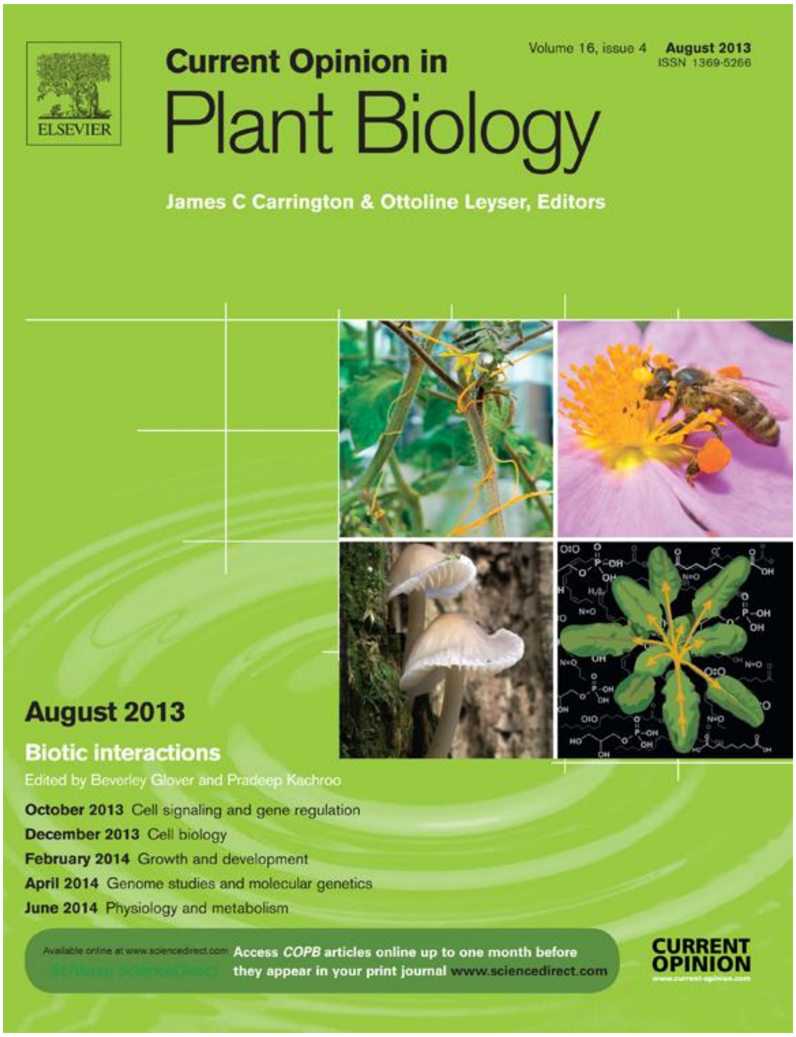

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Current Opinion in Plant Biology

A paleobiologic perspective on plant–insect interactions

Conrad C Labandeira[1,2,3,4]

Fossil plant–insect associations (PIAs) such as herbivory and pollination have become increasingly relevant to paleobiology and biology. Researchers studying fossil PIAs now employ procedures for assuring unbiased representation of field specimens, use of varied analytical quantitative techniques, and address ecological and evolutionarily important issues. For herbivory, the major developments are: Late Silurian–Middle Devonian (ca. 420–385 Ma[a]) origin of herbivory; Late Pennsylvanian (318–299 Ma) expansion of herbivory; Permian (299–252 Ma) herbivore colonization of new habitats; consequences of the end-Permian (252 Ma) global crisis; early Mesozoic (ca. 235–215 Ma) rediversification of plants and herbivores; end-Cretaceous (66.5 Ma) effects on extinction; and biological effects of the Paleocene–Eocene Thermal Maximum (PETM) (55.8 Ma). For pollination, salient issues include: Permian pollination evidence; the plant hosts of mid-Mesozoic (ca. 160–110 Ma) long-proboscid pollinators; and effect of the angiosperm revolution (ca. 125–90 Ma) on earlier pollinator relationships. Multispecies interaction studies, such as contrasting damage types with insect diversity and establishing robust food webs, expand the compass and relevance of past PIAs.

Addresses
[1] Smithsonian Institution, National Museum of Natural History, Department of Paleobiology, Washington, DC 20013, USA
[2] Rhodes University, Department of Geology, Grahamstown 6140, South Africa
[3] Capital Normal University, College of Life Sciences, Beijing 100048, China
[4] Department of Entomology and BEES Program, University of Maryland, College Park, MD 20742, USA

Corresponding author: Labandeira, Conrad C (labandec@si.edu)

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Introduction

The paleobiological study of plant–insect associations (PIAs) developed later than the allied fields of paleobotany and paleoentomology, or the study of modern PIAs. It was during the latter half of the twentieth century that an increase in the number of (largely descriptive) articles recorded the presence of fossil PIAs, eventually reaching a noticeable presence within paleobiology [1]. The discipline retained a primarily idiographic bent until the late 1990s, when the testing of hypotheses regarding changes in PIAs through time required various quantitative techniques to elucidate patterns of herbivory within and among bulk floras [2]. This transformation was spurred by studies from the Early Permian of Texas [3,4], and the Paleogene of the U.S. Western Interior [5], which increased the scope of analytical techniques [6,7]. A recent advancement is the effect of global climate change on plants and their insect herbivores [7], especially during the Paleocene–Eocene Thermal Maximum (PETM) [8••], and other Paleogene sites [9–14]. Current studies involve how plants and their insect herbivores respond to ecological crises such as mass extinctions [15,16], and the ecological expansion of new, globally dominant clades, including Mesozoic parasitoid insects [16,17•] and angiosperms [18,19•].

