

THE FOSSIL RECORD OF INSECT DIVERSITY AND DISPARITY

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ABSTRACT

The fossil record of insects documents a high proportion of modern higher-level taxa (67% for families), although this capture rate drops off considerably for lower-level taxa. This record is Lagerstätten-driven, and is deployed by complementary, parallel body- and trace-fossil components that reveal a wealth of taxonomic and ecological detail. A family-level analysis of this record shows that past insect diversity is governed by low origination and extinction rates, both decreasing toward the Recent. This feature, in addition to prolonged taxal durations, has conferred on insects significant immunity from extinction. Nevertheless, the most profound event in insect history, the end-Permian extinction, decimated the Paleozoic Insect Fauna but allowed survival of lineages that gave rise to the Modern Insect Fauna of the Mesozoic and Cenozoic.

Past insect ecomorphologic disparity can be documented as feeding attributes from the trace- and body-fossil records. Three such attributes are assessed in the insect fossil record: mouthpart class, functional feeding group, and dietary guild, which collectively are divided into 74 distinctive categories. A plot of durations of these categories disclose a distinct trend of ecomorphologic disparity peaking considerably earlier than taxonomic diversity, indicating that taxonomic diversification eventually partitioned earlier-created, major ecological roles. Entry into each of these categories has occurred iteratively and convergently between and within the Paleozoic and Modern Insect Faunas.

Insect history is divided into five phases. Initially there was (1) colonization of land in the earliest terrestrial ecosystems, followed by (2) taxic radiation and ecological penetration of plant tissues by numerous clades during the Late Carboniferous and Permian, a process that was curtailed by (3) the terminal Permian extinction. The (4) subsequent emergence of the Modern Insect Fauna in the Triassic and its rebound during the mid-Mesozoic was driven by ecological expansion into freshwater ecosystems, emergence of the parasitoid guild, and recolonization of new seed-plant lineages by phytophagous holometabolans. This process continued as (5)

modern associations were established as Cretaceous angiosperms became dominant and mid-Cenozoic temperate grasslands expanded. These data indicate that insect success is attributable to intricate, multiplicative, and probably extinction-buffered associations with other organisms, especially vascular plants.

INTRODUCTION

Of the approximately 35 macroscopic animal phyla on earth, arthropods by far contain the majority of species and possess an ecological breadth comparable to or surpassing other contenders. Within arthropods, terrestrial groups have experienced the greatest taxonomic expansion, occupying a previously vacant world sometime during the Late Silurian to Early Devonian, and diversifying to the current condition of unbridled presence in every major habitat on land and in freshwater, and secondarily penetrating shallow marine ecosystems. Several major arthropod groups are responsible for this ubiquity, namely arachnids (scorpions, spiders and mites), crustaceans (isopods, amphipods and decapods), myriapods (notably centipeds and millipeds), and especially hexapods (insects and relatives). The overwhelming bulk of this diversity is found among the insects, with current numbers of species estimated between 5 to 80 million. Thus, any assessment of the history of life on land obligately requires documentation of fossil insect diversity in both its taxonomic, morphologic and ecologic manifestations, as well as an understanding of why insects have become the premier success story. The conclusion of this brief review that elevated insect diversity has benefited enormously from intricate associations with other organisms, particularly vascular plants. To a lesser extent, interactions with animals—such as other insects that are hosts to parasitoids and vertebrates that are attacked by parasites—also are a source of insect success.

NATURE OF THE INSECT FOSSIL RECORD

Although terrestrial organisms have a more discontinuous and infrequently-encountered fossil record than their marine counterparts, the insect fossil record in particular has three strengths that historically have been undervalued. The first is a high capture percentage of taxa at the family level or above, by virtue of the sheer abundance of insect specimens in many deposits. All modern orders and 67 percent of extant families are known from the fossil record. However, unlike many other fossil groups, such as corals or mollusks, insect genera represented in the fossil record comprise only about 1 percent that of modern genera. Part of this difference is attributable to the lack of paleoentomologists to examine abundant insect specimens in numerous well-preserved deposits, most of which remain largely undescribed.

Second, fossil insects essentially are represented as a Lagerstätten-driven record of exceptionally preserved, profuse deposits occurring sporadically in several disparate environments. Fossil insect Lagerstätten include preservational modes as varied as ironstone concretions, lithographic limestones, amber, sinter deposits, and asphaltum, although it is the fine-grained, laminate, lacustrine deposits that contributes the greatest information in terms of number of insects available for study and the greatest representation in time (Permian to Recent) and space (virtually any persistent, locally drained landscape). Figure 1 depicts the temporal sequence of major modes of insect preservation.

Third, the record of fossil insects is separable into a well known body-fossil component (Hennig, 1981; Carpenter, 1992) and a poorly understood trace-fossil component that contains considerable, mostly unique, information on insect paleoecology, especially their associations with other organisms (Chaloner et al., 1991; Labandeira, 1997, 1998b). Very rarely are fossil insects associated with their plant or animal hosts *in flagrante delicto*. Thus, this parallel fossil record provides data on insect associations with other organisms that typically are absent in standard descriptions of insect body fossils (but see Schaarschmidt [1992] and Borkent [1995] for counter-examples). Relevant insect trace fossils are categorized into three distinctive types of

indirect evidence: the records of dispersed coprolites, plant damage, and gut contents. Additionally, there are aspects of the body-fossil records from both insects and plants that provide cogent inferences for the presence of associations with other organisms. Morphological features occurring on plant body fossils indicating associations with insects include reproductive structures such as nectaries and floral oil glands (Friis, 1985; Crepet and Nixon, 1996), and probably vegetative structures such as trichomes and latex canal systems (Scott and Taylor, 1983; Niklas, 1986; Farrell, et al. 1991). Equivalent structures on insect body fossils are primarily mouthpart structure and head shape (Labandeira, 1990, 1997), and to a lesser extent, ovipositors and surface features associated especially with pollination syndromes, such as femoral corbiculae, distinctive thoracic vestiture, and body brushes (Faegri and van der Pijl, 1980; Proctor, et al. 1996). Collectively these features provide not only data for qualitative assessments of the presence of particular plant-insect associations, but also, in the case of plant damage, opportunities for quantitative measuring of the extent of herbivory and plant host specificity (Greenfest and Labandeira, 1997; Beck and Labandeira, 1998, Wilf and Labandeira, 1999).

INSECT DIVERSITY AND DISPARITY THROUGH TIME

The insect fossil record broadly documents two different measures of organismic variety: taxonomic diversity and morphologic disparity. Taxonomic diversity typically is expressed as the global number of insect taxa occurring at specified geological-stage intervals, cumulated over their fossil history (Rohdendorf and Zherikhin, 1974; Wootton, 1990; Labandeira and Sepkoski, 1993; Jarzembowski and Ross, 1993, 1996). Taxonomic diversity has been evaluated at the family or ordinal levels, although currently these data are being refined by a compilation at the species level. These data (Dmitriev and Zherikhin, 1988; Rasnitsyn, 1988a; Ross and Jarzembowski, 1993; Labandeira, 1994), like cladistic and derivative phylogenetic studies of fossil and recent insects, are based on the fossil record and what is known of modern insect

relationships. The criticism that such studies are evidently "...based on the available literature" and are "...not enough critical on the original data" (Nel, 1998: 53) glosses over linkages of assignments of fossil taxa with conclusions from cladistic studies. Additionally ignored are numerical models that test how accurately paraphyletic taxa versus monophyletic clades capture underlying patterns of taxonomic diversity (Sepkoski and Kendrick, 1993). Results from these models indicate that under high paleontologic sampling levels, monophyletic clades capture somewhat more lineage information than paraphyletic groups. However, when sampling intensity is low, the reliability of monophyletic clades deteriorates, and paraphyletic groups capture more underlying lineage information, indicating that paraphyletic groups need not be rejected a priori as an important source of fossil diversity data (Sepkoski and Kendrick, 1993).

By contrast, morphologic diversity, also termed "disparity" to distinguish it from taxonomic measures (Foote, 1991). It is a measure of the morphological distinctness and, by extension in some cases, the number of ecologic roles that are occupied by taxa through time. The best documented ecological roles for fossil insects involve aspects of feeding, since the body-fossil record and the parallel and complementary trace-fossil record of insect-mediated damage can be accessed independently for data. Presently three measures have been investigated that separately provide assessments of insect ecomorphologic disparity through time. They are *the feeding apparatus* that insects use to consume food (mouthpart classes), *how insects feed* (functional feeding groups), and *what types of food* insects consume (dietary guilds). Thus the fundamental distinction between diversity and disparity, presented herein, is that diversity is an explicit measure of taxa number whereas disparity is a numerical assessment of ecological breadth. This distinction can be contrasted for elucidation of evolutionary patterns (Foote, 1996), such as whether the ecological partitioning of food resources is relevant in the generation of taxonomic diversity.

Taxonomic Diversity

In addition to refiguring the secular trend of family-level taxonomic diversity determined by Labandeira and Sepkoski (1993) (Fig. 2), we have decomposed this measure into its constituent elements, origination and extinction (Fig. 3). These two fundamental contributions to total global diversity can be expressed in three ways: raw values, values standardized to an interval length such that rates are appropriately comparable, and values normalized to then-existing total diversity. Most expressions of origination and extinction consist of background trends interrupted by sporadic, often sharp, peaks rising severalfold above the ambient trend, as predicted from a fossil record dominated by Lagerstätten.

