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# Paleobiology of middle Eocene plant-insect associations from the Pacific Northwest: A preliminary report

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## ABSTRACT

Well-preserved, middle Eocene floras from the Pacific Northwest, particularly the graben-fill deposit at Republic, Washington, offer an unique window for examination of some of the earliest documented, modern-aspect, plant-insect associations in the fossil record. Of special interest is fossil plant damage attributable to leaf mining and galling taxa that is very similar or identical to modern damage on the same host genera, indicating the geologically long-term persistence of some associations. Other types of middle Eocene, insect-mediated damage appear generalized and are not assignable to known types of modern associations, owing in part to imperfect taxonomic resolution of plant host, insect herbivore, or more likely, extinction. This preliminary report records the taxonomically diverse and morphologically detailed wealth of preserved foliar material in a Lagerstätte, which is important for addressing the macroevolutionary tempo of plant-insect associations. This relevance includes the prevalence of long-term associations, extinction of plant host and interacting insect herbivores, and the occurrence of host-switching at Cenozoic time scales for taxa presently confined to eastern Asia and North America.

**KEY WORDS:** plant-insect associations, leaf mining, galling, bud feeding, oviposition, leaf rolling, component community, plant hosts, Eocene, Republic Flora, Klondike Mountain Formation, paleobiogeography, extinction.

## INTRODUCTION

Insects and vascular plants have coexisted for at least 400 million years on land. For most of this time there is good fossil evidence of harmful, mutualistic, and beneficial associations between these two currently most diverse groups of terrestrial macroscopic organisms. We now know that approximately 300 million years ago insects and other arthropods were dietarily partitioning both dead and live plant tissues in essentially modern ways in coal-swamp forests (Labandeira and Beall, 1990; Chaloner et al., 1991; DiMichele and Hook, 1992; Labandeira, 1998a, 1998b). In these equatorial wetlands of the late Pennsylvanian, data now indicate that primitive, extinct lineages of marattialean tree ferns and seed ferns harbored insects that possessed the fundamental strategies that modern insects use for accessing plant tissue, including external chewing (Scott et al., 1992), boring (Labandeira et al., 1997), piercing-and-

sucking (Labandeira and Phillips, 1996a), galling (Labandeira and Phillips, 1996b), and spore and pollen consumption (Labandeira, 1998c).

During the Mesozoic, new lineages of insects on seed plants expanded the variations of these dietary themes (Grauvogel-Stamm and Kelber, 1996; Ash, 1997; Labandeira, 1998a), and by the mid Cretaceous, dominant angiosperm taxa were being consumed by insect herbivores. Some of these herbivore lineages have persisted essentially unchanged to the present day (Hodkinson, 1985; Kozlov, 1988; Labandeira et al., 1994; but see Kuschel et al., 1994, for an alternative view). However, it is in well-preserved, abundant, and diverse middle Eocene floras that the greatest potential exists for tracking modern-aspect, host-specific, plant-insect associations. This is because many of the earliest first appearances of modern plant and insect genera are documented from floras of Eocene