Examination of fossil insect pollination and related interactions has had a different history [2,7]. On the basis of the scarcity of evidence and lack of direct data, demonstrations of pollination have relied on the building of a case from multiple, independent sources of evidence [19•,20,21]. Initial interest in pollination focused on Late Carboniferous medullosan seedferns [22] (Glossary), attributable to their very large pollen grains and distinctive reproductive organs. This was followed by interest in pollination of mid-Mesozoic seedferns such as caytonialeans and bennettitaleans [19•,21–23], and early angiosperms [20,24]. Recently, there has been renewed interest in mid-Mesozoic insect–gymnosperm pollination, attributable to well preserved material from eastern Eurasia [19•,20,21,25]. Because evidence for pollination is rare in the fossil record, unlike more conspicuous herbivory, metrics were never developed to quantify pollination diversity or intensity.

Other fossil PAIs include very rare mimicry [26•] and various plant pathogens vectored by insects (CC Labandeira, R Prevec, unpublished data). These PIAs are ancient and are documented from the mid-Mesozoic [26•,27] and earlier. Nevertheless, this review will concentrate on herbivory and pollination in the fossil record in the context of recent empirical developments and relevant theoretical issues (Figure 1).

Herbivory

The earliest terrestrial ecosystems with recognizably megascopic life are from the Late Silurian to Middle Devonian, and display the earliest occurrences of several

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[a] The designation, Ma, or mega-annum, refers to millions of years ago. Also see Figure 1.

land-plant tissue types associated with stems. Some of these live tissues became consumed by small arthropod herbivores within several million years (m.y.) (Figure 1, cluster 1). The earliest arthropod feeding groups were piercer-and-suckers and pith borers in stems, and consumers of adjacent spores and sporangia [28,29•]. Later, during the Middle Devonian, there is evidence for consumption of foliose liverwort thalli (Labandeira, Tremblay, Bartowski, Hernick, unpublished data), in lieu of true vascular-plant leaves that later became ecologically conspicuous. By the end of the Devonian, all major organs and tissue types of land plants had evolved [28], but it was not until various times during the Carboniferous, in equatorial wetland environments, that the other tissue types become consumed, after an average lag time of 91 m.y. after they first occur in the fossil record [29•]. Reasons for these inordinately long lag times for herbivory of certain tissue types need to be explored, but probably involve atmospheric O_2 levels that plunged below the threshold for sustained active respiration of arthropod herbivores [30].

Increased herbivory ensued after a considerable rise of atmospheric O_2 levels in the Early Carboniferous, and by the mid-Late Carboniferous (Figures 1, cluster 2 and 2a), virtually all modern functional feeding groups, exophytic as well as endophytic, are present in humid equatorial habitats [1,2,16,31], with the exception of leaf miners. This time interval represents the first trophic evidence for the establishment of modern component communities, in which gallers, root feeders, wood borers and ovipositing insects were added as herbivores, providing a new baseline for food webs that appear more driven by herbivores than detritivores. In different environments of the Permian, these feeding styles colonized varied river-associated habitats in western Euramerica (southwestern USA) [3,4,32] (Figures 1, cluster 3 and 2b), and floristically distinctive glossopterid habitats of south-central Gondwana (South Africa's Karoo Basin) [33]. These herbivory trends were brought to a halt at the end-Permian (P-Tr) extinction. Preliminary evidence indicates that following the P-Tr ecological crisis, plant, insect, and associational diversity and intensity decreased significantly, was overly generalized in host-specificity, and did not recover to precrisis Permian levels until the early Late Triassic, 25 m.y. later [7,16,34,35] (Figures 1, cluster 4 and 2c). Reasons for this delayed rediversification are being explored [36], but equally impressive is the intensity and diversity of the herbivore rebound [16], replete with high host-plant specificities that rival the angiosperm diversification event 100 m.y. later [37].

Little is known of herbivore interactions in mid-Mesozoic ecosystems, although exploratory analyses (XL Ding, CC Labandeira, unpublished data) of two important, well-preserved sites in northeastern China, the Middle Jurassic Jiulongshan Formation and the mid-Early Cretaceous sites Yixian Formation, indicate substantial herbivory in some habitats that surrounded large lake basins. Non-herbivore PIAs also have been documented [19•,21,26•,38•], and will be integrated with results from quantitative analyses on bulk, site-specific floras to provide a robust portrait of a trophically diverse, preangiospermous food web. More is known, however, of PIAs resulting from the end-Cretaceous (K-Pg) event, which appears broadly similar to the P-Tr event. After the K-Pg crisis, there is a decrease in plant–insect interactional diversity during the Paleocene, rebounding during the latest Paleocene when levels of interactional diversity and intensity equaled that of the latest Cretaceous 10 m.y. earlier. The dramatic reduction of overall diversity, feeding intensity and host specialization following the K-Pg event (Figure 1, cluster 5) was documented for the Williston Basin [15,39], but not in other worldwide regions, where the boundary is absent or remains undiscovered [11]. Examination of the Denver Basin record would extend the North American patterns closer to the bolide impact site at Yucatan, but confirmation of the devastating effect of this major perturbation on PIAs awaits examination of other stratigraphic continuous intervals with well preserved floras outside of North America.

Herbivory patterns have been well documented for a six m.y. interval (59–53 Ma) that includes the PETM, a transient, 10^5 year long event at 55.8 Ma, during which there was an elevation of global mean annual temperature (MAT) by 5–7°C and a doubling of atmospheric CO_2 levels [8••,9]. Associated with PETM physical changes was a transformation of floral composition at mid-latitude sites such as those examined in Wyoming and a significant increase in herbivore intensity, as assessed by damage-type frequency data [8••] (Figures 1, cluster 5 and 2d). These patterns persist during a six m.y. interval that includes the post-PETM Early Eocene Climatic Optimum at 53–51 Ma [5,8••,9], after which there is a downward but fluctuating global trajectory in temperature and CO_2 levels, occasionally with counterintuitive results when compared to the earlier trends [12].

