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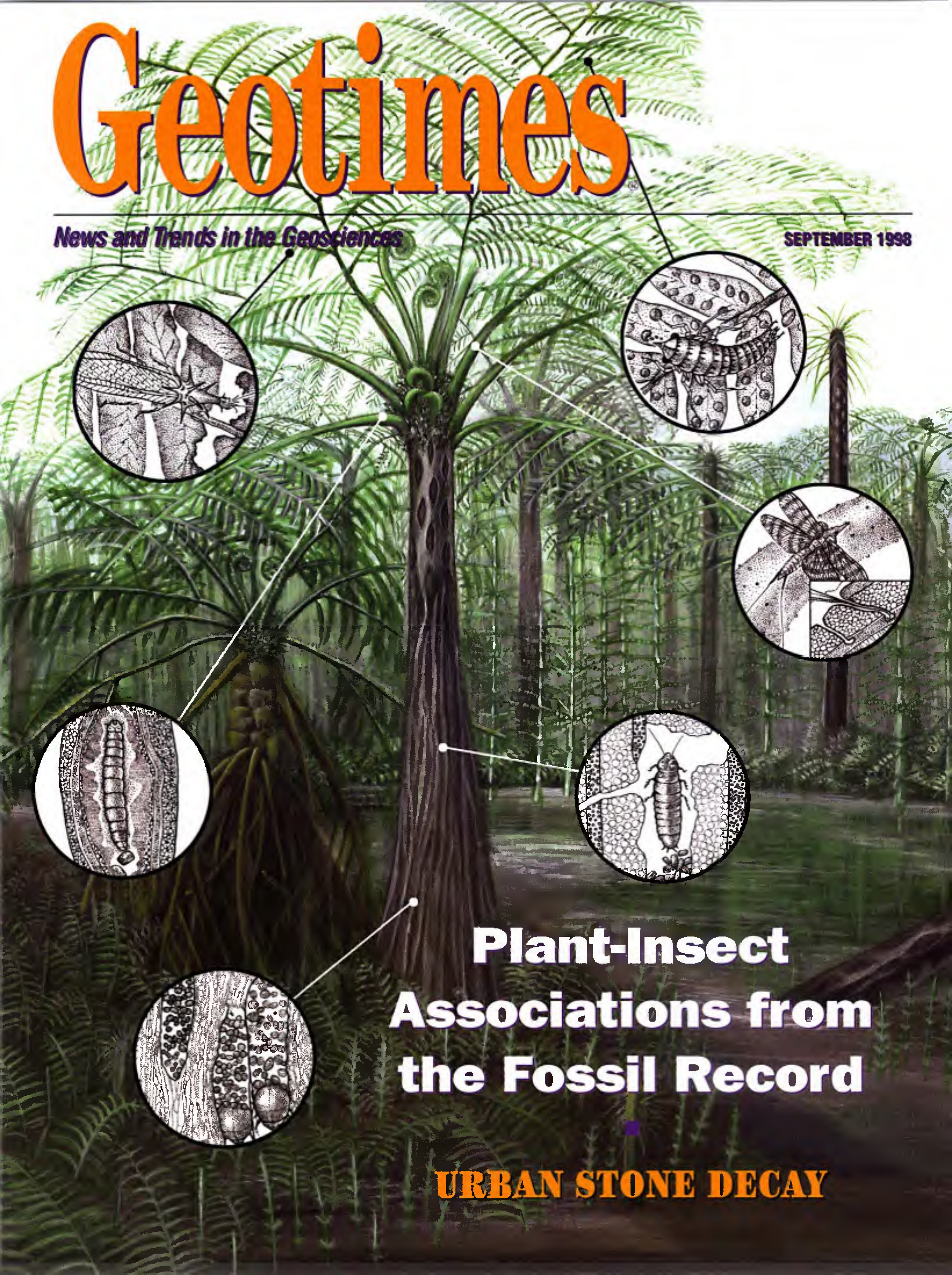


Plant-Insect Associations from the Fossil Record

URBAN STONE DECAY

Plant-Insect Associations FROM THE Fossil Record

The coarsest characterization of life on Earth is probably one of teeming diversity. As terrestrial organisms ourselves, we are impressed by the enormous variety of life on land, and in particular, by the countless taxa of insects and vascular plants that constitute much of the ecologic underpinning for terrestrial ecosystems. Any understanding of this diversity requires documentation of the associations among these two most pervasive groups of organisms. Historically, vascular plants and insects have provided the requisite numbers of species to support this ever-widening web of ecologic interdependence.