Total diversity—Insects possess a 400 million-year-long record of fossils, although the first 75 million years of this record is uninformative and is represented by only two orders of apterygote insects that occur as rare, scrappy material in three Early and Middle Devonian deposits (Hirst and Maulik, 1922; Shear et al., 1984; Labandeira, et al. 1988). The taxonomically informative portion of the insect record commences suddenly and in profusion at the Early Carboniferous/Late Carboniferous (=Mississippian/Pennsylvanian) boundary (Wootton, 1981; Brauckmann et al., 1995), and continues unabated to the Recent, punctuated by a modest decrease in diversity during the Late Pennsylvanian to Early Permian, and a major extinction event at the terminal Permian (Fig. 2). Within the post-Mississippian part of the record, one interval exhibits extremely depauperate representation of insect-bearing deposits worldwide: the Late Permian to Middle Triassic, straddling the end-Permian extinction. The Permian phase of this interval is marked by considerable habitat degradation in terrestrial ecosystems (Retallack, 1995; Retallack et al. 1996; Visscher et al., 1996; Erwin, 1998) and the post-extinction Triassic phase is characterized by extremely depauperate faunas worldwide prior to eventual rebound of taxa that are captured in Middle- and mostly Late Triassic deposits (Rasnitsyn, 1969; Sukacheva, 1973; Riek, 1976; Olsen, et al. 1978; Gall, 1996; Grimaldi and Fraser, 1999).

In the several Late Triassic deposits that are well-documented, known taxa consist overwhelmingly of lineages belonging to extant orders (Gall, 1996; Anderson et al., 1998a, 1998b; Grimaldi and Fraser, 1999), and there is minimal carryover from Late Paleozoic lineages. Some family-level lineages of orders whose diversity is centered in the Paleozoic survived the end-Permian event into the earlier Mesozoic, such as the “Protorthoptera” (Riek, 1953), Miomoptera (Marquat, 1991), and Glosselytrodea (Martynova, 1943), but most typically Paleozoic clades are not recorded in post-Permian deposits (Labandeira, 1994), including monurans, paleodictyopteroids, protodonates, protelytropterans, caloneurodeans, and hypoperlids (sensu Rohdendorf and Rasnitsyn, 1980) with the exception of the Geraridae (Fig. 3). These data demonstrate that the end-Permian event was the single most important event affecting insect diversity, separating the Paleozoic Insect Fauna from the Modern Insect Fauna at the highest taxonomic levels.

The global rebound of insect taxa after the end-Permian event is evident for Middle and especially Late Triassic Deposits in which basal, high-ranked clades of most of the modern insect orders became established. Although there is a slackening of diversification during the latest Triassic, throughout the Jurassic there is a steady increase of more derived clades within the Hemiptera, Coleoptera, Diptera and Hymenoptera, many which represent the invasion of a new ecological realms such as freshwater by filterers and collectors, colonization of a broadened range of host plants by various endophytic and exophytic lineages, and entry into other animals as parasitoids and thus trophically capitalizing on herbivore diversity itself. During this interval, subtle family-level increases occur among the much less diverse Odonata, Plecoptera, Orthoptera, Neuroptera, Mecoptera and Trichoptera (Fig. 3).

Near the end of the Jurassic, during Kimmeridgian times, there is a dramatic increase in family-level diversity attributable to high origination of taxa (Fig. 2), reflected in the spectacularly diverse Karatau lake deposits in Kazakhstan (Rohdendorf, 1968, Dmitriev and Ponomarenko, 1988, Rasnitsyn, 1988a, 1988b). Instructive in this regard is the presence of basal

phytophagous clades at Karatau and other later Jurassic deposits which were associated with nonangiospermous seed plants (Crowson, 1991, Farrell, 1998). The early Cretaceous represents a second post-Permian slackening of family-level origination, and much of the taxonomic diversification may be occurring at infrafamilial levels (Labandeira and Sepkoski, 1993; Farrell, 1998) and not reflected in family-level data. It is during this interval that there is a radiation of the Blattodea and perhaps the beginnings of the Mantodea and Isoptera (see Tillyard, 1936, Grimaldi, 1997), a secondary radiation of Psocoptera, and the expansion of the Lepidoptera, during which there was major, subordinal-level cladogenesis (Labandeira et al. 1994).

Throughout the Cretaceous and into the Paleogene, insect diversity increases overall, but at an abated rate and with stronger pulses, when compared to the Jurassic. The end of this phase is characterized by a spectacular jump of approximately 140 families, attributable to the Baltic Amber Lagerstätte, after which it asymptotes to the final diversity of 617 fossil families during the Pleistocene. This can be contrasted to the approximately 1000 extant hexapod families. Recent and ongoing updates of the data-base upon which Figure 2 is based indicates that approximately 67 percent of the currently recognized families (Naumann et al. 1991) have fossil records, and some now have earlier occurrences than was previously known in Labandeira (1994), indicating a modest shift of the secular trend upward in Figure 2, and a decrease in curve spikiness.

A few summary aspects from the fossil record of insect diversity are noteworthy. Family-level insect taxa are highly immune to extinction, with the singular exception of the demise of much of the Paleozoic Insect Fauna during the Late Permian. As discussed below, both insect origination and extinction rates have been low since this event, and have asymptoted to almost zero during the past 40 or so million years. Although the pull-of-the-recent (Raup, 1972, 1979) may exert a subtle bias on these trends, independent fossil evidence also indicates that insect taxa have exceptionally long geochronologic durations (Rayner and Waters, 1990; Kathirithamby and Grimaldi, 1993; Labandeira et al., 1994; Coope, 1995), contrary to the conclusions arrived by

Stanley (1979). Thus the force driving insect diversity is not high origination rates, but exceptionally low levels of extinction (Rohdendorf and Zherikhin, 1974; Labandeira and Sepkoski, 1993).

Origination—The unstandardized raw data for insect origination, is quite spiky, showing no overall trend in slope increase or decrease, although five conspicuous, Lagerstätten-associated peaks are evident (Fig. 4a). These intervals of exceptionally elevated levels of insect first appearances are, from older to younger, (1) a modest peak initiating the first significant appearance of insect taxa, centered on the Middle Pennsylvanian (Moscovian), associated with deposits at Mazon Creek in Illinois (USA), older strata of the Kusnetsk Basin in Russia, and the Saar Basin of Germany; (2) a modest Early Permian (Artinskian) peak from the insect fauna at Elmo, Kansas (USA), and its lateral correlative faunules; (3) a more pronounced peak of intermediate height documenting the Karatau compression fauna from the Late Jurassic (Kimmeridgian) of Kazakhstan; (4) a lesser peak representing several Early Cretaceous (Aptian) compression insect faunas from Mongolia, Russia, Australia, and Brazil; and (5) the highest peak, resulting from Late Eocene (Priabonian) Baltic amber deposits of northern Europe surrounding the Baltic Sea. When standardized to a monotonic time scale (Fig. 4b), origination exhibits a stable background rate when four major Lagerstätten-associated peaks are removed. These exceptionally elevated levels of first occurrences consist of a high peak corresponding to the Late Jurassic Karatau fauna and an intermediate-high peak representing the Late Eocene Baltic amber deposits, both mentioned above. Two new peaks also are present—an intermediate-low peak documenting several Late Triassic (Rhaetic) to Early Jurassic (Hettangian) lacustrine shale deposits, particularly at Issyk-Kul, in Kirgystan, and Shurab and Kizyl-Kiya, in Tajikistan; and a lower peak from Late Cretaceous (Santonian) amber from Taimyr, northern Russia. When standardized to then-existing diversity (Fig. 4c), the overall trend is one of semilogarithmic decrease from the Middle Pennsylvanian to the Recent (see

Eble, 1999), becoming more pronounced if the peaks corresponding to Baltic amber and perhaps the Karatau lacustrine deposits are removed.

Extinction—Overall trends of extinction are qualitatively similar to those of origination for all three types of data and important deviations generally involve the same deposits mentioned above. The only different pattern that emerges from the extinction data is that there is a decrease to zero during the past 90 million years, rather than the past 40 million years for origination data. The raw data indicate a flat background trend (Fig. 4d), with elevated extinction levels that modestly characterize the Upper Pennsylvanian (Gzelian + Kasimovian); a separate but dramatic rise during the Early Permian centered on the Artinskian; and a third pronounced peak reappearing during the later Early Cretaceous (Albian and Aptian). For time-standardized data (Fig. 4e), the background trend is typically flat and unchanging, although intervals of elevated extinction are more abundant and pronounced. There is continuation of the Lower Permian event from above, this time centered on the Late-Permian Capitanian + Wordian + Ufimian (“Guadlupian” of older usage); insertion of a Late Triassic spike during the Rhaetian, and a Jurassic spike during the Kimmeridgian, both which correspond to Central Asian lacustrine deposits prominent in origination data; and repeat of the late Early Cretaceous (Aptian + Albian) peak that includes several deposits from Mongolia, Russia, Australia, and Brazil, now extending to the early Late Cretaceous and incorporating amber from France, compression deposits from Botswana and Magadan (Russia), and terminating in a pronounced spike during the Santonian attributable to Taimyr amber from northern Russia. With regard to diversity-standardized extinction data (Fig. 4f), the Early Permian event is very pronounced, followed by a background decrease to the present, interrupted by a modest late Early Cretaceous (Aptian + Albian) peak; both peaks represent continuation from raw- and time-standardized data. Only two of the intervals of high origination are also times of high extinction: the Late Triassic to Early Jurassic (Rhaetian to Sinemurian) and the Late Jurassic (Kimmeridgian). However these parallelisms

only apply to time-standardized data, and these peaks are lost when data are calibrated to past levels of diversity.