At approximately the same time that deposits were being lain in North America that recorded major climatic events and trends during the late Paleocene to mid-Eocene, diverse floras were deposited in southern South America [40]. Four examined sites at Laguna del Hunco, in southern Argentina, display a greater diversity and intensity of herbivory in both finely resolved damage types and coarser grained functional feeding groups when compared to earlier, more depauperate rainforest floras from northern South America [41], and to contemporaneous floras in North America [40] (Figure 1, cluster 5). This significant increase in herbivore feeding diversity, particularly specialized interactions, may explain current, elevated PIA diversity in South America [42].

Figure 1

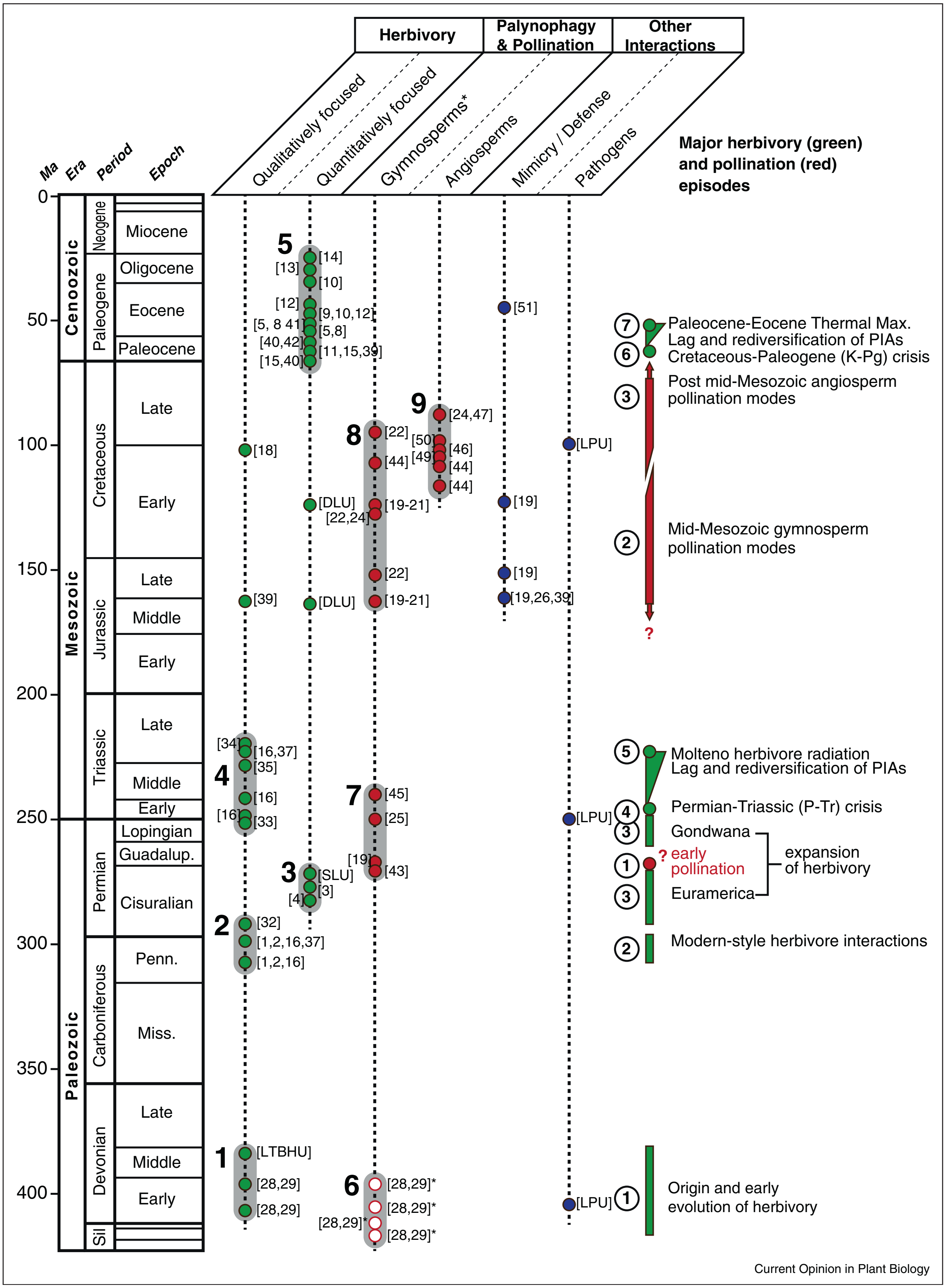

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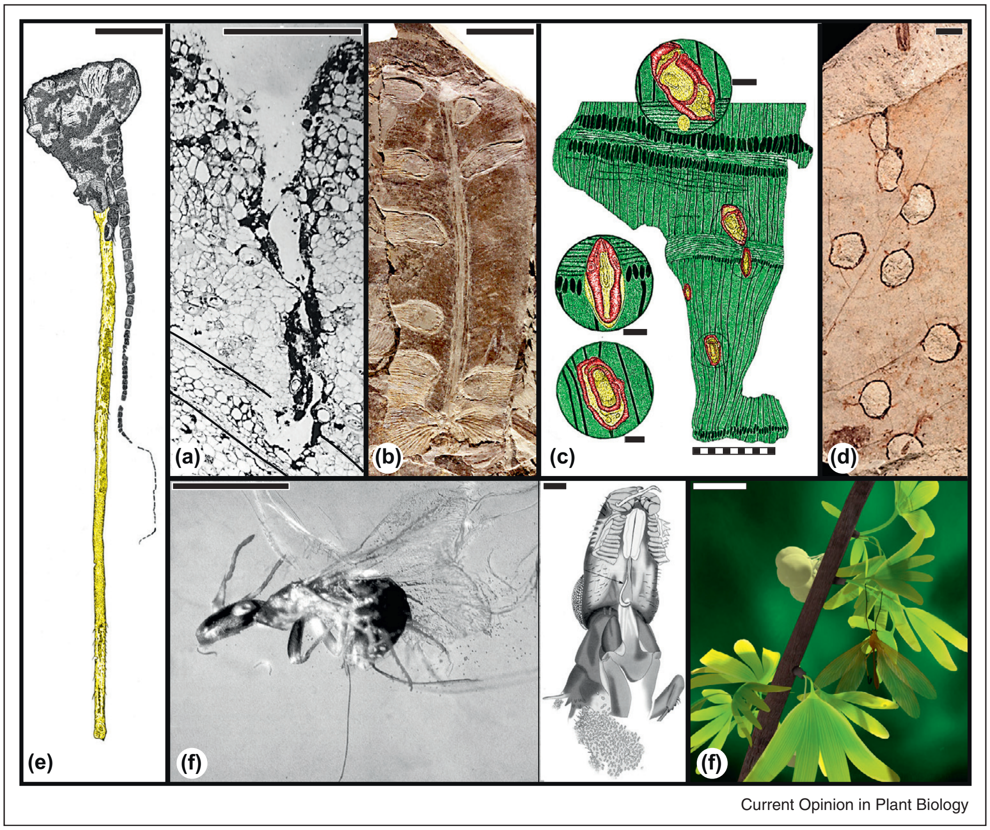
Figure 2



A gallery of fossil plant–insect interactions representing the perspectives of time interval, interaction type, preservational mode, and medium of illustration. Images **(a)**–**(d)** represent herbivory from Paleozoic (a, b), Mesozoic (c), and Cenozoic (d) deposits. At (a) is Late Pennsylvanian (ca. 305 Ma) piercing-and-sucking damage caused by mouthpart stylets of an extinct paleodictyopteroid insect extracting xylem and phloem (bracketed by the two diagonally parallel lines at lower-left), from the marattialean tree fern, *Psaronius chasei*, in an anatomically preserved peat [31]. Mattoon Fm., Illinois, USA; UIUC acetate peel 8227-Bbot, section 109. At (b) are Early Permian (ca. 296 Ma) *Ovofoligallites padjetti* galls in pinnular tissues of the medullosan seedfern, *Odontopteris readi*, induced by a probable early hemipteroid insect [32]. Archer City Fm., north-central Texas, USA; USNM 41165a. At (c) are Late Triassic (ca. 225 Ma) examples of dragonfly oviposition insertion scars on an equisetalean stem fragment of *Equisetites kapokensis*, from the Molteno Formation, South Africa. Colorized camera lucida drawing of compression material; scale bar at bottom-right in mm increments. At (d) is a strip of external foliage feeding showing extensive herbivory on Dicot Morphotype WW006, from the early onset of the Paleocene–Eocene Thermal Maximum (55.8 Ma) [8••]. Willwood Fm., Wyoming, USA; USNM530968. Images **(e)** and **(f)** represent