We know from the earliest fossils that only a few species of insects co-existed with primitive plants during the Early Devonian, principally as detritivores with monotonous diets of dead tissues, but also as a few nonspecialized herbivores. However, 400 million years later, after evolutionary radiations of land plants had produced complex ecosystems, approximately 280,000 species of vascular plants and several million to a few tens of millions of insects came to dominate the terrestrial world. Integral to this escalation of plant and insect numbers are the associations among these organisms, which — together with interacting fungi — represent a significant multiple of the individual diversities of the principal actors.

Consider a milkweed plant. Within a single photosynthesizing individual, a dozen species of herbivorous insect consumers can co-exist — each with a particular mouthpart structure for targeting a specific tissue type within leaves, stems, roots, and reproductive structures. These insects, in turn, are devoured internally by parasitoids or externally by parasites, each of which is attacked by hyperparasitoids, and all of which are preyed upon in complex ways by mobile and stationary insect predators.

How did such intricate trophic networks originate? Is there documentation in the fossil record, either from the organisms themselves or from their interactions, that can illuminate the general pattern of this increasing complexity? Can we say anything about species-generating processes that may be revealed by the fossil record of plant-insect associations?

by Conrad C. Labandeira

Macroevolutionary Study of Plant-Insect Associations

The answer to all of these questions is a qualified "yes," but so far, only preliminary results have been reached. Examination and interpretation of the fossil record of plant-insect interactions is a new field within paleobiology, historically ignored by both paleoentomologists and paleobotanists and rarely discussed by today's biologists studying the myriad associations between modern plants and insects. Virtually all of the existing paleobiological literature on this topic consists of descriptions of interesting interactions with fossil plants, and several recent hypotheses of how insects and plants associate at macroevolutionary time scales have not been addressed.

Consider a milkweed plant. Within a single photosynthesizing individual, a dozen species of herbivorous insect consumers can co-exist.

Recently, phylogenetic data have been marshaled to understand the macroevolutionary histories of selected lineages of extant insect herbivores and their respective host-plants, in lieu of direct fossil evidence. In this alternative approach, molecular-based phylogenies for plant hosts and their insect herbivores are established in order to determine if diversification occurred in parallel, as evidenced by the congruence of plant host and insect herbivore phylogenies (Figure 1). Rarely, however, are such studies explicitly calibrated by specimens from the fossil record; rather, they rely on a molecular clock for estimates of the origins of particular plant and insect taxa. Such an approach is not available for extinct lineages of associated plants and insects.

A more direct approach is to document highly invariant, repeatable types of insect damage on well-preserved fossil floras to establish distinctive patterns of tissue use by host herbivores. Temporal trends gleaned from this approach may reveal evolutionary radiations of certain herbivore clades onto plant taxa, or more particularly, the trajectory of host specificity through time. For host specificity by insects, a continuum is well known.

