

# The Fossil Record of Plant-Insect Dynamics

Conrad C. Labandeira<sup>1,2,3,4</sup> and Ellen D. Currano<sup>5</sup>

<sup>1</sup>Department of Paleobiology, National Museum of Natural History, Washington, District of Columbia 20013; email: labandec@si.edu

<sup>2</sup>Department of Geology, Rhodes University, Grahamstown 6140, South Africa

<sup>3</sup>College of Life Sciences, Capital Normal University, Beijing 100048, China

<sup>4</sup>Department of Entomology and BEES Program, University of Maryland, College Park, Maryland 20742

<sup>5</sup>Department of Geology and Environmental Earth Science, Miami University, Oxford, Ohio 45056; email: currane@miamioh.edu

Annu. Rev. Earth Planet. Sci. 2013. 41:287–311

First published online as a Review in Advance on  
March 7, 2013

The *Annual Review of Earth and Planetary Sciences* is  
online at earth.annualreviews.org

This article's doi:  
10.1146/annurev-earth-050212-124139

Copyright © 2013 by Annual Reviews.  
All rights reserved

## Keywords

damage type, end-Cretaceous event, functional feeding group, herbivory, Paleocene-Eocene Thermal Maximum, pollination

## Abstract

Progress toward understanding the dynamics of ancient plant-insect associations has addressed major patterns in the ecology and evolution of herbivory and pollination. This advancement involves development of more analytical ways of describing plant-insect associational patterns in time and space and an assessment of the role that the environment and internal biological processes have in their control. Current issues include the deep origins of terrestrial herbivory, the spread of herbivory across late Paleozoic landscapes, recoveries from sudden major crises, reaction to and accommodation of protracted environmental perturbations, and the nature of herbivory and pollination before the appearance of angiosperms during the mid-Mesozoic. These and other exploratory research themes provide a more complete account of a great nexus of ecological activity that has been wedged between the two most diverse organismic groups on land for the past 410 million years.

---

**Mimicry:** the resemblance of an insect to another organism in its environment, or to another unpalatable insect through camouflage

**Damage type (DT):** the basic defined and diagnosable unit of a plant-insect association in the fossil record

---

## INTRODUCTION

Continental arthropods and vascular plants unarguably are the most diverse multicellular organisms on the planet. If one conservatively tallies the average number of ecological associations or interactions of insects and mites found on a single host-plant species, then the number of interactions present today is a tenfold to a hundredfold multiple of the number of host plants (Strauss & Irwin 2004, Zheng & Dicke 2008). These figures result in tens to hundreds of millions of associations that presently occur, on the basis of a minimal estimate of one million described and known insect herbivore species (Schoonhoven et al. 2005). Throughout geologic time, this figure would be a vast number. Almost all of these associations are categorized into two types: herbivory and pollination. Herbivory, or the consumption of live plant tissue, has been the overwhelmingly dominant association through time, in part attributable to the variable but overall elevated host specificity of herbivores (Novotny & Basset 2005), whereas pollination has an opposite tendency of pollinating many typically unrelated host plants (Waser et al. 1996). Other associations include plants and insects exhibiting general to intimate connections with a variety of microscopic and macroscopic fungi (Vega & Blackwell 2004, Janson et al. 2008), physical and chemical defenses of plants to ward off insect herbivores (Krings et al. 2002, Royer et al. 2007, Futuyma & Agrawal 2009, Pott et al. 2012), and various types of deceptive camouflage and other categories of mimicry between plants and insects (Wedmann et al. 2007, Wang et al. 2012).

This multitude of associations in time and space has resulted from processes that occur at a broader environmental scale and also in the local habitat. These processes include (*a*) competition among species and (*b*) historical causes, such as the particular evolutionary trajectories of plant hosts and associated insect lineages (Pellmyr & Leebens-Mack 1999, Lopez-Vaamonde et al. 2006, McKenna et al. 2009, Winkler & Mitter 2009). For some time, it has been acknowledged that the mechanisms of how insects and plants come to be associated with each other involve responses to sudden and prolonged events of the global environment (Labandeira et al. 2002, Currano et al. 2010), as well as local ecological and evolutionary effects (Wappler & Denk 2011). For herbivory, detection of these patterns requires the examination of bulk floral data for determining community-wide and habitat-level patterns, as well as the examination of plant-host species data for specific lineages of the plant hosts and their herbivores, such as tracking the component community of herbivore species successively on a particular plant lineage through time. [The component community described by Root (1973) consists of all organisms trophically dependent on a plant-host species.] One goal of such studies is to establish the effects of major physical and biological events, such as mass extinctions or rapid diversification events. An equally important goal is the examination of associational changes in specific plant and insect lineages, such as shifts in insect herbivore and pollinating taxa accompanied by short-term turnovers of their plant hosts. One recently developed, utilitarian system for documenting such changes of herbivore taxa through time is the damage-type system, which provides definitions, comparative diagnoses, and related information about distinctive, categorizable types of insect damage, termed damage types (DTs) (Labandeira et al. 2007b).

In this review, we present new, emerging ways of examining and analyzing the fossil record of plants, insects, and their interactions through quantitative and qualitative analysis of the local communities and regional ecosystems in which they occur. Studies involving such a perspective extend to approximately the past 15 years and involve instrumental and especially analytical techniques for examining the plant-insect associational record. We discuss recent case studies and hope that similar approaches will be extended to the relevant, unexplored dynamics of the plant-insect associational record.

## SOLVING EVOLUTIONARY AND ECOLOGICAL PUZZLES

Plants and insects record their effects on each other in intricate ways. For the fossil record, the most widespread example is insect herbivore damage on plant leaves, but also on other organs such as stems (Sarzett et al. 2009, Petrulevičius et al. 2011, Moisan et al. 2012); seeds (Labandeira 2006a, Naugolnykh 2008); and, rarely, roots (Labandeira 1998). One recently examined system involves the evolution and origin of cynipid (gallwasp) galls on oak leaves in the Neogene of western North America, where distinctive gall shapes, host associations, and body-fossil records provide insights into the evolutionary biology of a fascinating relationship (Waggoner & Poteet 1996, Erwin & Schick 2007, Stone et al. 2009). More difficult to detect are plant reproductive structures that have been modified for the reception of insect mouthparts in pollination (Labandeira et al. 2007a). Mouthpart modifications, such as elongate proboscides, have an interlocking function as a hand-and-glove device for receiving plant reproductive structures (Labandeira 2010). Another consequence of pollinated plants is tissue consumption typically by larvae whose life cycle involves pollination as an adult (Klavins et al. 2005). The most intractable association to ascertain is mimicry, whereby wings or even entire insects uncannily resemble, respectively, smooth-margined leaflets or leaves (Wang et al. 2010), or entire highly lobed leaves (Wang et al. 2012) of coexisting plants in the same habitat.

The detective process begins with data collection. A fossil leaf assemblage for an herbivory study, and ideally for a pollination study, is retrieved from a methodically quarried pit. Adequately preserved to well-preserved specimens are collected in an unbiased way and constitute a sufficiently abundant sample, typically from several hundred to a few thousand specimens, to accurately represent the originally preserved flora. The specimens are identified for their plant-host morphotypes and insect DTs and are frequently analyzed in the context of other relevant data sets for trends based on time, biogeography, habitat, climate, plant host, or other variables of interest (Labandeira et al. 2007b). A battery of analytic techniques and instrumentation has been assembled to ferret out correlations and other patterns between plant hosts and their insect herbivores and pollinators (e.g., Currano et al. 2010, Labandeira 2010, Wappler et al. 2012).

Four case studies demonstrate the puzzle-solving nature of understanding the ecology and evolutionary biology of ancient plant-insect associations (**Figure 1**). These examples spotlight the eclectic uses of plant-insect associational data from the fossil record that may not be evident from an initial survey of the field. The first example comes from leaf mining (**Figure 1a**), specifically recognition of a stereotyped serpentine leaf mine (DT104) that has a distinctive frass trail alternating between either side of the mine and that is associated with a field of minuscule ovipositor probe marks surrounding the mine origin (Winkler et al. 2010). These and other features of the mine restrict its identity to the lineage Agromyzidae (leafmining flies), whose earliest body-fossil occurrence previously was in much younger strata but now is extended significantly earlier in time. Consequently, the earliest Agromyzidae now occur in the Early Paleocene of North America, and the origin of the larger fly clade to which the Agromyzidae family belongs, the Schizophora, is similarly extended earlier, with a probable latest Cretaceous origin. In addition, Paleocene Agromyzidae mines occur on an extinct woody species of sycamore, whereas the clade currently consists of miners that are almost exclusively on herbaceous plants, particularly grasses (Winkler et al. 2010), indicating a major host shift sometime during the mid-Cenozoic.

A second example is from external foliage feeding and involves the assessment of the highly stereotyped DT28 (Labandeira et al. 2007a), found on the ginger *Zingiberopsis* in Late Cretaceous and Paleogene deposits from the western interior of North America (Wilf et al. 2000). The distinctive surface-abrasion feeding mark of DT28 displays a suite of micromorphological modifications of host-plant tissues by mandible chew marks (**Figure 1b**) that exactly match the adult hispine

---

**Leaf mining:**  
larval feeding within host-plant leaf tissue, typically in a serpentine or blotch-like fashion but without eliciting a noticeable plant response

---



**Figure 1**

Plant-insect interactions that are important for solving evolutionary and ecological puzzles. (a) The leaf mine (DT104) on an early Paleocene sycamore host was made by an agromyzid fly, providing the earliest fossil date for not only the Agromyzidae but also its broader, encompassing lineage, the Schizophora, indicating a Late Cretaceous origin (Winkler et al. 2010). (b) Latest Cretaceous surface-feeding damage (DT28) on the ginger *Zingiberopsis*, showing the antiquity of a stereotyped association currently occurring in the Neotropics (Wilf et al. 2000). (c,d) Death-grip marks (DT212) astride the midrib of a middle Eocene dicot leaf from Messel, Germany, revealing the existence of a modern plant-ant-parasitoid fungus association that induced zombification of ants (Hughes et al. 2010). (e) A Middle Jurassic specimen of a long-proboscis scorpionfly (order Mecoptera) that exhibited specialized tubular mouthparts for fluid feeding on gymnosperms and associated pollination (Ren et al. 2009). Scale bars: solid, 1 cm; striped, 1 mm. Panels b and e are reproduced with permission from the American Association for the Advancement of Science; panels c and d are reproduced with permission from the Royal Society. Abbreviation: DT, damage type.

beetle damage of the modern neotropical taxon *Cephaloleiini* (Strong 1977). In addition, closely associated slot-hole feeding between two adjacent minor veins, typical of DT08 (Labandeira et al. 2007a), is an exact match for the larval stages of the same adult *Cephaloleiini* found on modern gingers and closely related heliconias. Because the match of two types of co-occurring damage, one larval and the other adult, on the same host-plant family (Zingiberaceae) has been found as

a set in the Late Cretaceous–Paleogene of the western interior and also in modern Mesoamerica, an extension of the association was made. This association subsequently was challenged on the grounds that certain beetle and moth larvae could produce a similar DT (Garcia-Robledo & Staines 2008), but the adult damage of the beetle larvae does not match that of the moth larvae; they differ in the pattern of chewed edges and lack any conspecific, early-instar moth larvae that would produce the associated slot-feeding damage. The fossil occurrence of the moth lineage, the more likely of the remote possibilities, does not occur earlier than mid-Cenozoic, on the basis of molecular phylogenetic grounds (Regier et al. 2012) and the fossil record (Sohn et al. 2012).

In the third example, a unique system of tritrophic interactions was investigated, involving the preserved chew marks on a leaf, an ant that made the foliar damage, and a parasitoid fungus that eventually killed the ant. This is the case of the zombie ants. The evidence begins with a distinctive “death grip” DT212 on a fossil leaf from the Middle Eocene lake deposit at Messel, Germany (**Figure 1c,d**), that matches the same damage produced by particular ant species in a modern Thai forest understory (Hughes et al. 2010). After the modern ant’s brain has been invaded by a parasitoid fungus, zombification ensues and induces a final death grip on the midvein of an accessible dicot leaf. Simultaneously, the ant dies and releases spores from a fungal fruiting body emerging from its head capsule, thus continuing the parasitoid fungus life cycle. This tritrophic leaf–ant–parasitoid fungus association consequently has been extended geographically and temporally to the middle Eocene of Germany.