Mesozoic and Cenozoic pollination. At (e) is a Middle Jurassic (165 Ma) head and mouthparts, proboscis in yellow, of *Lichnomesopsyche gloriae*, an extinct scorpionfly that probably probed for gymnosperm pollination drops [21]. Jiulongshan Fm., Inner Mongolia, China; CNU-MEC-NN-2005-024. At (f) is the Early Miocene (ca. 21 Ma) mutualism between an agaonid fig wasp *Tetrapus delclosi* (at left), and (at right) an associated clump of *Ficus* pollen processed by specialized mandibular appendages from the head underside [48]. La Toca Fm., Dominican Republic; AMNH DR-14-576. The reconstruction at (**g**) is mimicry between a hangingfly, *Juracimbrophlebia ginkgofolia* (the mimic), and a coexisting, multilobed ginkgoalean leaf, *Yimaia capituliformis* (the model), from the same locality as (e), based on specimens at Capital Normal University, Beijing, China [26•]. Scale bars: 1 mm; except for figure (f) (right), 0.1 mm. *Abbreviation*: Ma, millions of years.

(Figure 1 Legend) Geochronologic distribution of fossil plant–insect associational studies from the recent literature, including secondary sources, and the timing of significant episodes in plant–insect associations. Herbivory is indicated in green, pollination in red and other associations in black. References in brackets are keyed to data and events discussed in the text; circled numbers at right refer to major events mentioned in the text. Large-numbered, elliptically shaded study-site clusters suggest time intervals of comparatively high levels of recent interest, called out in the text. For those localities with an age-date range, the midpoint date was plotted. Some locality points for quantitatively focused data represent multiple sites, such as Green River and Messel for 47–48 Ma [9,10,12], and several USA Western Interior sites and Cerrejón, Colombia, for 58–59 Ma [39,41]. Open dots with asterisks indicate pollen feeding on pregymnospermous, free-sporing plants. *Abbreviations*: DLU (Ding, Labandeira, unpublished data); Guadalup., Guadalupian; LPU (Labandeira, Prevec, unpublished data); LTBHU, Labandeira, Tremblay (Bartowski, Hernick, unpublished data); Miss., Mississipian Subperiod; Penn., Pennsylvanian Subperiod; PIAs, plant–insect associations; Sil., Silurian; SLU (Schachat, Labandeira, unpublished data). *Includes Silurian and Devonian plant lineages that are not gymnospermous.

Pollination and related associations

In the fossil record, spores of vascular plants precede the earliest occurrence of pollen, as does their consumption by arthropods. Spore feeding, as demonstrated by spore-laden coprolites in late Silurian and Early Devonian deposits [28,29•] (Figure 1, cluster 6), was a precursor to pollen feeding, seen in later Paleozoic biotas [16,22] from insect gut contents [22], pollen grains that display circular holes indicating punch-and-sucking [43], and the earliest mouthparts with long tubular proboscides and pollen-macerating mandibles [19•,25] (Figure 1, cluster 7). This distinctive evidence strongly indicates that during the Late Pennsylvanian and Permian (306–252 Ma), pollen transfer occurred between insects and their seed-plant hosts. During the mid-Mesozoic, the punch-and-sucking pollination mode reappears in an association between thrips and ginkgoaleans [44••], and mandibulate insects, probably beetles, consumed cycad pollen sacs [45] (Figures 1, cluster 8 and 2e). Prominently, there are three, independently originating groups of long-proboscid insects — true flies [20], scorpionflies [21], and kalligrammatid lacewings [19•] — that represent multiple mouthpart convergences. One of the major challenges in understanding the repeated origin of the long-proboscid pollination mode is to determine which co-occurring gymnosperm ovulate organs were accommodated by elongate tubular mouthparts. Some long proboscides had sponge-like, accessory terminal structures for capillary uptake of fluids such as pollination drops, from a variety of receptive ovulate features including integumentary tubes, tubular clasping bracts, deep funnels, channels, and siphonate micropyles [19•,21]. Some tubular structures were lined with nectary-like structures, including resin glands, and glandular trichomes [21,22].

Various early angiosperm pollination types replaced earlier modes of gymnosperm pollination (Figures 1, cluster 9 and 2f). This dramatic turnover [19•] likely is attributable to a more efficient system of lures, rewards, and pollen capture by angiosperms, although such a hypothesis needs testing. Most early angiosperm pollination is generalized [24,46], although instances of specialization are known throughout the record, including beetles [47], fig wasps [48], bees [49•], and mosquitoes and mites caught in the act of feeding on pollen sacs [50••].

Current and future discipline-wide trends

Several approaches have contributed toward understanding PIAs in the fossil record (Figure 1). Most crucial are the unbiased collection of data, proper methods of data analysis, and importantly, inquiry based on sound evolutionary and ecological questions [6,7]. Historical trends of PIAs during the past 50 years have revealed an assessment of where the field has been and where it is headed (Figure 2). From this assessment, seven issues have garnered recent traction and are ripe for more mature evaluation.

1. A comprehensive understanding of the origin of herbivory is needed for the earliest terrestrial ecosystems. Currently, the data are very sparse, and the earliest occurrences originate from only four deposits [28]. The paucity of data may reflect actual rarity of early herbivory, or more likely represents a lack of searching, attributable to a major Middle Devonian to latest Early Mississippian [30] hiatus in the documented herbivore record (CC Labandeira, S Tremblay, KE Bartowski, LV Hernick, unpublished data).
2. The expansion of insect herbivory into new habitats during the Permian requires documentation in greater detail from additional sites. For the Early Permian of southwestern Euramerica, additional studies from north-central Texas (S Schachat, CC Labandeira, unpublished data) provide ecological insights into the different colonization patterns of plant hosts by insect herbivores in various habitats. For the Middle to Late Permian of Gondwanan South Africa, differences are emerging in herbivory patterns among glossopterid floras [33].
3. More recent data are needed for the immediate and longer-term consequences of major extinction events in terrestrial ecosystems. Work has begun to understand the patterns of pre-event and postevent patterns of PIAs during the P-Tr [16] and K-Pg [15] intervals. For the P-Tr case, radioisotopic age dates need to be established for reliable rate estimates of associational change.
4. Broad global assessments are required to record the gradual but profound environmental change that has affected plants and their insect herbivores. The Paleocene–Eocene Thermal Maximum has been most extensively examined, but the current data originate only from one set of localities in North America. It is unclear how universal the worldwide response is, and whether strata of the same age can be tapped in other terrestrial localities to elucidate a commonality of effects.
5. Recent efforts to understand pollinator-related mouthpart specializations of insects during the preangiospermous Mesozoic need to be balanced by a renewed focus on anatomical features of their likely targeted plant hosts, particularly bennettitaleans, caytonialeans, cheirolepidiaceous conifers and ginkgoaleans [19•,22,23]. Structures of gymnospermous ovulate and pollen organs that previously were enigmatic may be explained through an understanding of coeval insect mouthpart morphology and specializations.
6. Additional examples are required to document wing color-patterns for mid-Mesozoic insects that indicate mimicry and crypsis with contemporaneous plants (Figure 2g). It is likely that mid-Mesozoic data involving insect–ginkgoalean mimicry [26•] may be ecologically very similar to Cenozoic patterns with angiosperms [51], particularly in the face of almost complete turnover of important plant, insect and vertebrate lineages.

7. More integrated and intensive studies of multiple species associations are needed that include plants, their interactors (herbivores, pollinators, fungi, pathogens), and other trophic elements at local sites. A broader, multispecies perspective [52] would supplement emphases on single pairwise [53] or tritrophic [54••] interactions. One approach would examine bilateral PIAs in a modern source community where damage-type richness is contrasted with the linked insect richness responsible for the damage [55]. By contrast, construction of food webs can result in trophic networks that have high-resolution as well as high diversity, and are based on an accurate capture of all evident PIAs present in a local ecosystem, recently done for a 47 m.y. maar lake in Germany [56•]. The use of successive food webs with high trophic certainty may be the best approach toward addressing salient questions about ecological evolution of PIAs in deep time.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Labandeira CC: **Early history of arthropod and vascular plant associations**. *Annu Rev Earth Planet Sci* 1998, **26**:327-377.

2. Labandeira CC: **The history of associations between plants and animals**. In *Plant–Animal Interactions: An Evolutionary Approach.* Edited by Herrera C, Pellmyr O. Oxford, United Kingdom: Blackwell Science; 2002. 26–74, 248–261.

3. Beck AL, Labandeira CC: **Early Permian folivory on a gigantopterid-dominated riparian flora from north-central Texas**. *Palaeogeogr Palaeoclim Palaeoecol* 1998, **142**:139-173.

4. Labandeira CC, Allen EM: **Minimal insect herbivory for the Lower Permian Coprolite Bone Bed site of north-central Texas, USA, and comparison to other late Paleozoic floras**. *Palaeogeogr Palaeoclim Palaeoecol* 2007, **247**:197-219.

5. Wilf P, Labandeira CC: **Response of plant–insect associations to Paleocene–Eocene warming**. *Science* 1999, **284**:2154-2156.

6. Wilf P: **Insect-damaged fossil leaves record food web response to ancient climate change and extinction**. *New Phytol* 2008, **178**:486-502.

7. Labandeira CC, Currano ED: **The fossil record of plant–insect dynamics**. *Annu Rev Earth Planet Sci* 2013, **41** http://dx.doi.org/10.1146/annurev-earth-052120124139.

8. •• Currano ED, Labandeira CC, Wilf P: **Fossilized insect folivory tracks temperature for six million years**. *Ecol Monogr* 2010, **80**:547-567.

This study provides the first robust analysis of the effect of the Paleocene–Eocene Thermal Maximum on floras and their insect herbivory before, during and after this exceptional elevation in atmospheric temperature and CO_2 increase. This study analyzes in deep-time strata a process similar anthropogenic climate change that is occurring today (Figure 2d).

9. Wilf P, Labandeira CC, Johnson KR, Coley PD, Cutter AD: **Insect herbivory, plant defense and early Cenozoic climate change**. *Proc Natl Acad Sci U S A* 2001, **98**:6221-6226.

10. Smith DM: **A comparison of plant–insect associations in the middle Eocene Green River Formation and the Upper Eocene Florissant Formation and their climatic implications**. *Geol Soc Am Spec Pap* 2008, **435**:89-103.

11. Wappler T, Currano ED, Wilf P, Rust J, Labandeira CC: **No post-Cretaceous ecosystem depression in European forests? Rich insect-feeding damage on diverse middle Paleocene plants, Menat, France**. *Proc Roy Soc Lond B* 2009, **276**:4271-4277.

12. Wappler T, Labandeira CC, Rust J, Frankenhäuser H, Wilde V: **Testing for the effects and consequences of mid Paleogene climate change**. *PLoS ONE* 2012, **7**:e40744.

13. Currano ED, Jacobs BF, Pan AD, Tabor NJ: **Inferring ecological disturbance in the fossil record: a case study from the late Oligocene of Ethiopia**. *Palaeogeogr Palaeoclim Palaeoecol* 2011, **309**:242-252.

14. Wappler T: **Insect herbivory close to the Oligocene–Miocene transition — a quantitative analysis**. *Palaeogeogr Palaeoclim Palaeoecol* 2010, **292**:540-550.

15. Labandeira CC, Johnson KR, Wilf P: **Impact of the terminal Cretaceous event on plant–insect associations**. *Proc Natl Acad Sci U S A* 2002, **99**:2061-2066.

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

17. • Labandeira CC: **Evidence for outbreaks from the fossil record of insect herbivory**. In *Insect Outbreaks Revisited.* Edited by Barbosa P, Agrawal AA, Letorneau D. Chichester, United Kingdom: Blackwell Science; 2012:269-290.

This is the first exploration of data indicating pest outbreaks in the fossil record. It presents leaf-damage frequency and intensity data from external foliage feeders and leaf miners for inordinately high levels of folivory.

18. Labandeira CC, Dilcher DL, Davis DR, Wagner DL: **Ninety-seven million years of angiosperm–insect association: paleobiological insights into the meaning of coevolution**. *Proc Natl Acad Sci U S A* 1994, **91**:12278-12282.

19. • Labandeira CC: **The pollination of mid Mesozoic seed plants and the early history of long-proboscid insects**. *Ann Missouri Bot Gard* 2010, **97**:469-513.

This synthesis and review explores the preangiospermous, mid-Mesozoic, long-proboscid pollination mode by linking three lineages of long-proboscid insects with receptive plant reproductive features of gymnosperm ovules (Figure 2e).

20. Ren D: **Flower-associated Brachycera flies as fossil evidence for Jurassic angiosperms**. *Science* 1998, **280**:85-88.

21. Ren D, Labandeira CC, Santiago-Blay JA, Rasnitsyn AP, Shih CK, Bashkuev A, Logan MAV, Hotton CL, Dilcher DL: **A probable pollination mode before angiosperms: Eurasian, long-proboscid scorpionflies**. *Science* 2009, **326**:840-847.

22. Labandeira CC, Kvaček J, Mostovski MB: **Pollination drops, pollen and insect pollination of Mesozoic gymnosperms**. *Taxon* 2007, **56**:663-695.

23. Osborn JM, Taylor ML: **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.* Edited by Gee CT. Bloomington, Indiana, USA: Indiana Univ. Press; 2010:34-49.

24. Crepet WL, Nixon KC, Gandolfo MA: **An extinct calycanthoid taxon, *Jerseyanthus calycanthoides*, from the Late Cretaceous of New Jersey**. *Am J Bot* 2005, **92**:1475-1485.

25. Bashkuev AS: **Nedubroviidae, a new family of Mecoptera: the first Paleozoic long-proboscid scorpionflies**. *Zootaxa* 2011, **2895**:47-57.

26. • Wang YJ, Labandeira CC, Ding QL, Shih CK, Zhao YY, Ren D: **An extraordinary Jurassic mimicry between a hangingfly and**

ginkgo from China. *Proc Natl Acad Sci U S A* 2012, **109**: 20514-20519.

This study presents an unusual occurrence of Middle Jurassic mimicry between the whole body of scorpionfly and a species of co-occurring ginkgoalean with leaves that are nearly identical in shape, size, silhouette and surface texture. It extends modern styles of mimicry or crypsis to the preangiospermous Mesozoic (Figure 2g).

27. Sung GH, Poinar GO Jr, Spatafora JW: **The oldest fossil evidence of animal parasitism by fungi supports a Cretaceous diversification of fungal-arthropod symbioses**. *Mol Phylogen Evol* 2008, **49**:495-502.

28. Labandeira CC: **The origin of herbivory on land: the initial pattern of live tissue consumption by arthropods**. *Insect Sci* 2007, **14**:259-274.

29. • Labandeira CC: **Deep-time patterns of tissue consumption by terrestrial insect herbivores**. *Naturwissenschaften* 2013, **100**:355-364.

This paper presents fine-grained, plant histological data throughout the fossil record, but especially from early terrestrial ecosystems indicating that certain plant (especially photosynthetic) tissues were quickly consumed by arthropod herbivores. By contrast, other (mostly structural and meristematic) tissues had a ninefold longer lag time on average before they were subject to arthropod herbivory.

30. Ward P, Labandeira CC, Laurin M, Berner R: **Confirmation of Romer's Gap as a low oxygen interval constraining the timing of initial arthropod and vertebrate terrestrialization**. *Proc Natl Acad Sci U S A* 2006, **103**:16818-16822.

31. Labandeira CC, Phillips TL: **Insect fluid-feeding on Upper Pennsylvanian ferns (Palaeodictyoptera, Marattiales) and the early history of the piercing-and-sucking functional feeding group**. *Ann Entomol Soc Am* 1996, **89**:157-183 (Figure 2a).

32. Stull G, Labandeira CC, Chaney D, DiMichele WA: **The "seeds" on *Padgettia readi* Mamay are insect galls: reassignment of the plant to *Odontopteris* Brongniart, the gall to *Ovofoligallites* gen. nov., and the evolutionary implications thereof**. *J Paleontol* 2013, **87**:217-231 (see Figure 2b).

33. Prevec R, Labandeira CC, Neveling J, Gastaldo RA, Looy C, Bamford MA: **A portrait of a Gondwanan ecosystem: a new Late Permian locality from Kwa-Zulu Natal, South Africa**. *Rev Palaeobot Palynol* 2009, **156**:454-493.

34. Pott C, Labandeira CC, Krings M, Kerp H: **Fossil eggs and ovipositional damage on bennettitalean leaf cuticles from the Carnian (Upper Triassic) of Austria**. *J Paleontol* 2008, **82**:778-789.

35. Moisan P, Labandeira CC, Matushkina NA, Wappler T, Voigt S, Kerp H: **Lycopsid–arthropod associations and odonatopteran oviposition on herbaceous *Isoetites***. *Palaeogeogr Palaeoclim Palaeoecol* 2012, **344/345**:6-15.

36. Roopnarine PD, Angielczyk KD, Wang SC, Hertog R: **Trophic network models explain instability of Early Triassic terrestrial communities**. *Proc Roy Soc B: Biol Sci* 2007, **274**:2077-2086.

37. Labandeira CC: **The four phases of plant–arthropod associations in deep time**. *Geol Acta* 2006, **4**:409-438.

38. • Pott C, McLoughlin S, Wu SQ, Friis EM: **Trichomes on the leaves of *Anomozamites villosus* sp. nov. (Bennettitales) from the Daohugou beds (Middle Jurassic), Inner Mongolia, China: defense against herbivorous arthropods**. *Rev Palaeobot Palynol* 2012, **169**:48-60.

This study is the best demonstration from the fossil record for the role of trichomes as a distinct mechanism in antiherbivore defense. The trichomes protect the foliage of a bennettitalean plant host which may be linked to its suspected insect pollination.

39. Wilf P, Labandeira CC, Johnson KR, Ellis B: **Decoupled plant and insect diversity after the end-Cretaceous extinction**. *Science* 2006, **313**:1112-1115.

40. Wilf P, Labandeira CC, Johnson KR, Cúneo NR: **Richness of plant–insect associations in Eocene Patagonia: a legacy for South American biodiversity**. *Proc Natl Acad Sci U S A* 2005, **102**:8944-8948.

41. Wing SL, Herrera F, Jaramillo C, Gómez C, Wilf P, Labandeira CC: **Late Paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of Neotropical rainforest**. *Proc Natl Acad Sci U S A* 2009, **106**:18627-18632.

42. Price PW, Diniz IR, Morais HC, Marques ESA: **The abundance of insect herbivore species in the tropics: the high local richness of local species**. *Biotropica* 1995, **27**:468-478.

43. Wang J, Labandeira CC, Zhang ZF, Bek J, Pfefferkorn HW: **Permian *Circulipuncturites discinisporis* Labandeira, Wang, Zhang, Bek et Pfefferkorn gen. et sp. nov. (formerly *Discinispora*) from China, an ichnotaxon of punch-and-sucking insect on Noeggeranthialean spores**. *Rev Palaeobot Palynol* 2009, **156**:277-282.

44. •• Peñalver, Labandeira CC, Barrón E, Delclòs X, Nel P, Nel A, Tafforeau P, Soriano C: **Thrips pollination of Mesozoic gymnosperms**. *Proc Natl Acad Sci U S A* 2012, **109**:8623-8628.

On the basis of exquisitely preserved amber material, this study demonstrates an intricate pollinator relationship between an extinct lineage of thrips and its highly probable ginkgoalean host. A highly specialized body feature for capturing pollen, ring setae, is not found in any other extinct or extant insect and is analogous to the branched hairs of bees.

45. Klavins SD, Kellogg DW, Krings M, Taylor EL, Taylor TN: **Coprolites in a Middle Triassic cycad pollen cone: evidence for insect pollination in early cycads?** *Evol Ecol Res* 2005, **7**:479-488.

46. Hu S, Dilcher DL, Jarzen DM, Taylor DW: **Early steps of angiosperm–pollination coevolution**. *Proc Natl Acad Sci U S A* 2008, **105**:240-245.

47. Gandolfo MA, Nixon KC, Crepet WL: **Cretaceous flowers of Nymphaeaceae and implications for complex insect entrapment pollination mechanisms in early Angiosperms**. *Proc Natl Acad Sci U S A* 2004, **101**:8056-8060.

48. Peñalver E, Engel MS, Grimaldi DA: **Fig wasps in Dominican amber (Hymenoptera: Agaonidae)**. *Am Mus Novit* 2006, **3541**:1-16 (Figure 2f).

49. • Danforth BN, Poinar GO Jr: **Morphology, classification, and antiquity of *Melittosphex burmensis* (Apoidea: Mellitosphecidae) and implications for early bee evolution**. *J Paleontol* 2011, **85**:882-891.

This follow up study from an earlier study indicates that the earliest described bee was present during the late Early Cretaceous, soon after the origin of eudicots. The size and body modifications present in this specimen indicate that a specialized mode of pollination occurred early in bee history.

50. •• Hartkopf-Fröder C, Rust J, Wappler T, Friis EM, Viehofen A: **Mid-Cretaceous charred fossil flowers reveal direct observation of arthropod feeding strategies**. *Biol Lett* 2011 http://dx.doi.org/10.1098/rsb.2011.0696.

This exception discovery records a very rare instance in the fossil record where the mouthparts of an arthropod (a mite) was inserted into an angiosperm pollen sac. An association of a mosquito with the same chloranthaceous flower also indicates feeding on nectar.

51. Wedmann S, Bradler S, Rust J: **The first fossil leaf insect: 47 million years of specialized cryptic morphology and behavior**. *Proc Natl Acad Sci U S A* 2007, **104**:565-569.

52. Kaplan I, Denno RF: **Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory**. *Ecol Lett* 2007, **10**:977-994.

53. Wilf P, Labandeira CC, Kress JW, Staines CL, Windsor DM, Allen AL, Johnson KR: **Timing the radiations of leaf beetles: hispines on gingers from latest Cretaceous to Recent**. *Science* 2000, **289**:291-294.

54. •• Hughes D, Wappler T, Labandeira CC: **Life after death: ancient death-grip leaf-scars reveal ant–fungal parasitism**. *Biol Lett* 2011, **7**:67-70.

This study is the first use of distinctive fossil plant damage to establish a tritrophic interaction known from present biological research. The study links a clade of zombie ants that produce a characteristic death-grip leaf scar induced by a parasitoid fungus in control of the ant's brain.

55. Carvalho MR, Wilf P, Barrios H, Currano ED, Windsor DM, Jaramillo CA, Labandeira CC: **Tropical canopy insects link leaf damage in fossil and living forests**. *Geol Soc Am Abstr Prog* 2011, **43**:381.

56. • Labandeira CC, Labandeira CC, Williams RJ: **The Messel food web**. In *The World at the Time of Messel: Puzzles in Palaeobiology, Palaeoenvironment, and the History of Early Primates.* Edited by Lehmann T, Mossbrugger V. Frankfurt-am-Main, Germany: Schaal Senckenberg Gesellschaft für Naturforschung; 2011:95-97.

This preliminary study is the first time that a high-resolution and high certainty food web has been produced for any ancient ecosystem and spotlights the crucial importance of detailed plant–insect interactional data for the establishment of trophic links. It is the largest food web published and employs new network modeling and analytical approaches.

57. Anderson JM, Anderson HM, Cleal CJ: *Brief History of Gymnosperms: Classification, Biodiversity, Phytogeography and Ecology*. Pretoria, South Africa: South Africa National Biodiversity Institute; 2008, .

Glossary of extinct, major seed-plant groups (after [57])

Bennettitales: Gymnosperms with compact, many-ovular ‘gynoecia’ composed of a honeycomb-like aggregate of ovule bearing and (in some lineages) sterile cells. Middle Triassic–Oligocene.

Caytoniales: Gymnosperms consisting of single, bilaterally symmetrical, reflexed cupules fully enclosing 6 to >30 ovules. Late Triassic–Early Cretaceous.

Cheirolepidiaceae: Conifers bearing elliptical cones with megasporophyll units comprising large, free bracts; ovule-bearing scales complex, with 6–10 lobes and usually two ovules enclosed in cutinized sacs. Late Triassic–Paleocene.

Ginkgoales: Gymnosperms with short shoots bearing fascicles of leaves and reproductive organs; ovulate strobili lax, compact, and spicate, with many megasporophylls reduced to single or a pair of ovulate heads, each containing one to five ovules. Early Triassic? Eocene, one species Recent.

Glossopteridales: Gymnosperms with megasporophylls of bract/scale complexes in which megasporangia are variously palmate, many-ovuled structures attached to midrib of sterile bracts ranging from unmodified to reduced glossopterid leaves. Early to Late Permian.

Medullosales: Gymnosperms with radiospermic ovules borne singly on fronds or in loose clusters on dichotomously branched axes; vascularized nucellus free from integument. Middle Mississippian–Early Permian.

seedfern: A mostly late Paleozoic to late Mesozoic polyphyletic assemblage of seed plants with fern-like foliage and naked seeds. Including the Medullosales, Glossopteridales and Caytoniales. Synonym: pteridosperm.