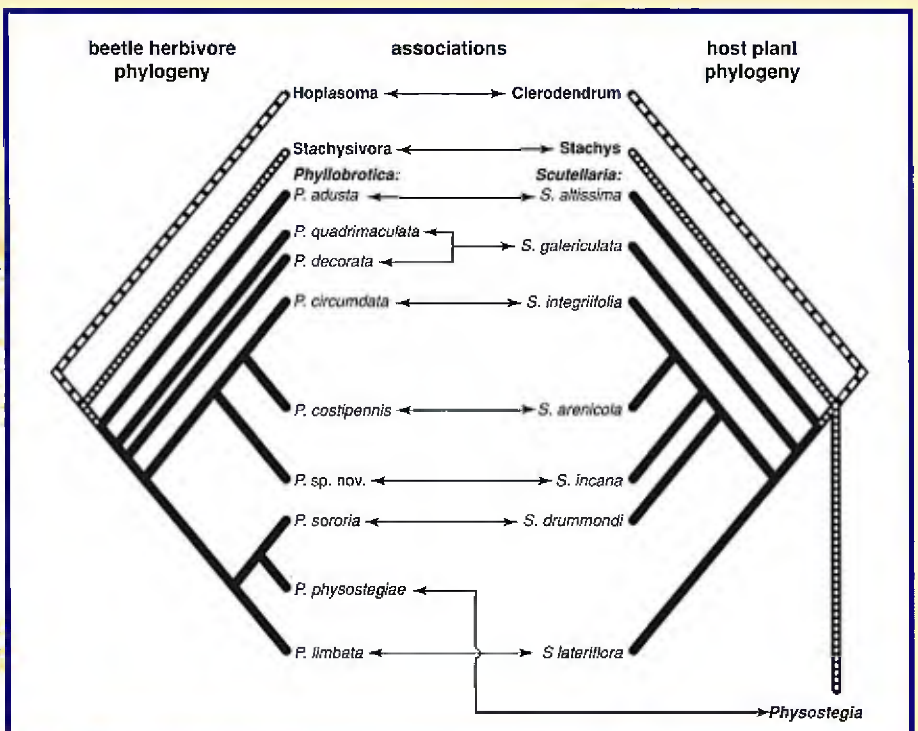
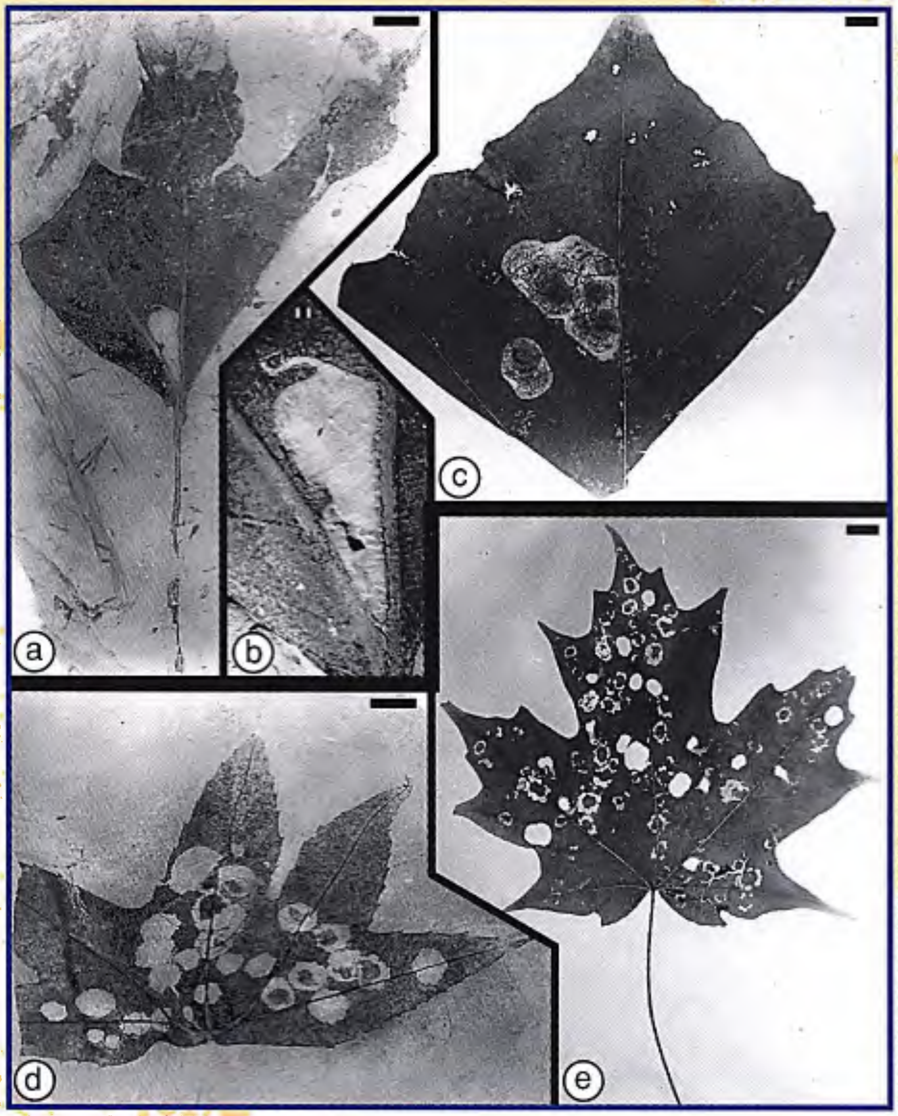


Figure 1. A comparison of the phylogenies of the *Phyllobrotica* clade of leaf beetles (Chrysomelidae) and their host-plant clade of *Scutellaria* and related mint taxa (Lamiaceae), taken and modified from Farrell and Mitter (1990). Note close correspondence between beetles and their host plants, with the notable exception of host switching of *P. physostegiae* on *Physostegia*.