The fourth case study involves discovery of the long-proboscisid pollination mode, now known to occur from the late Middle Jurassic (165 Mya) to the later Early Cretaceous (~100 Mya). For some time, paleobotanists mentioned in passing that some gymnosperm female (ovulate) reproductive organs possessed interesting surface orifices leading to internal channels, tubes, funnels, micropylar siphons, and other tubular structures that connected with an ovule or group of ovules (Harris 1940, 1951; Axsmith & Jacobs 2005; Crane & Herendeen 2009; Osborn & Taylor 2010). This suggested a unique but unspecified reproductive system. Also discussed were apparent rewards, such as glandular structures placed in orifices or near pollen sacs (Harris 1973, Kvaček 2000). Meanwhile, paleoentomologists were mostly concerned with the better and more consistently preserved wings for characters for systematic studies and paid less attention to often difficult-to-interpret, poorly preserved heads and mouthparts. Later, an interest in the relationship between the tubular structures of the receiving plant structures and the projecting long proboscides with food tubes of various insects (**Figure 1e**) led to the proposal of the mid-Mesozoic long-proboscisid mode of gymnosperm pollination (Ren et al. 2009, Labandeira 2010).

## INSECT HERBIVORY

Studies of plant hosts and their insect herbivores have concentrated sporadically on intervals spanning the Early Devonian to the Recent. Comparatively unstudied times involve the Early Devonian to Early Carboniferous (Mississippian) when herbivory initially was launched; the Early Triassic immediately after the end-Permian (P-Tr, Permo-Triassic) extinction; the mid-Late Triassic to the end of the Jurassic; and, surprisingly, the middle Miocene to Pleistocene, with a notable exception being Opler’s (1973) seminal demonstration of the significant antiquity of several modern leaf-miner associations. Almost all of the quantitative examinations to date have been confined to the Permian (Beck & Labandeira 1998, Adami-Rodrigues et al. 2004, Labandeira & Allen 2007, Prevec et al. 2009, Pinheiro et al. 2012), the latest Cretaceous to early Miocene (see **Supplemental Table 1**; follow the **Supplemental Materials** link from the Annual Reviews home page at <http://www.annualreviews.org>), and relevant modern studies (Smith & Nufio 2004; Adams et al. 2010, 2011). Examinations of other crucial episodes such as the radiation of

---

**Tritrophic interaction:** the presence of a trophic cascade that includes a host plant, its herbivore, and the herbivore’s parasitoid or predator

**Parasitoid:** a larva that slowly consumes its live insect host, saving its essential organs for consumption immediately before emergence from and death of the host

**Zombification:** the induction of neural control by a parasitoid of an ant or other animal host that results in eventual death

**Ovulate reproductive organ:** a female organ in seed plants that bears ovules, secretes fluids, and produces structures involved in pollination

---

---

**Piercing and sucking:**

the penetrative puncturing of plant and other tissues by insects that bear mouthparts modified into piercing stylets

**Galling:** a parasitic interaction typically by a subadult animal that invades host-plant tissue and exerts hormonal control for production of tissues used in its nutrition and protection

**Holometabolism:**

the complete developmental transformation in which an insect egg hatches a larva, which is transformed into a pupa, from which the adult emerges

---

plant-host and insect-herbivore diversity during the Late Triassic (Scott et al. 2004, Labandeira 2006a) and the expansion of the mid-Cenozoic grassland biome (Strömberg 2005) are noteworthy but are just beginning. Given this context, we discuss five of the more-studied episodes.

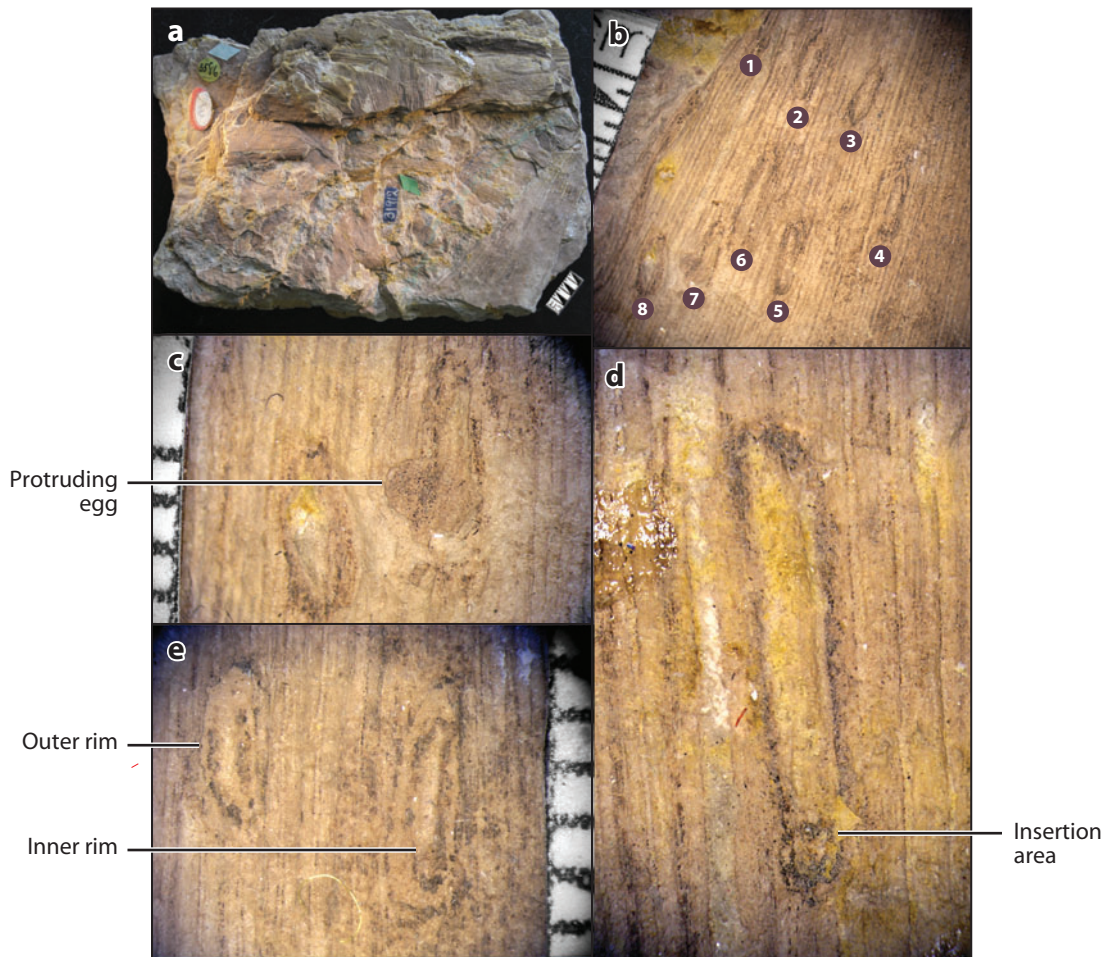
## The Initial Launch of Herbivory

Detritivory (the consumption of dead tissues) has been proposed as the exclusive mode of plant feeding during the time interval between the earliest compelling evidence for well-established terrestrial biotas—mostly of macroscopic plants, fungi, and arthropods of the Early Devonian—and the major development of coal-swamp and adjacent habitats during the Late Carboniferous (Pennsylvanian) (Shear & Kukalová-Peck 1990). The few studies of continental plant-arthropod associations during this interval documented the near or total exclusion of herbivory in a variety of settings within the paralic to the more inland deposits of Euramerica (Shear & Kukalová-Peck 1990, Edwards & Selden 1992). Although a few studies (Kevan et al. 1975, Banks & Colthart 1993) have demonstrated herbivore piercing and sucking and surface abrasion on stems, only recently have diverse associations such as hole feeding, margin feeding, surface abrasion, piercing and sucking, and galling been demonstrated on Middle Devonian liverworts, a land plant with photosynthetic, leaf-like equivalents (C.C. Labandeira, S. Tremblay, K. Bartowski & L. Hernick, submitted). For external foliage feeding, the next earliest occurrence is much later and on anatomically true leaves of an early seed fern from the late Mississippian of Australia (Iannuzzi & Labandeira 2008). This evidence, although sporadic, indicates that Devonian and Mississippian herbivory is more frequent than previously considered and perhaps was modulated by highly varying levels of the partial pressure of oxygen ( $pO_2$ ) (Berner 2009), which affected arthropod respiration and thus herbivore metabolic activity (Ward et al. 2006). The  $pO_2$  highs during this interval are approximately coincident with two pulses of arthropod herbivory. An earlier event corresponds to the initial consumption of sporangia and stem tissues in the Early Devonian. After a long lag, a second event unfolded in which leaves, seeds, true roots, and wood were consumed during the Late Mississippian and ensuing Pennsylvanian (Labandeira 2007).

## How Did Herbivory Expand on Vegetated Landscapes?

During this second pulse of herbivory, there was initial consumption of anatomically true leaves, seeds, true roots, and wood—organs that earlier were present but not herbivorized (Scott & Taylor 1983, Labandeira et al. 1997). The second, more extensive pulse is coincident with the first occurrences of 12 ordinal-level insect lineages, including mayflies, archaic “dragonflies,” piercing-and-sucking paleodictyopteroids, grasshopper-like orthopteroids, and the earliest holometabolous insects (Grimaldi & Engel 2005, Labandeira 2011). Ecological components of this diversification were herbivorous insects and mites that were external foliage feeders, piercers and suckers, gallers, pith borers, spore and pollen feeders, and root consumers. The partitioning of plant taxa by these herbivore guilds represents the first extensive and diverse component communities, as documented by histologically preserved permineralized compressions (Scott & Taylor 1983; Lesnikowska 1990; Labandeira & Phillips 1996, 2002; Labandeira et al. 1997). The apparently rapid cladogenetic and ecological events are associated with significantly increasing  $pO_2$  levels (Clapham & Karr 2012). The distinctive plant-herbivore associations of the Pennsylvanian and Early Permian wetlands were extirpated in Euramerica but were spatiotemporally displaced to similar, later Permian, peat-dominated habitats in Cathaysia (Glasspool et al. 2003, D’Rozario et al. 2011).

During the latest Pennsylvanian, various regions of Gondwana emerged from a glaciated regime as the supercontinent moved northward (Césari 2007). The first documented glossopterid



**Figure 2**

Middle Permian leaf specimens of a glossopterid seed-fern species showing the predominance of oviposition (DT100). The specimens are from the Paraná Basin, in Santa Catarina State, southeastern Brazil, and are part of the White collection (White 1908) at the National Museum of Natural History in Washington, DC. (a) A shale slab containing glossopterid foliage with individual leaves magnified in panels *b* and *c*. (b) Eight oviposition scars with reaction rims of callus tissue oriented parallel to venation. (c) Two ellipsoidal oviposition marks with an enveloping rim of scar tissue, one of which shows a protruding egg. (d) A magnified oviposition scar showing an insertion slit at the bottom and an upward-trending lesion with a surrounding scar. (e) Two oviposition scars showing inner and outer reaction rims. Scale bars indicate millimeter increments; the scale in panel *d* is approximately twice that in panels *c* and *e*.

seed-plant forests occurred during the earliest Permian (McLoughlin 2012), and by the end of the Early Permian, a diverse spectrum of associations occurred at one site, Hammanskraal in the Karoo Basin of South Africa, which displays a rich assortment of plant-insect associations, especially ovipositional damage (C.C. Labandeira & R. Prevec, personal observation). This predominance of ovipositional damage continues in Karoo floras of the Middle Permian (**Figure 2**) and intensifies with a broader spectrum of DTs during the Late Permian. By this time, varied glossopterid-dominated floras and their insect herbivores were well established in several swamp, lacustrine, and especially fluvial environments (Banerji 2004; Gastaldo et al. 2005; Prevec et al. 2009; McLoughlin 2011; C.C. Labandeira & R. Prevec, unpublished data).

---

**Oviposition:** the insertion by a female of insect eggs into host-plant tissues, resulting in scarring and callus formation

**Damage diversity (or damage richness):** the number of damage types on a leaf, plant host, or bulk flora

**Damage intensity:** the frequency of occurrence of damage types on a leaf, plant host, or bulk flora

**Specialization:** the feeding of insect herbivores on a single or perhaps a few phylogenetically related plant hosts

---

By contrast, studies of north-central Texas show significant differences from the Karoo Basin of Gondwana throughout the same Permian interval (Beck & Labandeira 1998; Labandeira & Allen 2007; S. Schachat & C.C. Labandeira, unpublished data). These studies document a much greater spectrum of major host-plant lineages, the dominance of external foliage feeding over oviposition, the earliest occurrence of insect outbreak-like phenomena, and a significantly different composition of insect herbivore component communities between the two supercontinents (Labandeira & Allen 2007; Labandeira 2012; S. Schachat & C.C. Labandeira, unpublished data). As insect herbivore colonization advanced toward more arid landscapes of continental interiors and away from wetland basins, it appears that plant-host xeromorphy in both southern Gondwana and southwestern Euramerica played an important role in the spectrum of insect damage.