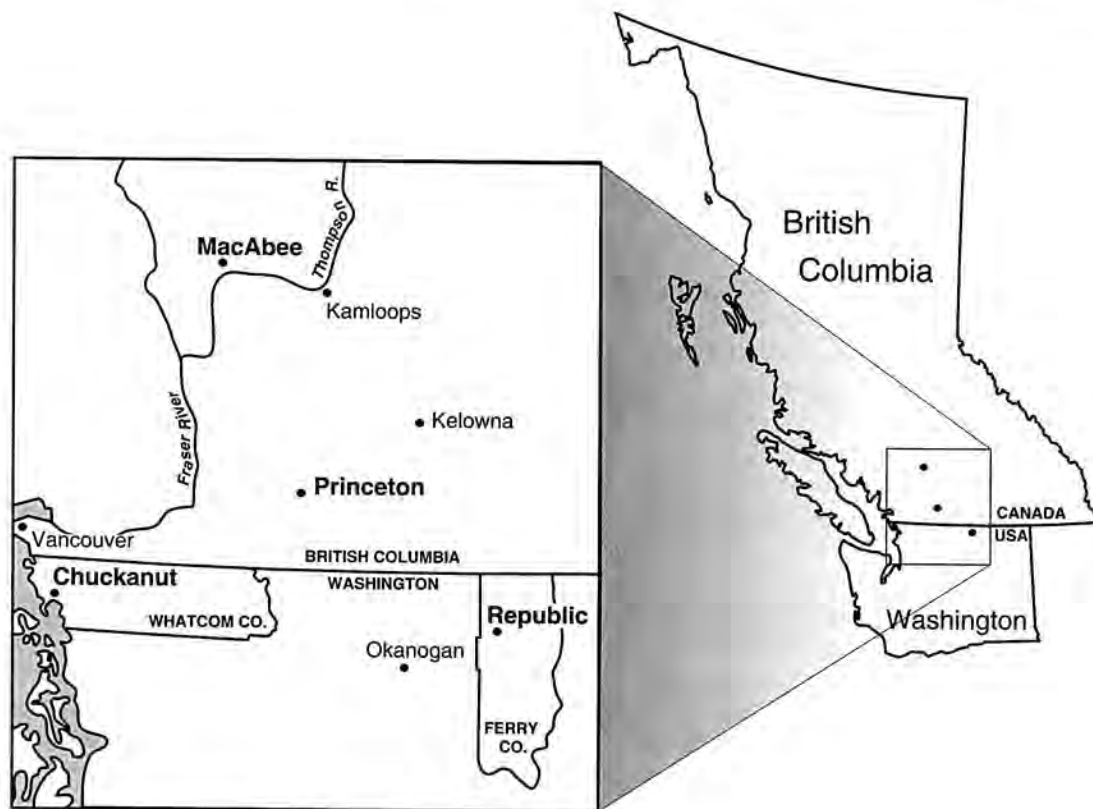
age, and in particular the early middle Eocene (49 Ma) site at Republic, Washington (Wolfe and Wehr, 1987, 1988; Wehr, 1995, 1998; Wehr and Manchester, 1996; Wilson, 1996). It is in this context that the well-preserved and highly stereotyped insect damage of the Republic Flora is important.

### IMPORTANCE OF THE REPUBLIC AND COEVAL FLORAS

Most lower to middle Eocene floras from North America are known from three principal regions: the Mississippi Embayment, particularly localities in Arkansas and Tennessee; the expansive Green River lake basins of Wyoming, Utah, and Colorado; and restricted lake basins in the Pacific Northwest, such as Republic in Washington and Princeton in British Columbia. Floras from the Pacific Northwest include one of the highest in documented fossil-plant diversity (Pigg and Stockey, 1996; Wehr, 1998). They originated in lacustrine and other depositional environments of the middle Eocene Okanogan Highlands of Washington State and British Columbia (Fig. 1; Wolfe and Wehr, 1987; Wehr, 1995, 1998). They represent a diverse sample

of warm-temperate to subtropical vegetation that was deposited in graben-fill basins of a tectonically active region (Wolfe and Wehr, 1991). At Republic during the middle Eocene the average temperature was 11°–13°C (52°–55°F), about 5°C (9°F) warmer than today, with a mean annual range of temperature of approximately 14°C (26°F), significantly less than the 24°C (44°F) of today (Wolfe and Wehr, 1987; Schorn and Wehr, 1996). The elevation is estimated at 2300 m (7500 ft), or about 1500 m (5000 ft) higher than today (Wolfe and Wehr, 1991). The vegetation grew under a warm microthermal to cool mesothermal climate in which precipitation was relatively balanced throughout the growing season (Schorn and Wehr, 1996). These conclusions, however, need to be confirmed by more accurate techniques of paleoclimatic estimation (e.g., Wilf, 1997).