Representing one extreme is one-to-one fidelity between an insect herbivore and its plant host; the other extreme is rampant host-switching or collective extinction (Figure 2).

A particularly intriguing method that has never been attempted in the fossil record is to track a well-established plant lineage of a few taxa through macroevolutionary time and monitor the spectrum of insect herbivores. Documentation of herbivore types through time can establish if some insect and plant lineages are ancient associations or whether older associations are being swamped constantly by more recently evolved insect herbivores. If the plant host is highly confined taxonomically — say, a group of related species, a genus, or a nondiverse family — the fossil record can be used to examine approximately what modern biologists term a "component community." A component community constitutes all the animal associates of a particular plant-host species (Figure 3). Tracking insect herbivory within a component community, based on recognition of damage types, can provide data on the entries, exits, and protracted associations of insect herbivore species in macroevolutionary time. Such paleobiological data could answer questions of high theoretical importance — such as whether co-evolved and longer-term associations occur between plants and insects, if primitive insects occur on primitive plants, or whether host-switching is associated with major paleoenvironmental changes or with the physical features of plant hosts.



CONRAD LABANDEIRA AND FINNEGAN MARSH, NATIONAL MUSEUM OF NATURAL HISTORY.

Figure 2. Two examples of associations between leaf-mining insects and their host plants, gleaned from the fossil record of plant damage. The upper part of the figure (**a**) depicts an ancient association between an insect herbivore, the leaf-mining moth *Ectoedemia*, and its host plant, an undescribed form closely related to the sycamore *Platanus*, from the mid-Cretaceous Dakota Formation of Kansas. The inset in the center (**b**) is an enlargement of this leaf mine, showing initial serpentine phase and subsequent blotch phase lodged between two primary veins. The leaf on the right (**c**) contains near-identical *Ectoedemia* damage on modern *Platanus* from Virginia. The lower pair show either temporal host-switching or extinction of both plant host and a species of the leaf-mining moth *Paraclemensia* or a closely related genus. The lower-left leaf (**d**) exhibits *Paraclemensia*-like damage on its Middle Eocene host plant *Macginitiea*, an extinct genus of the sycamore family from the Green River Formation of Utah. The lower-right leaf (**e**) features near-identical *Paraclemensia* damage on modern *Acer* from Vermont, a member of the maple family that is phylogenetically distant from sycamores. Scale bars: solid = **1.0** cm; striped = 0.1 cm.

Figure 3. A component community of insect herbivores on a hypothetical vascular plant. Included are piercer-and-suckers at top (**a, b**) and center right (**c**), borers at center (**d-g**), serpentine and blotch leaf miners at lower right (**h**), leaf and twig gallers at left (**i-k**), and external feeders at lower-left (**l**) and bottom (**m**). Modified from Johnson and Lyon (1991). Reprinted with permission from Cornell University Press. © 1991.

Increased Intensity of Insect Herbivory

A second general area of paleobiological investigation involves the evaluation of insect herbivory intensity through time. Quantifying the percentage of fossil leaf area removed by insects in fossil floras has been attempted only recently, although such studies are now routine in extant tropical to warm-temperate floras. For us to understand temporal trends in insect herbivory intensity — particularly within ecologically constrained plant-community types — requires a test of the "Red Queen Hypothesis." This hypothesis predicts that because insects continually adapt to circumvent defenses of their plant hosts while, conversely, plant hosts develop mechanisms to ward off insect herbivory, a progressive "arms race" takes place. In other words, both herbivore and host are "running faster and faster just to stay in place," similar to the plight of Alice and the Red Queen in *Through the Looking Glass*. Applying this rule to the fossil record of insect herbivory, the question becomes: Is there evidence for escalation among herbivores and their hosts, and if so, was it a gradually unfolding process to the present or was there a flurry of early activity, such as the invasion of live plant tissues during the expansion of Paleozoic forests?

This question has been investigated only recently, but the latter option appears closer to the truth. Both in terms of the near-modern ecological spectrum of herbivory from a Late Pennsylvanian coal-swamp forest from Illinois (cover and Figure 4) and the elevated intensity of live plant consumption at an Early Permian riparian forest from northern Texas, the evidence indicates that insect herbivory acquired a qualitative and quantitative head start in lowland equatorial forests during the Late Paleozoic. The currently reigning view of extensive and all-important Paleozoic insect detritivory to the exclusion of significant insect herbivory should be abandoned.

