

Ninety-seven million years of angiosperm–insect association: Paleobiological insights into the meaning of coevolution

(Cretaceous/Gracillariidae/Nepticulidae/Magnoliidae/platanoid)

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ABSTRACT From well preserved leaf damage of the mid-Cretaceous Dakota Flora (97 million years ago), three distinctive, insect-mediated feeding traces have been identified and assigned to two extant genera and one subfamily. These taxa are the leaf miners *Stigmella* and *Ectoedemia* of the Nepticulidae and Phyllocnistinae of the Gracillariidae. These fossils indicate that within 25 million years of early angiosperm radiation, the organs of woody dicots already were exploited in intricate and modern ways by insect herbivores. For *Ectoedemia* and its platanoid host, we document 97 million years of continuity for a plant–insect interaction. The early occurrence during the mid-Cretaceous of diverse and extensive herbivory on woody angiosperms may be associated with the innovation of deciduousness, in which a broadleaved angiosperm provided an efficient, but disposable, photosynthetic organ that withstood the increased cost of additional insect herbivory. Moreover, the group represented in this study, the leaf-mining Lepidoptera, exhibits a wide range of subordinal taxonomic differentiation and includes the Gracillariidae, a member of the most derived lepidopteran suborder, the Ditrysia. Ditrysiian presence during the mid-Cretaceous, in addition to lepidopteran body-fossil evidence from Early Cretaceous and Late Jurassic deposits, suggests that the radiation of major lepidopteran lineages probably occurred during the Late Jurassic on a gymnosperm-dominated flora.

Considerable recent attention has focused on the myriad associations between the two most diverse clades of extant macroscopic organisms—angiosperms and insects. In spite of this abundance of primary data (1, 2), few investigations have documented the macroevolutionary history of angiosperm–insect associations. Most studies involving the timing of origin of angiosperm–insect associations, particularly those of leaf-mining taxa, posit originations of host-specific insect herbivory during the Late Cenozoic (3–5) and, to a lesser degree, Early Cenozoic (6–8). Less commonly explicit hypotheses place essentially modern angiosperm–insect associations during the Cretaceous (9–11). Currently there is limited documentation of insect herbivores during the 40 million year Barremian to Turonian interval of angiosperm radiation (12–14) during which angiosperms became ecologically dominant in most terrestrial habitats (15, 16). This general absence of evidence for angiosperm–insect associations in the Cretaceous is attributable to (i) a lack of adequate fossil collections and (ii) selective analyses of potentially associated host and herbivore clades that emphasize apomorphic, recently derived, members of highly diverse encompassing clades (17–19) that extend to the Early Cretaceous or the earlier Mesozoic (20–22). While the possibility remains that selection of appropriate, basal clades of both

angiosperm hosts and their potentially coevolved insect herbivores may reveal older interactions (23), an alternative and more direct approach is the fossil record. Recent interest and published work in the fossil history of insect-mediated damage on angiosperms have provided critical physical evidence that directly links behaviorally stereotyped and taxonomically identifiable damage to modern host taxa that are still exploited today by the same herbivore clades (12, 14, 24). In principle, the direct evidence of fossil plant–insect interactions can address neontologically based hypotheses regarding the geochronologic duration, host specificity, and biogeographic distribution of modern angiosperm–insect associations. In this context, we report fossil evidence from insect-mediated plant damage from the Dakota Formation, an angiosperm-dominated flora deposited ≈25 million years into the radiation of angiosperms (15, 25).

Source of the Data: The Dakota Flora

Our data were collected from the Dakota Formation of earliest Cenomanian age (97 Ma), which originated from three warm-temperate sites representing coastal swamp, flood plain lake, and ox-bow channel deposits (25). These three sites comprise facies occurring on a flood plain, near a delta that faced a westward midcontinental seaway extending from the Arctic Ocean to the Gulf of Mexico (25–27). The bulk flora from the Dakota Formation is undoubtedly the most diverse mid-Cretaceous flora known, representing >400 species of angiosperms (28, 29) for which extensive, unbiased collections have been made. Material from three Dakota deposits in Kansas and Nebraska (the Braun Ranch, Rose Creek, and Hoisington localities) contains excellently preserved foliar material (25, 27–29), some of which contains damage by insects of varied life habits. Although previous studies of the Dakota flora have documented early evidence for insect dietary guilds and functional feeding groups during the early angiosperm radiation (13, 14, 25, 30), our evaluation of insect damage provides taxonomic identifications at the genus level. In addition, floral structure in the Dakota Flora suggest a variety of pollinators (31–33).

The Dakota Flora consists predominantly of plesiomorphic dicotyledonous angiosperms (15, 25, 34) and nonangiosperm taxa such as conifers (16, 34) and ferns (29). Although Rose Creek has been the only locality in which angiosperm megafossils have been intensively investigated (25, 29), preliminary data from other localities indicate that the general floristic conclusions reached for Rose Creek are consistent with the other sites as well. The most abundant and diverse components at Rose Creek are the orders Magnoliales, Laurales, and Illiciales (25) of the subclass Magnoliidae. Notably present as insect host plants are lauralean leaf

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Abbreviation: Ma, million years ago.

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species assigned to modern Chloranthaceae and Lauraceae and a few leaf species referable to mosaic combinations of several modern lauralean families. Other Rose Creek plants include two members of unknown ordinal affiliation within the Rosidae and four angiosperms that remain unassignable to subclass (25). Additional heavily herbivorized plants include from Braun Ranch and Hoisington an undescribed platanoid, a member of lower Hamamelidae, and at Hoisington the pinnately compound *Sapindopsis*, probably a primitive member of the Rosidae (25, 35).

Modern Insect Genera Associated with the Dakota Flora

From an ongoing and extensive examination of dicotyledonous angiosperm plant damage from the Dakota flora, three morphotypes of diagnostic leaf mines have been identified and are assigned to modern taxa (Fig. 1). Although other apparent lepidopteran leaf mines are present, of the distinctive leaf mines, *Stigmella* and *Ectoedemia* of the monotrysian lepidopteran family Nepticulidae and Phyllocnistinae of the

ditrysian lepidopteran family Gracillariidae are well represented. The latter mines could have been produced by *Phyllocnistis* or a closely related phyllocnistine genus (36). These leaf mines are preserved as internal excavations of parenchymatic and epidermal tissues in leaf compressions. They contain life-history detail of the larval miner, including oviposition site; fecal pellet distributional pattern; discrete, instar-related enlargement of mine width; and size, shape, and internal structure of the preemergence larval or pupation chamber.

The Nepticulidae is a near-cosmopolitan family of ≈ 600 described species of tiny monotrysian moths whose larvae feed on solid-tissue parenchyma as leaf miners or rarely in petiole galls, bark, and buds (37–40). Nepticulid species exhibit narrow host specificities, feeding principally on woody Hamamelidae, Rosidae, and Dilleniidae (40, 41). *Ectoedemia* and *Stigmella* are taxonomically and autecologically diverse and are assigned to distinct tribes within the Nepticulidae (41, 42). *Stigmella* is the most speciose nepticulid genus and exhibits the widest geographical distribution

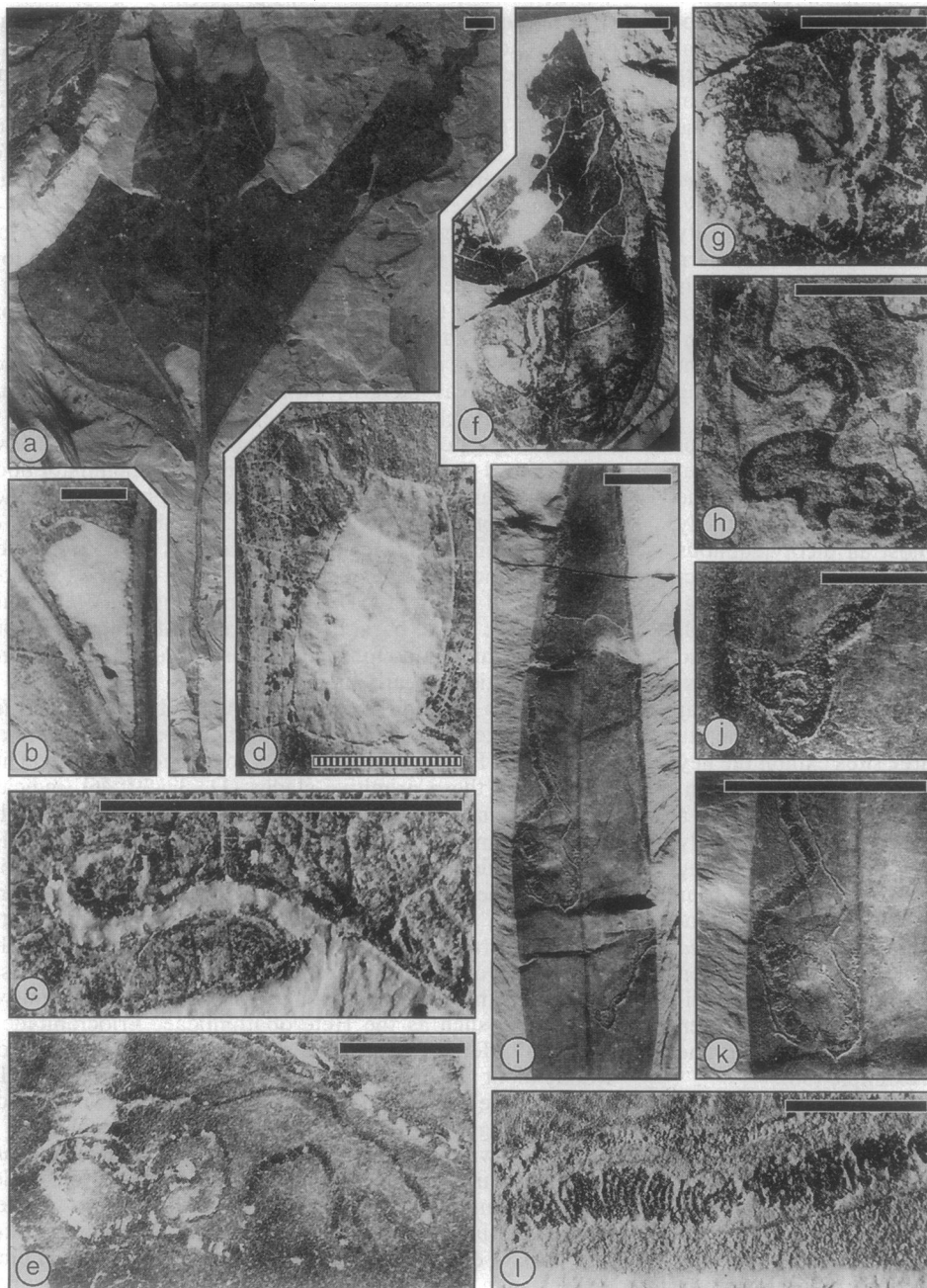


FIG. 1. Leaf-mining Lepidoptera from the mid-Cretaceous (97 Ma) Dakota Formation of Kansas. (a–d) The leaf-mining nepticulid *Ectoedemia* on undescribed platanooid hosts. (a) Leaf mine at left basal fork of primary veins of specimen (UF12701) from the Braun Ranch Locality. (b) Enlargement of same mine. (c) Detail of same mine showing serpentine early-instar portion. (d) *Ectoedemia* on platanooid specimen UF7255 from the Hoisington locality. (e–h) The leaf-mining nepticulid *Stigmella* on dicot hosts. (e) *Stigmella* on *Pandemophyllum kvacekii* (UF12712') from the Rose Creek locality. (f and g) *Stigmella* on *Dicotylophyllum* sp. (UF4811) from Hoisington. (f) Leaf mine. (g) Enlargement of mine terminus; note frass pattern. (h) Detail of mine terminus of *Stigmella* on *Anisodromum wolfei* (UF12718) from the Rose Creek locality. (i–l) A leaf-mining phyllocnistine gracillariid on *Densinervum* sp. (UF4818) from Braun Ranch. (i) Leaf mine. (j) Enlargement of oviposition site and early-instar tract. (k) Enlargement of pupation chamber. (l) Detail of frass trail. (a–c and e–l, bar 0.5 cm; d, bar = 0.25 cm.)

and the most eclectic plant host spectrum in the family (39, 40). Our identification of Dakota *Stigmella* is based on diagnostic leaf mines with an intermittently broken, medial, particulate trail of frass, terminating in a modestly expanded, frass-free chamber (Fig. 1 *e-h*). Ten leaf mines of *Stigmella* occur at all three localities on a diverse suite of dicotyledonous hosts representing the subclasses Magnoliidae [the lauraceous *Pandemophyllum kvacekii* (25)], Hamamelidae (an undescribed platanoid), and Rosidae [*Anisodromum wolfei* (25)], consistent with their currently extensive host breadth. Although extant *Stigmella* occurs on taxa of several angiospermous subclasses, no known Magnoliidae hosts have been documented (43).

Unlike *Stigmella*, *Ectoedemia* larvae construct an early serpentine mine that gradually widens for the first few instars, later becoming a conspicuous, full-depth blotch mine that frequently obliterates previously formed serpentine segments of the same mine (40, 44, 45) (Fig. 1 *a-d*). Collectively these unique features taxonomically circumscribe the culprit as *Ectoedemia*. Of the 12 identified leaf mines of *Ectoedemia* from the Dakota Formation (Fig. 1 *a-d*), 11 occur on a platanoid host common at Braun Ranch. This near monospecificity of *Ectoedemia* on platanoid hosts has important consequences for interpreting long-term angiosperm host/insect herbivore coevolution, particularly since leaf mines of the Cenomanian *Ectoedemia* are remarkably similar to those of extant *Ectoedemia platanella* on Nearctic *Platanus occidentalis*, the American sycamore. Although modern *Ectoedemia* comprises ≈ 200 described species occurring on several dicotyledonous subclasses and is distributed principally in the north-temperate Holarctic and secondarily in southern Africa (41, 42), the subgenus containing *E. platanella* is Nearctic and shows an overwhelming preference for hosts of Hamamelidae and Rosidae (37, 41). Similarly, the Platanaceae, a lower hamamelid family of six or seven extant species, is Holarctic and is a member of a lineage extending back to the Lower Cretaceous (25, 35).

The ditrysian Gracillariidae is the most diverse family of leaf-mining Lepidoptera, constituting ≈ 1700 described species in 70 genera (46). Of the three gracillariid subfamilies, the Phyllocnistinae is the most derived and has an extremely broad host range, encompassing almost all dicotyledonous subclasses (36–38). The first three or four instars of Phyllocnistinae are sap feeders that characteristically form a long, serpentine leaf mine with a central, zigzagging frass trail. Feeding is confined to the upper or lower epidermis and terminates in a small expansion in which pupation occurs, frequently near the leaf margin (37). The last larval instar does not feed and pupates within the mine terminus. Dakota Formation Phyllocnistinae from all three sites exhibit the key behavioral synapomorphy of the Phyllocnistinae, a median, continuous, and tightly sinusoidal frass trail resulting from a sap-feeding larva (Fig. 1*l*). Dakota Phyllocnistinae occur only on known plant hosts of Magnoliidae (Fig. 1 *i-k*), including two specimens on *Crassidenticulum decurrens* and four specimens on *Densinervum* sp., both assigned to the Chloranthaceae, and one specimen on the lauralean *Pabiana variloba* (25). These data suggest significant host colonization of Magnoliidae relatively early during the angiosperm radiation. A new genus of Phyllocnistinae has recently been reported from Chile on *Drimys* (Winteraceae) with leaf mine structure very similar to the Dakota example (36).

DISCUSSION

We document three well-preserved examples of angiosperm herbivory, two assigned to modern insect genera, occurring early within the initial angiosperm radiation. These interactions by lepidopteran leaf miners have implications for the timing and mode of colonization of insect herbivores on early

angiosperm hosts, as well as geologic longevity of some plant-insect associations. In this context, four issues are addressed.

Early Partitioning of Angiosperms by Insect Herbivores. Our current inventory of functional feeding groups from the Braun Ranch, Rose Creek, and Hoisington localities of the Dakota Formation consists of external leaf feeders, leaf miners, gallers, and probably piercer-and-suckers (13). With the possible exception of leaf miners (47–49), these functional feeding groups extend to the Paleozoic (14, 24), although apparently in modest ecological diversity. Nevertheless, it is evident that for leaf miners, the Dakota flora currently presents the earliest available evidence for significant resource partitioning of angiosperm leaves based on host plant taxonomic affiliation and leaf tissue type. *Ectoedemia* is targeting platanoids and may have been monophagous, whereas the Phyllocnistinae apparently were oligophagous, preferring hosts of Magnoliidae. Tissue-based specificity is illustrated by the preference of sap-feeding Phyllocnistinae for the epidermis, whereas the solid tissue-feeding *Stigmella* and *Ectoedemia* consume mostly palisade mesophyll (37, 39). Within the Nepticulidae, varied strategies of food consumption already were established since *Stigmella* constructs a serpentine mine (Fig. 1 *e* and *f*), whereas *Ectoedemia* forms a short serpentine mine that soon erupts into a blotch (Fig. 1 *b* and *d*) (38–40, 45, 46). In addition to these stereotyped leaf-mine strategies, much additional evidence exists for several external leaf-feeding types—center feeding, margin feeding, skeletonization, and surface abrasion (13)—documenting significant partitioning of angiosperm leaf organs based on host tissue type and taxonomic affiliation. Such fine-grained subdivision of angiosperm leaf resources is also evident in the slightly younger (91 Ma) Turonian flora from Kazakhstan (12, 17).

Although the data presented here provide direct evidence for insect larvae dietarily partitioning leaves of early angiosperms, much of the angiosperm radiation is believed to have been propelled by adult pollinators (11, 50). The known fossil record provides both flowers and likely pollinator body fossils for early angiosperms but lacks the physical evidence for pollinator interactions on plants. Notably, the adults of these leaf-miners and related incurvarioids bear abbreviated siphonate mouthparts capable of imbibing surface exudates or nectar in the field (51) and laboratory (D.L.W., unpublished data). Thus, basal heteroneurans (Monotrysis + Ditrysis) are candidates for nectar consumption and concomitant pollination of early angiosperms.

Deciduous Angiosperm Leaves As Accessible Food Items for Insects. Recent cladistic analyses of the basal lepidopteran taxa (ref. 3; Fig. 2), coupled with knowledge of the larval life histories of these primitive clades (11, 37–39, 46), indicate that leaf mining can be regarded as an apomorphy for the Heterobathmiina + Glossata clade (refs. 12, 42, and 60; Fig. 2). This clade includes all Lepidoptera minus the two most primitive lineages, the detritivorous and external leaf-feeding Zeugloptera and the Aglossata, consisting of endophytic borers of araucariaceous cones (46). Coincident with the appearance of leaf mining in the Heterobathmiina and basal Glossata is the occurrence of many constituent and primitive subclades—such as the Heterobathmiidae, Eriocranioidea, Nepticuloidea, Tischerioidea, and Incurvarioidea—on woody dicot angiosperms of high “apparency” (see ref. 61). Notably, the early association of Nepticulidae with woody dicots of high apparency (41, 62) such as Hamamelidae is consistent with conservative patterns of extant host plant association in some nepticulids (42, 55) and the great antiquity of extant species of *Stigmella* and *Ectoedemia* inferred from large, interspecific genetic distances (63). These latter two lines of evidence, plus the presence of nepticulid mines on Turonian trochodendroid (12) and earliest Cenomanian

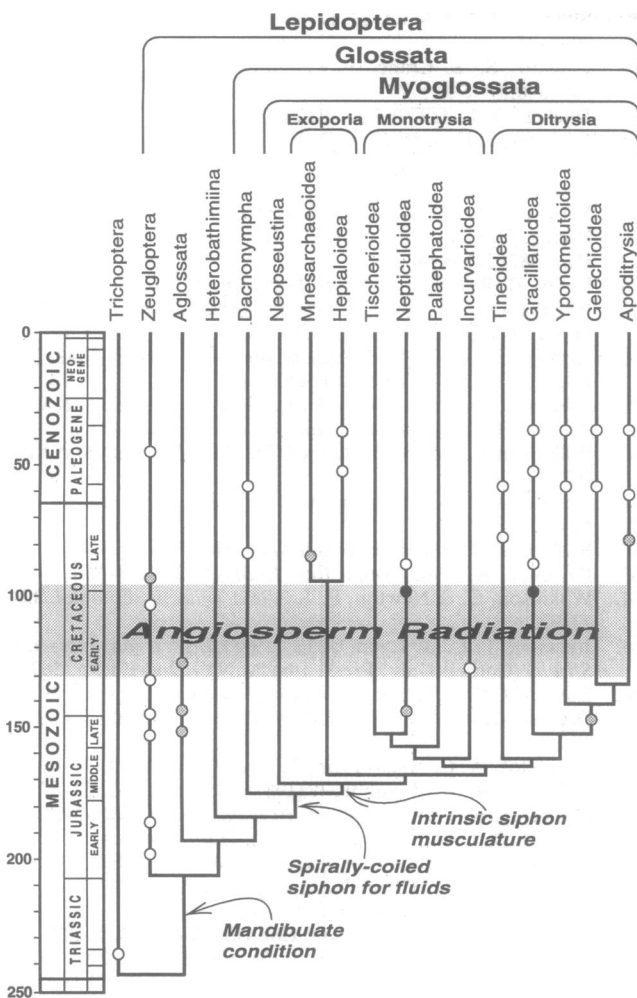


FIG. 2. Phylogeny of the Lepidoptera calibrated by fossil occurrences. Phylogeny is combined from several sources (52–55); fossil occurrences are from Whalley (56), Skalski (57), and this report. This angiosperm radiation spans the interval from 130 Ma, during which the oldest reports of pollen are commonly accepted as angiospermous (58), to 95 Ma, when angiosperms became the dominant vegetation in most areas where they are dominant today (16, 58). Time scale is from Harland *et al.* (59). Open circles, reliable assignments; shaded circles, probable assignments; solid circles, assignments of this study. The close similarity of the plesiomorphic and extinct lineage Eolepidopterygidae (56) was indicated by Skalski (57) to closely resemble the Aglossata, a suggestion that was incorporated in the cladogram. Only the earliest occurrence of the Trichoptera is shown; many Cenozoic occurrences of Lepidoptera are omitted.

platanoid and magnoliid leaves, suggest that woody and deciduous lower Hamamelidae and Magnoliidae were a favored target for several lineages of Lower Cretaceous leaf miners. This inference of early herbivore colonization is supported by recent cladistic analyses of angiosperm morphology and *rbcL* genes, which indicate that the lower hamamelid Platanaceae and Trochodendraceae are representatives of the two most basal lineages of nonmagnoliid dicots (64–66).

Although leaf mining has a significant pre-Cretaceous history, predominantly on seed ferns (24, 47–49), the frequency of leaves attacked and the amount of herbivorized tissue removed from leaves reached a qualitatively higher plateau during the mid-Cretaceous. This observation is reflected in the Cenomanian Dakota Flora (ref. 25; C.C.L. and D.L.D., unpublished observation). This increase in the diversity and intensity of herbivory has been explained as an evolutionary response of insects to the phytochemical diver-

sity in early angiosperm vegetative organs that was acquired for other reasons (see ref. 67). Such an explanation remains unconvincing, particularly in light of moderate predation levels on extant ferns and leafy gymnosperms (45, 68, 69) and the presence of highly effective, antiherbivore secondary compounds in angiosperms (20, 22, 69). Rather, we suggest that angiosperms offered a new, disposable food resource that became available to existing herbivores. This resource was a planated leaf that produced photosynthate during the course of a growing season, as it was simultaneously herbivorized. This key and widespread innovation of deciduousness in early angiosperm floras was a feature that occurred sporadically and rarely in older Mesophytic floras.

The Early Radiation of the Lepidoptera. The occurrence of all three subfamilies of gracillariid leaf miners at the Early/Late Cretaceous boundary (36) provides temporal calibration for the early radiation of the Lepidoptera (Fig. 2). The Gracillariidae is a member of the Ditrysia—the most derived lepidopteran lineage that constitutes 98% of all species in the order. The additional presence of the sister clade to the Ditrysia (54, 55), the Monotrysia in the form of the Nepticulidae, additionally supports the presence of the Heteroneura (Monotrysia + Ditrysia) during the Early Cretaceous. Also, an undescribed incurvarioid fossil from Lebanese amber of Barremian or Aptian age (56, 57) further constrains the minimum age of the Heteroneura to 120–125 Ma, penecontemporaneous with the earliest evidence for angiosperms and preceding their major ecological expansion (58). Earlier evidence is provided by an Upper Jurassic (Kimmeridgian) lepidopteran body fossil with a well developed maxillary siphon and large, three-segmented labial palp, assigned to the Ditrysia (70). Finally, leaf mines occurring in the corytosperm seed fern *Pachypteris* were described in an Upper Jurassic or Lower Cretaceous flora from Australia and have been assigned questionably to the Nepticulidae (47).

Most hypotheses of the early evolution of the Lepidoptera postulate a radiation contemporaneous with initial angiosperm diversification (5). The above trace-fossil and body-fossil data circumstantially indicate that the radiation of major lepidopteran clades probably occurred no later than the Late Jurassic on a gymnosperm-dominated flora. Since the oldest well-documented and currently widely accepted angiosperms originate from the Hauterivian or possibly Valanginian stages of the Lower Cretaceous (58), there is the strong indication that certain lineages of the Heterobathmiina + Glossata clade were either laterally transferred to newfound angiosperm hosts or were inherited from seed fern-feeding ancestors, or both.

The Fossil Record of Plant–Insect Interactions as a Source of Data and Inference. Although several authors have considered the fossil record of insect damage on plants too poor for detailed studies of interactions between identifiable hosts and herbivores (20, 22, 38), the material reported here and by other recent investigations have uncovered several exceptionally preserved floras with highly stereotyped, insect-mediated plant damage (12–14, 24, 25, 47). Much post-Jurassic angiosperm material contains insect damage frequently identifiable to the generic level. Examination and accurate identification of insect damage in fossil floras can provide minimal geochronologic dates for associations between plants and insects. Accordingly, these important dates and ecological associations can be used to test hypotheses generated by host–herbivore congruence or microevolutionary studies for the timing of origin and macroevolutionary history of plant–insect interactions.

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