Middle Eocene floras of the Pacific Northwest contain an exceptional spectrum of insect damage on a variety of plant hosts. Insect-mediated damage occurs especially on deciduous, arborescent, dicotyledonous angiosperm genera that currently occur in seasonal, warm- to cool-temperate habitats. Examples include *Acer* (maple), *Aesculus*



**Figure 1.** Location of fossil plant localities (boldfaced names) discussed in this study.

(buckeye), *Alnus* (alder), *Betula* (birch), *Comptonia* (sweetfern), and *Prunus* (cherry), as well as genera occurring in more aseasonal, warm-temperate to subtropical habitats, particularly, *Gordonia* (Carolina bay) and *Magnolia*.

Modern plant genera at Republic harbor insect associates as did lineages ancestral or otherwise closely related (*Macginitiea*, "*Paracrataegus*," "*Paraprunus*," *Plafkeria*) to modern genera found in temperate latitudes. Additionally, insect damage has been found on plant genera from lineages that no longer occur natively in western North America but exist only in eastern Asia and eastern North America. Notable examples include *Ginkgo* (maidenhair tree), *Cercidiphyllum* (katsura), and *Aucuba* (Japanese laurel), as well as *Sassafras* and *Gordonia* (Carolina bay); all are confined today to eastern Asia and eastern North America (Johnson, 1996; Manchester, 1999). Recent studies documenting isolated occurrences of insect-damaged foliar material from the middle Eocene of North America include Lewis and Carroll (1991), Lewis (1992, 1994), and Wehr (1995) for Republic; Grande (1984), Dayvault et al. (1995), and Johnson and Plumb (1995) for the Green River lake system; and Johnston (1993) for the Mississippi Embayment. Several brief reviews have documented insect faunas from the Eocene Pacific Northwest, including Lewis (1992), Douglas (1996), Wilson (1996), Wehr and Barksdale (1996), Wehr (1998), and Archibald (1998), some of which have commented on plant associations.

As many of these plant genera represent either relatively early occurrences or the earliest appearances of modern plant genera in the fossil record, floras of the Pacific Northwest offer a unique taphonomic window for paleobiologists and evolutionary biologists investigating the phylogenetic history and paleoecology of modern plant-insect associations (Fig. 1). This exceptional window is valuable, in part, because modern genetics and population ecology have significant implications for the history of plant-insect associations (Thompson, 1994; Futuyma et al., 1995), indicating that such associations may be very labile at macroevolutionary time scales (Zwölfer, 1982). Supportive evidence comes from examinations of extant butterflies (Janz and Nylin, 1998), leaf beetles (Becerra, 1997), bark beetles (Kelley and Farrell, 1998), planthoppers (Wilson et al., 1994), and ermine moths (Menken, 1996), which indicate that at least some insect herbivores and their host plants may be rapidly tracking plant host phenology and biochemistry, rather than host