Plant-Resource Use by Insects

The overall pattern that has emerged from an examination of the 400-million-year record of plant-insect associations suggests an increase in trophic complexity and a diversification of feeding strategies. However, there are a few surprises. Although the earliest terrestrial ecosystems were dominated by detritivores, there is now compelling evidence that as early as the latest Silurian to Early Devonian, piercing-and-sucking and externally feeding herbivores were consuming live plant stems, and borers were consuming hyphae-bearing fungal tissues.

Later, herbivore partitioning of plant tissues for the Late Pennsylvanian and Early Permian acquired a remarkably modern cast. For example, when assessed by functional feeding group (how insects feed), the host-plant *Psaronius* — a tree fern dominant in Late Pennsylvanian equatorial wetlands — harbored trophically diverse herbivores engaged in external foliage feeding (cover and Figure 4, upper-left inset), sporangia and spore consumption (upper right), piercing-and-sucking (center right), and galling (center left). Detritivores were present as stem and root borers (lower-right and lower-left insets, respectively). Assignments of one mite and five insect culprits to this component community on *Psaronius* are based on diagnostic features of the host-plant damage, coprolites with plant tissues occurring in the preserved peat deposit, and evidence from penecontemporaneous insect gut contents and mouthpart structures. When analyzed by dietary guild (what tissue is consumed), *Psaronius* herbivores were attacking virtually all tissue types — including foliage, entire sporangia or individual spores, the vascular tissues of stems and roots, and their surrounding tissues (parenchyma). Thus, modern modes of tissue-partitioning by insects existed by 300 million years ago and were organized into a component community of herbivores and detritivores.

Additionally, a pattern of host-specificity has been documented, such as the targeting of only a certain *Psaronius* organ in the cases of insects like the petiolar galler (35 specimens known) and the stem borer (seven specimens known). Other, but biovolumetrically subordinate, plants that also were attacked by herbivores include the seed-fern *Medullosa*, which displays extensive folivory (leaf-eating) of fern-like leaves, piercing-and-sucking of bell-shaped pollen organs, boring into stems and roots, and probable consumption of individual pollen grains that may have evolved into a mutualism similar to modern pollinators. Curiously, although cordaite conifers (an order of gymnospermous plants that have probably been extinct since the Mesozoic) were relatively rare within these swamp forests, most coprolites that have spores or pollen contain cordaitalean pollen.

After the Late Pennsylvanian, coal swamps waned in North America. Early Permian floras were characterized by a different suite of mostly seed plants, especially seed ferns, conifers, and cycadophytes, the latter distant relatives of cycads such as the modern sago palm. However, local patches were dominated by gigantopterids, a group of arborescent plants with uncertain taxonomic affinities that bore large, sturdy, and intricately veined leaves. A recent examination of a gigantopterid-dominated flora from the Lower Permian redbeds of northern Texas revealed extensive herbivory, particularly external feeding in the form of hole and margin consumption and skeletonization of gigantopterid foliage. An impressive level of herbivory — approximately 4 percent of the total surface area of gigantopterid leaves — was removed by insect herbivores. This represents about half the value for comparable modern tropical and subtropical angiospermous floras. Cycadophytes, ferns, and other plants were also consumed, but at lesser levels. These studies indicate that ecologically significant — indeed elevated — levels of herbivory were present during the Early Permian. In addition, distinct host-specificity occurred in both earlier peat-forming wetland forests and in the subsequent drier riparian habitats dominated by seed plants. The timing and biogeography of expansion of insect herbivory in a variety of distinctive plant communities needs to be narrowed by examining additional floras across this Late Pennsylvanian to Early Permian interval.

A dramatic extinction of most lineages of the Paleozoic insect fauna occurred during the Late Permian; the modern insect fauna, characterized by the major insect lineages of today, emerged during the Triassic. Although the taxonomic contrasts between these two evolutionary faunas are dramatic, the feeding strategies — assessed by mouthpart classes, functional feeding groups, and dietary guilds — maintained their integrity across this boundary. These Paleozoic feeding strategies are well represented during the Triassic, with entirely different taxa of interacting plants and insects. Examinations of Middle and Late Triassic plant-insect associations — such as those focusing on the Chinle Formation of the American Southwest and the Upper Buntsandstein, Lower Keuper, and Lettenkohle formations of France and Germany — indicate that all Late Paleozoic feeding strategies continued into the Mesozoic. The earliest known occurrence of leaf-mining is documented for the Late Triassic.

By the mid-to-late Jurassic, superbly preserved biotas in Central Asia, northern China, and the western United States provide strong evidence for pollination mutualisms between nonangiospermous seed plants, such as cycads, and insects that include weevils and flies. The support for these associations includes insect mouthpart structure, gut contents, damage patterns on plant reproductive organs, and certain plant reproductive structures. However, plant-insect associations during the Triassic to Jurassic are poorly understood when compared to the Late Pennsylvanian to Early Permian or to the subsequent Cretaceous.

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Figure 4. The component community of herbivores and detritivores in their Late Pennsylvanian (300 Ma) host plant *Psaronius*, a tree fern that dominated peat-substrate swamp forests of the Illinois Basin. All interactions are from insects, except the lower-right inset, which is a mite. The upper four of these associations indicate feeding of live plant tissue and are confined to the canopy.

During the Cretaceous, angiosperms began their extensive evolutionary and ecological radiation, providing new opportunities for partitioning vegetative resources and for elaborating mutualisms, such as pollination, that had been established earlier with seed plants. Interestingly, the rapid extension of mid-Cretaceous angiosperms is not matched by the appearance of major new herbivorous feeding strategies, virtually all of which were in existence during the earlier Mesozoic. Additionally, the overwhelming majority of modern insect families precede the appearance of the earliest angiosperms in the fossil record, indicating that herbivore associations with plants — including microscale exploitation of discrete tissue types, consumption of broad leaves, and pollination mutualisms — occurred among seed plants in general. Evidently, these associations were subsequently elaborated between insects at lower taxonomic levels and one particular (albeit currently diverse) lineage of seed plants, the angiosperms, resulting perhaps in more finely partitioned feeding strategies.

These consequences are best illustrated by numerous types of external foliage feeders (including margin and hole feeders, skeletonizers, and surface abraders), leaf miners, gallers, and other functional feeding groups documented from the mid-Cretaceous Dakota Formation of Kansas and Nebraska. Some of these interactions have persisted to the present, such as phylogenetically basal lineages of leaf-mining moths occurring on similarly basal lineages of woody angiosperms. Pollination syndromes became progressively elaborated during the Cretaceous and into the Cenozoic, paralleling similar fine-grained trends in plant-resource partitioning by herbivorous insects. During the mid-Cenozoic, more modern lineages of angiosperms emerged, especially grasses and members of the sunflower family. Their appearance introduced a substrate for associated insects that included leafhoppers, leaf beetles, and leaf-mining flies. This recent diversification was superimposed on older Mesozoic patterns, providing the broad and diverse spectrum of both ancient and modern associations seen today.

Current Status and Future Prospects

During the past two decades, an intellectual renaissance in the study of plant-insect interactions has taken place. In addition to the earliest and classic escape-and-radiation model mentioned above, four other major hypotheses have been proposed to account for observed patterns of plant-host use by insects. These alternative models involve differing temporal and spatial modes of insect speciation or adaptation to host plants, and vice-versa. Whether these modes of plant-insect association can be resolved within the temporal and spatial scales encountered in the fossil record is still uncertain. In principle they should — with well-preserved, diverse, and abundant floral successions representing brief, temporally constrained intervals within macroevolutionary time. Such approaches provide promise by placing in appropriate context the historical dimension of most of Earth's biodiversity.

Conrad C. Labandeira
Smithsonian Institution, National Museum of Natural History, NHB Paleobiology MRC-121, Washington, D.C. 20560

Dr. Labandeira received his doctorate from the University of Chicago, where he completed a dissertation on a classification of modern insect mouthparts and their representation in the fossil record. As a postdoctoral research fellow at the University of Illinois at Urbana-Champaign, he examined plant/arthropod associations in Pennsylvanian-age coal-swamp forests. Since 1992, he has been at the Smithsonian's National Museum of Natural History (NMNH), conducting research on insect diversity in the fossil record and, with other colleagues, examining the extent and variety of herbivory in Late Pennsylvanian and Early Permian floras and the ecology of Cretaceous insect associates of early angiosperms. They are currently working on the spectrum and intensity of insect herbivory from three Eocene floras. Labandeira is curator of fossil arthropods in the Department of Paleobiology at NMNH.

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