### What Were the Effects of Ecosystem Change on Landscapes?

The dynamics and tempo of plant-insect interactions in the geological record are profoundly influenced by biotic and abiotic environmental perturbations. The Parasitoid Revolution and the Angiosperm Revolution are two examples of biotic events that restructured plant-insect food webs. The Parasitoid Revolution represented the emergence of a new feeding guild consisting principally of members of the Hymenoptera (small wasps) but also Diptera (brachyceran flies), which are parasitoids that feed largely on larval herbivorous insects (Labandeira 2002a). The diversification of major parasitoid lineages during the Jurassic introduced a major top-down regulator of insect herbivores that, together with existing predators, forever changed the trophic structure of insect herbivore communities and their associated food webs. With the addition of parasitoids, resource-driven bottom-up regulation became proportionately less effective, as modern studies show that parasitoids are more effective than predators, particularly those that target endophytic herbivores that feed within plant tissues (Memmot et al. 1994). In contrast to the Parasitoid Revolution, the Angiosperm Revolution, another biotic perturbation, was a mid-Cretaceous resource-driven enhancement of plant-insect associational diversity that resulted in the creation of new opportunities for insect herbivores and pollinators (Grimaldi 1999, Krassilov & Shuklina 2008). Abiotic environmental perturbations include the P-Tr and Cretaceous-Paleogene (K-Pg) crises and climate change, discussed in detail below.

**Permo-Triassic event.** Preliminary work on plant-insect interactions from glossopterid-dominated floras of the Karoo Basin in South Africa indicates that moderately diverse and modest levels of damage occurred in a variety of habitats prior to the P-Tr event (Prevec et al. 2009; C.C. Labandeira & R. Prevec, unpublished data). Poorly preserved, fragmentary Karoo floras in Early Triassic deposits immediately after the P-Tr crisis suggest a profound downturn in plant and insect diversity and the near absence of plant-insect associations (Labandeira 2005, 2006a), although the Eurasian data are richer (Krassilov & Karasev 2008, Shcherbakov 2008). This dramatic fall in Karoo associational diversity was reversed sometime during the Middle Triassic, when plant diversity was relatively low, but as new plant lineages appeared, the latter became speciose during the Late Triassic. Similarly, Middle Triassic damage diversity and damage intensity were low but very generalized, and the insect herbivores responsible for the damage experienced a rebound before the Late Triassic, seemingly in synchrony with their plant hosts (R. Prevec, C.C. Labandeira, E.D. Currano, J.M. Anderson, H.M. Anderson, unpublished data). Upon diversification of horsetails, ferns, and several major seed-plant lineages during the early Late Triassic, plant-insect associations became significantly diverse in the total number of DTs, exhibited greater host specialization, and emphasized internal feeding over external feeding (Scott et al. 2004, Labandeira 2006a). The Late Triassic radiation of plant hosts and their herbivores may have reached a level

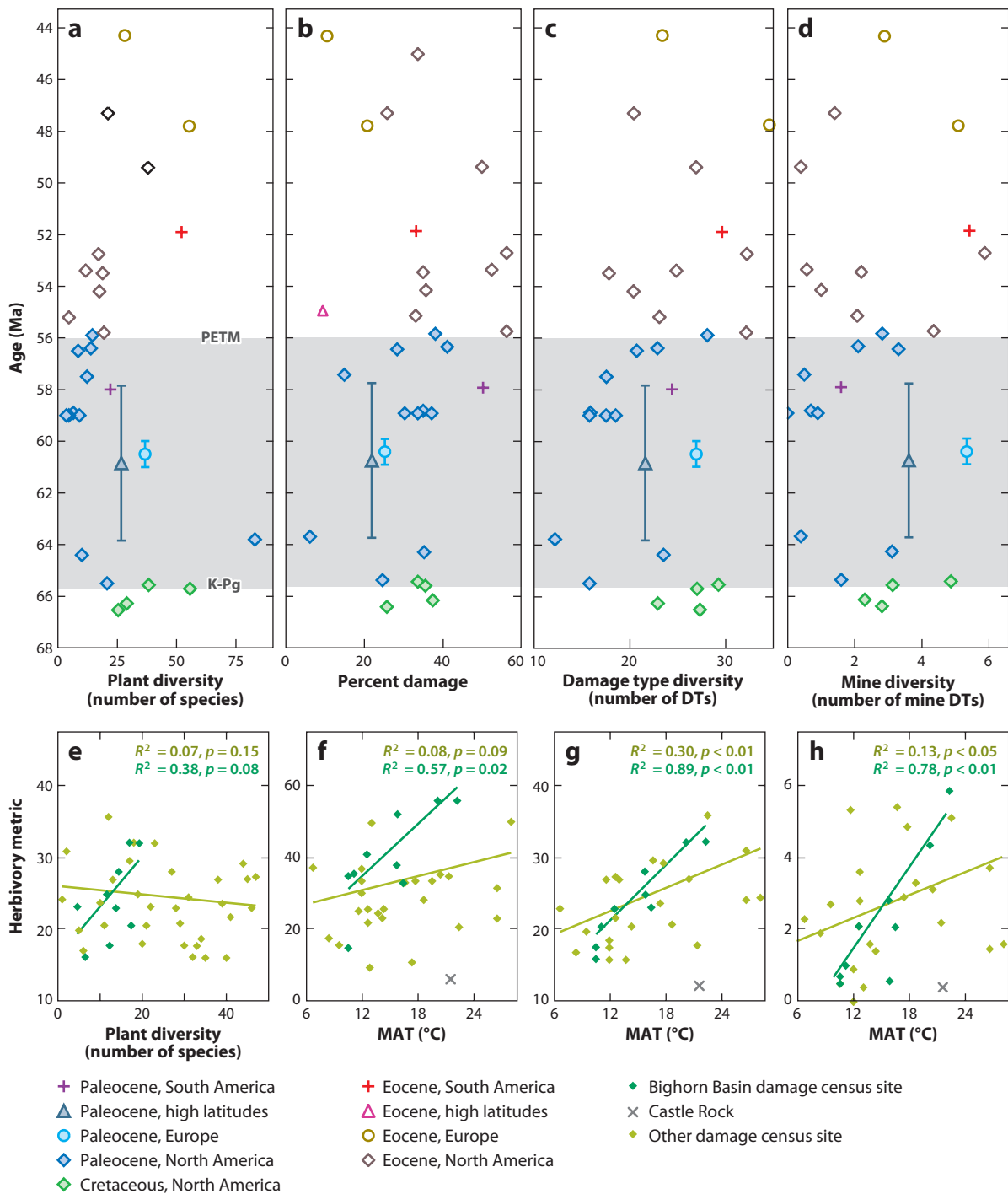


## REGIONAL PATTERNS OF THE CRETACEOUS-PALEOGENE EXTINCTION?

The significant extinction and prolonged recovery interval in the western interior of the United States (**Figure 3**) is commonly considered the baseline for our understanding of terrestrial ecosystem response to the Cretaceous-Paleogene (K-Pg) impact. However, recent data from other continents suggest that the net effects of the bolide impact decrease with increasing distance from the Chicxulub crater in Mexico. Both floral and insect damage diversity at the 58-Ma-old Cerrejón site in Colombia (8 Ma postimpact; 2,100 km modern distance from Chicxulub) are notably low for a tropical forest (Wing et al. 2009). By contrast, the middle Paleocene Menat site in France (5–6 Ma; 8,500 km) (Wappler et al. 2009) and the late early to middle Paleocene Firkanten flora from Spitsbergen (age poorly constrained to 2.9–6.8 Ma post-K-Pg boundary; 8,000 km) (Wappler & Denk 2011) show the combinations of high floral, total damage type, and mining diversity that suggest balanced and fully functional ecosystems completely unlike those in Cerrejón or the United States [e.g., southwestern North Dakota (10 Ma; 3,100 km)]. These results are consistent with paleobotanical studies showing high Paleocene plant diversity in Chubut, Argentina (4.3 Ma; 7,700 km) (Iglesias et al. 2007) and rapid postimpact ecosystem recovery in New Zealand (a few thousand years; 12,300 km) (Vajda et al. 2001). We emphasize that more data, particularly from the late Cretaceous, are needed to test this pattern.

of intensity and diversity of interactions similar to that of the angiosperm radiation (Labandeira 2006b). After the Late Triassic increase in herbivory, little is known about global trends and other patterns in Jurassic floras. Current research is under way (Vasilenko 2005, 2006; Pott et al. 2008; C.C. Labandeira & J.A. Santiago-Blay, unpublished data), and preliminary results indicate that bennettitaleans may be the most herbivorized group of plants during this interval (Pott et al. 2008, 2012; Popa & Zaharia 2011; Meller et al. 2011; Q. Ding & C.C. Labandeira, unpublished data).

**Cretaceous-Paleogene event.** Compared with the P-Tr event, much more is known about the effects of the K-Pg event, particularly in North America (Labandeira et al. 2002). Current evidence suggests that floras from the Williston Basin in North America underwent a significant decline in plant taxa and plant-insect associations, especially a decline in host-specialized DTs (Labandeira et al. 2002). Quantitative insect damage data from Early Paleogene sites in Montana, Wyoming, and Colorado demonstrate that terrestrial ecosystems remained depauperate and ecologically unstable for 10 million years (see **Figure 3** and **Supplemental Table 1**). An imbalance in specialized associational diversity is illustrated by leaf-mine DT diversity in two contrasting floras. One diverse flora from the Denver Basin of central Colorado exhibits the virtual absence of leaf mining, whereas a depauperate flora of similar age from the Williston Basin of eastern Montana displays an unusually rich spectrum of leaf mining (Wilf et al. 2006). Stable terrestrial ecosystems, as evidenced by moderately diverse floras with total and leaf-mine DT diversity at Late Cretaceous preimpact levels, do not occur in the western interior until the latest Paleocene (see sidebar, Regional Patterns of the Cretaceous-Paleogene Extinction?). As currently known, both the K-Pg and P-Tr crises resulted in geochronologically sudden ecological rearrangements concomitant with mass extinction and major turnovers in plant-insect associations (Labandeira et al. 2002). The major comparative difference is condensation of the recovery interval from 65.5 to 55.8 Ma [ $\sim$ 10 million years for the K-Pg interval, compared to from 252 Ma to  $\sim$ 228 Ma ( $\sim$ 24 million years) for the P-Tr interval, which was two-and-a-half times longer (Labandeira 2006a, Wilf et al. 2006)].



**Hothouse earth conditions.** Unlike the P-Tr and K-Pg events, the Paleocene-Eocene Thermal Maximum (PETM) is a longer event ( $10^5$  years) embedded in a protracted period of elevated temperatures from the latest Paleocene to the middle Eocene. An influx of  $^{13}\text{C}$ -depleted carbon into the atmosphere during the onset of the PETM caused the partial pressure of carbon dioxide ( $p\text{CO}_2$ ) to approximately double and global temperatures to increase by at least  $5^\circ\text{C}$  (Kennett & Stott 1991, Koch et al. 1992, Zachos et al. 2003). In a study from 59 to 52.7 Mya in the Bighorn Basin of Wyoming, insect damage diversity and abundance were sampled from nine floras before, during, and after the PETM (Currano et al. 2008, 2010). The results indicate that increased levels of insect-mediated damage diversity and to a lesser extent damage frequency are correlated with the short-lived PETM, in particular with increased temperature but not with changes in floral diversity, as shown in **Figure 4** (Currano et al. 2008, 2010).

The only other Bighorn Basin flora with comparable damage diversity, frequency, and specialization is from the Early Eocene Climatic Optimum (EECO, 53–51 Mya), when the mean annual temperature (MAT) was approximately  $2^\circ\text{C}$  warmer than during the PETM (Wing et al. 2000). The high damage diversity, particularly specialized damage diversity, suggests that PETM forests were balanced, fully functional ecosystems, in contrast to those of the Early Triassic or early Paleocene. Thus, either the rate of temperature change was slow enough to allow plants and insects to migrate or adapt or the temporal resolution of the fossil record is too low to distinguish stressed ecosystems at the onset of the PETM. However, elevated damage intensity during the PETM may indicate ecosystem stress owing to elevated  $p\text{CO}_2$ , which often leads to decreased leaf nitrogen concentrations (Bazzaz 1990, Lincoln et al. 1993) and higher insect feeding rates (Watt et al. 1995). Dwarfing in terrestrial vertebrates (Clyde & Gingerich 1998, Secord et al. 2012) and soil-dwelling invertebrates (Smith et al. 2009) also supports a decrease in food quality.

The best archive of southern neotropical plant-insect associational diversity during the EECO occurs at Laguna del Hunco (52 Mya) (Wilf et al. 2005). Four separate sites from Laguna del Hunco were sampled and compared with sites of a similar age in western North America (sites from Washington, Utah, and Wyoming). Significantly more damage was found at the South American sites, regardless of whether functional feeding groups or DTs were analyzed. In addition, a rank order of insect functional feeding group and DT diversity showed a disproportionate representation of Laguna del Hunco plant hosts exhibiting greater feeding diversity than hosts from the three sites in North America. These data indicate that an early Cenozoic history of elevated herbivore damage intensity and a high level of specialized associations were present on diverse plant hosts during a warm interval of the early Eocene. This ancient pattern may explain the high diversity levels of plants and their insect associates today in neotropical South America (Gentry 1988, Price et al. 1995).