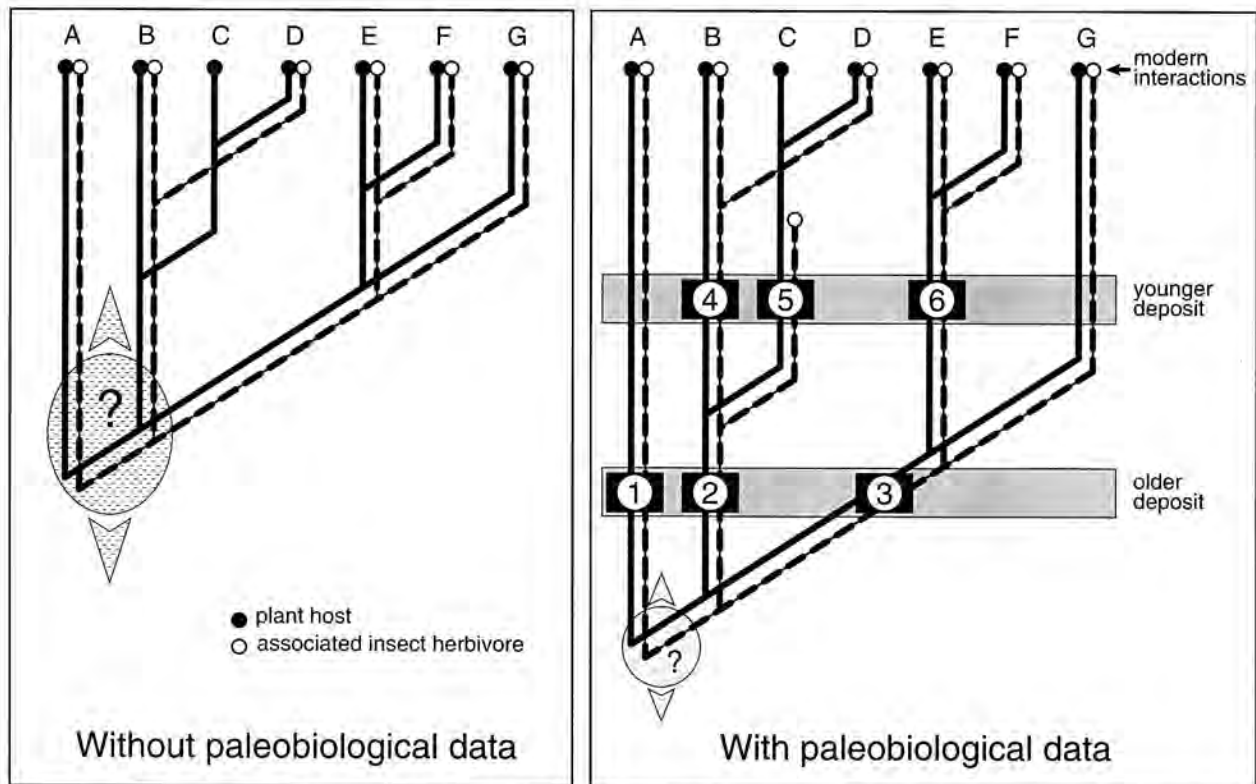
taxonomy per se (Jaenike, 1990; Mitter and Farrell, 1991). However, more integrative synopses that include historical data (see also Farrell and Mitter, 1990) allow for considerable plant host-insect herbivore fidelity during geologic time, suggesting that modern associations may be quite ancient. In fact, studies using a variety of approaches have predicted extensions of modern associations to the early Cenozoic (Moran, 1989; O'Dowd et al., 1991; Pellmyr and Leebens-Mack, 1999), the late Cretaceous (Zwölfer, 1978; Farrell and Mitter, 1994; Labandeira et al., 1994; Futuyma and Mitter, 1996), and possibly the late Jurassic to early Cretaceous (Farrell, 1998). These and other studies of modern and ancient plant-insect associations, shown schematically in Figure 2, can benefit from identifications of middle Eocene plant hosts and their insect herbivores, if for no other reason than to provide calibration to a geologic time scale (Labandeira, 2002).

