



The Fossil Record of Insect Extinction: New Approaches and Future Directions

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ABSTRACT: The fossil record of insect extinction at the family level is characterized by two basic modes: background extinction, which represents an ambient level of taxa extirpation, and mass extinctions, which are occasional severe events in which taxa are eliminated significantly above background levels. The most significant mass extinction, at the end-Permian (Permian–Triassic; P-T), divides the history of insects into two major evolutionary faunas: an earlier Paleozoic Evolutionary Fauna of apterygotes, paleopterans, and basal clades of orthopteroids and hemipteroids; and a subsequent Modern Evolutionary Fauna of more derived clades of orthopteroids and hemipteroids and especially holometabolous insects. In addition to the P-T event, four other extinctions are documented by multiple types of data: Late Pennsylvanian, Late Jurassic, later

Early Cretaceous; and the end-Cretaceous (Cretaceous–Paleocene; K-P). There also is an analogous record of insect origination that is characterized by major, above-background events.

Four methods are used to detect insect extinction in the fossil record. The taxic approach is widely used, whereby the temporal durations of fossil taxa are tallied for each geologic unit of interest and analyzed in a manner analogous to demography used in ecology. By contrast, the phylogenetic approach uses clades as the basic units of interest. A recent approach uses proxy data such as quantification of plant–insect associations across major boundaries in lieu of an insect body–fossil record. Last, the clustering of times of origin from modern coevolved plant–insect associations provides data for likely interruptions from major paleoenvironmental perturbations. Pluralism, emphasizing multiple approaches to determine the ecological dynamics of insects during an extinction, is the best strategy to evaluate insect demise or survival in the fossil record. **Key words:** extinction, origination, biodiversity, fossil insects

The origination and extinction of species are among the truths of the biological world. These two processes, occurring in tandem or sequentially, and often causally linked, define the biological trajectory of life. This history, in the marine and continental (land plus freshwater) realms, is characterized by continual turnover of species that contributes to background extinction. Normal species turnover is punctuated by occasional bouts of catastrophic wipe-out, known as mass extinction (Raup 1991).

Extinction affects all forms of life, particularly when a mass extinction event claims as many as 96% of all species—an estimate established from longevity data for marine taxa at the Permian–Triassic (P-T) boundary 251 million years (m.y.) ago (Raup 1979a). The immensity of this extirpation can be extrapolated to continental species such as insects, given the fundamentally different taxonomic compositions of Late Permian and Triassic insect faunas (Labandeira and Sepkoski 1993, Jarzembowski and Ross 1996).

For insects, the P-T extinction was the most profound event in the history of the clade and separates two major evolutionary faunas at higher taxonomic levels (Jarzembowski and Ross 1996, Zherikhin 2002; Fig. 1). Although there is temporal overlap of some lineages, the Paleozoic insect fauna, dominant from the Early Devonian to Late Permian, consists of basal clades of apterygotes, paleopterans, orthopteroids, and hemipteroids. The post-Paleozoic modern insect fauna, dominant from Early Triassic to the Holocene, comprises more derived clades of odonates, orthopteroids, and hemipteroids, but especially the broad spectrum of holometabolous insects that currently account for the vast majority of extant insect species (Kristensen 1999; Fig. 1).

Nevertheless, there is constant adjustment of the position of insect clades across the boundary;

for example, the discovery of a probable paleodictyopteran, in Upper Triassic strata, representing a clade formerly confined entirely to the Paleozoic (Bechly 1997, Nel et al. 1999a; Fig. 2), or alternatively, recognition of taxa that have the opposite effect, such as a representative of the nominally post-Permian odonatopteran clade Panodonata occurring in the Permian (Nel et al. 1999b). One way of assessing the importance of this extinction is that major clades of the Middle and Late Triassic insect faunas are more similar to those of today, 230 m.y. later, than to those of the later Permian, only a few tens of millions of years earlier (Fig. 1).

In addition to this “mother of all extinctions” (Erwin 1993), other more modest extinctions also exceed background levels. Two other extinctions are an event during the Late Pennsylvanian, probably reflecting the demise of Euramerican coal swamp taxa at the end of the Middle Pennsylvanian (Labandeira and Phillips 2002), and the Cretaceous–Paleocene (K-P) event, which was responsible for the extinction of host-specialist herbivores at least for North America (Labandeira et al. 2002a, 2002b), and probably elsewhere. Both of these events were determined principally by taxic and ecological studies, although other types of data suggest significant extinction as well. In general, these and other extinctions represent detectible decreases on a general trend of an exponential increase in insect family-level diversity since the Late Paleozoic.

Extinction is a taxon-based phenomenon that occurs within an ecological context of associations with other organisms. The presence of food webs involving insects extends to the earliest continental ecosystems, which have been dominated macroscopically by vascular plants, arthropods (overwhelmingly insects, but also myriapods and arachnids), and tetrapods. Together with other continental taxa, life on land currently constitutes ≈85% of all global species (May 1994).

When considering the fossil record, however, a similar proportion of species are marine (Raup 1976), suggesting a severe bias against continental organisms (Raup 1976). Nevertheless, given that

(1) ≈56% of all extant species are insects (May et al. 1995), (2) that insect species on average persist for about 10 m.y. based on studies of late Cenozoic and Holocene insects (Coope 1990) and the older fossil record (Labandeira and Sepkoski 1993), and (3) a conservative estimate of 3 million species currently exist (Benton 2001), then it is likely that minimally 10% or somewhat more of all plant and animal species to ever have lived are insects (May et al. 1995) and that they have dominated the continental fossil record from the late Paleozoic to the Holocene. This preponderance of insect species in continental deposits for the past 330 m.y. is evidenced by their numerical abundance, as well as diversity in deposits as diverse as lake-deposited shales and mudstones, ironstone concretions, Mesozoic lithographic limestones, amber, and more recent hot spring, asphaltum, and glacial deposits (Labandeira 1999).

A very rough estimate for described and known fossil insect species is 25,000. This evidently is a very small proportion of the species that once existed and represents ≈0.5% of known, extant insect diversity, (also see Carpenter 1992). Nevertheless, the fossil insect record is better than once thought; and it considerably exceeds that of the only other comparable major terrestrial animal group—the vertebrates—in terms of taxonomic representation (Labandeira and Sepkoski 1993) and also provides documentation for patterns of trophic and mouth-part evolution (Labandeira 1997).

Diversity, Origination, and Extinction in the Fossil Insect Record

To evaluate insect extinction in the fossil record, two other metrics need to be considered: total diversity and origination (Figs. 3 and 4b). Origination is a tally of the numbers of first appearances of taxa of interest in the fossil insect record for a particular time unit; essentially it is the inverse of extinction, which is a tally of their disappearances. Total diversity is a count of all known insect families occurring at a particular time; it provides the secular trend of increase or decrease of taxa during geologic time.

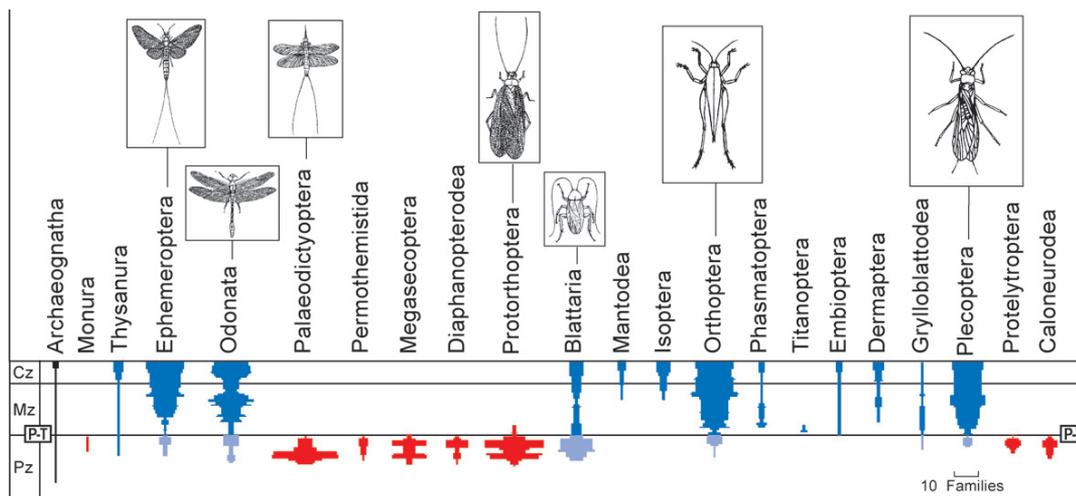


Fig. 1. Family level diversity for some Paleozoic orders, reported in Labandeira and Sepkoski (1993) as the upper panel in their Fig. 2. Abbreviations: Pz, Paleozoic; Mz, Mesozoic; Cz, Cenozoic. Note end-Permian mass extinction at the Paleozoic-Mesozoic era boundary. Some orders with distinctive Paleozoic clades are indicated by a lighter shade of blue.

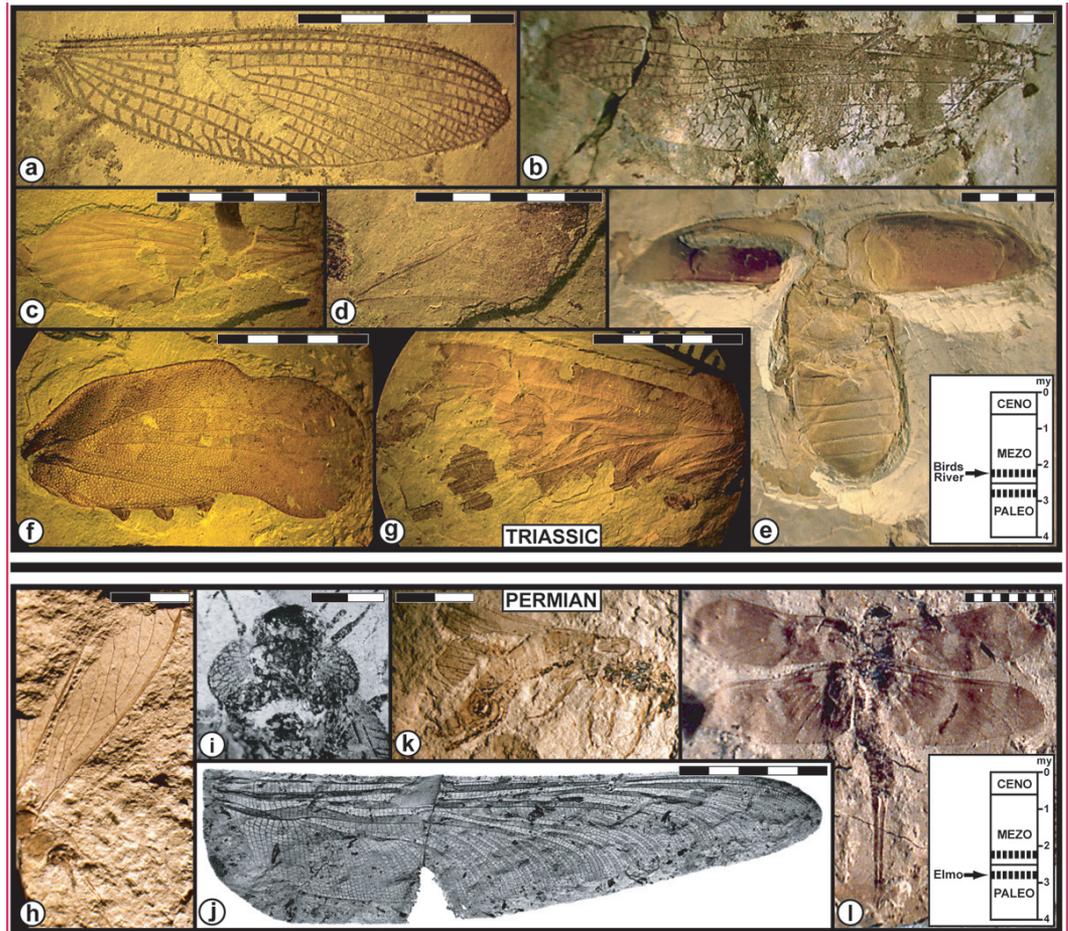


Fig. 2. Insect fossils from the Late Triassic Molteno Formation (Birds River site of the Karoo Basin, South Africa) whose lineages mostly originated after the end-Permian mass extinction (**a** to **g**). Illustrated are **a**, *Litophlebia optata* Riek (Ephemeroptera: Litophlebiidae); **b**, *Triassoneura andersoni* Riek (Odonata: uncertain family); **c**, *Protorthophlebia capensis* (Riek) (Mecoptera: Orthophlebiidae); **d**, *Moltenia rieki* Schlüter (Hymenoptera: Xyelidae?); **e**, Coleoptera, probably assignable to the Ademosynidae; **f**, *Tennentsia protuberans* Riek (Hemiptera: Dymorphoptilidae); and **g**, *Mesoses magna* Riek (“Paratrichoptera:” Mesosetidae), most likely affiliated with an antliophoran stem group. Below the P-T extinction divider are examples of Paleozoic insect body fossils from major lineages of the mid-Permian (Wellington Formation of Elmo, KS) that failed to survive into the Triassic (**h** to **l**). Illustrated are **h**, *Protohymen permianus* Tillyard (Diaphanopteroidea: Protohymenidae), with a beak of piercing-and-sucking mouthparts; **i**, *Lemmatophora typa* Sellards (Protorthoptera: Lemmatophoridae), illustrating pronotal lateral lobes; **j**, the large wing of *Kennedyia mirabilis* Tillyard (Protodonata: Kennedyidae); **k**, another view of *Asthenohymen*, showing ovipositor at lower left (arrow); and **l**, *Dunbaria fasciipennis* Tillyard (Palaeodictyoptera: Spilapteridae), showing wing color pattern. Figure **i** from Carpenter (1966) and **j** from Beckemeyer (2000). Bars at lower right indicate the geochronologic position of the Elmo and Birds River sites.

All three kinds of data typically are recorded at the level of the geologic stage, or epoch in the case of the Carboniferous and sometimes Middle and Late Permian. Devonian to Pleistocene stages are time units that range in duration from 1.3 (Induan) to 18.3 (Visean) m.y., with a mean length of ≈ 7.1 m.y (Fig. 3), although these values are subject to significant change as better calibration methods become available. The level of taxonomic analysis can range from the species to the order. Traditionally analysis has been at the level of the family, owing mostly to the practical issue of compiling a vast database of fossil insect taxa at lower ranks (genera and species occurrence data currently are being assembled by several researchers).

As it turns out, the family level is a good predictor of underlying species diversity and has been extensively applied as the “higher taxon approach” used by biologists charting the distribution, ecological correlates, and diversity patterns of tropical insect faunas. Use of this approach is attributable principally to difficulties inherent in documenting and describing all relevant extant insect species in exceptionally diverse insect faunas (Gaston and Williams 1993, Williams and Gaston 1994, Balmford et al. 1996, Lee 1997). Such studies have demonstrated high levels of correlation between family level diversity and underlying speciosity, a relationship that has been demonstrated in the fossil record as well (Bambach and Sepkoski 1992).

Although the data used in this and previous studies is at the family level, it is probably the genus level that produces the strongest signal between taxonomic specificity on one hand and the vagaries of error-prone species-level determinations on the other hand. The latter was amply demonstrated by Schneider's (1977) study of significant variation in wing venation within extant and extinct cockroach "species".

Once tabulations of total diversity, originations, and extinctions have been established for the 57 geologic stages and epochs since the earliest occurrences of insects in the Early Devonian, several methods are used to treat the raw data, including time standardization to a monotonic geologic time scale and diversity standardization to present-day diversity within a taxonomic level. In this contribution, I use raw data at the family level.

Diversity. The most generalized description of family-level insect diversity is that of an exponential increase beginning during the Pennsylvanian Subperiod and continuing to the Holocene (Fig. 3). However, there is indication of a logistic tapering-off of this expansion, especially evident in suprafamilial data such as orders (Ross and Jarzembowski 1993a, Jarzembowski 2001). This is explained by a decrease in diversification for the past 245 m.y. from the rate that was established during the late Paleozoic and early Mesozoic (Labandeira and Sepkoski 1993) and indicates that a modern level of ≈ 1100 families is a level of saturation based on the expected family-level capture rate from the fossil record. Other explanations such as the "pull of the Recent," in which the more modern part of the fossil record is better sampled than the older deposits (Raup 1979b), may accentuate an exponential rise. Considerable effort during the past three decades, however, has focused on the older part of the fossil record, especially Mesozoic deposits, and thus has deemphasized more recent occurrences.

Superimposed on this trend are a few noteworthy deviations. The most important is the severe decline at P-T boundary interval (Fig. 3, which reflects the profound environmental degradation that affected marine and continental taxa (Retalack 1995, Visscher et al. 1996, Erwin 1998). A more subdued, earlier event occurred during the Early Permian, reflecting the demise of archaic, larger-bodied insect taxa associated with the Pennsylvanian-age swamp biotas of the paleocontinent Euramerica; these taxa were replaced by smaller taxa inhabiting more mesic and arid environments in the same region. There also was a modest event during the Middle to Late Jurassic, before the large jump associated with first occurrences of many modern insect families, such as those found in faunas from Southern England and Central Asia, and the lacustrine shales of Karatau in Kazakhstan and Baissa in transbaikalian Russia. Subsequent minor decreases are recorded for the early Early Cretaceous, and early Late Cretaceous, but they represent proportionately modest excursions when compared with standing family-level diversity. These downturns have been commented on, such

as the one at the early Late Cretaceous (Ross et al. 2000, Grimaldi et al. 2002, Zherikhin, 2002), which evidently is related to modernization of the insect fauna and the extirpation of some archaic clades that survived the P-T extinction or originated during the earlier Mesozoic.

The most significant trend during the Cenozoic has been the dramatic increase in insect families during the late Eocene to early Oligocene, attributable to spectacular, mostly lacustrine Lagerstätten (exceptionally preserved fossil deposits) of Baltic amber and Messel in northern Europe, and the Green River and Florissant deposits of the western United States. These Lagerstätten contain abundant, well-preserved, and diverse fossils that have attracted the attention of paleoentomologists for more than 100 years.

Origination. Explanations for factors associated with originations and extinctions involve details about the completeness and the geographic and ecologic context of particular intervals of the fossil insect record; knowledge of related biological events, especially disruptive events or radiations in the evolutionary history of vascular plants; and assessments of sudden to prolonged, major environmental perturbations during the earth's past. A notable aspect of origination and extinction is that they frequently are coupled (compare Fig. 4a with 4b), providing unusually high levels of both within the same geologic stage and indicating major clade turnover and possible competitive replacement (Briggs 1998).

An alternative for this coincidence of elevated origination and extinction is poor sampling, such as a significantly incomplete fossil record. However, stages during which both are synchronous occur among the most highly sampled intervals of the fossil insect record.

Data for fossil insect origination are quite spiky, but they show five peaks above the ambient, background level (Fig. 4a, arrows 1–5). This background level of origination averages ≈ 20 families per geologic stage, but has a large variation from zero to a persistent plateau of ≈ 45 families. The background origination values remain constant throughout the late Paleozoic to late Paleogene, but essentially are zero during the Devonian to Mississippian and for the past 20 m.y. The five bouts of exceptional origination, significantly exceeding the background level, are

- (1) the Middle Pennsylvanian Moscovian Stage,
- (2) an Early Permian peak during the Artinskian Stage,
- (3) a more pronounced uptick during the Late Jurassic Kimmeridgian Stage,
- (4) a more subdued but still significant rise during the Aptian Stage of the Early Cretaceous, and
- (5) a maximal increase in the Priabonian Stage of the late Eocene.

The Middle Triassic does exhibit a robust increase in origination, from a baseline of zero at the P-T boundary, but apparently it does not rise significantly above background levels.

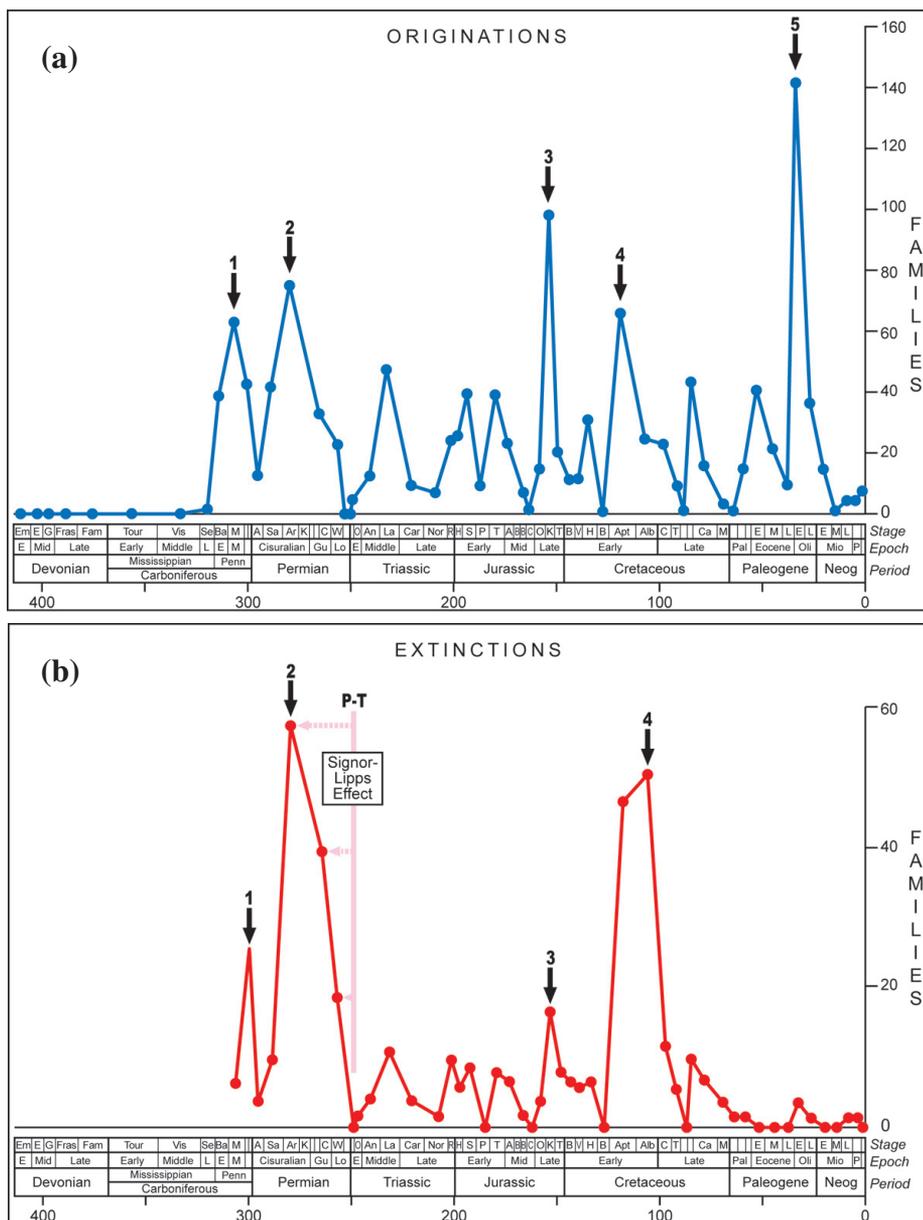


Fig. 4. Raw data on origination (a) and extinction (b) are presented for fossil insect families, based on Labandeira's (1994) compendium of fossil insect families. For the later half of the Permian, the Bajocian and Bathonian of the Jurassic, and much of the Paleogene and Neogene, data representing two or (uncommonly) three stages are combined into a single point.

Because the Late Paleozoic insect record overwhelmingly is centered in the equatorial latitudinal belt that includes principally Euramerica, explanations for the causes of insect origination during the Pennsylvanian (Fig. 4a, arrow 1) reside in biome-wide processes occurring throughout wetland and associated environments. The appearance of a major radiation of diverse, basal pterygote clades during the Pennsylvanian was associated with the colonization of peat swamp forests dominated by lycophytes, calamite horsetails, herbaceous ferns, gymnospermous cordaites, and especially toward the close of the subperiod, arborescent ferns and seed ferns. The typical habitus of Pennsylvanian insects was one often of large size, and presence of archaic external body features, and there was dominance by odonatan, paleodictyopteroid, and orthopteroid lineages.

By contrast, the diversity rise during the Early Permian, peaking at the Artinskian Stage (Fig. 3b, arrow 2), represents the appearance of taxa that were smaller and bore somatic modifications appropriate for mesic to xeric environments. This spectrum of

taxa consisted of derived Pennsylvanian clades, as well as new basal lineages of hemipteroid and holometabolous insects. Members of these clades inhabited principally riparian, lacustrine, and coastal ecosystems populated with floras dominated by gymnosperms, such as cycadophytes, gigantopterid (Laurasian) and glossopterid (Gondwanan) seed ferns, cordaites, and primitive conifers. Although not one of the five major origination events, the Middle Triassic blip is a rebound phase following the P-T extinction, characterized by the appearance of many of the major insect clades that occur today.

During the Late Jurassic (Fig. 4a, arrow 3), a major increase of family-level diversity occurs that is attributable to spectacular deposits and collecting efforts in central Asia. However, this increase records several real, biological phenomena that were transforming terrestrial insect faunas. Specifically, these taxa represent mostly the latter expansion phase of phytophagous and parasitoid groups that originated throughout the Jurassic and were trophically connected to new food resources

resulting from the diversification of advanced seed plants and a global increase in new insect taxa, both of which served as hosts, respectively, for herbivore and parasitoid colonization (Rasnitsyn 1988b, Labandeira 2002b).

The less dramatic increase in origination during the Aptian (Fig. 4a, arrow 4) likewise has multiple explanations. Major changes in Mesozoic lotic and lentic freshwater ecosystems to an ecologically more modern one (Sinichenkova and Zherikhin 1996), and changes in the soil fauna on land provided new family-level taxa that entered the fossil record. Interestingly, the Cretaceous radiation of angiosperms did not promote contemporaneous family-level increases in insects—a pattern that has been reproduced in several separate analyses (Rasnitsyn 1988a, Labandeira and Sepkoski 1993, Jarzembowski and Ross 1996) and is attributable to major phytophagous insect clades having an earlier Mesozoic origin with gymnospermous seed plants (Labandeira 1997).

The most dramatic increase in origination is during the Late Eocene, coeval with the spectacular Lagerstätten of Baltic amber and the Florissant lake beds in Colorado, and probably representing an accumulation of first fossil occurrences that actually have origins in the earlier Cenozoic and late Mesozoic (Fig. 4a, arrow 5). This peak is being projected backward into the Cretaceous from new occurrences, although the Paleocene probably represents a time interval of depressed origination following the K-P extinction event that affected host specialists, at least in North America.

Extinction. Ultimate causes for insect extinction most likely involve environmental degradation, although their immediate manifestation is in the context of a local ecological community involving associations with other organisms. Because there is a distinct range in the severity of extinction in the fossil record, the background extinction level is typically separated from mass extinction. Although data from marine invertebrates indicate that a continuum may link these two modes (Raup 1991), for insects the records of background and mass extinction are very different, and impart differing evolutionary dynamics separating taxa with the ambient level of extinction from those that succumb to mass dieoff at major events. Specifically, background extinction is very flat and consists of a persistent Mesozoic plateau of about 10 families per stage, interrupted occasionally by an extinction spike (Fig. 4b). These four extinction events range from about a two- to more than fivefold increase above background levels that encompass one to three geologic stages.

The significant extinction event during the Late Pennsylvanian (Fig. 4b, arrow 1) is associated with a significant ecological change based on a Euramerican floral and plant–insect associational record. At the end of the Middle Pennsylvanian, there was a major extinction of the dominant wetland communities on peat and mineral substrates in Euramerica (Phillips et al. 1974, Pfefferkorn and Thomson 1982), which resulted in a major replacement of

ecosystems dominated by lycopods, calamites, herbaceous ferns, and lower-statured seed ferns by arborescent marattialean fern and medullosan seed fern communities. Additionally, the detritivore-rich trophic structure of the Middle Pennsylvanian was supplemented by major exophytic and endophytic herbivores feeding on live tissues of the new arborescent taxa (Labandeira and Phillips 1996, 2002), consistent with an insect extinction. This new Late Pennsylvanian wetland ecosystem, replete with new taxa of plants and insects, persisted into the Permian in some paleocontinents; but it was rapidly replaced in Euramerica by gymnosperm-dominated communities, as peat-swamp-associated insects gave rise to taxa occurring in drier habitats with mineralic soils (Gastaldo et al. 1996, DiMichele et al. 2001).

The second major extinction event (Fig. 4b, arrow 2) was by far the largest in the history of insects, and it is characterized by the loss of numerous families that apparently cover three geologic intervals preceding the P-T event. One explanation for this delayed decrease is the Signor–Lipps effect, modeled initially to explain the extinction pattern of marine microorganisms at the K-P extinction (Signor and Lipps 1982). Their results, corroborated in subsequent studies, indicate that the last occurrences of variably preserved or moderately sampled fossil taxa at a major extinction will be recorded in a stepwise fashion back onto immediately earlier time units from the actual event. Thus there is a stair-stepped pattern to last fossil occurrences that segregates taxa with a poorer fossil record from those with a better record. This pattern gives an impression that there are a series of earlier extinction events when in fact, they are an effect of a single, more massive extinction.

In the case of vertebrate taxa at the end of the P-T in the Karoo Basin of South Africa, subsequent additional and intensive sampling effort revealed that the stair-stepped pattern was largely removed with the ends of ranges extending much closer to the boundary (Smith and Ward 2001). Given the much coarser-grained and comparatively poorer insect fossil record during the Late Permian, however, it is possible that the P-T extinction actually occurred during the mid- to Late Permian rather than at the last stage of the Permian, encompassing the three time intervals preceding the event (Fig. 4b). An alternative explanation is that sample size is insufficient to demonstrate the Signor–Lipps effect, even though the pattern (Fig. 4b) is consistent with it. Both explanations are consistent with the total diversity data in Fig. 3 and in the turnover of other terrestrial taxa (Retallack 1995).

After the “mother of all extinctions,” there is indication of a distinct Middle Triassic rebound as the early phase of the modern insect fauna was established. It is not until the Late Jurassic (Kimmeridgian Stage) that there is evidence for a third major extinction event (Fig. 4b, arrow 3), coinciding with the origin of many new taxa, discussed earlier. The taxa that became extinct undoubtedly represent less competitive, earlier Mesozoic

Because there is a distinct range in the severity of extinction in the fossil record, the background extinction level is typically separated from mass extinction.

lineages, some of which survived the P-T event, particularly as new preangiospermous seed plant and insect food resources were being expanded for colonization by a wealth of herbivores and parasitoids. The subsequent angiosperm radiation had no or even a negative effect on family-level insect diversity (Labandeira and Sepkoski 1993, Ross and Jarzembowski 1993a, Jarzembowski and Ross 1996, Gorelick 2001) and probably involved insect diversification at the infrafamilial level for phytophagous clades that were previously established on gymnospermous hosts.

There was a major extinction event, however, during the Albian and Aptian stages of the mid-Cretaceous, (Fig. 4b, arrow 4) which has more than one explanation. Many of the involved taxa represent the extirpation of older Mesozoic freshwater taxa that were replaced by clades that formed in a more modern, Cretaceous ecosystem setting; others represent the final extinguishment of older, mostly phytophagous, clades that perhaps were noncompetitive in exploiting increased angiosperm food resources. The same process affected earlier Mesozoic clades of predators. After this event, there is no evidence for an extinction event from the body-fossil record at the family level (Whalley 1987, Jarzembowski 1989), although ecological data indicates a major event for the K-P boundary in North America at the infrafamilial level (see below) and possibly for the Paleogene (Poinar et al. 1999). Family level diversity data indicate that extinction levels during the past 80 m.y. have asymptoted to a level of zero.

There has been considerable discussion of significant extinction, including insects, in extant ecosystems (Wilson 2002). The causes of this extinction have been attributed to direct anthropogenic consequences, such as the introduction of feral insectivorous organisms, or to the more indirect effects of global climatic change. Although present-day extinction is significant, direct comparisons to those of the fossil record are difficult because for the past there is reduced temporal resolution, a reliance on geographically widespread taxa, and that assessments are made at the family rather than lower taxonomic levels (Jablonski 1994). Bringing fossil insect data closer to the more finely resolved data of the present will allow a greater quantitative comparison between mass extinctions of deep time and those of today.

Detecting Extinction in the Insect Fossil Record

Four basic approaches are available for understanding insect extinction in the fossil record (Fig. 5). The taxic approach (Fig. 5a) overwhelmingly has been the most frequently used (Rohdendorf and Zherikhin 1974, Dmitriev and Zherikhin 1988, Labandeira and Sepkoski 1993, Ross and Jarzembowski 1993a, Jarzembowski and Ross 1996). It is dependent on extensive databases that list the global geochronologic occurrence of fossil insect taxa that historically have been determined at the family level (Dmitriev and Zherikhin 1988,

Rasnitsyn 1988a, Ross and Jarzembowski 1993b, Labandeira 1994). Increasingly these databases also record ecological, depositional, and morphometric attributes. Therefore, they describe not only the spatiotemporal and geologic context of fossil occurrences, but also the life habits, body structure, preservational context, and other documentable features of the fossil insect record.

By contrast, the phylogenetic approach considers clades as the units of interest. Unlike the taxic approach, it provides genealogical links among the lowest-level analyzed taxa (Hennig 1965; Fig. 5b). However, phylogenetic approaches have not been used to gather quantitative data for fossil insect diversity studies (e.g., Grimaldi and Agosti 2000, Engel 2001), more because of paramount concerns of intertaxal relationships than of documenting diversity trends in the “standing crop” of insect taxa. An example using the family level history and phylogeny of snakeflies is provided in Fig. 6, indicating extinction of three major lineages during the later Cretaceous.

Another approach has been to document plant-insect associations in the all-too-frequent absence of relevant body-fossil data in more stratigraphically focused intervals that span an extinction event (Labandeira et al. 2002a, 2002b; Fig. 5c). Such ecological data provide an alternative framework for assessing insect diversity, origination, and extinction patterns, specifically through the effects of herbivorous insects on plants. However, such an approach is relevant for only primary consumers of plants, herbivorous insects, which constitute 50–60% of all extant species (Price 1997), but they also constitute the majority of body-fossil occurrences in many insect-bearing deposits. A major extinction of herbivores, however, should have major, cascading consequences on dependent insects such as predators, parasitoids, and parasites (Godfray et al. 1999).

Although never explicitly applied to extinction in the fossil record, many molecular studies of co-evolved plant and insect taxa from the present have provided estimates of the temporal ranges for the period of initial association of host-herbivore systems. A sufficient number of these temporal ranges, gleaned from various studies in the plant-insect associational literature, can document temporal gaps that indicate the presence of significant disruptive events separating clusters of associations linking older associated plant and insect clades from newer such clades (Labandeira 2002a; Fig. 5d).

These four distinct approaches represent different ways of recording data relevant to insect extinction. Collectively they have the advantage of maximally using diverse types of taxonomic, ecological, and other data and methodologies for evaluating smaller-to larger-scale patterns from various geologic intervals.

Taxic Approach. The oldest approach uses taxonomic ranks, such as the family, to understand extinction in the fossil insect record. This has been done by tabulating the numbers of taxa that originate, become extinct, or persist through successive geochronologic intervals during a specified interval

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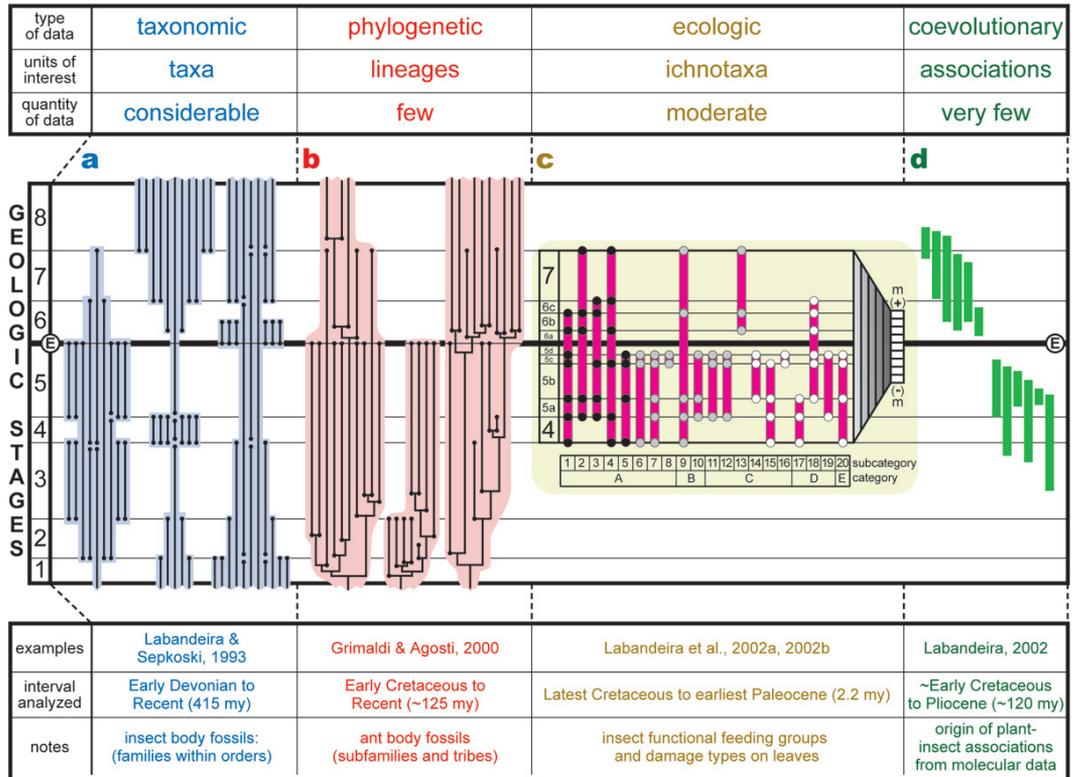


Fig. 5. Four major types of data for detection of extinction in the insect fossil record. Data are schematic for illustrative purposes. Taxonomic and cladistic data at left are presented as vertical lines that represent durations and terminal dots designate either originations (below) or extinctions (above) for a given taxon or lineage. For taxonomic data, lowest-level taxa are encompassed in blue diversity spindles to indicate the next higher rank; for cladistic data lineages are designated by inclusive red envelopes. The taxonomic data are a clade-by-clade breakdown of global, taxonomically comprehensive data presented in Fig. 1. More finely resolved ecologic data are represented as stratigraphic occurrences in meters above and below a putative extinction datum, circled as “E”; finer-grained stratigraphic resolution is indicated by zonation at left, labeled in lower-case letters. Data points express occurrences of ichnotaxa; attributes may refer to qualities such as plant-host specificity. The estimates for the timing of coevolutionary associations, at right, are based principally on molecular sequence data from insect herbivores and their associated plant-host taxa. The plots of vertical bars would be assembled from a compilation of the literature.

of time (Fig. 5a). To date, the range-through method of compilation has been used, in which the time interval between a taxon’s first and last occurrence is taken as the range of its duration, regardless of its presence or absence in intervening stages. This approach is not concerned with the precise genealogical relationships of the taxa being counted other than their membership in the next-higher major clade, such as families within an order (Fig. 2) or genera within families (see Sepkoski and Kendrick 1993).

The logic for the taxic approach was borrowed from the classical demography used in population ecology, namely the model proposed by A. J. Lotka and V. Volterra during the 1920s. Their model expressed exponential or logistic increases in numbers of individuals over time based on the size of the initial population, birth and death rates, survivorship, and the presence of a dampening factor that limits eventual growth (Wilson and Bossert 1971). J. J. Sepkoski and others during the late 1970s and early 1980s applied this demographical approach to the fossil record of marine invertebrates. Their work resulted in considerable advances in understanding the diversity dynamics and macroevolutionary pat-

terns based on the appearance, radiation, demise, or persistence of major taxa in the fossil record (Gould et al. 1977; Sepkoski 1978, 1981).

This general approach was applied to the fossil insect record initially by Zherikhin and Rohdendorf in 1974, and subsequently and independently by several investigators during the late 1980s and early 1990s. The major evolutionary patterns of insect diversity repeatedly have been borne out by these studies. The collection of data at the genus level (Ross and Jarzembowski 1993a, Jarzembowski 2001), with certain caveats, will allow a more finely resolved analysis of the fossil record that may be more sensitive to biogeography, clade membership, preservation, and ecological attributes such as associations with other organisms. Additionally, a trend toward placing fossil insect data within a more finely resolved stratigraphic context, extending stage-level data to zones within stages, will provide more circumscribed data in the range of tens of thousands to a few million years.

Phylogenetic Approach. Recent advances in placing fossil insect taxa into a cladistic context offers an opportunity to chart the diversity and

other attributes of monophyletic lineages through time, including feeding styles or other life history traits. Lineages with varied ecological features can be used to ascertain the differential effects of environmental change or major biological events (Fig. 5b). However, this requires the establishment of monophyletic lineages, and the analysis of fossil insect taxa can be notoriously difficult. It is fraught with problems, such as the lack of important structural data for taxonomic assignments and phylogenetic placement, the temporally and spatially discontinuous nature of the fossil insects for evaluation of variation, and the absence of comparable molecular data that often define extant lineages. Perhaps the most important consequence of the phylogenetic approach in the future will be to provide well-established lineages and more inclusive clades that can be used to document the effects of sudden or prolonged global or more regional events on turnover, survivorship, and extirpation. This will provide a clade-centered, biologically realistic, unit of analysis. This approach also requires a significant effort from communities of systematists to phylogenetically resolve the internal and external relationships of historically intractable and polyphyletic groups such as the Paleozoic “Proorthoptera” and “Hypoperlida.” The presence of inadequately defined clades, particularly in the older fossil record (Béthoux and Nel 2002), offer major challenges to sustained progress.

Ecological Proxy Data. The fossil record of insects consists not only of body fossils, but also documents their interactions with sedimentary substrates in the form of tracks, trails, burrows, nests, and other domiciles (Miller and Labandeira 2002, Genise et al. 2002), as well as their associations with plants in the form of recognizable and ecologically important types of plant damage (Wilf and Labandeira 1999). These ichnological data have the advantage of representing distinctive feeding behaviors, the trophic use of plants, and other pervasive ecological effects of insects in lieu of the actual presence of the insects themselves (Fig. 5c). Consequently, for critical intervals when the bodies of insects are rarely preserved, their associations

nonetheless are recorded, often in profusion, on physical and biological substrates. For insect-mediated damage on plants, there is a rich and underappreciated fossil record of plant fossils that is considerably more abundant and preservationally complete than that of the insects themselves, particularly at extinction boundaries. Also, whereas an insect only dies once, the same individual often would have processed in the same deposit scores of leaves with evidence of its presence in the form of feeding and ovipositional damage. Recording presence-absence data for explicitly defined insect damage types is crucial for understanding the effect of mass extinction events on insect diversity, including the P-T and K-P events (see Nel 1998), where plant fossil deposits are comparatively abundant in the absence of insignificant numbers of insect body fossils.

One of my studies assessed patterns of insect herbivory at K-P boundary event for the geographically extensive Williston Basin in central North America (Labandeira et al. 2002a, 2002b). We examined a 183-m continuous stratigraphic section containing 140 floras representing 106 discrete horizons, of which the 14 most abundant were used to infer patterns of insect herbivory and host specialization across the boundary (Fig. 7). This boundary interval consisted of 2.2 m.y.—1.4 m.y. below and 0.8 m.y. above—that were calibrated to a well-established record of normal and reversed paleomagnetic polarity data that also were linked to radioisotope age dates (Hartman et al. 2002). Consequently, stratigraphic resolution was considerably greater than that achievable for almost any other time sequence of the insect body-fossil record. The results of this study indicated that the K-P extinction dramatically affected the diversity and frequency of bulk herbivory across the boundary and was especially harsh on host-specialized associations (Fig. 8).

Four explicit criteria, often used in combination, were used to recognize herbivory; three levels of host plant specialization were determined from the known ecologies of descendant taxa; and the damage distribution patterns were tabulated on

Recording presence-absence data for explicitly defined insect damage types is crucial for understanding the effect of mass extinction events on insect diversity

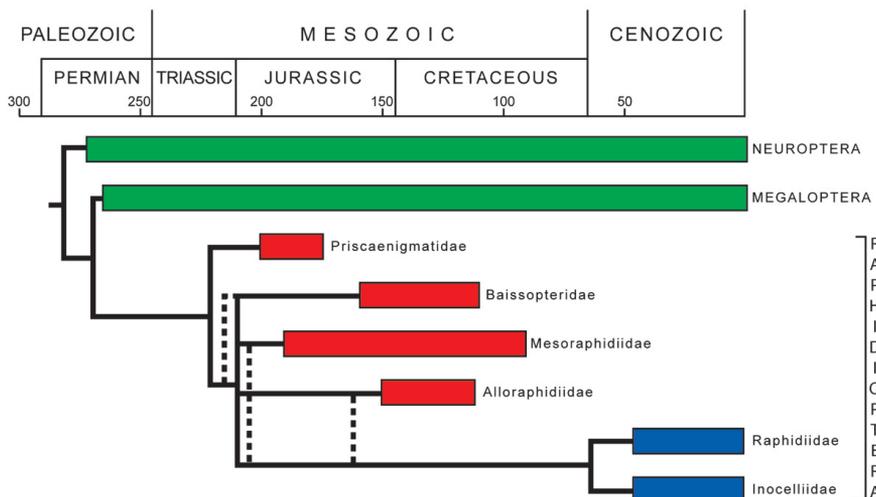


Fig. 6. Phylogeny of the Raphidioptera (Engel 2002), indicating a mid-Cretaceous extinction of three Mesozoic, family-level taxa, and the survival of the two extant clades.

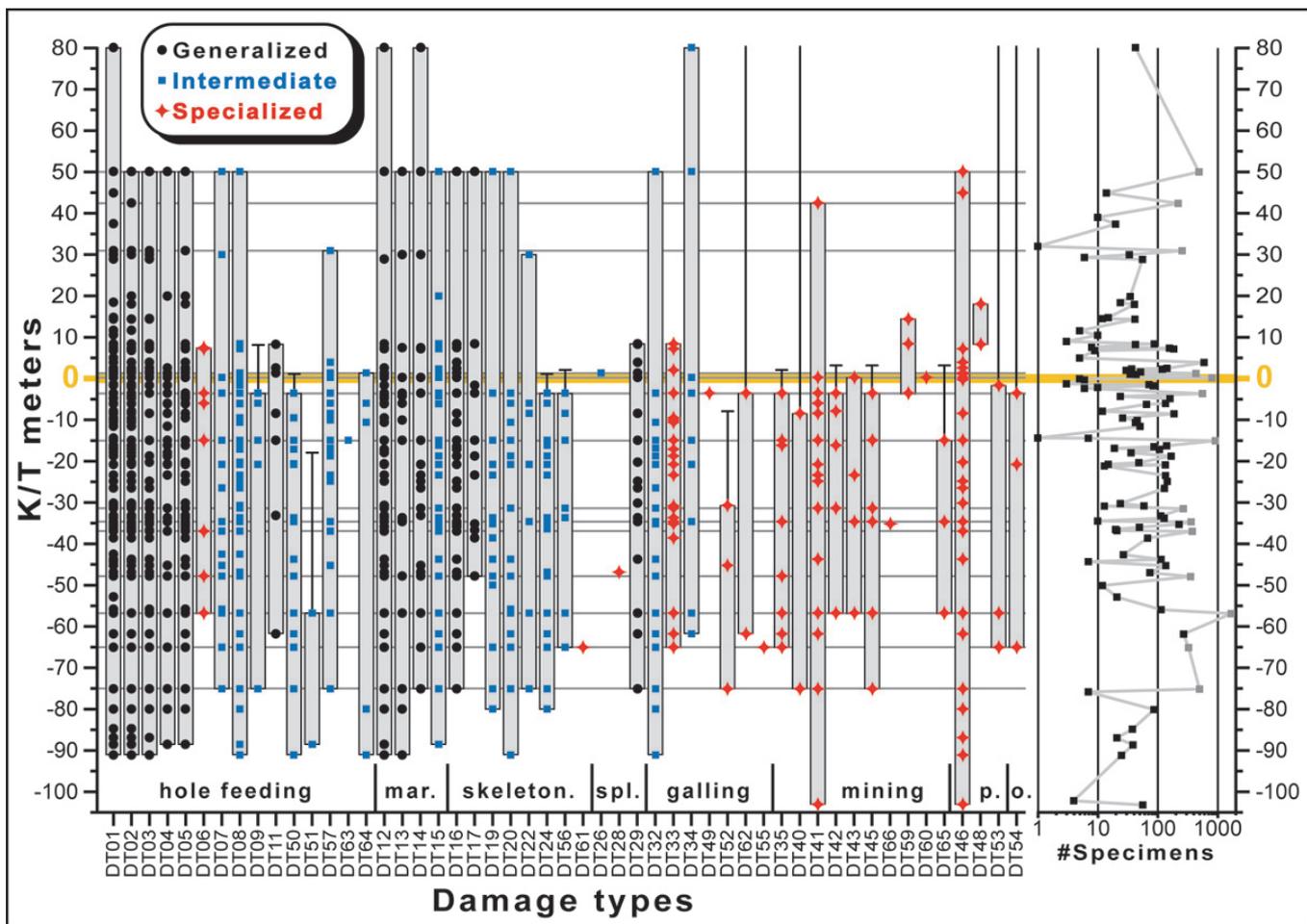


Fig. 7. Sampling data and stratigraphic context of insect damage types from a 183-m stratigraphic interval of the Williston Basin, ND, representing a 2.2 m.y. interval straddling the Cretaceous–Paleocene (K–P) boundary. The K–P boundary is indicated as a horizontal orange line at the “0” datum; levels below and above the boundary indicate discrete horizons from which recovered damage types on leaf fossils are indicated according to classification at bottom. Breadth of associations indicated by damage types are indicated as generalized, intermediate, and specialized, based on several criteria. Statistical confidence intervals of 50% are provided for those damage types occurring in the uppermost Cretaceous that approach the boundary; based on fossil-record distribution and completeness for each analyzed damage type. Total specimen frequencies for each horizon given as a logarithmic scale at right. Abbreviations: mar., margin feeding; skeleton., skeletonization; spl., specialized external foliage feeding; p., piercing-and-sucking; and o., oviposition. Figure reproduced from Labandeira et al. (2002b); for additional details, see Labandeira et al. (2002b).

the original plant hosts. Some generalized damage types were determined to be variable with respect to generally unknown insect culprits. These frequency and diversity data—based on highly recognizable and repeated damage types, including many stereotyped host-specialized associations—presented a community-based ecological picture of the type and intensity of insect associations on a temporally constrained floral succession across a major extinction that otherwise was unavailable for taxic or phylogenetic analysis. This study provided a unique perspective of plant-host use and herbivore trophic breadth across an interval of insect extinction. These data, currently confined to a single regional basin in North America, need to be corroborated by examining similar sequences in other basinwide studies worldwide.

An analogous, coarser-grained study has been initiated to document patterns of plant–insect associational extinction across the more severe

P–T extinction event. Similar modifications of this approach could be used to study the possibility of late Paleozoic to middle Mesozoic colonization, extinction, and recolonization of freshwater lake and river habitats by infaunal and epifaunal insects (Miller and Labandeira 2002). An examination of the behavioral diversity of trace-fossils across such key boundaries, linked when possible to biological taxa, could document the geochronological timing of sediment use by lotic and lentic insects.

Timing the Origin of Coevolutionary Associations. Recently, studies that examined congruence in the associations between particular plant clades and their insect herbivores also have provided estimates for the initial origin of those relationships. (Farrell 1998, Labandeira 2002a). Increasingly this approach has used variable rates in the molecular evolution of plant and insect clades, as well as greater precision of calibration points, when possible, from fossil occurrences (Fig. 3d). A compi-

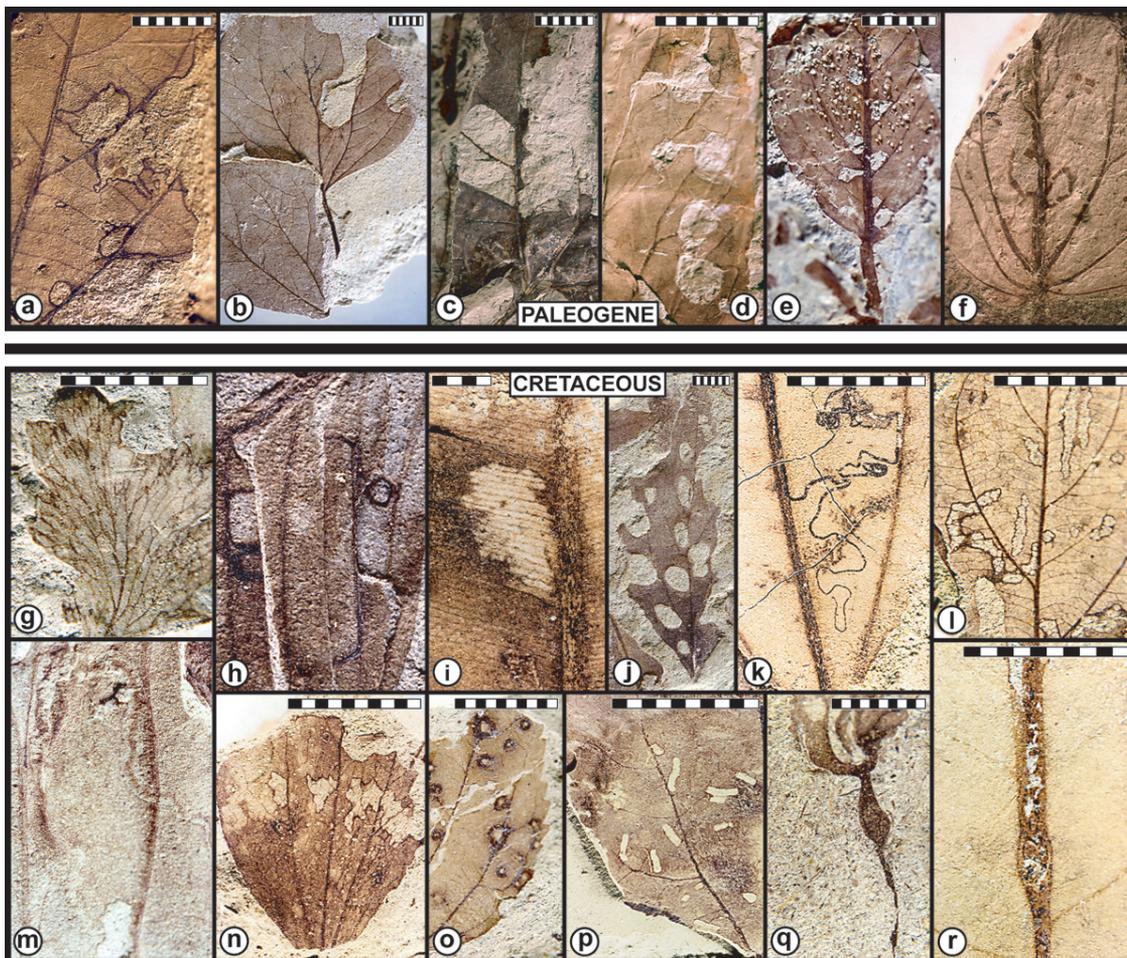


Fig. 8. Spectrum of plant–insect associations documented in Labandeira et al. (2002a, 2002b) and Fig. 7 that either survived the K-P extinction or arose subsequently during the Paleocene (a to f), or alternatively became extinct in the Williston Basin and probably throughout western North America before the boundary event (g to r). The stratigraphic units from which the flora and associated damage originates are the Hell Creek Formation (HC), exclusively latest Cretaceous age, and the Fort Union Formation (FU), of almost entirely early Paleocene age. Damage type (DT number), plant host taxon and morphotype (HC or FU number), meter distance above (+) or below (–) the K-P boundary, and specimen identifications of the Denver Museum of Nature and Science are provided as follows. For Early Paleocene leaves: **a**, margin and hole feeding (DT2,3,14,15) on *Pterospermites cordata* (Dilleniidae, FU61), loc. 898 (+8.2 m), 20052a; **b**, margin feeding (DT15) on *Cercidiphyllum genatrix* (Cercidiphyllaceae, FU43), loc. 562 (+8.4 m), 20044; **c**, free feeding (DT26) on a leaf assignable to *Cornus* (Cornaceae, FU31), loc. 2217 (+0.2 m), 20035; **d**, margin hole feeding (DT64) on an unidentified dicot (FU35), loc. 2217 (+2.5 m), 20034; **f**, leaf mine with a large terminal chamber on the unidentified dicot *Paranymphea crassifolia* (FU1), loc. 563 (+14.4 m), 20055; and **e**, hole feeding at primary vein angles (DT57) on “*Populus*” *nebrascensis* (Trochodendraceae, DT22), loc. 2217 (+2.5 m), 20020. For Late Maastrichtian leaves: **g**, margin feeding on a filicalean fern (HC241), loc. 2087 (–34.4 m), 19963; **h**, hole and margin feeding on *Metasequoia* sp. 2 (Cupressaceae, HC35), loc. 567 (–56.0 m), 13104; **i**, strip feeding on *Nilssonia yukonensis* (Cycadales, HC164), loc. 571 (–65.0 m), 7128; **j**, extensive hole feeding (DT4) on a possible platanaceous leaf (?HC330), 7595b; **k**, mines with initial coiled phase (DT45) on *Marmarthia pearsonii* (Laurales, HC162), loc. 900 (–2.8 m), 7325; **l**, serpentine skeletonization (DT20) on an unidentified dicot (HC254), loc. 1855 (–20.0 m), 20003a; **m**, hole feeding at primary vein angles (DT57) and leaf mine (DT41) on a urticalean dicot (HC81), loc. 2203 (–56.0 m), 19619; **n**, bud feeding (DT6) on “*Cinnamomum*” *lineaefolia* (Trochodendraceae, HC92), loc. 567 (–56.0 m), 19950; **o**, hole feeding with thick callus (DT11) on *Cercidiphyllum ellipticum* (Cercidiphyllaceae, HC212), loc. 1491 (–56.0 m), 19059; **p**, slot hole feeding (DT8) on a cercidiphyllacean leaf (HC229), loc. 2203 (–56.0 m), 19610a; **q**, petiolar gall (DT55) on an unknown dicot unassignable to a morphotype, loc. 571 (–65.0 m), 18876; and **r**, incipient midrib gall (DT33) on a magnoliid dicot (HC43), loc. 2091 (–8.95 m), 20011.

lation from the literature of time-estimate ranges for numerous associations provides an assessment of major patterns not only in the clustering of the timing of associations, but also for recording major gaps that would indicate significant environmental perturbation. For example, the contrast of older plant–insect associations during the earlier Pa-

leogene from more recent Neogene radiations of phytophagous insects on similar herbaceous plant clades (Fig. 2.4 in Labandeira 2002a), indicates a major disruption during the mid-Cenozoic. This shift is perhaps attributable to aridification, shifting vegetation patterns, and an ensuing response by insect herbivores.

A Broadened Perspective

Relevant data for examining insect extinction come in many forms: geochronologic ranges of taxa based on body fossils, the phylogenetic history of extinct and extant lineages from morphologic and molecular data, patterns of insect herbivore-mediated plant damage on fossil leaves at crucial intervals, and the timing of the origin of modern plant–insect associations. Other kinds of data and approaches probably are waiting to be applied or discovered. This diversity of data is dedicated to the examination of a single phenomenon—namely insect extinction—and requires a plurality of methodologies, depending on the time span and areal representation investigated and questions asked.

Of these four approaches, the taxic approach is the most empirical and robust. It has encompassed the greatest number of analyzed units—more than 1000 fossil insect families distributed throughout the 415-m.y. insect fossil record among several independent studies. The possibility now exists for refinements at the generic and species level, although the major trends of insect diversity, origination, and extinction probably will remain the same. For the taxic approach, it is not important that analyzed taxa be natural lineages because the fundamental premise is demographic evaluation of cohorts of species spanning geologic time. A side benefit of this approach is that data frequently are analyzed in terms of origination and extinction rates, typically at a global scale, but also by ecological guild, biogeographical region, or other units of interest. These units are relevant for testing evolutionary or paleoenvironmentally based hypotheses that invoke significant changes in taxa through geologic time.

By contrast, examining the history of extinct and extant supraspecific lineages within a phylogenetic context provides the opportunity to analyze actual clades and the effectiveness of key synapomorphies and associated ecological attributes during environmental crises. Currently such studies take two forms: first, the study of the effects of particular environmental and biological events on the history of modern lineages, principally confined to the Cenozoic; and second, the much less common examination of extinct, typically older lineages that have responded to various crises, often as opportunities for diversification. Both types of cladistically based phylogenetic examinations would be informative; but there are too few studies, especially for taxa with older fossil records. Such studies would have to increase considerably on a clade-by-clade basis, especially at important extinction events. These studies are particularly necessary if finely resolved insect occurrence data were available so that a detectable and resolved pattern can emerge that parallels the taxic approach. Given the paucity of insect body fossils at such crucial events as the P-T and K-P extinctions, it is highly likely that ecological proxy data and the timing of coevolved associations (the latter especially for the Neogene) will

have the greatest resolving power for teasing out insect diversity and ecological patterns.

The End-Cretaceous (K-P) Insect Extinction

Multiple approaches toward understanding a mass extinction, involving different types of mutually exclusive data, can be used to evaluate the complexities of how insects succumbed and responded to a particular global event. For the K-P extinction—characterized by the demise of continental organisms such as vascular plants, freshwater mollusks, dinosaurs, pterosaurs, and a variety of mammalian lineages—family level taxic data from several sources have indicated that there was not an extinction event for insects (Dmitriev and Zherikhin 1988, Labandeira and Sepkoski 1993, Jarzembowski and Ross 1996).

Nevertheless, phylogenetic data from a variety of non-insectan sources indicate a profound disruption of continental ecosystems (Hartman et al. 2002), implicating insect involvement in devastated food webs and indicating that insects should have experienced major deleterious effects. Limited phylogenetic data suggest the demise of a some lineages of collembolans, sternorrhynchans, scarabeoid beetles, and ants toward the latest Cretaceous (Heie and Pike 1992, Scholtz and Chown 1995, Grimaldi and Agosti 2000, Christiansen and Pike 2002). The data, however, are too few and are counterbalanced by studies of extinction resistant clades, such as leaf-mining moths, flies, phytophagous beetles, and spiders (Kozlov 1988, Rayner and Waters 1990, Farrell 1998, Penney et al. 2003).

Data from the timing of coevolutionary associations are ambivalent and too few. Some studies indicate commencement or termination of associations at the boundary, whereas others suggest continuity. In lieu of a worldwide absence of insect body–fossil deposits that are stratigraphically highly resolved and occur in sufficient preservational quality, abundance, and diversity that could address the issue of a K-P insect extinction, all four types of evidence point to an extinction event among lower-ranked insect clades, below that of the family. Although documented for herbivores, the K-P event probably caused a trophic cascade affecting other herbivore-dependent taxa, such as parasitoids and predators. This suggests that the K-P extinction was geologically rapid and not attributable to prolonged clade interaction wherein less competitive plant-associated lineages were gradually extinguished and then annihilated before the boundary (Briggs 1998). Significantly, the K-P event displays a different pattern from the other extinction events that couple origination with extinction.

Conclusions

The fossil record of insect extinction, origination, and diversity provides the only empirical account of how the most diverse group of macroscopic organisms has responded to major disruptions during the geologic past. These include sudden or protracted environmental perturbations, specific challenges from competitors and other interacting

organisms, and the changing biologic context such as associations with plants or the colonization of animal hosts by insect parasitoids. Distilling this fossil record into important taxonomic, phylogenetic, and ecologic data provides an important foundation for assessing the connections, if any, among insect diversity, extinction, and origination, and for assessing their susceptibility to major extrinsic or intrinsic global change, or biologic revolutions such as major shifts in vegetational composition.

Each of the four approaches that explore patterns of insect extinction in the fossil record has its own strengths. When combined, as in an assessment of the K-P event, these approaches provide a powerful tool for analyzing the evolutionary and ecological dynamics of insects before, during, and after important crises in the history of life. To expand the investigation of insect extinction, considerably more data are needed at the genus and species level, particularly ecological proxy data, phylogenetic data, and ecologically coded taxic data. Such an effort would broaden our understanding of insect extinction to include not only which taxa or clades perished or survived, but, equally important the crucial ecological correlates underlying insect response during such crises.

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