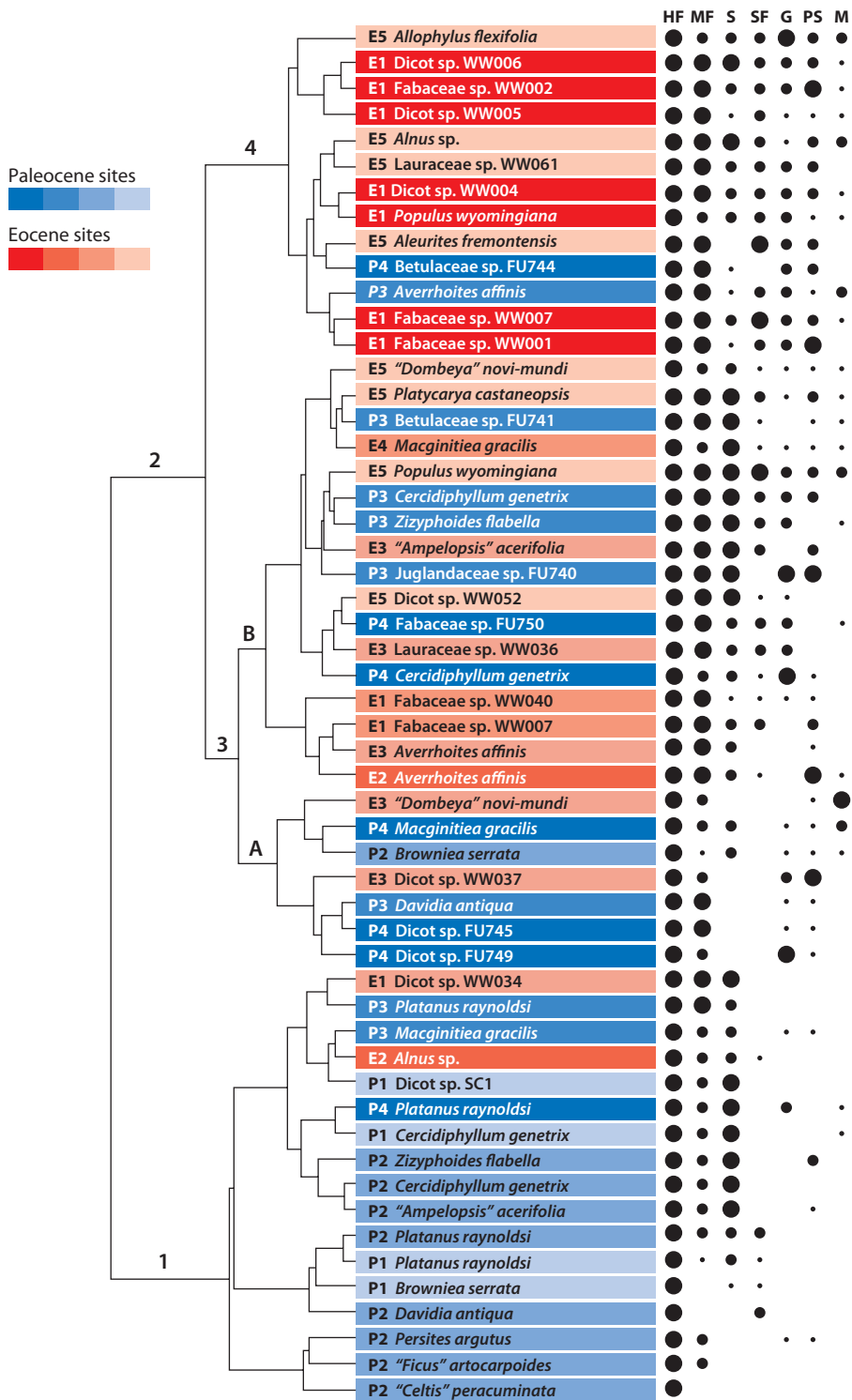
---

**Functional feeding groups:** the fundamental kinds of plant-insect interactions (external foliage feeding, piercing and sucking, oviposition, leaf mining, galling, seed predation, and wood boring)

---

### Figure 3

Quantitatively censused insect damage on bulk floral assemblages from the Late Cretaceous and Early Paleogene. The floras included in this data set are listed in **Supplemental Table 1** (follow the **Supplemental Materials** link from the Annual Reviews home page at <http://www.annualreviews.org>). (a) The number of dicot leaves at each site is rarefied to 400 leaves. (b) Percentage of leaves at each site with insect herbivore damage. (c) Total damage diversity (number of damage types, or DTs) on each flora standardized to 400 leaves by averaging damage diversity for 5,000 random subsamples of 400 leaves without replacement. (d) Sampled standardized mine diversity on the bulk floras, calculated as in panel c. (e) Plant diversity at each site as in panel a versus total damage diversity as in panel c. (f) Mean annual temperature (MAT) versus percentage of leaves at each site with insect herbivore damage as in panel b. (g) MAT versus total damage diversity as in panel c. (h) MAT versus mine diversity as in panel d. The early Paleocene Castle Rock flora is considered an outlier because of the effects of the Cretaceous–Paleogene impact event. The Mexican Hat flora is not included in panels f–h because there is no published MAT estimate. Regression lines in panels e–h are from a linear model.



The sustained warmth of the EECO continued throughout the early Eocene. Two maar lake sites in Germany, at 47.8 Mya (Messel) and 44.3 Mya (Eckfeld), capture the initial decline from hothouse conditions. These sites document an elevated level of plant-insect associations compared with sites of similar age in western North America and southern South America (Wappler et al. 2012). However, in Germany, elevated temperature and  $p\text{CO}_2$  produced disproportionate herbivory on evergreen over deciduous angiosperms, a trend opposite to that seen in penecontemporaneous sites of the Green River flora in Wyoming (Wilf & Labandeira 1999, Wilf et al. 2001). This trend is explained by historical enrichment of evergreen taxa in western Europe, also borne out by diverse and apparently long-standing trophic links among herbivores and evergreen source plants at Messel (Labandeira et al. 2011, Wappler et al. 2012). The Messel food web (**Figure 5**) represents a highly integrated, continental ecosystem of 700 taxonomically highly resolved, trophically unique taxa, dominated by plants and arthropods (71% of the total); the latter are overwhelmingly herbivores and pollinators (Labandeira et al. 2011). Plant-insect associational links and their trophic cascades form the majority of the web links, providing a realistic capture of ecosystem structure that historically has been neglected in almost all modern and fossil food webs analyzed to date (but see Pocock et al. 2012). The ameliorated paleoclimate and decreased diversity and abundance of plant-insect interactions of the later Eocene and Oligocene (Wappler 2010, Currano et al. 2011) contrasted dramatically with those of middle Eocene Messel and Eckfeld.

The specific examples above demonstrate that warming and elevated  $p\text{CO}_2$  affect plant-insect interactions. Insect damage diversity and frequency strongly, significantly, and positively correlate with the MAT over six million years within the Bighorn Basin (Currano et al. 2010). Furthermore, there are weak but significant positive correlations between DT diversity and MAT when data from all of the latest Cretaceous and Paleogene insect damage censuses are compiled (**Figure 3**). That these weak correlations exist at all is surprising given the number of other factors affecting plant-insect herbivore interactions, including but not limited to latitude, continent, geologic age, phylogeny, nutrient availability, and climate factors other than temperature. Additionally, multiple scientists collected the insect damage data, and a variety of methods were used to reconstruct the MAT at each site. The fossil record makes it clear that elevated insect herbivory in natural and managed ecosystems will be a consequence of current anthropogenic increases in temperature and  $p\text{CO}_2$ .

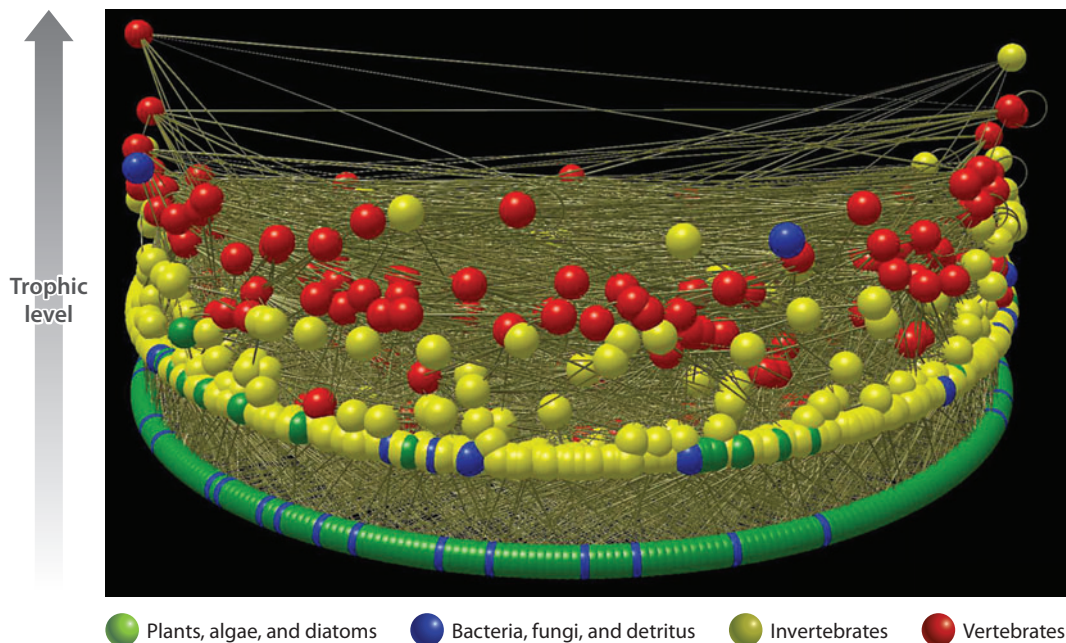
## How Are Modern and Fossil Herbivory Connected?

One approach to understanding the importance of insect damage on fossil leaves is to analyze modern floras using the same research protocol used for fossil material. Several modern studies have established herbivory patterns analogous to those within fossil associational data, such as

←

### Figure 4

Cluster analysis of insect damage on individual plant species at each fossil site on the basis of the relative abundances of the seven feeding groups and subgroups. Plant hosts with at least 20 leaf specimens each were included in the analysis, and species are color coded according to the sites at which they occur. Leaf morphotypes that had not been formally named were assigned to Fort Union (FU) or Willwood (WW) Formation morphotype feeding group on each plant host. Black circles are scaled according to the relative abundances of each functional feeding group on each plant host. The numbered clusters 1, 2, 3A and 3B, and 4 are explained further in Currano et al. (2010). The general pattern reveals that galling, piercing and sucking, and mining damage types are more abundant on host plants from warm Eocene sites. Feeding category abbreviations are as follows: HF, hole feeding; MF, margin feeding; S, skeletonization; SF, surface feeding; G, galling; PS, piercing and sucking; and M, leaf mining.



**Figure 5**

Visualization of the Messel forest food web. Spheres represent taxa and lines represent feeding links. Links that loop refer to cannibalism. The vertical axis corresponds to trophic level. Plants, algae, and diatoms are shown in green; bacteria, fungi, and detritus in blue; invertebrates in yellow; and vertebrates in red (although the colors of the links are not easily distinguished at this scale). Feeding links are tied up disproportionately among the land plants (*green*) and primary consumers (*yellow*), overwhelmingly herbivores and pollinators and their consumers (Labandeira et al. 2011).

spatiotemporal variation in diversity and intensity of feeding guilds among sites (Smith & Nufio 2004), effects of leaf toughness and predation between monocot and dicot angiosperms (Grubb et al. 2008), diversity and intensity of latitudinal gradients (Adams et al. 2010), and differences in temperate versus tropical specialization (Adams et al. 2011). One fundamental issue involves how accurately associational data retrieved from fossil sites match analogous modern data when the latter are appropriately standardized. One study (Carvalho et al. 2011) tested the correlation between the leaf-chewing DT diversity made by mandibulate insects and the diversity of the mandibulate insects (at various developmental stages) responsible for the leaf damage on 24 plant-host species from two different Panamanian forests. This correlation was found to be robust in modern forests across a range of hosts and their herbivores, regardless of mouthpart and behavioral convergences across insect groups or their developmental stages. As an alternative to the study of Smith & Nufio (2004), this study validates the assumptions of paleobiological studies that rely on DT diversity as a means of comparing herbivory through time. Additionally, it provides an actualistic example that supports use of bulk herbivory values in assessing the evolution of fossil herbivore assemblages through time.

## INSECT POLLINATION

Herbivory affects the development and efficiency of a plant's photosynthetic organs, representing a cost to a plant. By contrast, insect pollination is advantageous to plants through enhancement

of reproductive fitness. However, insect pollination comes with a cost, resulting in a cost-benefit resonance with herbivory and an ecological tension between these two dominant insect-related parts of a plant's life.

### How Ancient Is Pollination?

The origins of active insect pollination lie in the earlier consumption of pollen and prepollen in wind-pollinated plants with incidental and passive insect-vectored pollination. This process undoubtedly occurred during the early Mesozoic, and more remotely during the late Paleozoic (Labandeira et al. 2007a), but except for the angiosperms, it never resulted in pollinated plant lineages that underwent any significant diversification (Gorelick 2001). Although pollen and its developmental precursors constitute the rewards of accessible solid grains, parallel rewards also existed in seed plants that typically produced pollen-related fluids such as pollen drops (gymnosperms) and later nectars (angiosperms). Insects with specialized mandibulate (chewing) and long-proboscid (siphoning) mouthparts are known from the Permian of Russia (Rasnitsyn 1977, Labandeira 2010), indicating that both pollen and pollination drop rewards, respectively, were being actively consumed. For plants, large-size pollen from the Pennsylvanian would be inefficient as an abiotic dispersal mode (Schwendemann et al. 2007). In addition, Permian pollinate and ovulate reproductive organs consistent with insect pollination are known (Archangelsky & Cúneo 1987).

### Which Groups Were Responsible for Mid-Mesozoic Pollination?

We mentioned above the match of some peculiar elongate, tubular structures in gymnosperm ovulate organs with contemporaneous long-proboscid insect mouthparts (Labandeira 2010). Several studies indicate that multiple lineages of mid-Mesozoic insects developed siphonate proboscides of different lengths, diameters, and aspect ratios (**Figure 6**) for imbibing fluids such as pollen drops from a wide variety of gymnospermous hosts (Ren et al. 2009, Labandeira 2010). These matches depended on the fit of the proboscis to the receiving tube-like structure of the ovulate organ (Ren et al. 2009; Labandeira 2010; C.C. Labandeira, Q. Yang, J.A. Santiago-Blay, W. Wu, C.L. Hotton, A. Monteiro, Y. Wang, C. Shih, T. Rose, D. Dilcher & D. Ren, submitted) and occasionally the pollinate organ (Labandeira 2010) and may have been aided by colorful displays (Briscoe & Chittka 2001). These structural specializations were present by the late Middle Jurassic (165 Mya), which is the current date for the oldest definitive pollinating insects (Ren et al. 2009, Labandeira 2010). Relevant mid-Mesozoic insect clades included several lineages of true flies (Ren 1998); three lineages of scorpionflies belonging to the Aneuretopsychina clade (Ren et al. 2009); and the nonsophogrammatine Kalligrammatidae, representing four subfamilies of large butterfly-like lacewings (C.C. Labandeira, Q. Yang, J.A. Santiago-Blay, W. Wu, C.L. Hotton, A. Monteiro, Y. Wang, C. Shih, T. Rose, D. Dilcher & D. Ren, submitted). Collectively, these insect taxa represent at least 85 described and known species across the Eurasian mid-Mesozoic. Proposed pollinated plants possessing features consistent with accommodation by long-proboscid insects were members of corystospermalean and caytonialean seed ferns, ginkgophytes (e.g., czekanowskialeans), cheirolepidiacean conifers, gnetaleans, and bennettitaleans (Harris 1940, 1973; Retallack & Dilcher 1988; Stockey & Rothwell 2003; Labandeira et al. 2007a, 2012b; Crane & Herendeen 2009; Ren et al. 2009; Labandeira 2010; Rydin & Friis 2010). Other possible modes of insect pollination on gymnosperms were pollen-feeding mandibulate insects, such as beetles and katydid-like orthopteroids for cheirolepidiacean conifers, cycads, and bennettitaleans

---

#### Mandibulate mouthparts:

chewing mouthparts characterized by mandibles and other elements that slice, tear, or crush plant and other tissues

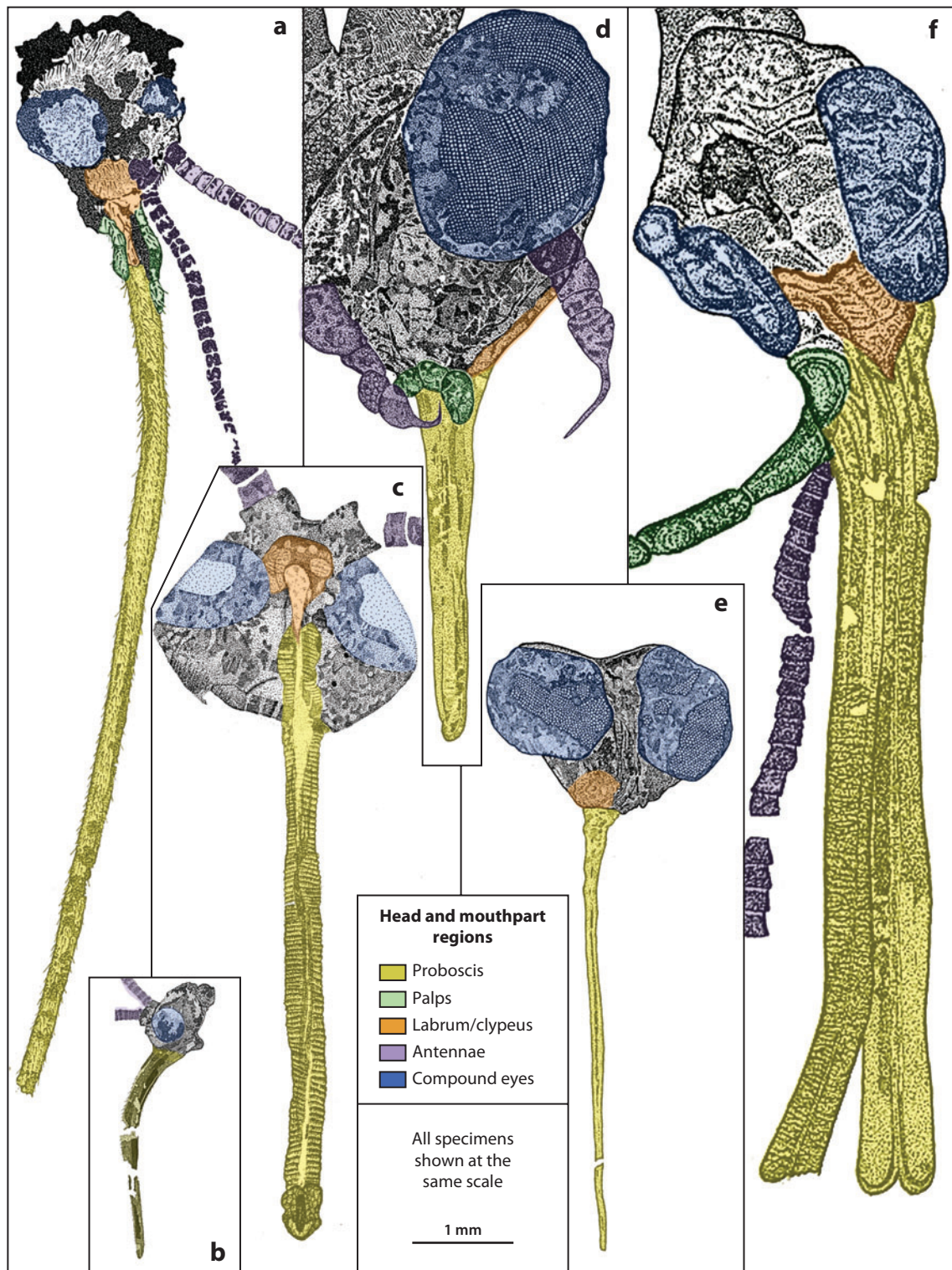
#### Long-proboscid mouthparts:

specialized mouthparts in which maxillary or labial head elements become considerably elongated to form a siphon for surface fluid feeding

#### Pollinate reproductive organ:

a male organ in seed plants that bears pollen variously in sacs or other contained structures, sometimes accessed by insect pollinators

---





(Klavins et al. 2005, Labandeira et al. 2007a, Labandeira 2010, Pott et al. 2010), and specialist lineages of punch-and-sucking thrips for cycads and ginkgoaleans, wherein stout, stylet-bearing mouthparts are used to puncture spores or pollen to extract protoplasts (Terry 2002, Peñalver et al. 2012).

## How Did the Angiosperm Revolution Affect Pollination?

The emergence of major angiosperm clades during an interval from 120 to 100 Mya replaced older pollination modes involving gymnosperms with new associations of angiosperms. Three patterns express this transformation (Labandeira 2010): (a) the extinction of most gymnosperms and their pollinators (some melanthripid thrips, many beetles, orthopteroids, scorpionflies, kalligrammatid lacewings); (b) the lateral transfer of some lineages of brachyceran flies to angiosperms (tanglevein flies, flower-loving flies, pangionine horse flies); and (c) the origination of new lineages associated with the pollination of early angiosperms (thripid thrips, moths, bees). Early in angiosperm evolution, initial pollinator associations included flowers with special fly traps (Gandolfo et al. 2004); small bowl-shaped flowers that were muted in color and mostly lacking nectarial rewards and that were pollinated by small thrips, nematocerous flies, moths, wasps, and probably bees (Luo & Li 1999; Thien et al. 2000, 2009; Hu et al. 2008; Danforth & Poinar 2011; Hartkopf-Fröder et al. 2011); and flowers with structures for advanced bee pollination (Crepet & Nixon 1998). Later, during the mid-Late Cretaceous, heath-like flowers with modestly deep throated floral tubes signal the earliest occurrence of an abbreviated long-proboscid mode that would accommodate short to modestly elongate, probing mouthparts, such as those of larger wasps, smaller bees, or moths with short siphonate proboscides (Nixon & Crepet 1993, Schönenberger & Friis 2001). Further structural elaborations of flowers continued into the Paleogene, such as more-differentiated nectarial tissue and bilaterally symmetrical flowers for specialized pollination (Crepet 1979, Taylor & Crepet 1987). More recent, Late Paleogene–Early Neogene occurrences include the familiar fig-fig wasp (Peñalver et al. 2006, Compton et al. 2010), yucca-yucca moth (Pellmyr & Leebens-Mack 1999), and orchid-bee pollination mutualisms, the latter involving pseudocopulatory deceit, wherein a male pollinating insect attempts to mate with a modified floral structure that closely resembles the species' female (Ramírez et al. 2007).

---

### Figure 6

Long-proboscid insects from the Jiulongshan and Yixian Formations of northeastern China during the mid-Mesozoic, before the ecologically significant appearance of angiosperms. Specimens are size standardized. Three lineages of long-proboscid scorpionflies of the order Mecoptera (scorpionflies) are represented: (a) the Mesopsychidae (*Lichnomesopsyche gloriae*), (b) the Pseudopolycentropodidae (*Pseudopolycentropus janeanae*), and (c) the Aneuretopsychidae (*Jeholopsyche liaoningensis*) (Ren et al. 2009). In the order Diptera (true flies), long-proboscid insects comprise (d) the Nemestrinidae (*Florinemestrius pulcherrimus*) and (e) *Protonemestrius jurassicus* (Ren 1998). From the order Neuroptera (lacewings, antlions, and relatives), panel f shows an undescribed kalligrammatid lacewing. Note the variation in proboscis length, shape, aspect ratio, terminus modification, and surface ornamentation in associated structures such as palps, in these convergently evolved insects. The specimens depicted in panels a, b, and f are from the Jiulongshan Formation at Daohugou, of late Middle Jurassic age; those in panels c, d, and e are from the Yixian Formation at Huangbanjiguo, of mid–Early Cretaceous age. Labandeira (2010) provides additional details. Panels a–c are reproduced, with permission, from the American Association for the Advancement of Science; panels d and e are reproduced, with permission, from the Missouri Botanical Garden Press.

## SUMMARY POINTS

1. Examination of the fossil record of plant-insect dynamics is a fruitful way to understand deep-time terrestrial ecology at the local habitat level. This fossil archive offers an important opportunity for understanding broader, community-level patterns in time and space, providing an ecologic component to major evolutionary trends.
2. Deciphering plant-insect dynamics of the past requires assembling a case using a detective-like approach based on a variety of direct, indirect, and circumstantial evidence. Such an inquiry also requires a battery of analytical tools for robustly demonstrating associational patterns.
3. Arthropod herbivory was initiated during the Early Devonian within early detritivore-based terrestrial ecosystems. This early herbivory is characterized by two pulses: one during the Early Devonian and a second, more extensive one commencing at the Mississippian–Pennsylvanian boundary.
4. Continuation of the second herbivory pulse into the Permian resulted in the spread of plant-insect interactions across vegetated landscapes in a variety of habitats, including those with xeromorphic vegetation.
5. The P-Tr and K-Pg ecological crises had a devastating effect on plant-insect associations, resulting in major lags in plant-host recovery and their subsequent colonization by insect herbivores.
6. The PETM expressed a transient, short-lived increase in temperature and  $p\text{CO}_2$  levels within a longer term, several-million-year Eocene warm interval. Both are associated with increases in insect herbivory.
7. Although pollination is an ancient association with roots in the late Paleozoic, there was establishment of distinctive mid-Mesozoic modes of feeding on pollen and the pollen drops in some gymnosperm reproductive organs, including the long-proboscid pollination mode.
8. Early angiosperms and their repertoire of insects extinguished mid-Mesozoic modes of pollination and reinvented pollination during the mid-Cretaceous, initially with generalist associations and later with specialist associations during the Late Cretaceous and Paleogene.

## FUTURE ISSUES

1. The ecological change of insect herbivore component communities in well-preserved, recurring, and geologically long-lived plant hosts needs to be investigated. Candidates include (a) the Pennsylvanian–Early Permian medullosan seed fern *Macroneuropteris scheuchzeri*, (b) the Jurassic bennettitalean *Anomozamites-Williamsonia-Weltrichia-Bucklandia* plant, and (c) the Late Cretaceous–Recent sycamore lineage of *Sapindopsis-Platanites-Platanus*.
2. The radiation of plant hosts and their insect herbivores following the P-Tr crisis in the Karoo Basin of South Africa must be explored in greater detail.

3. The number of worldwide K-Pg data sets for understanding the global patterns of the end-Cretaceous crisis for early Paleogene plant-insect associations needs to be expanded. Possibilities include the Denver Basin in Colorado and the Raton Basin in Colorado and New Mexico.
4. The Eocene–Miocene plant-insect associations in northeastern Africa should be examined, and their links to a known ecological and paleoclimatological history of the region need to be established.
5. The past trophic role of plant-insect associations in establishing highly resolved food webs in well-preserved, deep-time deposits should be evaluated. Possibilities include extensive lake deposits in western Eurasia of Jurassic and Early Cretaceous age.
6. The fidelity at which the fossil record captures insect damage on the basis of modern damage-spectra studies should be ascertained in more detail.
7. Jurassic floras need to be evaluated for insect damage and evidence of pollination. In addition, a relationship between bennettitalean herbivory levels and their possible pollination needs to be explored.
8. Knowledge is needed of the complete spectrum of pollination modes during the preangiospermous mid-Mesozoic. One focus is the timing of origin of the siphonate proboscis in early insect lineages.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

## ACKNOWLEDGMENTS

We thank the editorial board of *Annual Review of Earth and Planetary Sciences* for inviting us to contribute this review. We thank our numerous colleagues who have worked with us and influenced our thoughts on plant-insect interactions. Finnegan Marsh produced **Figures 1, 2, 5, and 6**. This is contribution 250 of the Evolution of Terrestrial Ecosystems consortium at the National Museum of Natural History in Washington, DC.

## LITERATURE CITED

- Adami-Rodrigues K, de Souza PA, Iannuzzi R, Pinto ID. 2004. *Herbivoria em floras Gonduânicas do Neopaleozóico do Rio Grande do Sul: análise quantitativa*. *Rev. Bras. Paleontol.* 7:93–102
- Adams JM, Ahn S, Ainuddin N, Lee ML. 2011. A further test of a palaeoecological thermometer: Tropical forests have more herbivore damage than temperate forests. *Rev. Palaeobot. Palynol.* 164:60–66
- Adams JM, Brusa A, Ahn S, Ainuddin AN. 2010. Present-day testing of a paleoecological pattern: Is there a latitudinal difference in the diversity of insect leaf-feeding damage? *Rev. Palaeobot. Palynol.* 162:63–70
- Archangelisky S, Cúneo NR. 1987. Ferugliocladaeace, a new conifer family from the Permian of Argentina. *Rev. Palaeobot. Palynol.* 51:3–30
- Axsmith BJ, Jacobs BF. 2005. The conifer *Frenelopsis ramosissima* (Cheirolepidiaceae) in the Lower Cretaceous of Texas: systematic, biogeographical and paleoecological implications. *Int. J. Plant Sci.* 166:327–37
- Banerji J. 2004. Evidence of insect-plant interactions from the Upper Gondwana Sequence (Lower Cretaceous) in the Rajmahal Basin, India. *Gondwana Res.* 7:205–10

- Banks HP, Colthart BJ. 1993. Plant-animal-fungal interactions in Early Devonian trimerophytes from Gaspé, Canada. *Am. J. Bot.* 80:992–1001
- Bazzaz FA. 1990. The response of natural ecosystems to the rising global CO<sub>2</sub> levels. *Annu. Rev. Ecol. Syst.* 21:167–96
- Beck AL, Labandeira CC. 1998. Early Permian insect folivory on a giantopterid-dominated riparian flora from north-central Texas. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 142:139–73
- Berner RA. 2009. Phanerozoic atmospheric oxygen: new results using the GEOCARBSULF model. *Am. J. Sci.* 309:603–6
- Briscoe AD, Chittka L. 2001. The evolution of color vision in insects. *Annu. Rev. Entomol.* 46:471–510
- Carvalho MR, Wilf P, Barrios H, Currano ED, Windsor DM, et al. 2011. Tropical canopy insects link leaf damage in fossil and living forests. *Geol. Soc. Am. Abstr. Prog.* 43:381 (Abstr.)
- Césari SN. 2007. Palynological biozones and radiometric data at the Carboniferous-Permian boundary in western Gondwana. *Gondwana Res.* 11:529–36
- Clapham ME, Karr JA. 2012. Environmental and biotic controls on the evolutionary history of insect body size. *Proc. Natl. Acad. Sci. USA* 109:10927–30
- Clyde WC, Gingerich PD. 1998. Mammalian community response to the latest Paleocene thermal maximum: an isotaphonomic study in the northern Bighorn Basin, Wyoming. *Geology* 26:1011–14
- Compton SG, Ball AD, Collinson ME, Hayes P, Rasnitsyn AP, Ross AJ. 2010. Ancient fig wasps indicate at least 34 Myr of stasis in their mutualism with fig trees. *Biol. Lett.* 6:838–42
- Crane PR, Herendeen PS. 2009. Bennettitales from the Grisethorpe Bed (Middle Jurassic) at Cayton Bay, Yorkshire, UK. *Am. J. Bot.* 96:284–95
- Crepet WL. 1979. Insect pollination: a paleontological perspective. *BioScience* 29:102–8
- Crepet WL, Nixon KC. 1998. Fossil Clusiaceae from the Late Cretaceous (Turonian) of New Jersey and implications regarding the history of bee pollination. *Am. J. Bot.* 85:1122–33
- Currano ED, Jacobs BF, Pan AD, Tabor NJ. 2011. Inferring ecological disturbance in the fossil record: a case study from the late Oligocene of Ethiopia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 309:242–52
- Currano ED, Labandeira CC, Wilf P. 2010. Fossilized insect folivory tracks temperature for six million years. *Ecol. Monogr.* 80:547–67
- Currano ED, Wilf P, Wing SL, Labandeira CC, Lovelock EC, Royer DL. 2008. Sharply increased insect herbivory during the Paleocene-Eocene Thermal Maximum. *Proc. Natl. Acad. Sci. USA* 105:1960–64
- Danforth BN, Poinar GO Jr. 2011. Morphology, classification, and antiquity of *Melittosphex burmensis* (Apoidea: Melittosphecidae) and implications for early bee evolution. *J. Paleontol.* 85:882–91**
- D’Rozario A, Labandeira CC, Guo WY, Yao YF, Li CS. 2011. Spatiotemporal extension of the Euramerican *Psaronius* component community to the Late Permian of Cathaysia: in situ coprolites in a *P. housuoensis* stem from Yunnan Province, southwest China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 306:127–33
- Edwards D, Selden PA. 1992. The development of early terrestrial ecosystems. *Bot. J. Scotl.* 46:337–66
- Erwin DM, Schick KN. 2007. New Miocene oak galls (Cynipini) and their bearing on the history of cynipid wasps in western North America. *J. Paleontol.* 81:568–80
- Futuyma DJ, Agrawal AA. 2009. Macroevolution and the biological diversity of plants and herbivores. *Proc. Natl. Acad. Sci. USA* 106:18054–61
- Gandolfo MA, Nixon KC, Crepet WL. 2004. Cretaceous flowers of Nymphaeaceae and implications for complex insect entrapment pollination mechanisms in early angiosperms. *Proc. Natl. Acad. Sci. USA* 101:8056–60
- García-Robledo C, Staines CL. 2008. Herbivory in gingers from latest Cretaceous to present: Is the ichnogenus *Cephaloeichnites* (Hispinæ: Coleoptera) a rolled-leaf beetle? *J. Paleontol.* 82:1035–37
- Gastaldo RA, Adendorff R, Bamford M, Labandeira CC, Neveling J, Sims H. 2005. Taphonomic trends of macrofloral assemblages across the Permian-Triassic boundary, Karoo Basin, South Africa. *Palaios* 20:480–98
- Gentry AH. 1988. Tree species richness of upper Amazonian forests. *Proc. Natl. Acad. Sci. USA* 85:156–57
- Glasspool IJ, Hilton J, Collinson ME, Wang SJ. 2003. Foliar herbivory in Late Paleozoic Cathaysian giantopterids. *Rev. Palaeobot. Palynol.* 127:125–32
- Gorelick R. 2001. Did insect pollination cause increased seed plant diversity? *Biol. J. Linn. Soc.* 74:407–27

---

Danforth & Poinar  
2011: The first  
description of a bee  
from Early Cretaceous;  
documents this key  
pollinator group among  
early angiosperms.

---

**Grimaldi D. 1999. The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Ann. Mo. Bot. Gard.* 86:373–406**

Grimaldi D, Engel MS. 2005. *Evolution of the Insects*. New York: Cambridge Univ. Press. 755 pp.

Grubb PJ, Jackson RV, Barberis IM, Bee JN, Coomes DA, et al. 2008. Monocot leaves are eaten less than dicot leaves in tropical lowland rain forests: correlations with toughness and leaf predation. *Ann. Bot.* 101:1379–89

Harris TM. 1940. *Caytonia*. *Ann. Bot.* 4:713–34

Harris TM. 1951. The fructification of *Czekanowskia* and its allies. *Philos. Trans. R. Soc. B* 235:483–508

Harris TM. 1973. *The strange Bennettitales*. Presented at 19th Sir Albert Charles Seward Mem. Lect., 1970, pp. 1–11, Birbal Sahni Inst. Palaeobot., Lucknow, India

Hartkopf-Fröder C, Rust J, Wappler T, Friis EM, Viehofen A. 2011. Mid-Cretaceous charred fossil flowers reveal direct observation of arthropod feeding strategies. *Biol. Lett.* 8:295–98

Hu SS, Dilcher DL, Jarzen DM, Taylor DW. 2008. Early steps of angiosperm-pollinator coevolution. *Proc. Natl. Acad. Sci. USA* 105:240–45

Hughes DP, Wappler T, Labandeira CC. 2010. Ancient death-grip leaf scars reveal ant-fungal parasitism. *Biol. Lett.* 7:67–70

Iannuzzi R, Labandeira CC. 2008. The oldest record and early history of insect folivory. *Ann. Entomol. Soc. Am.* 101:79–94

Iglesias A, Wilf P, Johnson KR, Zamuner AB, Cúneo NR, et al. 2007. A Paleocene lowland macroflora from Patagonia reveals significantly greater richness than North American analogs. *Geology* 35:947–50

Janson EM, Stiremann JO III, Singer MS, Abbot P. 2008. Phytophagous insect-microbe mutualisms and adaptive evolutionary diversification. *Evolution* 62:997–1012

Kennett JP, Stott LD. 1991. Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene. *Nature* 353:225–29

**Kevan PG, Chaloner WG, Savile DBO. 1975. Interrelationships of early terrestrial arthropods and plants. *Palaeontology* 18:391–417**

Klavins SD, Kellogg DW, Krings M, Taylor EL, Taylor TN. 2005. Coprolites in a Middle Triassic cycad pollen cone: evidence for insect pollination in early cycads? *Evol. Ecol. Res.* 7:479–88

Koch PL, Zachos JC, Gingerich PD. 1992. Correlation between isotope records in marine and continental carbon reservoirs near the Paleocene/Eocene boundary. *Nature* 358:319–22

Krassilov V, Karasev E. 2008. First evidence of plant–arthropod interaction at the Permian–Triassic boundary in the Volga Basin, European Russia. *Alavesia* 2:247–52

Krassilov V, Shuklina S. 2008. Arthropod trace diversity on fossil leaves from the mid-Cretaceous of Negev, Israel. *Alavesia* 2:239–45

Krings M, Taylor TN, Kellogg DW. 2002. Touch-sensitive glandular trichomes: a mode of defence against herbivorous arthropods in the Carboniferous. *Evol. Ecol. Res.* 4:779–86

**Kvaček J. 2000. *Frenelopsis alata* and its microsporangiate and ovuliferous reproductive structures from the Cenomanian of Bohemia (Czech Republic, Central Europe). *Rev. Palaeobot. Palynol.* 112:51–78**

Labandeira CC. 1998. Early history of arthropod and vascular plant associations. *Annu. Rev. Earth Planet. Sci.* 26:329–77

Labandeira CC. 2002a. The paleobiology of predators, parasitoids, and parasites: accommodation and death in the fossil record of terrestrial invertebrates. *Paleontol. Soc. Pap.* 8:211–50

Labandeira CC. 2002b. The history of associations between plants and animals. In *Plant–Animal Interactions: An Evolutionary Approach*, ed. C Herrera, O Pellmyr, pp. 26–74, 248–61. Oxford, UK: Blackwell

Labandeira CC. 2005. The fossil record of insect extinction: new approaches and future directions. *Ann. Entomol.* 51:14–29

Labandeira CC. 2006a. Silurian to Triassic plant and insect clades and their associations: new data, a review, and interpretations. *Arthropod Syst. Phylogeny* 64:53–94

Labandeira CC. 2006b. The four phases of plant–arthropod associations in deep time. *Geol. Acta* 4:409–38

Labandeira CC. 2007. The origin of herbivory on land: the initial pattern of live tissue consumption by arthropods. *Insect Sci.* 14:259–74

---

Grimaldi 1999: A broad, updated review of evidence between emerging mid-Cretaceous angiosperms and their insect associates.

---

---

Kevan, Chaloner & Savile 1975: The seminal paper that established the presence of herbivory and spore consumption during the Devonian.

---

---

Kvaček 2000: The first detailed, microanatomical study from superb material of the reproductive peculiarities of a cheirolepidiacean conifer.

---

- Labandeira CC. 2010. The pollination of mid-Mesozoic seed plants and the early history of long-proboscid insects. *Ann. Mo. Bot. Gard.* 97:469–513
- Labandeira CC. 2011. Evidence for an earliest Late Carboniferous divergence and early larval ecology and diversification of major Holometabola. *Entomol. Am.* 117:9–21
- Labandeira CC. 2012. Evidence for outbreaks from the fossil record of insect herbivory. In *Insect Outbreaks Revisited*, ed. P Barbosa, AA Agrawal, D Letorneau, pp. 269–90. Oxford, UK: Blackwell
- Labandeira CC, Allen EM. 2007. Minimal insect herbivory for the Lower Permian Coprolite Bone Bed site of north-central Texas, USA, and comparison to other Late Paleozoic floras. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 247:197–219
- Labandeira CC, Dunne JA, Williams RJ. 2011. The Messel food web. *Proc. Int. Senckenberg Conf., 22nd, Frankfurt, Nov. 15–19*, ed. T Lehmann, V Mossbrugger, S Schaal, pp. 95–97. Frankfurt: Senckenberg Ges. Naturforsch.
- Labandeira CC, Johnson KR, Wilf P. 2002. Impact of the terminal Cretaceous event on plant-insect associations. *Proc. Natl. Acad. Sci. USA* 99:2061–66
- Labandeira CC, Kvaček J, Mostovski MB. 2007a. Pollination fluids, pollen, and insect pollination of Mesozoic gymnosperms. *Taxon* 56:663–95
- Labandeira CC, Phillips TL. 1996. Insect fluid-feeding on Upper Pennsylvanian tree ferns (Palaeodictyoptera, Marattiales) and the early history of the piercing-and-sucking functional feeding group. *Ann. Entomol. Soc. Am.* 89:157–83
- Labandeira CC, Phillips TL. 2002. Stem borings and petiole galls from Pennsylvanian tree ferns of Illinois, USA: implications for the origin of the borer and galling functional-feeding-groups and holometabolous insects. *Palaeontogr. Abt. A* 264:1–84
- Labandeira CC, Phillips TL, Norton RL. 1997. Oribatid mites and decomposition of plant tissues in Paleozoic coal-swamp forests. *Palaios* 12:317–51
- Labandeira CC, Wilf P, Johnson KR, Marsh F. 2007b. *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils*. Washington, DC: Smithsonian. Inst. Version 3.0. <http://paleobiology.si.edu/pdfs/InsectDamageGuide3.01.pdf>
- Lesnikowska AD. 1990. Evidence for herbivory in the tree fern petioles from the Calhoun Coal (Upper Pennsylvanian) of Illinois. *Palaios* 5:76–80
- Lincoln DE, Fajer ED, Johnson RH. 1993. Plant-insect herbivore interactions in elevated CO<sub>2</sub> environments. *Trends Ecol. Evol.* 8:64–68
- Lopez-Vaamonde C, Wikström N, Labandeira CC, Goodman S, Godfray HCJ, Cook JM. 2006. Fossil-calibrated molecular phylogenies reveal that leaf-mining moths radiated millions of years after their host plants. *J. Evol. Biol.* 19:1314–26**
- Luo Y-B, Li Z-Y. 1999. Pollination ecology of *Chloranthus serratus* (Thunb.) Roem. et Schult. and *Cb. fortunei* (A. Gray) Solms-Laub. (Chloranthaceae). *Ann. Bot.* 83:489–99
- McKenna DD, Sequeira AS, Marvaldi AE, Farrell BD. 2009. Temporal lags and overlap in the diversification of weevils and flowering plants. *Proc. Natl. Acad. Sci. USA* 106:7083–88
- McLoughlin S. 2011. New records of leaf galls and arthropod oviposition scars in Permian-Triassic Gondwanan gymnosperms. *Aust. J. Bot.* 59:156–69
- McLoughlin S. 2012. *Glossopteris*—insights into the architecture and relationships of an iconic Permian Gondwanan plant. *J. Bot. Soc. Bengal* 65:1–14
- Meller B, Ponomarenko AG, Vasilenko DV, Fischer TC, Aschauer B. 2011. First beetle elytra, abdomen (Coleoptera) and a mine trace from Lunz (Carnian, Late Triassic, Lunz-am-See, Austria) and their taphonomical and evolutionary aspects. *Palaeontology* 54:97–110
- Memmot J, Godfray HCJ, Gauld ID. 1994. The structure of a tropical host parasitoid community. *J. Anim. Ecol.* 63:521–40
- Moisan P, Labandeira CC, Matushkina NA, Wappler T, Voigt S, Kerp H. 2012. Lycopsid-dragonfly associations and odonatopteran oviposition on Triassic herbaceous *Isoetes*. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 344/345:6–15
- Naugolnykh SV. 2008. A new gymnosperm *Sylvocarpus armatus* gen. et sp. nov. from the Lower Permian of the Ural Mountains. *Paleontol. J.* 42:431–39

---

Lopez-Vaamonde et al. 2006: Provided support from molecular phylogeny and fossils that moth leaf miner colonization occurred long after their plant hosts appeared.

---

- Nixon KC, Crepet WL. 1993. Late Cretaceous fossil flowers of ericalean affinity. *Am. J. Bot.* 80:616–23
- Novotny V, Basset Y. 2005. Host specificity of insect herbivores in tropical forests. *Proc. R. Soc. B* 272:1083–90**
- Opler PA. 1973. Fossil lepidopterous leaf mines demonstrate the age of some insect-plant relationships. *Science* 179:1321–23**
- Osborn JM, Taylor ML. 2010. Pollen and coprolite structure in *Cycadeoidea* (Bennettitales): implications for understanding pollination and mating systems in Mesozoic cycadeoids. In *Plants in Deep Mesozoic Time: Morphological Innovations, Phylogeny, and Ecosystems*, ed. CT Gee, pp. 34–49. Bloomington: Indiana Univ. Press
- Pellmyr O, Leebens-Mack J. 1999. Forty million years of mutualism: evidence for Eocene origin of the yucca-yucca moth association. *Proc. Natl. Acad. Sci. USA* 96:9178–83
- Peñalver E, Engel MS, Grimaldi DA. 2006. Fig wasps in Dominican amber (Hymenoptera: Agaonidae). *Am. Mus. Novit.* 3541:1–16
- Peñalver E, Labandeira CC, Barrón E, Delclòs X, Nel P, et al. 2012. Thrips pollination of Mesozoic gymnosperms. *Proc. Natl. Acad. Sci. USA* 109:8623–28
- Petrulevičius JF, Wappler T, Nel A, Rust J. 2011. The diversity of Odonata and their endophytic ovipositions from the Upper Oligocene Fossilagerstätte of Rott (Rhineland, Germany). *ZooKeys* 130:67–89
- Pinheiro ERD, Iannuzzi R, Tybusch GP. 2012. Specificity of leaf damage in the Permian “*Glossopteris* flora”: a quantitative approach. *Rev. Palaeobot. Palynol.* 174:113–21
- Pocock MJO, Evans DM, Memmot J. 2012. The robustness and restoration of a network of ecological networks. *Science* 335:973–77
- Popa ME, Zaharia A. 2011. Early Jurassic ovipositories on bennettitalean leaves from Romania. *Acta Palaeontol. Rom.* 7:285–90
- Pott C, Krings M, Kerp H, Friis EM. 2010. Reconstruction of a bennettitalean flower from the Carnian (Upper Triassic) of Lunz, Lower Austria. *Rev. Palaeobot. Palynol.* 159:94–111
- Pott C, Labandeira CC, Krings M, Kerp H. 2008. Fossil insect eggs and ovipositional damage on bennettitalean leaf cuticles from the Carnian (Upper Triassic) of Austria. *J. Paleontol.* 82:778–89
- Pott C, McLoughlin S, Wu SQ, Friis EM. 2012. Trichomes on the leaves of *Anomozamites villosus* sp. nov. (Bennettitales) from the Daohugou beds (Middle Jurassic), Inner Mongolia, China: mechanical defense against herbivorous arthropods. *Rev. Palaeobot. Palynol.* 169:48–60
- Prevec R, Labandeira CC, Neveling J, Gastaldo RA, Looy C, Bamford MA. 2009. A portrait of a Gondwanan ecosystem: a new Late Permian locality from Kwa-Zulu Natal, South Africa. *Rev. Palaeobot. Palynol.* 156:454–93
- Price PW, Diniz IR, Morais HC, Marques ESA. 1995. The abundance of insect herbivore species in the tropics: the high local richness of local species. *Biotropica* 27:468–78
- Ramírez SR, Gravaendeel B, Singer RB, Marshall CR, Pierce NE. 2007. Dating the origin of the Orchidaceae from a fossil orchid with its pollinator. *Nature* 448:1042–45
- Rasnitsyn AP. 1977. New Paleozoic and Mesozoic insects. *Paleontol. J.* 11:60–73
- Regier JC, Mitter C, Solís MA, Hayden JE, Landry B, et al. 2012. A molecular phylogeny for the pyraloid moths (Lepidoptera: Pyraloidea) and its implications for higher-level classification. *Syst. Entomol.* 37:635–56
- Ren D. 1998. Flower-associated Brachycera flies as fossil evidence for Jurassic angiosperm origins. *Science* 280:85–88**
- Ren D, Labandeira CC, Santiago-Blay JA, Rasnitsyn AP, Shih CK, et al. 2009. A probable pollination mode before angiosperms: Eurasian, long-proboscis scorpionflies. *Science* 326:840–47
- Retallack GJ, Dilcher DL. 1988. Reconstructions of selected seed ferns. *Ann. Mo. Bot. Gard.* 75:1010–57
- Root RB. 1973. Organization of plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* 43:95–124
- Royer DL, Sack L, Wilf P, Lusk CH, Jordan GJ, et al. 2007. Fossil leaf economics quantified: calibration, Eocene case study, and implications. *Paleobiology* 34:574–89
- Rydin C, Friis EM. 2010. A new Early Cretaceous relative of the Gnetales: *Siphonospermum simplex* gen. et sp. nov. from the Yixian Formation of northeast China. *BMC Evol. Biol.* 10:183

---

**Novotny & Basset 2005:** Demonstrated that feeding guilds in the tropics are not as host specialized as formerly thought.

---

**Opler 1973:** The first fossil-based study indicating that modern, host-specific leaf-mine types have an antiquity, extending deep into the fossil record.

---



---

**Ren 1998:** The first demonstration of the long-proboscis pollination mode occurring in an essentially preangiospermous mid-Mesozoic flora.

---

---

Scott & Taylor 1983:  
A widely cited paper  
integrating many  
concepts and topics  
about Carboniferous  
plant-insect  
associations.

---

- Sarzetti LC, Labandeira CC, Muzón J, Wilf P, Cúneo NR, et al. 2009. Odonatan endophytic oviposition from the Eocene of Patagonia: the genus *Paleoovoidius* and implications for dragonfly behavioral stasis. *J. Paleontol.* 83:431–47
- Schönenberger J, Friis EM. 2001. Fossil flowers of ericalean affinity from the Late Cretaceous of Southern Sweden. *Am. J. Bot.* 88:467–80
- Schoonhoven LM, van Loon JJA, Dicke M. 2005. *Insect-Plant Biology*. Oxford, UK: Oxford Univ. Press. 421 pp. 2nd ed.
- Schwendemann AB, Wang G, Mertz ML, McWilliams RT, Thatcher SL, et al. 2007. Aerodynamics of saccate grains and its implications for pollination. *Am. J. Bot.* 94:1371–82
- Scott AC, Anderson JM, Anderson HM. 2004. Evidence of plant-insect interactions in the Upper Triassic Molteno Formation of South Africa. *J. Geol. Soc.* 161:401–10
- Scott AC, Taylor TN. 1983. Plant-animal interactions during the Upper Carboniferous. *Bot. Rev.* 49:259–307**
- Secord R, Bloch JI, Chester SGB, Boyer DM, Wood AR, et al. 2012. Evolution of the earliest horses driven by climate change in the Paleocene-Eocene Thermal Maximum. *Science* 335:959–62
- Shcherbakov DE. 2008. Insect recovery after the Permian/Triassic crisis. *Alavesia* 2:125–31
- Shear WA, Kukulová-Peck J. 1990. The ecology of Paleozoic terrestrial arthropods: the fossil evidence. *Can. J. Zool.* 68:1807–34
- Smith DM, Nufio CR. 2004. Levels of herbivory in two Costa Rican rain forests: implications for studies of fossil herbivory. *Biotropica* 36:318–26
- Smith JJ, Hasiotis ST, Kraus MJ, Woody DT. 2009. Transient dwarfism of soil fauna during the Paleocene-Eocene Thermal Maximum. *Proc. Natl. Acad. Sci. USA* 106:17655–60
- Sohn JA, Labandeira CC, Davis D, Mitter C. 2012. An annotated catalog of fossil and subfossil Lepidoptera (Insecta: Holometabola) of the world. *Zootaxa* 3286:1–132
- Stockey RA, Rothwell GW. 2003. Anatomically preserved *Williamsonia* (Williamsoniaceae): evidence for bennettitalean reproduction in the Late Cretaceous of western North America. *Int. J. Plant Sci.* 164:251–62
- Stone GN, Hernandez-Lopez A, Nicholls JA, di Pierro E, Pujade-Villar J, et al. 2009. Extreme host plant conservatism during at least 20 million years of host plant pursuit by oak gallwasps. *Evolution* 63:854–69
- Strauss SY, Irwin RE. 2004. Ecological and evolutionary consequences of multispecies plant-animal interactions. *Annu. Rev. Ecol. Evol. Syst.* 35:435–66
- Strömberg CAE. 2005. Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. *Proc. Natl. Acad. Sci. USA* 102:11980–84
- Strong DR. 1977. Rolled-leaf hispine beetles (Chrysomelidae) and their Zingiberales host plants in middle America. *Biotropica* 9:156–69
- Taylor DW, Crepet WL. 1987. Fossil floral evidence of Malpighiaceae and an early plant-pollinator relationship. *Am. J. Bot.* 74:274–86
- Terry I. 2002. Thrips: the primeval pollinators? *Thrips and Topoviruses: Proc. 7th Int. Symp. Thysanoptera*, pp. 157–62. Canberra: Aust. Natl. Insect Collect.
- Thien LB, Azuma H, Kawano S. 2000. New perspectives on the pollination biology of basal angiosperms. *Int. J. Plant Sci.* 161:S225–35
- Thien LB, Bernhardt P, Devall MS, Chen ZD, Luo YB, et al. 2009. Pollination biology of basal angiosperms (ANITA grade). *Am. J. Bot.* 96:166–82
- Vajda V, Raine JI, Hollis CJ. 2001. Indication of global deforestation at the Cretaceous-Tertiary boundary by New Zealand fern spike. *Science* 294:1700–2
- Vasilenko DV. 2005. Damages on Mesozoic plants from the Transbaikalian locality Chernovskie Kopi. *Paleontol. J.* 39:628–33
- Vasilenko DV. 2006. Margin feeding damage on the leaves of conifers and Ginkgoales from the Mesozoic of Transbaikalia. *Paleontol. J.* 40:286–89
- Vega FE, Blackwell M, eds. 2004. *Insect-Fungal Associations: Ecology and Evolution*. Oxford, UK: Oxford Univ. Press. 336 pp.
- Waggoner BM, Potet MF. 1996. Unusual oak leaf galls from the middle Miocene of northwestern Nevada. *J. Paleontol.* 70:1080–84



- Wang YJ, Labandeira CC, Shih CK, Ding QL, Wang C, et al. 2012. Jurassic mimicry between a hangingfly and a ginkgo from China. *Proc. Natl. Acad. Sci. USA* 109:20514–19
- Wang YJ, Liu Z, Wang X, Shih C, Zhao Y, et al. 2010. Ancient pinnate leaf mimesis among lacewings. *Proc. Natl. Acad. Sci. USA* 107:16212–15
- Wappler T. 2010. Insect herbivory close to the Oligocene–Miocene transition—A quantitative analysis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 292:540–50
- Wappler T, Currano ED, Wilf P, Labandeira CC. 2009. No post-Cretaceous ecosystem depression in European forests? Rich insect-feeding damage on diverse middle Palaeocene plants, Menat, France. *Proc. R. Soc. B* 276:4271–77
- Wappler T, Denk T. 2011. Herbivory in early Tertiary Arctic forests. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 310:283–95
- Wappler T, Labandeira CC, Rust J, Frankenhäuser H, Wilde V. 2012. Testing for the effects and consequences of mid Paleogene climate change on insect herbivory. *PLoS ONE* 7:e40744
- Ward P, Labandeira CC, Laurin M, Berner R. 2006. Confirmation of Romer’s Gap as a low oxygen interval constraining the timing of initial arthropod and vertebrate terrestrialization. *Proc. Natl. Acad. Sci. USA* 103:16818–22
- Waser NM, Chittka L, Price MV, Williams NM, Ollerton J. 1996. Generalization in pollination systems and why it matters. *Ecology* 77:1043–60
- Watt AD, Whittaker JB, Docherty M, Brooks G, Lindsay E, Salt DT. 1995. The impact of elevated atmospheric CO<sub>2</sub> on insect herbivores. In *Insects in a Changing Environment*, ed. R Harrington, N Stork, pp. 198–217. San Diego: Academic
- Wedmann S, Bradler S, Rust J. 2007. The first fossil leaf insect: 47 million years of specialized cryptic morphology and behavior. *Proc. Natl. Acad. Sci. USA* 104:565–69
- White D. 1908. Report on the fossil flora of the coal measures of Brazil. *Comissão Estud. Minas Carvão Pedra, Relat. Final* 3:337–617
- Wilf P. 2008. Insect-damaged fossil leaves record food web response to ancient climate change and extinction. *New Phytol.* 178:486–502
- Wilf P, Labandeira CC. 1999. Response of plant-insect associations to Paleocene-Eocene warming. *Science* 284:2153–56**
- Wilf P, Labandeira CC, Johnson KR, Coley PD, Cutter AD. 2001. Insect herbivory, plant defense, and early Cenozoic climate change. *Proc. Natl. Acad. Sci. USA* 98:6221–26
- Wilf P, Labandeira CC, Johnson KR, Cúneo NR. 2005. Richness of plant-insect associations in Eocene Patagonia: a legacy for South American biodiversity. *Proc. Natl. Acad. Sci. USA* 102:8944–48
- Wilf P, Labandeira CC, Johnson KR, Ellis B. 2006. Decoupled plant and insect diversity after the end-Cretaceous extinction. *Science* 313:1112–15
- Wilf P, Labandeira CC, Kress JW, Staines CL, Windsor DM, et al. 2000. Timing the radiations of leaf beetles: hispines on gingers from latest Cretaceous to recent. *Science* 289:291–94
- Wing SL, Bao H, Koch PL. 2000. An early Eocene cool period? Evidence for continental cooling during the warmest part of the Cenozoic. In *Warm Climates in Earth History*, ed. BT Huber, KG MacLeod, SL Wing, pp. 197–237. Cambridge, UK: Cambridge Univ. Press
- Wing SL, Herrera F, Jaramillo C, Gómez C, Wilf P, Labandeira CC. 2009. Late Paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of neotropical rainforests. *Proc. Natl. Acad. Sci. USA* 106:18627–32
- Winkler IS, Labandeira CC, Wappler T, Wilf P. 2010. Diptera (Agromyzidae) leaf mines from the Paleogene of North America and Germany: implications for host use evolution and an early origin for the Agromyzidae. *J. Paleontol.* 84:935–54
- Winkler IS, Mitter C. 2009. The phylogenetic dimension of insect-plant interactions: a review of recent evidence. In *Specialization, Speciation and Radiation: The Evolutionary Biology of Herbivorous Insects*, ed. K Tillmon, pp. 240–63. Berkeley/Los Angeles: Univ. Calif. Press
- Zachos JC, Wara MW, Bohaty S, Delaney ML, Petrizzo MR, et al. 2003. A transient rise in tropical sea surface temperature during the Paleocene-Eocene Thermal Maximum. *Science* 302:1551–54
- Zheng SJ, Dicke M. 2008. Ecological genomics of plant-insect interactions: from gene to community. *Plant Physiol.* 146:812–17

---

**Wilf & Labandeira 1999: The first paper to quantify insect damage and introduce analytical methods for tracking fossil insect herbivory.**

---



# Contents

On Escalation <i>Geerat J. Vermeij</i> .....	1
The Meaning of Stromatolites <i>Tanja Bosak, Andrew H. Knoll, and Alexander P. Petroff</i> .....	21
The Anthropocene <i>William F. Ruddiman</i> .....	45
Global Cooling by Grassland Soils of the Geological Past and Near Future <i>Gregory J. Retallack</i> .....	69
Psychrophiles <i>Khawar S. Siddiqui, Timothy J. Williams, David Wilkins, Sheree Yau, Michelle A. Allen, Mark V. Brown, Federico M. Lauro, and Ricardo Cavicchioli</i> .....	87
Initiation and Evolution of Plate Tectonics on Earth: Theories and Observations <i>Jun Korenaga</i> .....	117
Experimental Dynamos and the Dynamics of Planetary Cores <i>Peter Olson</i> .....	153
Extracting Earth's Elastic Wave Response from Noise Measurements <i>Roel Snieder and Eric Larose</i> .....	183
Miller-Urey and Beyond: What Have We Learned About Prebiotic Organic Synthesis Reactions in the Past 60 Years? <i>Thomas M. McCollom</i> .....	207
The Science of Geoengineering <i>Ken Caldeira, Govindasamy Bala, and Long Cao</i> .....	231
Shock Events in the Solar System: The Message from Minerals in Terrestrial Planets and Asteroids <i>Philippe Gillet and Ahmed El Goresy</i> .....	257
The Fossil Record of Plant-Insect Dynamics <i>Conrad C. Labandeira and Ellen D. Currano</i> .....	287

The Betic-Rif Arc and Its Orogenic Hinterland: A Review <i>John P. Platt, Whitney M. Bebr, Katherine Jobanesen, and Jason R. Williams</i> .....	313
Assessing the Use of Archaeal Lipids as Marine Environmental Proxies <i>Ann Pearson and Anitra E. Ingalls</i> .....	359
Heat Flow, Heat Generation, and the Thermal State of the Lithosphere <i>Kevin P. Furlong and David S. Chapman</i> .....	385
The Isotopic Anatomies of Molecules and Minerals <i>John M. Eiler</i> .....	411
The Behavior of the Lithosphere on Seismic to Geologic Timescales <i>A.B. Watts, S.J. Zhong, and J. Hunter</i> .....	443
The Formation and Dynamics of Super-Earth Planets <i>Nader Haghighipour</i> .....	469
Kimberlite Volcanism <i>R.S.J. Sparks</i> .....	497
Differentiated Planetesimals and the Parent Bodies of Chondrites <i>Benjamin P. Weiss and Linda T. Elkins-Tanton</i> .....	529
Splendid and Seldom Isolated: The Paleobiogeography of Patagonia <i>Peter Wilf, N. Rubén Cúneo, Ignacio H. Escapa, Diego Pol, and Michael O. Woodburne</i> .....	561
Electrical Conductivity of Mantle Minerals: Role of Water in Conductivity Anomalies <i>Takashi Yoshino and Tomoo Katsura</i> .....	605
The Late Paleozoic Ice Age: An Evolving Paradigm <i>Isabel P. Montañez and Christopher J. Poulsen</i> .....	629
Composition and State of the Core <i>Kei Hirose, Stéphane Labrosse, and John Hernlund</i> .....	657
Enceladus: An Active Ice World in the Saturn System <i>John R. Spencer and Francis Nimmo</i> .....	693
Earth's Background Free Oscillations <i>Kiwamu Nishida</i> .....	719
Global Warming and Neotropical Rainforests: A Historical Perspective <i>Carlos Jaramillo and Andrés Cárdenas</i> .....	741
The Scotia Arc: Genesis, Evolution, Global Significance <i>Ian W.D. Dalziel, Lawrence A. Lawver, Ian O. Norton, and Lisa M. Gabagan</i> .....	767