## REPRESENTATIVE PLANT-INSECT ASSOCIATIONS

### Introduction

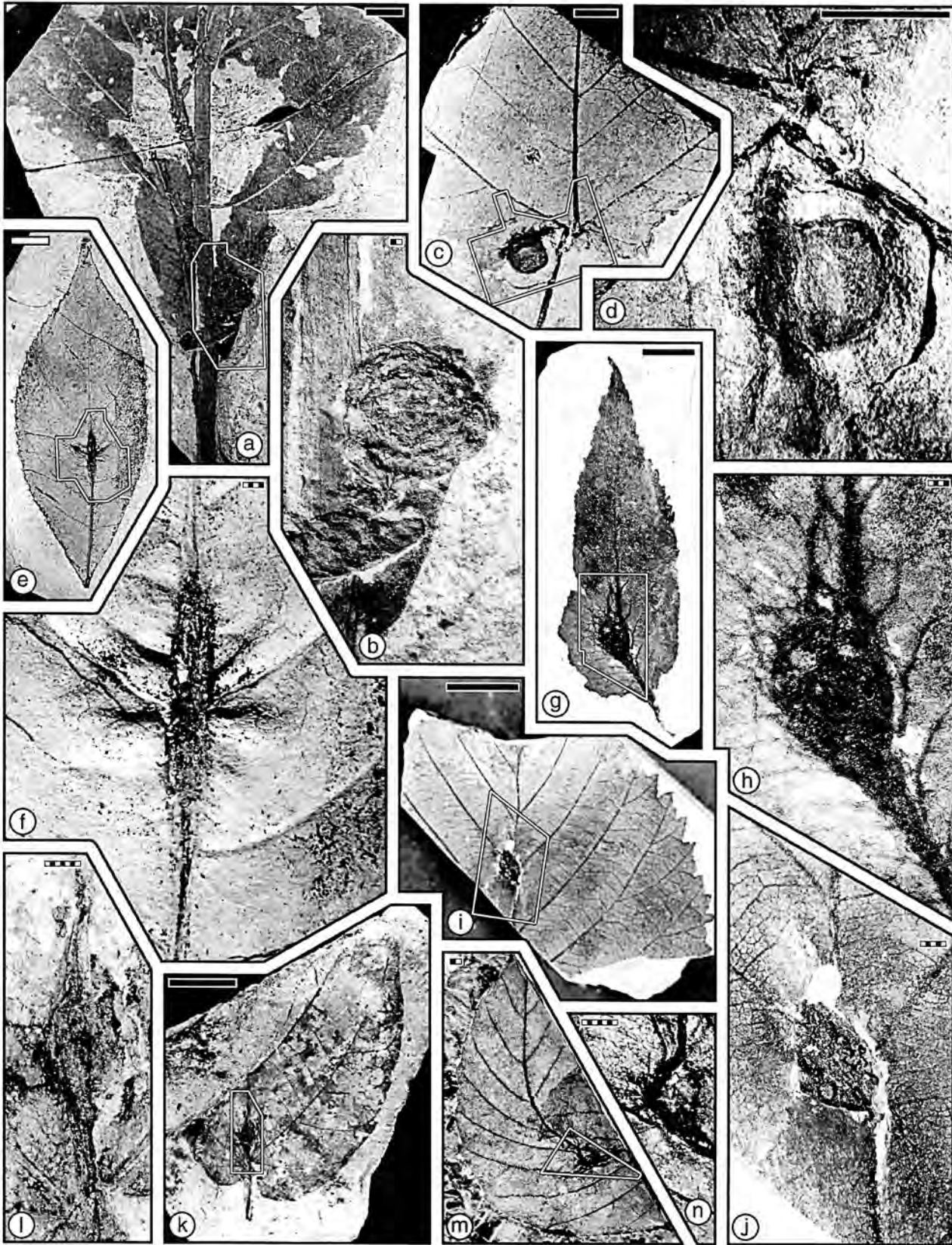
Plant damage resulting from a broad spectrum of insects, representing twelve families from the five most diverse orders of insects (Hemiptera, Coleoptera, Hymenoptera, Diptera, and Lepidoptera), is documented in Figures 3 to 6 for Republic and three other penecontemporaneous floras. The damage produced by representatives of these insect taxa occurs on at least 15 families of diverse plant hosts, including ferns, Ginkgoaceae, and four dicotyledonous subclasses (Magnoliidae, Hamamelidae, Dilleniidae, and Rosidae). In terms of the basic feeding types of insects, the most commonly encountered groups are external foliage feeders, especially skeletonizers and hole feeders, followed by gallers, leaf miners, and rare leaf rollers and bud borers. Additionally, there is significant evidence for ovipositional damage on leaves.

This spectrum is dissimilar to the only other diverse fossil floras in which plant-insect interactions have been examined comprehensively — the mid Cretaceous Dakota Flora and late Cretaceous Hell Creek Flora — wherein external foliage feeding and leaf miners are common, galling is relatively rare, and ovipositional damage, leaf rolling, and bud boring are rare to absent (Stephenson, 1991; Labandeira et al., 1994). In some ways it parallels the patterns of damage documented for the latest Paleocene to early Eocene for the greater Green River Basin (Wilf and Labandeira, 1999). At



**Figure 2.** Importance of paleobiological data in determining phylogeny and temporal context of modern plant-insect associations (designated from A-G). At left are arbitrary phylogenies of plant host taxa and their coevolved insect herbivore taxa. Note lack of temporal resolving power based on biological data only. If molecular data were used in the construction of these phylogenies, temporal calibration could be made independently by inferring times of divergence based on distinctiveness of constituent taxa both from plant hosts and their insect herbivores. However, such methods rely on several assumptions, including constancy in rate of molecular change in taxa under consideration. At right, independent temporal calibration of phylogenies at left based upon occurrences of fossil plant-insect associations, numbered 1-6. These dates represent minimal ages of occurrence of associations. Note that plant taxon C is now known to have had an extinct insect associate.

**Figure 3, facing page.** Examples of galling on stems, midribs, and leaf blades of woody dicotyledonous angiosperms and example of a leaf roll on *Ulmus*. Probable culprits are gall wasps (Hymenoptera: Cynipidae) for *a-d* and gall midges (Diptera: Cecidomyiidae) for *e-k*. Leaf rolling plantlice are the probable culprits for *m* and *n*. Scales: solid bars indicate 1 cm; and each unit on striped bars indicates 0.1 cm. DT in caption refers to damage types listed in Table 1. Museum acronyms for Figures 3-6 are: UWBM, Burke Memorial Museum, University of Washington, Seattle; and SR, Stonerose Interpretive Center, Republic, Washington. *a*, Stem gall on "*Paraprunus*" sp. (Rosaceae); UWBM 76828, loc. B4600, Republic; plant host identified by J. Wolfe; DT55. *b*, Enlargement of galled stem in *a*. *c*, Foliar gall on margin of *Acer* sp. (Aceraceae); UWBM 56312a, loc. B3389, Princeton; plant host identified by J. Wolfe; DT32. *d*, Enlargement of galled leaf margin in *c*. *e*, Midrib gall on *Gordonia* sp. (Theaceae); UWBM 36832, loc. B4131, Republic; plant host identified by J. Wolfe; DT67. *f*, Enlargement of galled midrib region in *e*. *g*, Midrib gall on an unknown dicot; UWBM 36967, loc. B4294, Princeton; plant host identified by J. Wolfe; DT33. *h*, Detail of galled midrib region in *g*. *i*, Midrib gall with exit holes on *Tsukada davidiiifolia* Wolfe & Wehr (Davidiaceae, extinct genus); UWBM 52174, loc. 3389, Princeton; plant host identified by W. Wehr; DT33. *j*, Detail of galled midrib region in *i*; note several, well-defined spheroidal chambers within the gall. *k*, Midrib gall on *Plafkeria* sp. (Tiliaceae, extinct genus); UWBM 71116, loc. A0307, Republic; plant host identified by J. Wolfe; DT67. *l*, Detail of galled midrib region in *k*. *m*, Leaf roll on *Ulmus* sp. (Ulmaceae), with characteristic deformed midrib; UWBM 66233, loc. B4294, Princeton; plant host identified by W. Wehr; DT33. Note overlapping regions of leaf blade at center-right. *n*, Detail of midrib region in *m*.



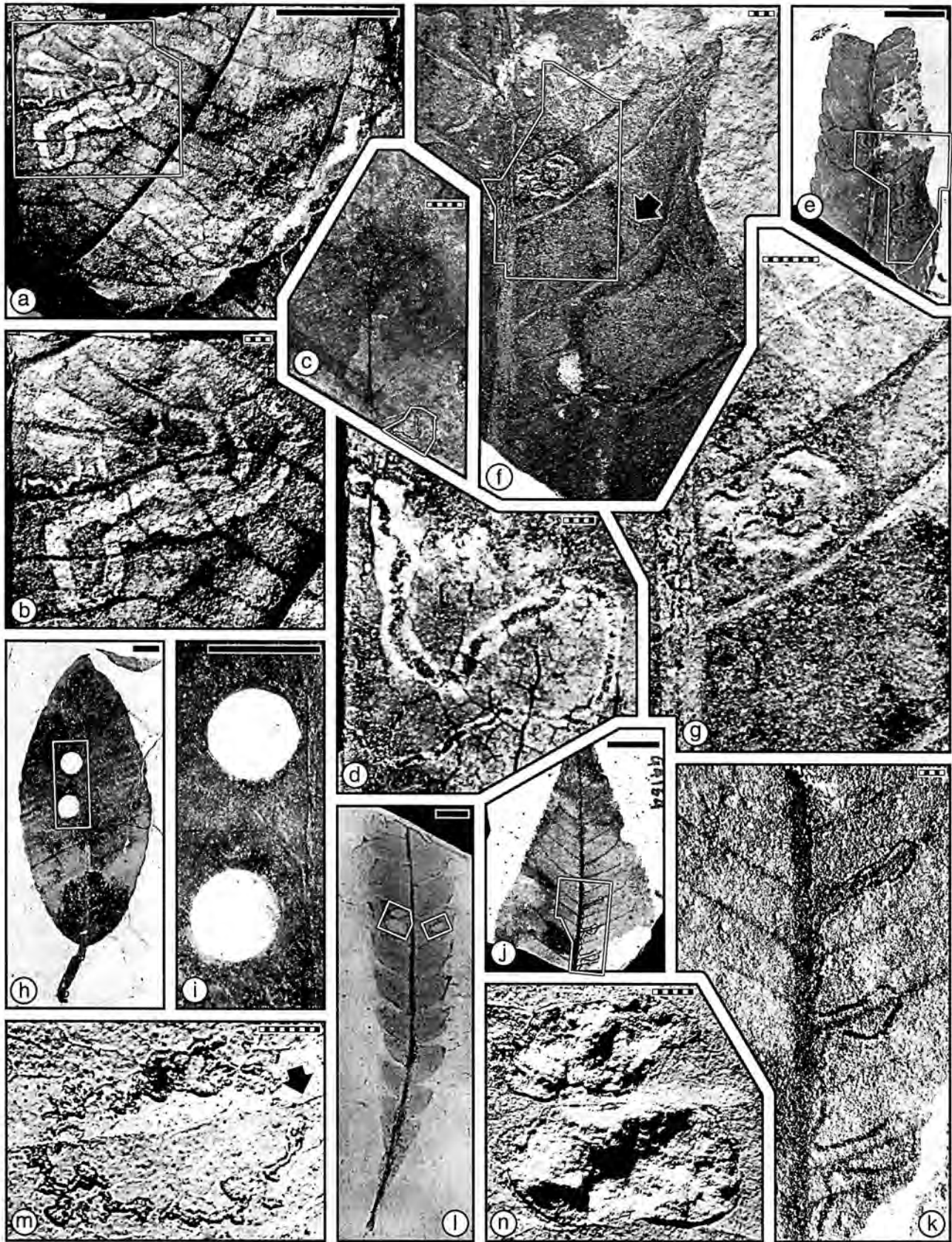
Republic and associated floras, the spectrum of interactions include: midrib, foliar, and stem galls (Fig. 3*a-l*); leaf rolls (Fig. 3*m-n*); serpentine, blotch, and shield-bearer leaf mines, as well as the larval cases of a casebearer leaf miner (Figs. 4, 6*e-f*). Additionally, margin feeding, hole feeding, skeletonization, ovipositional damage (Figs. 5, 6*g-p*), and bud feeding (Fig. 6*a-d*) are present. The plant-insect interactions illustrated in Figures 3 to 6 occur on 29 plant host taxa, twenty (69%) of which are from Republic, six (21%) are from Princeton, two (7%) are from McAbee, and one (3%) is from Chuckanut (Fig. 1). If unpublished materials from other museum specimens are included, 41 separate associations are known for the Republic and coeval floras (Table 1).

It is highly probable that some of these middle Eocene insect associations no longer occur in the modern flora. However, other insect associations may have survived intact among modern descendants of these same plant host lineages, although they currently occur in the disjunct geographical ranges of eastern North America and eastern Asia. This survival is attributable to the close geographical juxtaposition of North America and Eurasia during the middle Eocene, followed by the subsequent separation and differentiation of their respective plant and insect faunas (Linsley, 1963; Tiffney, 1985a, 1985b; Manchester, 1999). Consequently, both Eurasia and North America must be included in any search for modern descendants of insects associated with plant host lineages traceable to the middle Eocene of the Pacific Northwest.

Those plant host lineages still extant in North America and Eurasia that had extensive north-temperate geographic distributions during the geologic past may still possess slowly evolving, ancient insect associations (Linsley, 1963; Moran, 1989; Mitter and Farrell, 1991; Labandeira, et al., 1994). By contrast, plant host lineages that underwent population bottlenecks during the Neogene and currently occur in North American or Eurasian refugia probably lost insect herbivores that were present during the middle Eocene. Probable examples of this phenomenon include *Ginkgo*, *Cercidiphyllum*, and *Aucuba*. A related and important issue in documenting potential descendants of middle Eocene phytophagous insects is the disparate entomological effort in recording insects and their plant hosts in Asia, as opposed to North America and Europe. The lack of adequate systematic and plant host data for modern East Asian insects may result in erroneous inferences regarding the absence of ancient insect associations on modern plants. Coevolved insect lineages occurring on middle Eocene plants may, in fact, still persist with their plant host lineages in Asia, but they remain undocumented. Many of these currently disjunct plant hosts have been discovered during the past century and remain poorly known, as is true for their insect herbivores.

Complete documentation of insect-related associations from the Republic Flora, housed in the Burke Memorial Museum (University of Washington) in Seattle and at the Stonerose Interpretive Center in Republic, Washington, will

**Figure 4, facing page.** Examples of leaf mining. Scales: solid bars indicate 1 cm; and each unit on striped bars indicates 0.1 cm. DT in caption refers to damage types listed in Table 1. See caption to Figure 3 for museum acronyms. *a*, Leaf mine of *Stigmella* (Lepidoptera: Nepticulidae) on an unknown dicotyledonous angiosperm; UWBM 57293a, loc. B5495, Chuckanut; DT39. *b*, Enlargement of mined area in *a*. *c*, Leaf mine of a phyllocnistine (Lepidoptera: Gracillariidae) on an unknown dicotyledonous angiosperm; UWBM 94055a, loc. B5751, McAbee; DT41. *d*, Detail of mined area in *c* showing an undulatory frass trail. *e*, Leaf mines of *Stigmella* (Lepidoptera: Nepticulidae) on aff. *Sorbus* (Rosaceae); UWBM 76477, loc. A0307, Republic; plant host identified by W. Wehr; DT39. *f*, Detail of blotch mine in right-center in *e* showing early instar linear serpentine mine near midrib (black arrow), followed by subsequent blotch mining phase at bottom. *g*, Additional detail of early instar phase of serpentine mining in *f*, showing early confinement of mine by primary and secondary venation, followed by escape to leaf margin prior to blotch formation. *h*, Leaf mine typical of aff. *Incurvaria* (Lepidoptera: Incurvariidae), on *Aucuba* sp. (Cornaceae); UWBM 71371, loc. B2737, Republic; plant host identified by J. Wolfe; DT38. *i*, