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Science, New Series, Vol. 261, No. 5119 (Jul. 16, 1993), 310-315.

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Insect Diversity in the Fossil Record

Conrad C. Labandeira and J. John Sepkoski, Jr.

Insects possess a surprisingly extensive fossil record. Compilation of the geochronologic ranges of insect families demonstrates that their diversity exceeds that of preserved vertebrate tetrapods through 91 percent of their evolutionary history. The great diversity of insects was achieved not by high origination rates but rather by low extinction rates comparable to the low rates of slowly evolving marine invertebrate groups. The great radiation of modern insects began 245 million years ago and was not accelerated by the expansion of angiosperms during the Cretaceous period. The basic trophic machinery of insects was in place nearly 100 million years before angiosperms appeared in the fossil record.

Investigations of diversity, or taxonomic richness, in the fossil record have provided a wealth of information about the history of life, identifying intervals of massive radiations, great extinctions, and relative evolutionary quiescence. Most of these studies have concerned taxa above the species level (mainly genera and families), and a variety of fossil groups have been examined, including marine animals (1, 2), plankton (3), terrestrial vertebrates (4, 5), plants (6), and even Precambrian microbes (7). However, the most diverse class on Earth today, the Insecta, has received much less attention (8).

The reasons for this lack of attention include the perception that insects are rarely preserved as fossils and the fact that descriptions of fossil insects, especially from the Mesozoic era, are sparse in English-language publications. However, the fossil record of insects is indeed extensive, but much of the primary study has been published in older German and more recent Russian literature (9). In this article, we review this literature on fossil insects and address (i) their fossil diversity; (ii) their rates of evolution; (iii) their diversification with respect to the radiation of angiosperms; and (iv) their evolution of ecological breadth in relation to expanding angiosperm resources.

Our database is a compilation of the geochronologic ranges of 1263 insect families. These data were derived from 472 literature sources comprising several compendiums (10) that were extensively supplemented and updated with numerous other sources (11–15). The rank of family was chosen for several reasons. (i) This taxonomic level has been analyzed in other studies of fossil diversity (1, 2, 4, 5) and

seems to correlate well with underlying species diversity (16, 17). (ii) Families are less susceptible to irregular and biased sampling than are fossil species and genera (18), so that an evolutionary signal is better maintained at this level. (iii) Families of insects, especially extant ones, are reasonably well established through consensus among researchers, whereas fossil species and genera are more idiosyncratically defined and less frequently correspond to good phylogenetic or phenetic units (19). (iv) Insect families individually possess discrete, often highly stereotyped life habits, and their morphologies directly reflect their trophic guilds, which are informative in diversity studies (20). We recognize that some of the families in our database may not correspond precisely to monophyletic groups as defined by cladistic methodology. However, the inclusion of paraphyletic families in diversity studies has not been found to detract from general evolutionary signals in both empirical (17) and experimental (21) investigations.

Fossil Insect Diversity

The fossil record of insects is hardly poor when compared to other major taxa. The 1263 families recognized for fossil specimens exceeds the approximately 825 families described for fossil tetrapod vertebrates (22). Figure 1 illustrates that the preserved diversity of insect families exceeds that of the much more intensively studied tetrapods at all times except for a 34-million-year interval during the latest Devonian period and Early Carboniferous period.

Insect fossil diversity is not restricted to a few, easily preserved higher taxa but is contributed by a wide range of living and extinct orders, as illustrated in Fig. 2. All of the 30 commonly recognized extant orders (15, 23) are represented as fossils. All but one of these orders have diversities in the late Tertiary period that are approximately

proportional to their extant familial diversities (15, 23): The linear correlation (r) between the numbers of living and of latest Tertiary families for the 30 orders is 0.954 (0.932 for logarithms). The one outlier is the Lepidoptera (moths and butterflies), which has only about half the fossil diversity that would be expected from their Recent families. The Lepidoptera is characterized by relatively large individuals with lightly sclerotized bodies that are not well represented in *Lagerstätten* (extraordinary fossil deposits) of the Tertiary, which preserve diverse representatives of other groups. Elimination of the Lepidoptera increases the linear fit between extant and latest Tertiary familial diversities such that $r = 0.985$. In summary, it appears that the most recent part of the fossil record has captured insect families in a largely unbiased fashion with respect to ordinal membership. Thus, it is not unreasonable to assume that older parts of the record have behaved similarly.

Few fossil insects are known from the first 60 million years of their 390-million-year history (24) (Fig. 1). This paucity probably results from a lack of appropriate terrestrial deposits that preserved insects. Sometime during the Early Carboniferous, before 325 million years ago, a massive radiation began, followed by peaks in fossil insect diversity during the Late Carboniferous and middle Permian. The diversity

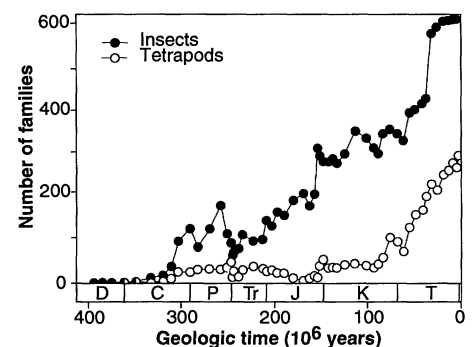


Fig. 1. Family-level diversity of fossil insects through geologic time (24), plotted at the level of stratigraphic stages and compared to the diversity of terrestrial tetrapod vertebrate families. We computed diversity with the range-through method, which assumes that a family was present in all time intervals between its first and last appearance (including the Recent), even if not directly sampled in all intervals. Abbreviations are D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; and T, Tertiary.

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minimum between these peaks probably is artifactual, reflecting sparse collecting sites between the various siderite concretion faunas of the Upper Carboniferous (for example, Mazon Creek from Illinois and Montceau-les-Mines from France) and the lake-bed faunas from the middle Permian (for example, Elmo from Kansas and Chekarda from European Russia).

The subsequent Triassic minimum in insect diversity also could be a consequence of a dearth of Lower Triassic insect-bearing deposits. However, we believe it is more likely real, reflecting the terminal Permian mass extinction, which severely affected marine animals (25) and terrestrial tetrapods (5). As Fig. 2 documents, 8 of the 27 orders of insects that have Paleozoic occurrences evidently did not survive the Permian; four of these orders (Palaeodictyoptera, Permothemistida, Megasecoptera, and Diaphanopteroidea) constitute the Palaeodictyopteroidea, which is the only supraordinal taxon within the Insecta ever to become extinct. There are another three orders that entered the Triassic with reduced diversities and evidently became extinct during that period. After the demise of Paleozoic groups, about half of the orders that survive to the Recent underwent modest to spectacular diversifications during the Triassic and Jurassic, continuing to the Recent in most cases. This shift in phylogenetic pattern of diversification is the most pronounced event during the history of insects and is largely attributable to the end-Permian mass extinction.

For the Insecta as a whole (Fig. 1), preserved familial diversity increases almost steadily after the Permian-Triassic bottleneck and rises sharply in the middle Tertiary. This final jump is undoubtedly artifactual, reflecting the spectacular insect faunas preserved in the Baltic amber of Europe and Florissant lake deposits of Colorado. As older ambers and compression fossil deposits receive more study, especially those from the Cretaceous (26), many families first represented in these Tertiary deposits probably will have their ranges pushed back into the Mesozoic. We expect that eventually the marked mid-Tertiary rise in fossil diversity will be largely extended into the late Mesozoic.

Rates of Evolution

The rise in familial diversity among insects after the Permian is remarkable not only for its magnitude but also for its mechanism. Origination rates of families were no higher than during the Paleozoic, but extinction rates were much lower. It is difficult to measure rates of taxic evolution for fossil insect families because many first and last appearances are tied to extraordinary fossil

deposits and because nearly half of all known families are still extant. These factors make standard survivorship analysis complicated (27). An alternative method for assessing extinction rates is Lyellian survivorship analysis (28). Lyellian survivorship curves display the proportion of taxa in any interval of geologic time that are still alive today. Groups that undergo rapid extinction are characterized by proportions that rapidly decay backward through time, whereas those with low extinction rates decay only slowly.

We compared Lyellian survivorship curves for insects (Fig. 3) with curves for two

other taxonomic groups, the tetrapod vertebrates (22) and the marine bivalves (29). Tetrapods are the only other major group of terrestrial animals with a good fossil record, and bivalves are traditionally considered to have one of the lowest rates of extinction (30). As Fig. 3 illustrates, insect families exhibit low rates of familial turnover throughout much of their recent history: Tertiary insect faunas were composed almost exclusively of living families, and even 100 million years ago (middle Cretaceous), 84% of the fauna consisted of members of extant families. Only during the Jurassic and earlier did extinct families con-

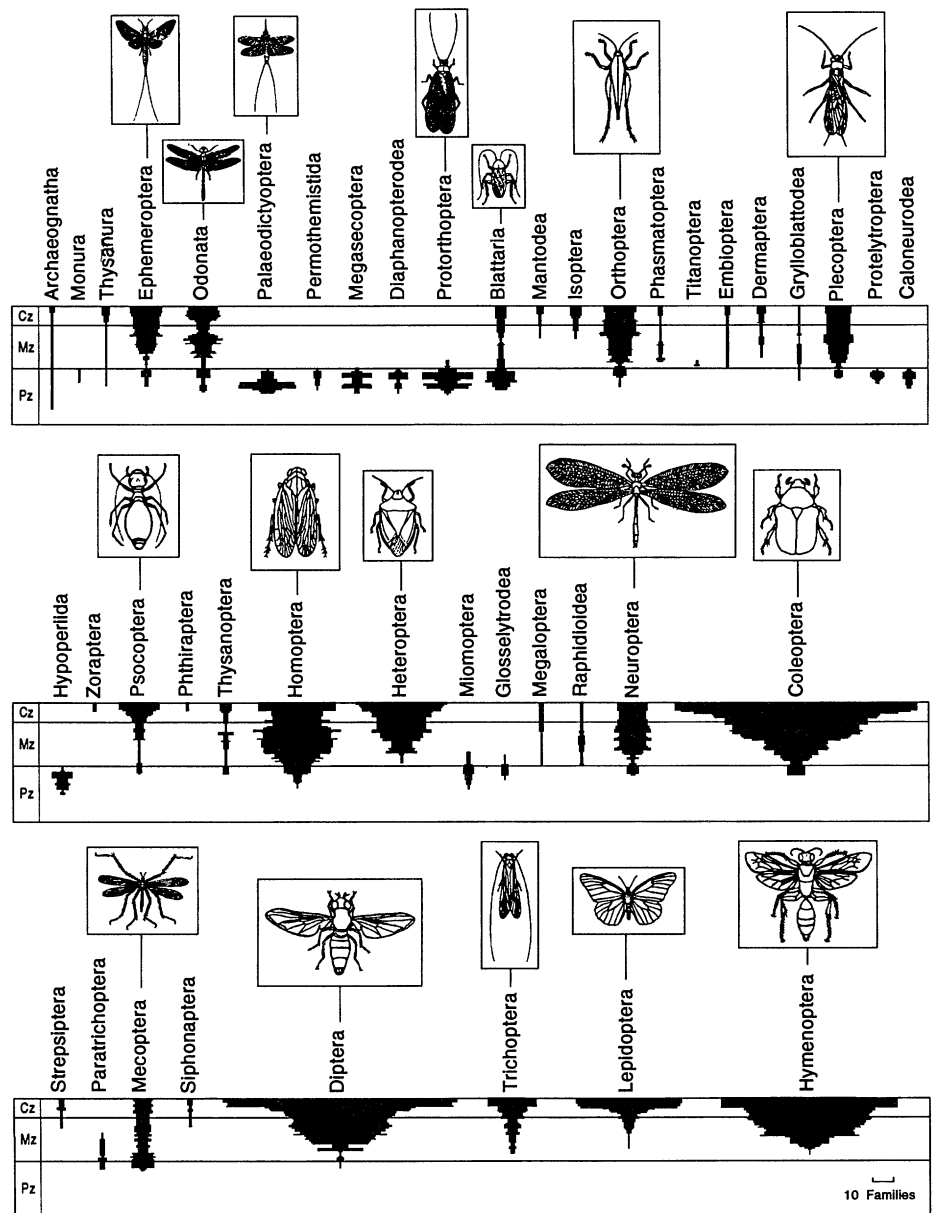


Fig. 2. Spindle diagrams displaying diversities of fossil families within insect orders in stratigraphic stages of the Phanerozoic. A scale bar is shown in the lower right. Abbreviations are Pz, Paleozoic (Silurian through Permian); Mz, Mesozoic; and Cz, Cenozoic. Boxed illustrations (not to scale) depict typical adult representatives of the more important orders. Angiospermous plants make their fossil appearance approximately two-thirds of the way up the band for the Mesozoic (that is, just above the "M" in Mz).

stitute the majority of global insect diversity (31). This pattern contrasts dramatically with that of the tetrapods, in which fewer than 20% of extant families are present in faunas 100 million years ago and fewer than 10% are present at the Jurassic-Cretaceous boundary. The more appropriate comparison seems to be between insects and the slowly evolving marine bivalves. From the Jurassic-Cretaceous boundary to the Recent, bivalves experienced higher rates of extinction than insects, although before the Jurassic-Cretaceous boundary they had lower rates of extinction than insects. Slightly more than half of marine bivalve families from the Early Triassic are still extant, but fewer than 10% of insect families are. For insects, the lower extinction rates after the end of the Jurassic reflect in large part the transition from the archaic, extinct orders of the Paleozoic Era, which experienced high extinction rates, to the more derived orders of the Mesozoic and Cenozoic, whose families suffered only half the extinction rates of their predecessors. This kind of secular decline in extinction seems to be general to both terrestrial and marine animals (32).

The low extinction rates of insect families during the Mesozoic and Cenozoic are subject to more than one interpretation. It is possible that some paleoentomologists have used generalized taxonomic concepts of extant families, shoehorning into extant taxa fossil species that are only distantly related to and morphologically distinct from living species (10). Such practice would result in modern insect families having inordinately long geologic ranges. Alternatively, the extinction resistance of insect families may reflect only species richness (33) and not species behavior. Indeed, many extant families of insects have species numbers in the thousands (34), whereas tetrapod and bivalve families possess one to at most hundreds of species. However, when genera and species within insect families are considered, they, too, exhibit remarkable geologic persistence. For example, the modern beetle genus *Tetraphalerus* closely resembles 153-million-year-old Jurassic fossils (35), and the modern crane fly

genus *Helius* and leaf-mining moth genus *Stigmella* have been identified from 93-million-year-old and 89-million-year-old deposits, respectively (36). Many insect specimens of Eocene to Miocene age are easily placed within modern genera (14, 37) and even modern species (38). In the younger part of the fossil insect record, Pliocene aphids have been determined to be conspecific with modern species (39), and Coope (40) and Matthews (41) were able to place almost all fossil beetle specimens from Pliocene and Pleistocene lake deposits in Britain and northern Canada, respectively, into modern species on the basis of characters of the genitalia; assignment was possible despite profound changes in the biogeographic distributions of descendant populations. Tetrapods, on the other hand, experienced major turnovers during the late Pliocene and latest Pleistocene (42), and few living species are more than a million years old. Thus, the depressed extinction rates among insect families in the fossil record may reflect the intrinsic evolutionary behavior of their constituent species (43).

Angiosperms and Insect Diversity

The extraordinary diversity of living insects has been attributed by some workers to the diversity of angiospermous plants (44), which first appear as fossils in the Lower Cretaceous. This notion is buttressed by exhaustive examples of intricate ecological coupling between the two groups, especially with regard to insect herbivory and pollination (45). Indeed, the great expansion of insect families toward the Recent would appear consistent with this proposition. But additional evidence is needed: It must be demonstrated that rates of diversification of insects increased as angiosperms diversified to dominate virtually all terrestrial plant communities.

The null model for patterns of diversification of radiating groups is exponential expansion (28). Each incremental increase in diversity augments the number of taxa that potentially can be produced in the next time interval, such that numbers of

taxa can grow like compound interest. Thus, any group that maintains a constant rate of diversification will have the logarithm of its diversity plot as a straight-line function of geologic time (46).

As shown in Fig. 4, the familial diversity of insects exhibits a roughly log-linear trend from the Middle Triassic through the Early Cretaceous. Variation around this trend probably reflects only the uneven temporal distribution of rich insect-bearing deposits; for example, the spectacularly fossiliferous lake beds at Karatau, Kazakhstan (47), contribute a large positive outlier over the Late Jurassic. Interestingly, the exponential trend extrapolates to nearly the modern diversity of insects, which we take to be 977 families (15, 23). This extrapolation might suggest that insects have been undergoing exponential diversification for the last 245 million years. However, we doubt this is the case: Although the insect record is rich, only 63% of extant insect families are represented as fossils, and there is no reason to believe that early Mesozoic fossil deposits were capturing substantially larger proportions of the insect fauna. Thus, if insects indeed experienced exponential diversification, there should be more extant families than are actually observed. This result suggests that the global insect fauna of more recent times has been approaching saturation such that rates of diversification have slowed. Indeed, the deviation in preserved diversity below the exponential trend seen over the last 100 million years is consistent with this inference (46). An alternative explanation is that extinction events have depressed insect diversity below the exponential trend; however, other than the terminal Permian event, no mass extinction, including the Cretaceous-Tertiary event, seems to have had a major effect on insects (48).

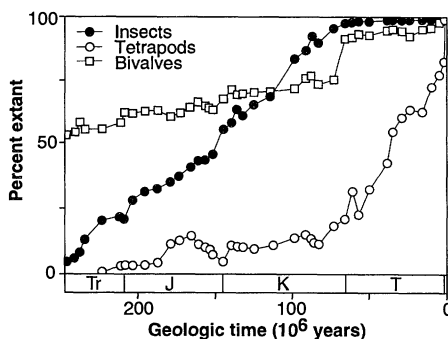


Fig. 3. Lyellian survivorship curves showing proportions of extant families as a function of time (24) for insects, terrestrial vertebrate tetrapods, and marine bivalves. Steeper curves indicate a higher extinction rate among families in the group. However, these curves need not be monotonic because radiations of short-lived families can temporarily depress Lyellian proportions. The low extinction rates of insects, especially relative to tetrapods, mean that even with a relatively discontinuous fossil record, insect families can be traced from one *Lagerstätte* to another, providing a reasonably continuous record of insect diversity. Data are plotted for stratigraphic stages, and abbreviations are the same as in Fig. 1.

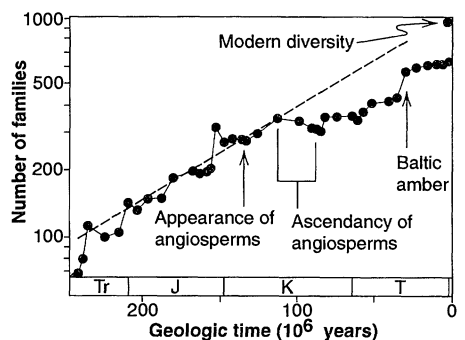


Fig. 4. Insect familial diversity from the Triassic to the Recent, plotted on semilogarithmic coordinates. The dashed line is interpretative, illustrating possible exponential diversification beginning in the Triassic and possibly continuing into the Early Cretaceous. The temporal positions of the Baltic amber and important events in the history of angiosperms are labeled. Time scale and abbreviations are the same as in Fig. 1.

The more startling interpretation that can be drawn from the data (Fig. 4) is that the appearance and expansion of angiosperms had no influence on insect familial diversification. Present data on the earliest occurrences of definitive angiosperm pollen and macrofossils indicate that these flowering plants may have originated during the Hauterivian stage of the Early Cretaceous (49). However, some cladistic analyses and fossil identifications (50) would place the origin as early as the Triassic, although the absence of definitive fossil material indicates that the group could not have been abundant and ecologically important before the Cretaceous. Whenever these plants originated, the fossil data indicate that angiosperms experienced a tremendous radiation in all geographic regions during the Albian and Cenomanian stages of the middle Cretaceous (51). However, there is no signature of this event in the family-level record of insects. Instead, the data in Fig. 4 suggest that insect diversification actually slackened as angiosperms radiated. Even if the drop in diversity below the exponential trend during the Cretaceous were a result of a lack of preservation or inadequate sampling of insect fossils (26), the fact remains that the post-Paleozoic radiation of insect families commenced more than 100 million years before angiosperms appeared in the fossil record. Within the Insecta, orders that have radiated strongly during the Mesozoic and Cenozoic, such as the Coleoptera (beetles), Diptera (true flies), and Hymenoptera

(wasps, ants, and bees), all apparently began their expansions during the Triassic and Jurassic (Fig. 2), long before the ascendancy of angiosperms. Consequently, if there were any effect on insect diversification, angiosperms must have had an impact at taxonomic levels below the rank of family, where indeed many species appear highly co-evolved with flowering plants (44, 45). Alternatively, it is possible that it was the earlier diversification of insects that partly propelled the rapid expansion of angiosperms during the mid-Cretaceous (52).

Ecological Roles of Ancient Insects

Part of the presumption that angiosperms fueled the diversification of insects involves the inference that the diverse tissues and organs, particularly leaves and flowers, of these advanced land plants provided an expanded spectrum of ecological resources that could be exploited by various guilds of herbivorous and pollinating insects (45). For the fossil record, direct inferences regarding how insects exploited plant resources have been drawn largely from three sources of evidence: (i) preserved host tissue damage, (ii) insect gut contents, and (iii) fecal pellet composition from herbivores (53). Although this evidence is a significant (if underappreciated) part of the fossil record, there have been only a few efforts in using it to assemble a comprehensive view of the diversity of major insect feeding guilds through time. An alternative way to characterize how plant resources

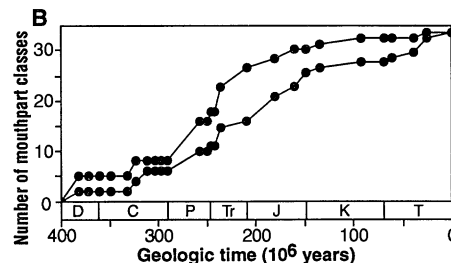
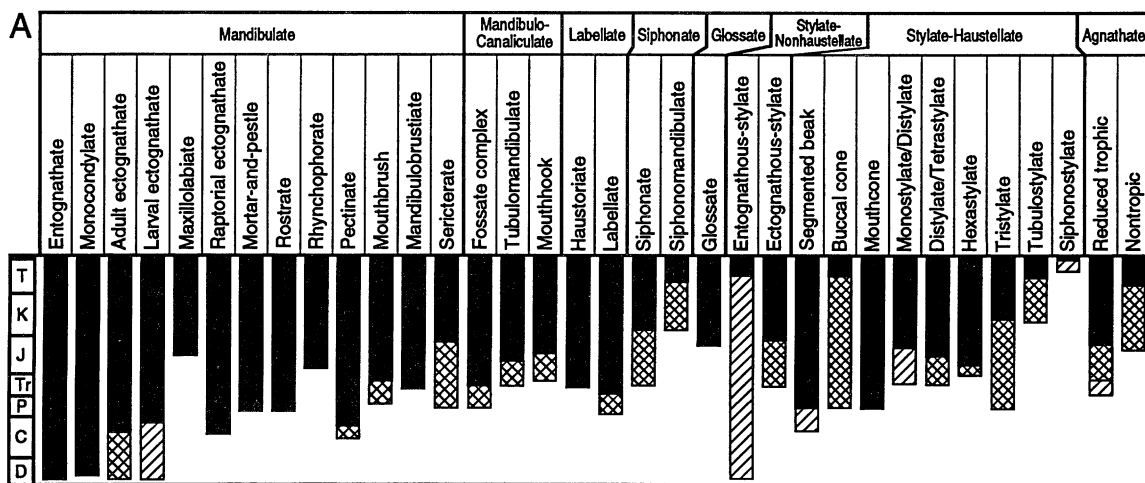
have been exploited is to group all insects into guilds on the basis of preservable morphological features that function during feeding activities. Mouthpart structure is ideally suited for recognizing such guilds because it is a morphological expression of feeding type.

By means of a multivariate phenetic analysis (34), we grouped mouthpart characters of 1365 extant species of insects into 34 fundamental mouthpart classes (Fig. 5A), each representing a distinct adaptive facies for manipulating, consuming, and processing a particular food type. Each morphologically based class can be equated with an ecological guild, and each is composed of a particular ensemble of taxonomic clades. The mouthpart classes vary considerably in constituent species diversity, and most cross phylogenetic boundaries, encompassing lineages that independently acquired the same mouthpart type and thus gained entrance into the same feeding guild. Therefore, the mouthpart classes reflect ecological disparity and not necessarily taxonomic diversity.

The geochronological distribution of mouthpart classes represented among living insects (Fig. 5A) and their diversity through time (Fig. 5B) indicate that the number of feeding guilds among insects expanded well before the appearance of fossil angiosperms. By the Middle Jurassic, 65% (low estimate) to 88% (high estimate) of all modern insect mouthpart classes were present (54), including several (for example, rhynchophorate, haustoriolate, and la-

Fig. 5. The history of mouthpart classes represented among living insects [updated from (34)]. **(A)** Geochronologic ranges of mouthpart classes. The solid pattern indicates direct evidence for the occurrence from fossil material and therefore marks the minimum age of origin; the cross-hatched pattern indicates indirect evidence from the occurrence of sister-group taxa; and the hatched pattern indicates more remote indirect evidence such as

trace fossils and the presence of apparently conspecific developmental (that is, ontogenetic) stages other than the stage under consideration. **(B)** Mouthpart class diversity as a function of time (24), plotted at the level of stratigraphic series. The upper mouthpart diversity curve represents inferred presence based on all evidence, whereas the lower curve is based on direct body fossil evidence alone [solid bars in (A)]. The upper curve may be the more realistic measure of true mouthpart diversity. Abbreviations are the same as in Fig. 1.



bellate) that are presently associated with flowering plants. After the expansion of angiosperms, only 1 (low estimate) to 7 (high estimate) of the 34 mouthpart classes are known to have originated. However, these have poor fossil records, and only one (siphonmandibulate) is associated with flowering plants. Thus, by using mouthpart classes as proxies for ecological disparity, we conclude that virtually all major insect feeding types were in place considerably before angiosperms became serious contenders in terrestrial ecosystems. Evidence from the fossil record of vascular plant-insect interactions (53) also supports this inference.

Conclusion

Insects are not an invisible part of the fossil record. They have a rich history that must be reconciled with evolutionary interpretations of the taxonomic diversity and morphological and ecological disparity of modern insects. We have examined a few synoptic aspects of the fossil record of insects, and the results contradict several notions about what macroevolutionary patterns can be seen among fossil insects and about how modern insect diversity can be interpreted.

At the family level, fossil insect diversity through most of the Phanerozoic exceeds that of tetrapod vertebrates, as might be expected from the great difference in their modern diversities. But what is unexpected is that modern insect diversity results not from high rates of origination but rather from low rates of extinction. These low rates were established early during the Mesozoic era, and the great radiation of insects began more than 100 million years before the ascendancy of angiosperms. This diversification was based in part on a wide range of previously evolved trophic adaptations that allowed insects to enter into new food-based ecological guilds during the late Paleozoic to mid-Mesozoic eras. The morphologies and correlated membership in major guilds were retained into the later Mesozoic and Cenozoic eras when they became co-opted by angiosperms, allowing, perhaps, for continued increases in family-level diversity. Whereas seed plants in general, and not angiosperms in particular, provided the stage for the spectacular evolutionary history of insects, it is also possible that the exploitative destruction of angiosperm communities today could reverse 245 million years of evolutionary success.

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 55. Data on insect family ranges and mouthpart classes are available from C.C.L. We thank D. Chaney and F. Marsh for assistance in drafting the figures and D. H. Erwin, D. J. Futuyma, J. Kukulová-Peck, and A. P. Rasnitsyn for critical commentary. Research received support from the National Aeronautics and Space Administration under grants NAG 2-282 and NAGW-1693 to J.J.S. This is Evolution of Terrestrial Ecosystems Contribution no. 12.

A Cold Suboceanic Mantle Belt at the Earth's Equator

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An exceptionally low degree of melting of the upper mantle in the equatorial part of the mid-Atlantic Ridge is indicated by the chemical composition of mantle-derived mid-ocean ridge peridotites and basalts. These data imply that mantle temperatures below the equatorial Atlantic are at least ~150°C cooler than those below the normal mid-Atlantic Ridge, suggesting that isotherms are depressed and the mantle is downwelling in the equatorial Atlantic. An equatorial minimum of the zero-age crustal elevation of the East Pacific Rise suggests a similar situation in the Pacific. If so, an oceanic upper mantle cold equatorial belt separates hotter mantle regimes and perhaps distinct chemical and isotopic domains in the Northern and Southern hemispheres. Gravity data suggest the presence of high density material in the oceanic equatorial upper mantle, which is consistent with its inferred low temperature and undepleted composition. The equatorial distribution of cold, dense upper mantle may be ultimately an effect of the Earth's rotation.

A basic tenet of the theory of plate tectonics states that upper mantle isotherms rise beneath mid-ocean ridges because of the upwelling of hot mantle material, which as a result undergoes partial melting. The melt fraction migrates upward, cools, and forms the oceanic crust. The degree of melting undergone by mantle peridotites upwelling

beneath mid-ocean ridges can be estimated either from the chemical composition of the melt fraction (mid-ocean ridge basalts or MORBs) or the solid residue left behind after partial melting (mid-ocean ridge peridotites or MORPs). These estimates are based on experimental work on the melting of peridotites under different pressure and temperature conditions (1, 2) and on assumptions as to the initial composition of the upwelling upper mantle material (1, 3). Estimates based on the composition of peridotite samples recovered along the mid-Atlantic Ridge (MAR) suggest that the degree of melting of the upper mantle along

the MAR ranges from ~8 to ~25% and varies regionally over long (~1000 km) and short (~100 km) scales (4–6). Estimates derived independently from the composition of MORBs (7) agree in general with those obtained from MORPs.

Recent studies of MORPs and MORBs from the central MAR have suggested that the upper mantle in some areas of the equatorial Atlantic has undergone little or no melting; thus, the mantle appears to be relatively cold in these areas (6, 8). We present additional data and discuss possible causes and implications of an equatorial belt of cold upper mantle in the Atlantic and east Pacific.

Partial Melting of Atlantic Mantle Peridotites

The mantle-equilibrated minerals found in MORPs include olivine (ol), orthopyroxene (opx), clinopyroxene (cpx), and spinel (sp). The composition of these phases has been determined in many peridotites from the north and equatorial Atlantic (5, 6, 9, 10). Peridotites from the equatorial region are of particular interest in this context. Near the equator, the MAR axis is offset by major transform faults, including the Romanche fracture zone (FZ) (~950-km offset) at the equator, the St. Paul FZ just north of the equator, and the Chain FZ just south of it (Fig. 1).

We found that the composition of peridotites sampled from several sites along the Romanche FZ (Fig. 1) is different from that of other MORPs. For instance, their mantle-equilibrated phases have higher concentrations of incompatible elements (elements such as Al that partition with the melt) and lower concentrations of refractory elements (elements such as Mg and Cr that stay with the solid residue during partial melting) than MORPs from the Atlantic and Indian oceans (Fig. 2). Representative samples show a modal content of clinopyroxene higher than that of other MORPs (Fig. 3).

Laboratory experiments and theoretical modeling show that the modal and mineral composition of mantle peridotites changes as a result of partial melting (1, 2, 11). Assuming an initial pyrolytic modal composition for parental upper mantle beneath the ridge (3), partial melting at 10 kbar causes a rapid decrease in the content of clinopyroxene (and eventually its disappearance when the degree of melting is over about 20%), a slower decrease of orthopyroxene, and an increase of olivine (1, 2). Moreover, the initial chemical composition of the primary phases is modified by partial melting, so that the ratio of refractory elements to incompatible elements increases with an increased degree of melting (1, 2).

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