturus intermedius* from the Eocene Lake Messel (FRG). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 173:75–85.
- RICHTER, R., AND G. STORCH. 1980. Beiträge zur Ernährungsbiologie eozäner Fledermause aus der "Grube Messel." *Natur und Museum*, 110:353–367.
- RIEK, E. F. 1970. Lower Cretaceous fleas. *Nature*, 227:746–747.
- RITZKOWSKI, S. 1997. K-Ar-Alterbestimmungen der bernsteinführenden Sedimente des Samlandes (Paläogen, Bezirk Kaliningrad). *Metalla Bochum*, 66:19–23.
- ROHDENDORF, B. B., AND A. P. RASNITSYN. 1980. Historical Development of the Class Insecta. USSR Academy of Sciences, Moscow [in Russian].
- ROLFE, W. D. I. 1985. Aspects of the Carboniferous terrestrial arthropod community, p. 303–316. In J. T. Dutro, Jr. and H. W. Pfefferkorn (eds.), *Comptes Rendus de Neuvième Congrès International de Stratigraphie et de Géologie du Carbonifère*, 5. Southern Illinois University Press, Carbondale, IL.
- ROLFE, W. D. I., F. R. SCHRAM, G. PACAUD, D. SOTTY, AND S. SECRETAN. 1982. A remarkable Stephanian biota from Montceau-les-Mines, France. *Journal of Paleontology*, 56:426–428.
- ROTH, B. 1986. Land mollusks (Gastropoda: Pulmonata) from early Tertiary Bozeman Group, Montana. *Proceedings of the California Academy of Sciences*, 44:237–267.

LABANDEIRA—PREDATORS, PARASITOIDS, AND PARASITES

- ROWLEY, W. A., AND M. CORNFORD. 1972. Scanning electron microscopy of the pit of the maxillary palp of selected species of *Culicoides*. Canadian Journal of Zoology, 50:1207–1210.
- RUIZ-TRILLO, I., M. RIUTORT, D. T. J. LITTLEWOOD, E. A. LHERNIOU, AND J. BAGUÑA. 1999. Acoel flatworms: earliest extant bilaterian metazoans, not members of Platyhelminthes. Science, 283:1919–1923.
- SAMWAYS, M. J., R. OSBORN, AND T. L. SAUNDERS. 1997. Mandible form relative to the main food type in ladybirds (Coleoptera: Coccinellidae). Biocontrol Science and Technology, 7:275–286.
- SCHLEE, D., AND W. GLÖCKNER. 1978. Bernstein. Stuttgarter Beiträge zur Naturkunde (C), 8:1–72.
- SCHMID-HEMPEL, P. 1998. Parasites in Social Insects. Princeton University Press, Princeton, NJ, 409 p.
- SCHMIDT, W., M. SCHURMANN, AND M. TEICHMÜLLER. 1958. Biß-Spuren an Früchten des Miozän-Waldes der niederrheinischen Braunkohlen-formation. Fortschritte in der Geologie von Rheinland und Westfalen, 2:563–572.
- SCHOONHOVEN, L. M., T. JERMY, AND J. J. A. VAN LOON. 1998. Insect-Plant Biology: From Physiology to Evolution. Chapman and Hall, London, 409 p.
- SCHRAM, F. R. 1973. Pseudocoelomates and a nemertine from the Illinois Pennsylvanian. Journal of Paleontology, 47:985–989.
- SCHRAM, F. R. 1986. Crustacea. Oxford University Press, Oxford, UK, 606 p.
- SCHRAM, F. R., R. M. FELDMAN, AND M. J. COPELAND. 1978. The Late Devonian Palaeopalaemonidae and the earliest decapod crustaceans. Journal of Paleontology, 52:1375–1387.
- SCHUH, R. T., AND J. A. SLATER. 1995. True Bugs of the World (Hemiptera: Heteroptera). Cornell University Press, Ithaca, NY, 337 p.
- SCIACCHITANO, J. 1955. Su un gordio fossile. Monitore Zoologico Italiano, 63:57–61.
- SCOTT, A. C., AND T. N. TAYLOR. 1983. Plant/animal interactions during the Upper Carboniferous. Botanical Review, 49:259–307.
- SCOURFIELD, D. J. 1926. On a new type of crustacean from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire)—*Lepidocaris rhyniensis* gen. and sp. nov. Philosophical Transactions of the Royal Society of London, 214:153–187.
- SCUDDER, S. H. 1895. Revision of the American fossil cockroaches with descriptions of new forms. Bulletin of the United States Geological Survey, 124:1–176.
- SELDEN, P. A. 1996. Fossil mesothelae spiders. Nature, 379:498–499.
- SHAROV, A. G. 1973. Morphological features and way of life of Palaeodictyoptera, p. 49–63. In G. Y. Bei-Benko (ed.), 24<sup>th</sup> Annual Lectures in Memory of N. A. Kholodkovskogo, 24. Academy of Sciences, Moscow.
- SHEAR, W. A., AND P. M. BONAMO. 1988. Devonobiomorpha, a new order of centipedes (Chilopoda) from the Middle Devonian of Gilboa, New York state, USA, and the phylogeny of centiped orders. American Museum Novitates, 2927:1–30.
- SHEAR, W. A., AND J. KUKALOVÁ-PECK. 1990. The ecology of Paleozoic terrestrial arthropods: the fossil evidence. Canadian Journal of Zoology, 68:1807–1834.
- SHEAR, W. A., AND P. A. SELDEN. 2001. Rustling in the undergrowth: animals in early terrestrial ecosystems, p. 29–51. In P. G. Gensel and D. Edwards (eds.), Plants Invade the Land: Evolutionary and Environmental Perspectives. Columbia University Press, New York.
- SHEAR, W. A., W. SCHAWALLER, AND P. M. BONAMO. 1989b. Record of Palaeozoic pseudoscorpions. Nature, 341:527–529.
- SHEAR, W. A., J. M. PALMER, J. A. CODDINGTON, AND P. M. BONAMO. 1989a. A Devonian spinneret: early evidence of spiders and silk use. Science, 246:479–481.
- SIH, A. 1987. Nutritional ecology of aquatic insect predators, p. 579–607. In F. Slansky, Jr. and J. G. Rodriguez (eds.), Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. John Wiley & Sons, New York.
- SMIT, F. G. A. M. 1972. On some adaptive structures in Siphonaptera. Folia Parasitologica, 19:5–17.
- SMITH, J. J. B. 1985. Feeding mechanisms, p. 33–85. In G. A. Kerkut and L. E. Gilbert (eds.), Comprehensive Insect Physiology, Biochemistry, and Pharmacology, 4. Pergamon Press, Oxford, UK.
- SNODGRASS, R. E. 1952. A Textbook of Arthropod Anatomy. Cornell University Press, Ithaca, NY, 363 p.
- SOLEM, A., AND E. L. YOCHELSON. 1979. North American Paleozoic land snails, with a summary of other Paleozoic nonmarine snails. United States Geological Survey Professional Paper, 1072:1–42.
- SOUTHCOTT, R. V., AND R. T. LANGE. 1971. Acarine and other microfossils from the Maslin Eocene, South Australia. Records of the South Australian Museum, 16:1–21.
- STORCH, G., AND G. RICHTER. 1992. The ant-eater *Eurotamandua*: a South American in Europe, p. 209–215. In S. Schaal and W. Ziegler (eds.), Messel—An Insight into the History of Life and of the Earth. Oxford University Press, Oxford, UK.

- STØRMER, L. 1963. *Gigantoscorpio willsi*, a new scorpion from the Lower Carboniferous of Scotland and its associated preying microorganisms. *Skrifter Utgitt av Det Norske Videnskaps-Akademi i Oslo*, 8:1–171.
- STØRMER, L. 1969. Oldest known terrestrial arachnids. *Science*, 164:1276–1277.
- STRICKER, S. A. 1983. SEM and polarization microscopy of nemertean stylets. *Journal of Morphology*, 175:153–169.
- SUKACHEVA, I. D. 1982. Historical development of the order Phryganeida. *Transactions of the Paleontological Institute*, 197:1–111 [in Russian].
- SZADZIEWSKI, R. 1996. Biting midges from Lower Cretaceous amber of Lebanon and Upper Cretaceous amber of Taimyr (Diptera, Ceratopogonidae). *Studia Dipterologica*, 3:23–86.
- TASCH, P. 1957. Flora and fauna of the Rhynie Chert: a paleoecological reevaluation of published evidence. *University of Wichita Bulletin*, 36:1–24.
- TASNÁDI-KUBACSKA, A. 1962. *Paläopathologie*, Vol. 2. Gustav Fischer, Jena, Germany, 269 p.
- TAYLOR, T. N. 1981. Pollen and pollen organ evolution in early seed plants, p. 1–25. In K. J. Niklas (ed.), *Paleobotany, Paleoecology, and Evolution*, 2. Praeger, New York.
- THOMPSON, I. D., AND D. S. JONES. 1980. A possible onychophoran from the Middle Pennsylvanian Mazon Creek of northern Illinois. *Journal of Paleontology*, 54:588–596.
- THULBORN, R. A. 1991. Morphology, preservation and palaeobiological significance of dinosaur coprolites. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 83:341–366.
- TILLIER, S., M. MASSELOT, AND A. TILLIER. 1996. Phylogenetic relationships of the pulmonate gastropods from rRNA sequences, and tempo and age of the stylommatophoran radiation, p. 267–284. In J. Taylor (ed.), *Origin and Evolutionary Radiation of the Mollusca*. Oxford University Press, Oxford, UK.
- TRACEY, S., J. A. TODD, AND D. H. ERWIN. 1993. Mollusca: Gastropoda, p. 131–167. In M. J. Benton (ed.), *The Fossil Record 2*. Chapman & Hall, London.
- TRAUB, R., AND H. STARCKE. 1980. Fleas. Balkema, Rotterdam, 420 p.
- VERMEIJ, G. J. 1987. *Evolution and Escalation: An Ecological History of Life*. Princeton University Press, Princeton, NJ, 527 p.
- VERMEIJ, G. J., AND D. R. LINDBERG. 2000. Delayed herbivory and the assembly of marine benthic ecosystems. *Paleobiology*, 26:419–430.
- VINSON, S. B., AND P. BARBOSA. 1987. Interrelationships of nutritional ecology of parasitoids, p. 673–695. In F. Slansky, Jr. and J. G. Rodriguez (eds.), *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates*. John Wiley & Sons, New York.
- VOIGT, E. 1938. Ein fossiler Saitenwurm (*Gordius tenuifibrosus* n. sp.) aus der eozänen Braunkohle des Geiseltales. *Nova Acta Leopoldina*, N.F., 5:351–360.
- VOIGT, E. 1952. Ein Haareinschluss mit Phthirapteren-Eiern im Bernstein. *Mitteilungen der Geologische Staatsinstitut in Hamburg*, 21:59–74.
- VOIGT, E. 1957. Ein parasitischer Nematode in fossiler Coleopteren—Musculatur aus der eozänen Braunkohle des Geiseltales bei Halle (Saale). *Paläontologische Zeitschrift*, 31:35–39.
- VON KOENIGSWALD, W., G. G. RICHTER, AND G. STORCH. 1981. Nachweis von Hornschuppen beim *Eomanis waldi* aus der ‘Grube Messel’ beim Darmstadt (Mammalia, Pholidota). *Senckenbergiana Lethaea*, 61:291–298.
- WAAGE, J. K. 1979. The evolution of insect/vertebrate associations. *Biological Journal of the Linnean Society*, 12:187–224.
- WALKER, E. M. 1932. Prognathism and hypognathism in insects. *Canadian Entomologist*, 44:223–229.
- WALOSSEK, D., AND K. J. MÜLLER. 1994. Pentastomid parasites from the Lower Paleozoic of Sweden. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, 85:1–37.
- WALOSSEK, D., J. E. REPETSKI, AND K. J. MÜLLER. 1994. *Heymonsicambria taylori* n. sp. (Articulata: Pentastomida) from Upper Cambrian/Lower Ordovician boundary beds of Newfoundland, Canada. *Canadian Journal of Earth Sciences*, 31:1664–1671.
- WALTER, D., AND H. PROCTOR. 1999. *Mites: Ecology, Evolution and Behaviour*. University of New South Wales Press, Sydney, 322 p.
- WEITSCHAT, W., AND W. WICHARD. 1998. *Atlas der Pflanzen und Tiere im Baltischen Bernstein*. Friedrich Pfeil, Munich, 256 p.
- WHEELER, Q. D. 1990. Insect diversity and cladistic constraints. *Annals of the Entomological Society of America*, 83:1031–1047.

*LABANDEIRA—PREDATORS, PARASITOIDS, AND PARASITES*

- WHITFIELD, J. B. 1998. Phylogeny and evolution of host-parasitoid interactions in Hymenoptera. *Annual Review of Entomology*, 43:129–151.
- WIEGMANN, B. M., C. MITTER, AND B. FARRELL. 1993. Diversification of carnivorous parasitic insects: extraordinary radiation or specialized dead end? *American Naturalist*, 142:738–754.
- WILSON, E. O. 1992. *The Diversity of Life*. Harvard University Press, Cambridge, MA, 424 p.
- WILLS, M. 1993. Miscellanea, p. 555–560. In M. Benton, (ed.), *The Fossil Record 2*. Chapman and Hall, London.
- WIRTH, W. W., AND A. A. HUBERT. 1989. The *Culicoides* of Southeast Asia (Diptera, Nematocera). *Memoirs of the American Entomological Institute*, 44:1–508.
- WITHYCOMBE, C. L. 1922. Notes on the biology of some British Neuroptera (Planipennia). *Transactions of the Entomological Society of London*, 1922:501–594.
- YEATES, D. K., AND D. GREATHEAD. 1997. The evolutionary pattern of host use in the Bombyliidae (Diptera): a diverse family of parasitoid flies. *Biological Journal of the Linnean Society*, 60:149–185.
- ZHERIKHIN, V. V. 1989. Oligocene seed beetles and acorn weevils (Coleoptera: Bruchidae, Curculionidae) from the Bol'shoy Svetlovodnaya River (Northern Primorye). *Cenozoic of the Far East*, 1989:145–150.
- ZUMPT, F. 1965. *Myiasis in Man and Animals in the Old World*. Butterworth, London.