Ecomorphologic Disparity

Ecomorphologic disparity data are based on Labandeira (1990, 1997) for mouthpart classes, and a compilation currently in press (Labandeira, 2001) for functional feeding groups and dietary guilds. The latter compilation documents 466 occurrences of functional feeding groups and 398 occurrences of dietary guilds in the fossil record from the primary literature of insect body-fossils and especially trace-fossils. These condensed data are presented in this brief review as Fig. 5.

Mouthpart classes— It has been recognized for some time that the astounding variety of insect mouthparts is divisible into discrete morphological types, each representing a major and distinctive structural solution to feeding on a particular type of food (Metcalf, 1929; Chaudonneret, 1990). A recent phenetic classification of modern hexapod mouthparts resulted in the recognition of 34 discrete types, and later two extinct fossil mouthparts were added. (See Fig. 5d and Table 1 for mouthpart classes and taxal membership.) The temporal distribution of these mouthpart classes are shown in Fig. 5d, based on earliest fossil occurrences of clades that bear the modern mouthpart classes and the preserved fossil record of mouthparts (Labandeira, 1990, 1997). Most of these mouthpart classes individually represent multiple, phylogenetically convergent, solutions toward a particular mode of feeding, and some have been invented as many as 6 or 7 times from unrelated family- or ordinal-level taxa.

Functional feeding groups—Rather than emphasizing the body-fossil record and known phylogenies of insect clades in the example of mouthpart classes (Carpenter, 1971; Labandeira, 1997), the trace-fossil record of insect damage on plants, insect gut contents and coprolites, and insect-associated reproductive and vegetative features of plants, can be exploited to understand the history of how insects have fed and what foods they have consumed (Chaloner et al., 1991;

Labandeira, 1998b, 1998c). With regard to feeding modes, the fossil record of functional feeding groups has been partitioned into 20 basic categories identifiable in the fossil record (Fig. 5c), which constitute the fundamental ways that insects consume food (Labandeira, 2001). Each of these modes have evolved convergently and repeatedly within the Paleozoic and the Modern Insect Faunas, and among clades within these two evolutionary faunas. Although this lability among insect taxa in time and space conceptually parallels the situation of extensive convergence in mouthpart classes, the two are not congruent: multiple mouthpart classes or subgroupings within mouthpart classes can achieve the same functional way of procuring and consuming and processing food. For example, consumption of mesophyll-located sap within vascular plants is accomplished by piercing-and-sucking insects possessing ectognathous-stylate, segmented beak, mouthcone, and robust beak mouthpart types.

Dietary guilds—Whereas mouthpart classes circumscribe the *apparatus that insects use to feed*, and functional feeding groups address *how insects feed*, dietary guilds state *what is consumed*. Taxal membership in the 20 basic dietary guilds (Fig. 5b), when contrasted to mouthpart classes and functional feeding groups, is the most labile of the three ecomorphological categories. This is attributable to the exceptional variety of food that insects consume, the plurality of modes in which the same food type can be consumed, and the evolutionary plasticity of dietary shifts within insect clades (Heming, 1993; Pierce, 1995). For example, whereas pollen is considered a solid, particulate food, it can be consumed by a variety of ways using diverse mouthpart types and functional feeding approaches. Mandibulate insects consume pollen by modification of the maxillae into brushes that sweep pollen into the oral cavity, with or without mandibular maceration of grains (adult-ectognathate; Schicha, 1967; Crowson, 1981); some piercing-and-sucking insects puncture the pollen wall to suck out protoplasts (mouthcone; Kirk, 1984; Heming, 1993); many fluid-feeding insects, notably syrphid flies, consume pollen intact (labellate; Holloway, 1976; Haslett, 1983); and other insects digest pollen by specialized

mouthparts and postoral processing within an osmotically specialized gut (glossate; Parker, 1926; Peng et al., 1985).

Taxonomic Diversity and Ecomorphological Disparity Contrasted

A frequently observed feature of the long-term evolutionary dynamics of most invertebrate clades is that taxonomic diversification increases semiexponentially or logistically whereas corresponding morphological and ecological breadth rapidly increases significantly earlier (Foote 1997). These disjunct patterns are interpreted as the early generation of most to almost all of fundamental morphology, followed by subsequent and more rapid increases in taxonomic diversification to efficiently pack and narrowly partition previously occupied morphological space (Foote, 1993). The available evidence indicates that this characterization also applies to insects (Fig. 6; Eble, 1999). Like other invertebrate clades, there have been disruptions of these secular trends by extinction, including a Late Pennsylvanian to Early Permian extirpation, the end-Permian event that eliminated most of the Paleozoic Insect Fauna, an early Jurassic event (Ponomarenko, 1996), and tentative evidence for insect turnover at the Cretaceous/Tertiary boundary (Labandeira et al., 1999) not detected by several family-level analyses (Labandeira and Sepkoski, 1993; Jarzembowski and Ross, 1993). Notably, while taxonomic diversity has risen steadfastly, albeit with setbacks, ecological measures of feeding strategies—mouthpart classes, functional feeding groups, and dietary guilds—have remained relatively stable since their major increase during the Late Paleozoic to Early Mesozoic. This has occurred in face of the fact that the participants in these ecological roles have originated from taxonomically unrelated clades between and within the Paleozoic and Modern Insect Faunas. Approximately 60 percent of these 74 ecomorphological categories were present during the Late Paleozoic, and virtually all the others originated by the mid-Cretaceous.

The disjunction between taxonomic diversity and morphologic/ecologic disparity provides implications for the role of insects in structuring terrestrial and freshwater ecosystems. Although

species-level packing was probably less intense during the Paleozoic and Mesozoic than today when global insect diversity was less (but see Anderson et al., 1998b), compilation of insect ecological categories indicate that major ecological roles were mostly in place during the Late Paleozoic and Early Mesozoic, a condition buttressed, at least for herbivores, by site-specific examinations of associations between plants and their insect associates (Grauvogel-Stamm and Kelber, 1996; Ash, 1997; Labandeira, 1998b, 1998c). Exceptions to this pattern, however, are notable: the absence of the parasitoid guild prior to the Jurassic radiation of basal apocritan clades (Gauld and Bolton, 1988; Rasnitsyn, 1988b), and the absence of ants and other social insects such as termites and bees before the early Cretaceous. Both groups of insects currently exert a tremendous role in top-to-down regulation of plants and insect herbivores by establishing a dynamic alternative for the third trophic level of predatory insects. It is unclear what enemy-free space was available to insect herbivores during the Late Paleozoic and Early Mesozoic, and if predation of insects by other insects during this interval was ecologically equivalent to the pressure that parasitoids and social insects currently exert in the regulation of herbivore abundance. Perhaps the additional intricacies of parasitoid attack and the dynamic antiherbivore mutualisms of ants and plants (Beattie, 1985; Jolivet, 1996) stimulated the taxonomic diversification observed in the mid-Mesozoic fossil record.

IMPORTANT PHASES IN THE HISTORY OF INSECT DIVERSITY

Five phases characterize the 400-million-year fossil history of hexapods in terrestrial and freshwater ecosystems (Fig. 5a). Recognition of these phases may be partly attributable to imperfections in the insect fossil record, particularly in the prolonged absences of insects that characterize the 55 million-year hiatus from the Middle Devonian to the latest Mississippian, and the 15 million-year gap from the mid-Permian to the mid-Triassic. However, the rest of the insect fossil record indeed is sufficiently well-documented, taxonomically diverse, and ecologically instructive to provide a basis for the following summary.

Insects in the Earliest Terrestrial Communities

The earliest hexapod fossils occur in Early and Middle Devonian clastic, terrestrial deposits at three sites occurring in northern Euramerica (Labandeira et al., 1988). These sites are dominated by algae, bryophytes, primitive vascular plants, massive, enigmatic fungi (Gensel and Andrews, 1984), and arthropods including arthropleurid, millipede and centipede myriapods (Almond, 1985), trigonotarbid, pseudoscorpionid, and acarid arachnids (Dunlop, 1996), and collembolan and archaeognathan insects (Hirst and Maulik, 1926; Shear et al., 1984; Labandeira et al., 1988). The terrestrial arthropod record in general and the hexapod record in particular is extremely fragmentary (Shear and Kukalová-Peck, 1990), and few conclusions can be generated, other than the presence of a relatively simple food chain of primary producers, decomposers, detritivores, herbivores, and carnivores, based on all the available evidence, including mouthpart morphology, coprolites, damaged plant tissues, and ecological comparisons of bradytelic lineages to their modern descendants (Kevan et al., 1975; Labandeira, et al. 1988; Shear and Kukalová-Peck, 1990; Banks and Colthart, 1993; Hotton et al., 1996).

Expansion of Diversity during the Late Paleozoic

After the hiatus of 55 million years, the insect fossil record resumes during the latest Early Carboniferous (Brauckmann et al., 1995), and within about 18 million years, 15 orders of insects are represented in lowland equatorial environments from the Middle Pennsylvanian of Euramerica (Labandeira, 1994). This fauna constitutes the core of the Paleozoic Insect Fauna, and is dominated by paleopterous and orthopteroid (*sensu lato*) clades, supplemented by apterygotes, primitive hemipteroids, and rare basal holometabolans (Kukalová-Peck, 1991; Labandeira & Phillips, 1996b). Latest Carboniferous and Early Permian taxa represent subsequent additions of less humid-adapted, smaller-bodied taxa, some which were progenitors of the subsequent Modern Insect Fauna (Wootton, 1990).

One of the earliest and best-documented glimpses into the Paleozoic Insect Fauna is at Mazon Creek, in the Illinois Basin of North America, from the Carbondale Formation of latest Middle Pennsylvanian (late Moscovian) age. A wide variety of almost 200 well-preserved insect species occur in this deposit (Carpenter, 1997; Kukalová-Peck, 1997) that includes soft-part structures, often with detail of mouthparts and appendages. Mazon Creek provides the earliest evidence for diverse insects occurring in any ecosystem, although the particular paleoenvironment was a lowland woodland ecosystem occurring along the emergent flanks of a delta that prograded into an epeiric sea (Baird, 1997). This fauna is dominated by paleodictyopteroid and odonatoid Palaeoptera and generalized “protorthopteran” orthopteroids, although some members of the clearly polyphyletic “Protorthoptera” have been assigned to basal hemipteroids upon closer examination (Rasnitsyn, 1977; Rohdendorf and Rasnitsyn, 1980; Kukalová-Peck and Brauckmann, 1992). Apparently the Mazon Creek insect fauna consisted of some large to gigantic forms by comparison to modern insect standards, and formed a relatively complete trophic web of detritivores, insectivores, and herbivores, the latter judging from extensive plant damage occurring particularly on pteridosperm vegetation (Scott and Taylor, 1983; Labandeira and Beall, 1990). This fauna was largely extinguished at the end of the Middle Pennsylvanian, and replaced by different lineages during the early Kasimovian that were associated with an emergent Euramerican flora dominated by tree-ferns and subordinately by new groups of pteridosperms (Phillips et al., 1974; Pfefferkorn and Gillespie, 1980). These latter insect taxa occur in such Late Pennsylvanian localities as Montceau-les-Mines and Commentry in France.

Also from the Illinois Basin is an exceptional coal-ball deposit of permineralized, three-dimensionally preserved, plant tissues that exhibit anatomical detail resolvable to the cellular level. This deposit, the Calhoun Coal of the Mattoon Formation, represents a swamp forest rooted on a peat substrate, is of early Late Pennsylvanian (Kasimovian) age, and provides some of the best anatomically preserved plant tissues in the fossil record. Notably, it includes rare and

significant arthropod-mediated damage of plant tissues, indicating that virtually all dead and live plant tissues were consumed by arthropod detritivores and herbivores. Included in this inventory are piercing-and-sucking of tree-fern petioles and pteridosperm prepollen organs (Retallack and Dilcher, 1988; Labandeira and Phillips, 1996a; Labandeira 1998b), galling of tree-fern rhachises (Labandeira and Phillips, 1996b), sporivory of at least two tree-fern spore types and pollinivory of medullosan prepollen and cordaitalean pollen organs (Labandeira and Phillips, in prep.), borings into dead and live tissues of tree-fern and pteridosperm stems and petioles, and extensive external feeding of *Alethopteris* pteridosperm foliage (Labandeira and Phillips, in prep.). Additionally, there was extensive detritivory by oribatid mites of a broad variety of decaying, indurated tissues such as wood and sclerenchyma, and the softer tissues of foliage and roots. Oribatid mites were the predominant degraders of plant litter into comminuted organic debris within this ecosystem. This deposit, together with an additional evidence of diverse external-foliage feeding from the Lower Permian of Texas, reveals that, with the exception of leaf-mining (but see Müller, 1982), all major herbivore functional feeding groups on land were established by the Late Paleozoic (Fig. 5c).

The Permian contains two deposits of note, Elmo from Kansas, U.S.A., of Artinskian age (Carpenter, 1930, 1933), and the somewhat younger Chekarda deposit of Russia, of Kungurian age (Novokshonov, 1998). Most of what is known of these Early Permian insect faunas originates from these two and other stratigraphically-associated but minor deposits. Judging from their taxonomic composition, the Early Permian represents the early radiation of phylogenetically basal hemipteroid and holometabolous clades, most of which did not survive the Permian, and were replaced by more persistent and advanced descendants that formed the core of the Modern Insect Fauna during the early Mesozoic.

The Great Permian Extinction

The most profound event affecting the course of life on land was the end-Permian extinction, which also had drastic effects in the marine realm (Erwin, 1993). By comparison to the marine record, terrestrial deposits are more sporadic and less informative, albeit recent multidisciplinary research has documented dramatic changes of the physical environment and in patterns of fungal, plant, and insect diversity across the Late Permian to Early Triassic boundary. During the Late Permian, and following a prolonged interval of Late Carboniferous to Early Permian glaciation, much of the continental world was characterized by warm and especially arid continental interiors, as evidenced by extensive redbed deposits, evaporites, reef carbonates, and high-latitude coals (Waugh, 1973; Zharkov, 1981; Retallack et al., 1996; also see Yemane, 1993). The sedimentological record of the latest Permian reveals unusual patterns of increased rates of erosion and acidification of clay minerals that parallel dramatic, negative $\delta^{13}\text{C}$ and $^{87}\text{Sr}/^{86}\text{Sr}$ isotope excursions (Denison et al., 1994; Morante, 1996), suggesting major landscape devegetation (Retallack, 1999). This pattern is consistent with a much-noted fungal spike immediately prior to earliest Triassic deposits (Visscher, et al., 1996), perhaps also attributable to extensive vegetative dieback. Coincident with these patterns is the worldwide cessation of reef and coal deposits, both intimately tied to continental ecosystems, and their delayed reappearance 6 m.y. later during the Middle Triassic (Flügel, 1994; Retallack et al. 1996).

Throughout the Permian and deployed diachronously among various continental regions, there was a major floral transition from typical “Paleophytic” aspect flora dominated by arborescent lycopods and sphenophytes, ferns, pteridosperms, and cordaites, to a “Mesophytic” one of conifers, ginkgophytes, cycadophytes, and new clades of ferns and pteridosperms (Knoll, 1984; Niklas, et al., 1985; DiMichele and Aronson, 1992). In local sections, such as the Sydney Basin of eastern Australia, there was an abrupt change from a high-diversity flora rich in glossopterid pteridosperms to a low-diversity one dominated by *Dicroidium* pteridosperms, voltzialean conifers, and other pteridosperm lineages—a shift coincident with the abrupt

changeover from the latest Permian *Dulhuntyispora parvithola* palynomorph zone to the earliest Triassic *Protohaploxylinus microcorpus* zone (Retallack, 1995, 1999). Similarly, the distinctive Paleozoic Insect Fauna was extirpated during the Late Permian, although the relative contributions of (1) an Early Permian extinction event, (2) later Permian ecological replacement of competitively different Carboniferous lineages by more modern lineages, and (3) the end-Permian event, are difficult to pin down. It is quite likely that the demise of the Paleozoic Insect Fauna matched the Paleophytic to Mesophytic floral transition, particularly if major hostplant associations were established earlier (Niklas, 1986; DiMichele and Hook, 1992; Jarzembowski and Ross, 1996). It is known that many lineages surviving the end-Permian event constituted the basis of the distinctive hemipteroid- and holometabolous-dominated Modern Insect Fauna of the Mesozoic and Cenozoic. The earliest well-documented Mesozoic deposits contain reasonably diverse insect faunas of late-Middle and Late Triassic age from disparate localities worldwide (Riek, 1955; Rasnitsyn, 1969; Sukacheva, 1973; Olsen et al., 1978; Gall, 1996; Anderson et al., 1998a; Grimaldi and Fraser, 1999). These deposits are overwhelmingly dominated by taxa of the Modern Insect Fauna and exhibit comparatively little carryover of Permian taxa. Interestingly, the absence of any Early Triassic and early-Middle insect deposits of note parallels the absence of coal and carbonate reefs, indicating an interval of minimal diversity following the terminal Permian event.

Mesozoic Rebound and Subsequent Ecological Expansion

Although evidence for a rebound of insect taxa following the terminal Permian extinctions is evident in late-Middle and Late Triassic deposits, it was not until the Middle Jurassic that family-level diversity reached the Paleozoic maximum. The modern increase in family-level diversification commenced in the Triassic, and during the Jurassic it was promoted by three groups of organisms that invaded environments with expanded food resources. The first environment was fresh water, spurred by the radiation of nematoceran Diptera, basal

Trichoptera, hydrocorisan Heteroptera, adepagan and polyphagan Coleoptera (Kalugina and Kovalev, 1985; Ponomarenko, 1996; Labandeira, 1997), and other groups whose naiads and larvae played important trophic roles as filterers, scrapers, gatherers, shredders and predators in aquatic ecosystems. These functional feeding groups, and the associated expansion of mouthpart classes—larval ectognathate, pectinate, mouthbrush, mandibulobrustiate, segmented beak, among others—mark the beginning of modern trophic partitioning of freshwater ecosystems. The peak of this invasion is centered in the Early Jurassic, although it persisted into the Cretaceous, during which complex trophic networks typical of modern freshwater ecosystems were present in several lake types (Sinichenkova and Zherikhin, 1996).

The two other ecological invasions occurred on land: colonization of other insects by parasitoids, and associations between new lineages of seed plants and various phytophagous holometabolous and orthopteroid insects. The diversification of basal apocritan Hymenoptera began during the early Jurassic and continued into the mid-Cretaceous (Rasnitsyn, 1969, 1988b), consisting of parasitic but principally parasitoid groups that endozoically attack other insects. This consequence had a profound effect on the top-to-down regulation of trophic networks by establishing on herbivorous insects a qualitatively new type of predation based on subtle behavioral cues or biochemical signals from their host plants (Godfray, 1994). Similarly, there was expansion of herbivory on diverse tissues among newly-emerging plant clades during the preangiospermous mid-Mesozoic. Considerable evidence from the trace-fossil record of plant-insect associations documents the presence of specialized types of insect herbivory, such as leaf-mining in seed ferns (Rozefelds, 1988), galls in conifers (Grauvogel-Stamm and Kelber, 1996; Ash, 1997) and bennettitaleans (Alvin, et al., 1967), wood boring of conifers (Jarzembowski, 1990; Tidwell and Ash, 1990), and pollinivory of conifers, ephedroids, and seed-ferns (Krassilov and Rasnitsyn, 1983; Krassilov, et al., 1997). Separate evidence from mouthpart morphology indicate that during the Jurassic primitive weevils were consuming deep plant tissues (Crowson, 1991; Gratshev and Zherikhin, 1995) and brachyceran flies were obtaining nectar or similar

substances from unknown seed plants (Mostovski, 1988; Ren, 1998; Labandeira, 1998a). Modern pollination syndromes involving cycads and beetles are probably ancient associations extending to the Jurassic (Crowson, 1991; Norstog and Nicholls, 1997; Farrell, 1998), and similar interactions are known for Early Cretaceous bennettitaleans and their presumed beetle inhabitants (Delevoryas, 1968; Crepet, 1972). By the time that angiosperms became ecologically dominant during the mid-Cretaceous, virtually all of the major associations between vascular plants and herbivorous insects were established, although the invention of the angiospermous flower offered additional opportunities for highly-faithful mutualisms and coevolution (Crepet and Nixon, 1996).

Angiosperms and the Evolution of Modern Associations

By the early Late Cretaceous, angiosperms were dominant in most environments (but see Wing, 1993), and the global insect fauna consisted of clades that overwhelmingly are assignable to modern families. The appearance of social insects, namely termites and ants, is documented during the Early Cretaceous (Brandão et al., 1989; Martínez-Delclòs and Martinell, 1995), and advanced social bees are known from the Late Cretaceous (Michener and Grimaldi, 1988), but do not become significant as fossils until mid-Cenozoic times. Although site-specific mid-Cretaceous abundances were probably low by modern standards (Wilson, 1987), the appearance of social insects must have had a significant impact on plants and their herbivores later in the Cenozoic, if the extensive associations between modern plants and ants (Beattie, 1985; Jolivet, 1996) are any guide. By contrast, the radiation of major clades of Lepidoptera is an Early Cretaceous or even Late Jurassic event (Connor and Taverner, 1997; Kristensen and Skalski, 1998), and well-preserved mid-Cretaceous angiosperm floras bear considerable lepidopteran leaf-miner damage (Kozlov, 1988; Labandeira, et al., 1994), albeit there also is significant damage from gallers, and stereotyped patterns of external feeding attributable to chrysomelid and curculionid beetles (Labandeira et al., 1994, 1995). Although family-level documentation of

diversity has consistently indicated that insects were unaffected by the Cretaceous/Tertiary extinction (Whalley, 1988, Jarzembowski, 1989; Labandeira, 1992), examination of biostratigraphically well-calibrated and diverse floras across this boundary in the Williston Basin of North Dakota indicates that, at least for insect herbivores, there was significant disappearance of leaf-damage morphotypes at the terminal event (Labandeira et al., 1999). Perhaps the last major event in the history of phytophagous insects was their invasion of the Grassland Biome and the evolution of obligate graminivory in numerous clades of insects, including mandibulate acridids (Boys, 1981), piercing-and-sucking cicadellids (Ross, 1970; Whitcomb et al., 1987), and leaf-mining agromyzids (Spencer, 1990).

Trace-fossil documentation of the associations between insects and their Mesozoic tetrapod hosts is considerably poorer than record of plant-insect associations mentioned above. However, more is known about Cenozoic insects and their mammalian and avian hosts (Traub, 1980; Lyal, 1987; Kim, 1988), since the ecologies of their modern descendants is probably reliable. With regard to the Cretaceous, the principal associations are blood-feeding dipterans and dinosaurs, parasitic flea-like insects on unknown hosts, carrion feeding on crustacean and dinosaurian carcasses, and a trophic web among conifers, herbivorous ornithopods and dung beetles. Recently, Borkent (1995) has used mouthpart microstructure and functional morphology to deduce that two or three species of biting midges from the Upper Cretaceous (Campanian) of Alberta fed on the blood of large vertebrates, most likely hadrosaurs. Additionally, another family of blood-feeding lower Diptera, the monogeneric Corethrellidae, have been found in Lower Cretaceous (?Barremian) Lebanese amber (Szadziewski, 1995). Members of *Corethrella* currently feed obligately on frogs and are attracted by their calls (Borkent and Szadziewski, 1992), suggesting that this is an ancient association. In addition to biting midges, fossils very similar to fleas are known from the Lower Cretaceous (Aptian) of Australia (Jell and Duncan, 1986), although this assignment is contentious (Poinar, 1995). These flea-like insects are large by modern standards and were probably ectoparasitic since they bear distinctive pronotal and

tergal combs, stylate mouthparts, and laterally compressed bodies. Associations of insects and tetrapods also occurred after death, since calliphorid pupae have been found associated with crustaceans in Late Cretaceous (Campanian) deposits of the Edmonton Formation of Alberta, Canada (McAlpine, 1970) and dermestid-like borings are known from dinosaur bones in penecontemporaneous deposits (Rogers, 1992), suggesting consumption of decomposing flesh, like modern members of these families. Lastly, there now is good evidence for dung beetles processing dinosaurian excreta, demonstrated by distinctive backfilled burrows and tunnel geometry in conifer-laden coprolites produced by ornithopod dinosaurs (Chin and Gill, 1996).

CONCLUSION

Beginning with the terminal Permian extinction that extinguished the Paleozoic Insect Fauna, insect origination and extinction has progressively decreased toward the Recent, reaching an asymptote approaching zero during the Cenozoic. This pattern indicates that insect success, as measured by family-level diversity, is attributable to a low probability of extinction. This conclusion also is borne out by long geochronologic durations of insect genera determined from the body-fossil record, as well as the ability of modern pest species to form insecticide-resistant mutations while maintaining species-level integrity. While this pattern is very different from considerably more shorter-lived vertebrates (Labandeira and Sepkoski, 1993), it is similar to vascular plant families (Eble, 1999), which are also long-lived. Perhaps this coincidence merits further study, particularly since insects and plants constitute the overwhelmingly bulk of diversity on land and have a long history of association.

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TABLE

Taxonomic composition of mouthpart classes (from Labandeira, 1990).

<i>mouthpart series</i>	<i>no.</i>	<i>mouthpart class</i>	<i>included taxa</i>	<i>life stage</i>	<i>membership</i>
MANDIBULATE	1.	Entognathate	Collembola, Diplura	nymphs,	10
	2.	Monocondylate	Archaeognatha	nymphs, adults	3
	3.	Adult-ectognathate	Zygentoma; Blattodea; Mantodea; Phasmatodea; Grylloblattodea; Orthoptera; Isoptera; Dermaptera; Embioptera; Plecoptera; Zoraptera; Megaloptera; Neuroptera; Megalo- ptera; Raphidioidea; Coleoptera; Lepidoptera (Zeugloptera); Hymeno- ptera (Symphyta, Apocrita- "Parasitica")	adults, naiads of Plecoptera, a few larvae	291
	4.	Larval-ectognathate	Coleoptera; Mecoptera; Siphon- aptera; Diptera (Anisopodidae); Trichoptera (Phryganopsychidae); Lepidoptera (Zeugloptera)	larvae	164
	5.	Maxillolabiate	Hymenoptera (Apocrita)	adults	24
	6.	Raptorial- ectognathate	Odonata	adults	22
	7.	Mortar-and-pestle	Psocoptea; Phthiraptera (Amblycera, Ishnocera)	nymphs, adults	27
	8.	Rostrate	Mecoptera; Neuroptera (Nemopteridae)	adults	13
	9.	Rhynchophorate	Coleoptera (Curculionioidea)	adults	18
	10.	Pectinate	Ephemeroptera	naiads	26
	11.	Mouthbrush	Diptera (Nematocera); Coleoptera (Buprestidae); Lepidoptera (Gracillariidae)	larvae	3
	12.	Mandibulobrustiate	Trichoptera	larvae	28
	13.	Sericterate	Lepidoptera (Glossata); Hymeno- ptera	larvae	125

<i>mouthpart series</i>	<i>no.</i>	<i>mouthpart class</i>	<i>included taxa</i>	<i>life stage</i>	<i>membership</i>
MANDIBULO-CANALICULATE	14.	Fossate Complex	Neuroptera	larvae	15
	15.	Tubulomandibulate	Coleoptera (Hygrobiidae, Dytisci-, dae, Gyrinidae, Haliplidae, Lampyridae, Telegeusidae, Drilidae, Lycidae, Phenogodidae, Cantharidae, Brachypsectridae, Omethidae)	larvae	20
	16.	Mouthhook	Diptera (Cecidomyiidae, Brachycera)	larvae	55
LABELLATE	17.	Haustoriolate	Trichoptera	adults	30
	18.	Labellate	Diptera (Tipuloidea, Tanyderidae, Ptychopteridae, Bibionoidea, Brachycera); Mecoptera (Nannochoristidae)	adults	5
SIPHONATE	19.	Siphonate	Coleoptera (?Hydrophilidae, Meloidae, Rhipiphoridae)	adults	5
	20.	Siphonomandibulate	Coleoptera (?Hydrophilidae, Meloidae, Rhipiphoridae)	adults	5
GLOSSATE	21.	Glossate	Neuroptera (Nemopteridae); Hymenoptera (?Torymidae, Sapygidae, Scolioidea, Vespoidea, Sphecoidea, Apoidea)	adults	29
STYLATE-NONHAUSTELLATE	22.	Entognathous-stylate	Protura; Collembola (Neanuridae)	nymphs, adults	4
	23.	Ectognathous-stylate	Orthoptera (Cooloolidae); Coleoptera (Sphaeridae, Rhysodidae, Leiodidae, Cerylonidae, Corylophidea, Eucinetidae)	adults, a larva	13
STYLATE-HAUSTELLATE	24.	Segmented beak	Hemiptera	nymphs, adults	118
	25.	Buccal Cone	Phthiraptera (Anoplura, Mallophaga -Haematomyzidae)	nymphs, adults	6
	26.	Mouthcone	Thysanoptera	nymphs, adults	9
	27.	Monostylate/ Distylate	Diptera (Asilidae, Acroceridae, Empididae, Bombyliidae)	adults	8

<i>mouthpart series</i>	<i>no.</i>	<i>mouthpart class</i>	<i>included taxa</i>	<i>life stage</i>	<i>membership</i>
STYLATE- HAUSTELLATE	28.	Distylate/ Tetrastylate	Diptera (Anisopodidae, Mydidae, Rhagionidae, Therevidae, Ironomyiidae)	adults	9
	29.	Hexastylate	Diptera (Nematocera, Tabanoidea)	adults	27
	30.	Tristylate	Siphonaptera	adults	15
	31.	Tubulostylate	Diptera (Glossinidae, Hippoboscidae, Streblidae, Nycteribidae)	adults	10
	32.	Siphonostylate	Lepidoptera (Noctuidae)	adults	2
REDUCED	33.	Reduced trophic	Homoptera (Neococcoidea); Coleoptera (Eucnemidae, Rhipiphoridae); Strepsiptera; Diptera (Nymphomyiidae, Hyperoscleidae, Gastrophilidae, Acroceridae); Lepidoptera (Zygaenoidea); Hymenoptera (Apocrita-“Parasitica”)	nymphs, some larvae and adults	52
	34.	Nontrophic	Ephemeroptera; Lepidoptera (Hepialoidea, Lasiocampidae, Saturniidae)	adults	9

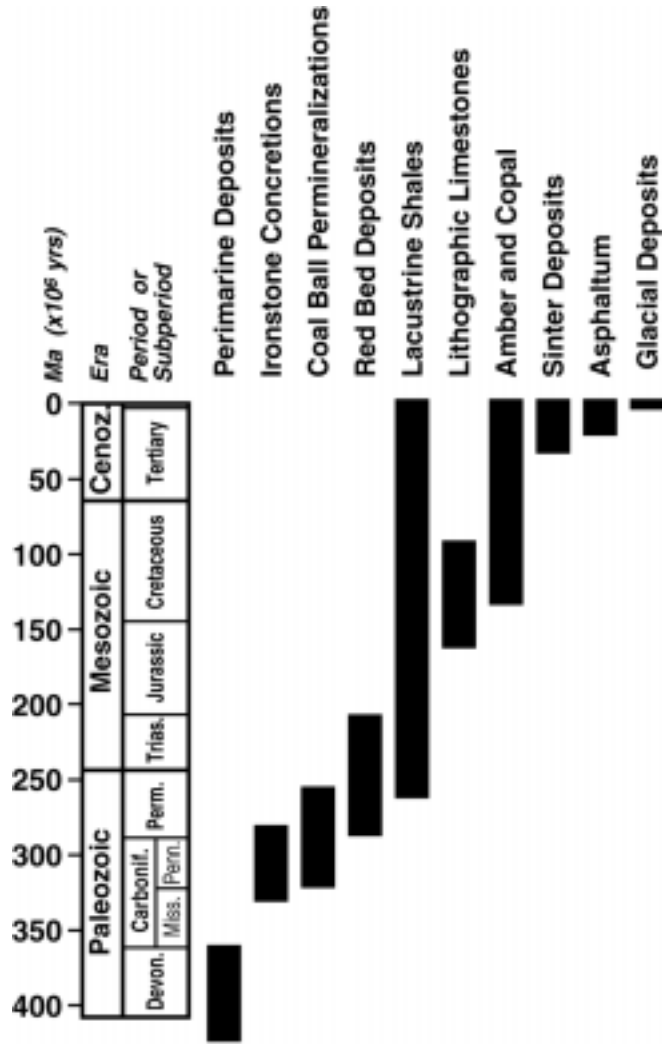


Figure 1

Figure 1. Geochronologic distribution of major types of insect-bearing deposits. Abbreviations: Devon.=Devonian, Carbonif.=Carboniferous, Miss.=Mississippian, Penn.=Pennsylvanian, Perm. = Permian, Trias. = Triassic, Cenoz. = Cenozoic.

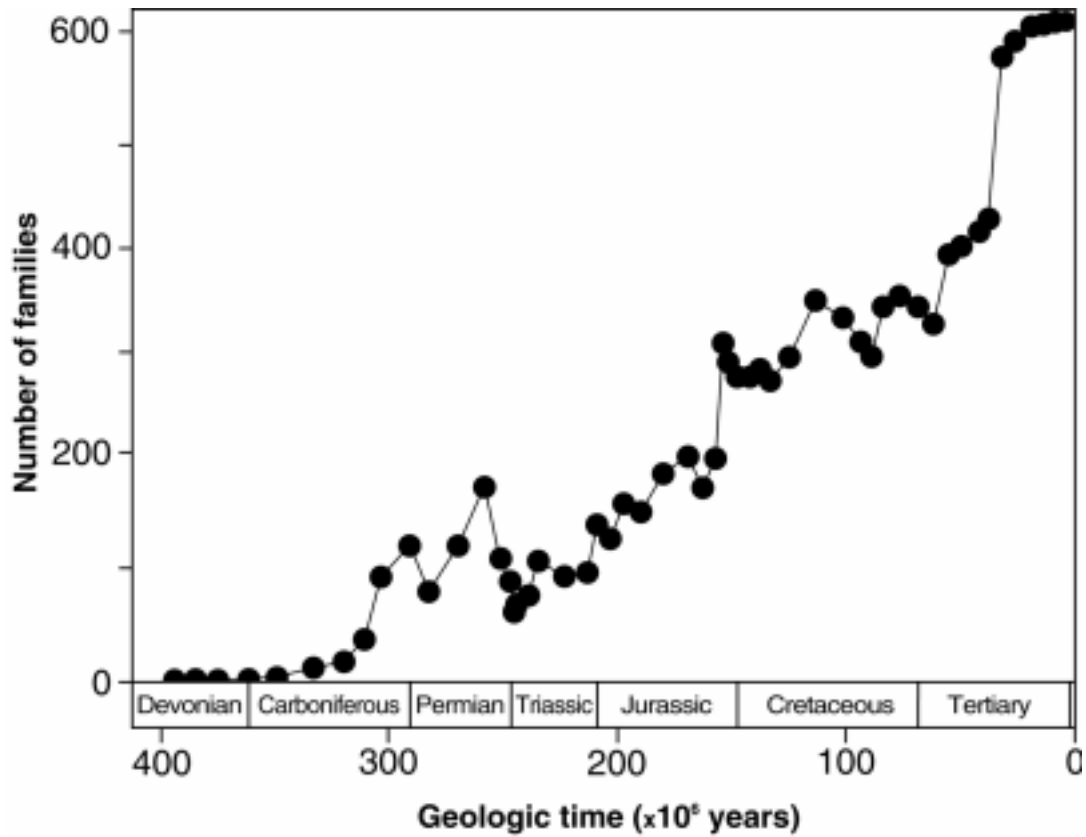
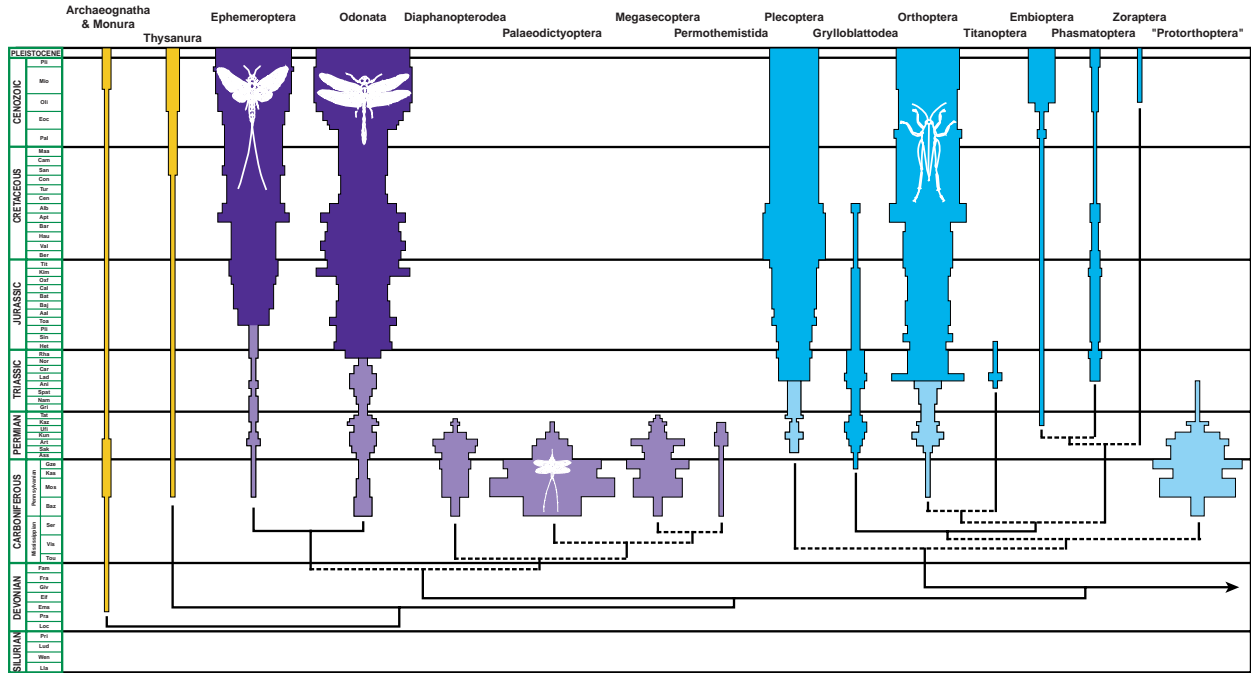
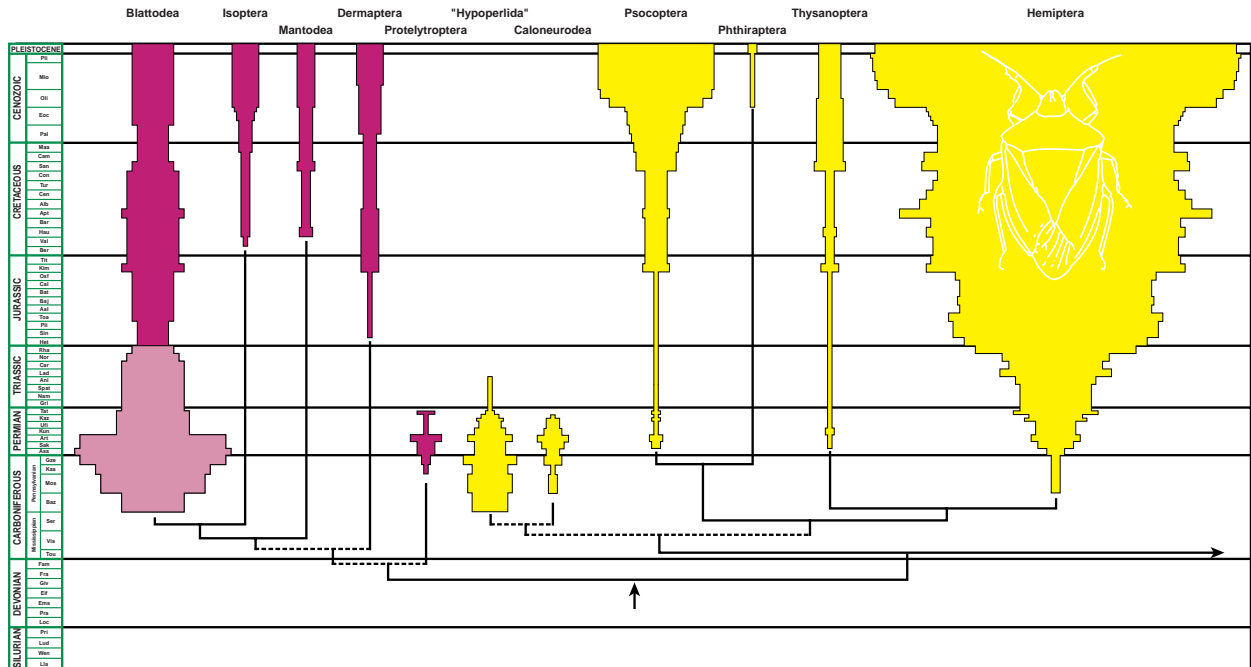


Figure 2

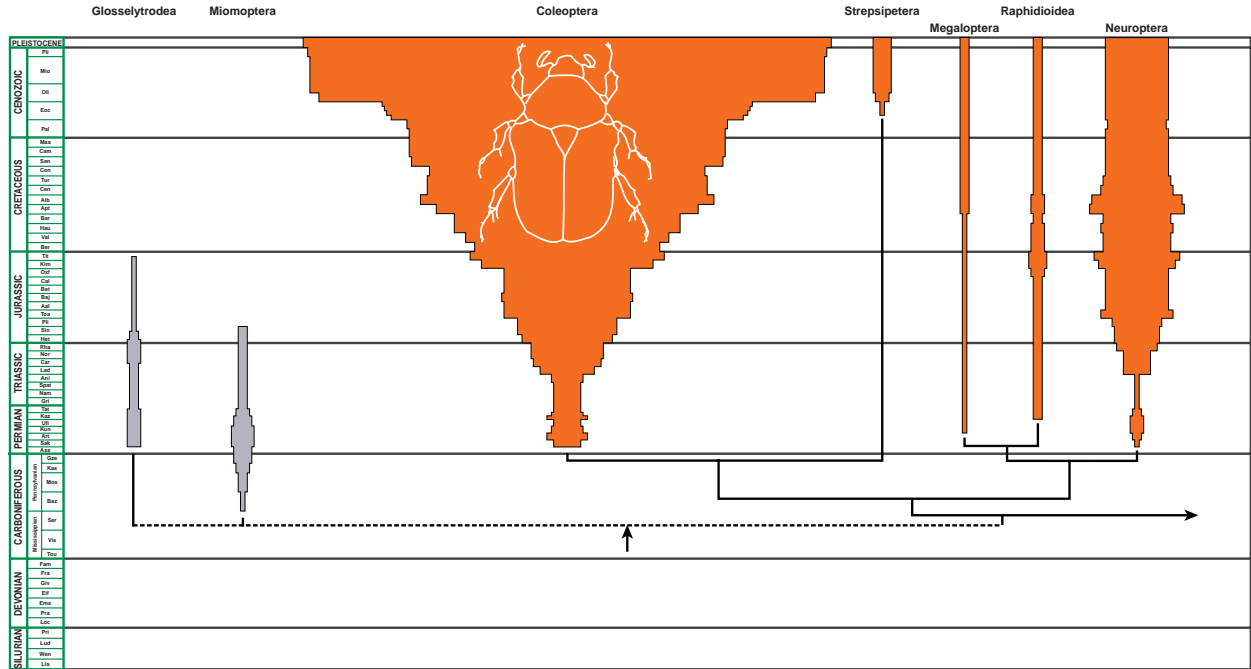
Figure 2. Family-level diversity of fossil insects, resolved to the level of stratigraphic stages, and using the range-through method. From Labandeira and Sepkoski (1993), based on data in Labandeira (1994).



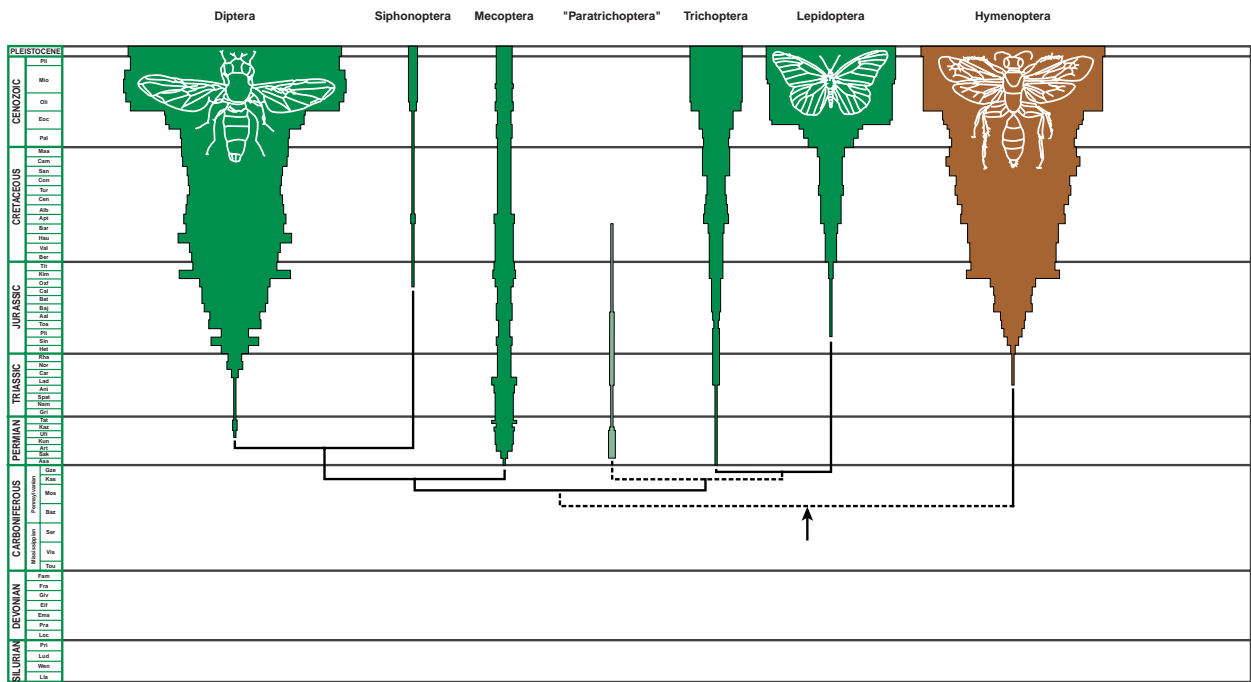
3a



3b



3c



3d

Figure 3. Family-level diversity of major insect clades through time, placed in phylogenetic context. **a**, Clades representing apterygotes, Palaeoptera, Plecoptera and basal orthopteroids. **b**, Clades representing advanced orthopteroids and Hemipteroidea. **c**, Clades representing basal Holometabola and neuropteroid groups. **d**, Clades representing panorpoid groups and the Hymenoptera. Phylogenetic relationships are a composite from various sources, including Rohdendorf and Rasnitsyn (1980), Hennig (1981), Wheeler (1989), Kukalová-Peck (1991), and Kristensen (1995). Dotted lateral connectors are inferred associations whereas solid lines are relatively secure relationships. Abbreviations: Pz=Paleozoic, Mz=Mesozoic, Cz=Cenozoic. Spindle diagram colors: grey = Paleozoic Insect Fauna, black = Modern Insect Fauna. Diversity data based on Labandeira (1994), modified somewhat from Labandeira and Sepkoski (1993).

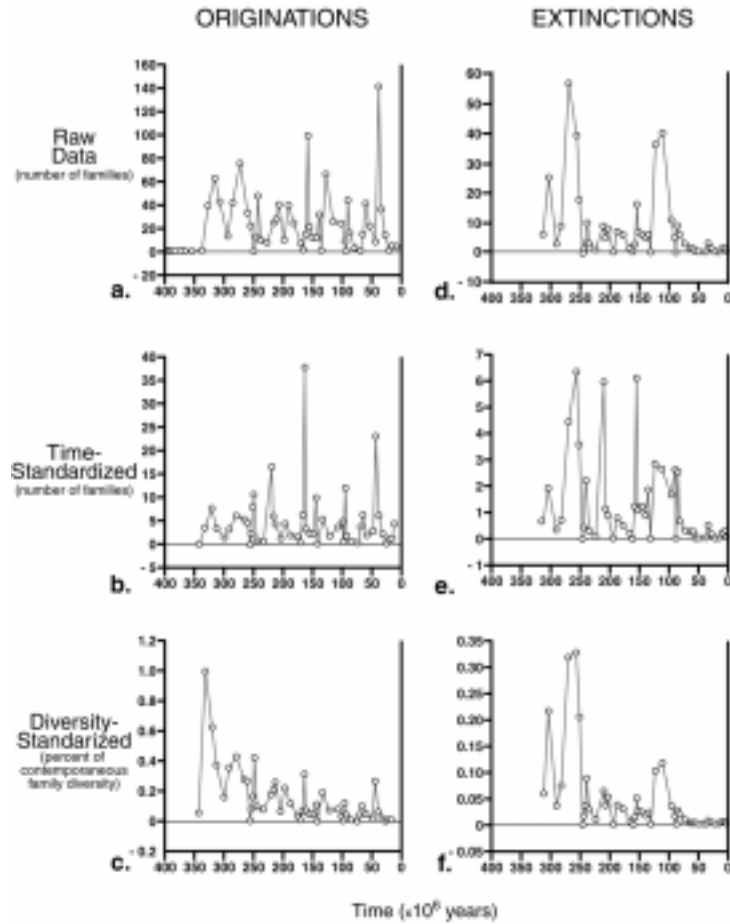


Figure 4

Figure 4. Family-level origination and extinction data for fossil insects (left and right columns, respectively), based on Labandeira (1994). Raw untreated data are shown at top row; data standardized by time, expressed as originations or extinctions per million years, are given in the middle row; and data expressed as originations or extinctions for existing standing diversity is provided at the bottom row. Data referred to in text: *a*, Raw origination data; *b*, Time-standardized origination data; *c*, Diversity-standardized origination data, *d*, Raw extinction data; *e*, Time-standardized extinction data; *f*, Diversity-standardized extinction data.

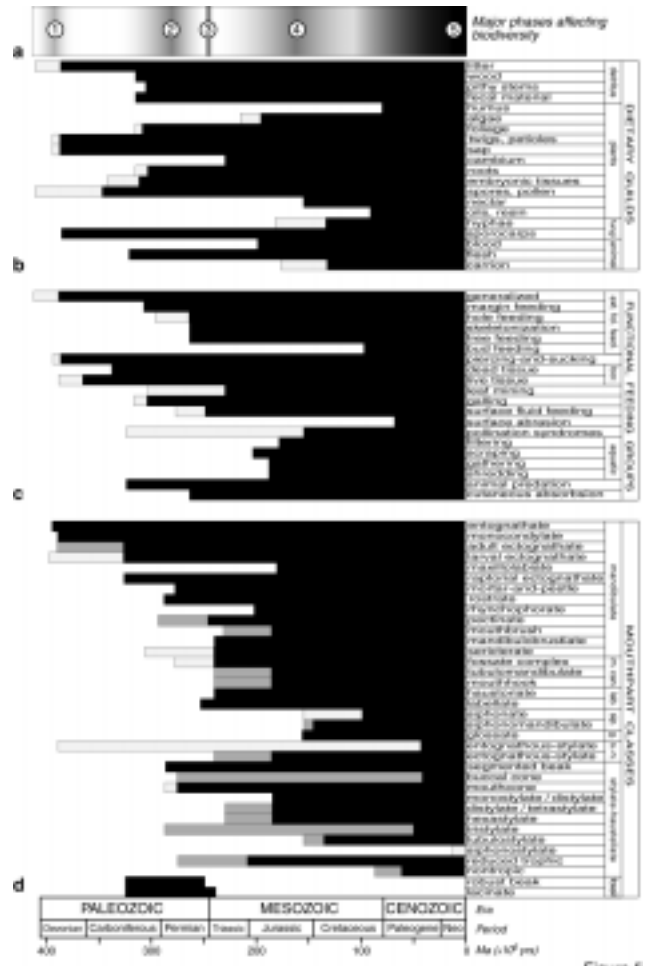


Figure 5

Figure 5. Measures of fossil insect ecomorphologic diversity. *a*, Major phases affecting the biodiversity of insects, as revealed in the fossil record, discussed in the text. *b*, Distribution of fossil dietary guilds, abstracted from data in Labandeira (2001). *c*, Distribution of fossil functional feeding groups, abstracted from data in Labandeira (2001). Abbreviations: ext. fol. feed. = external foliage feeders; bor. = borers. *d*, Distribution of mouthpart classes, modified from Labandeira (1990, 1997). Mouthpart series abbreviations: m. can. = mandibulo-canaliculate; lab. = labellate; sip. = siphonate; g. = glossate; s.-n. = stylate-nonhaustellate; red. = reduced. Conventions for shading are: black, direct evidence; dark grey, compelling indirect evidence; light grey, less compelling indirect evidence. Timeline abbreviation: Neo. = Neogene.

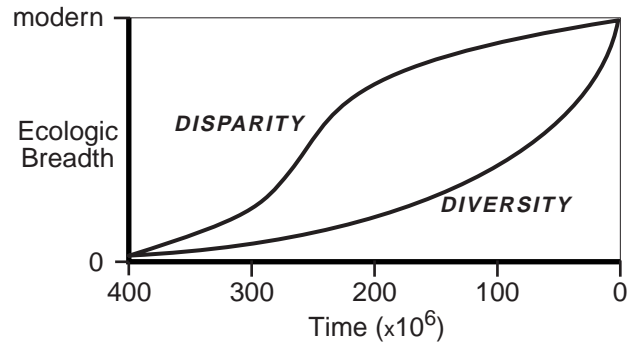


Figure 6

Figure 6. Schematic comparison between the increase of taxonomic diversity versus ecologic disparity in the insect fossil record.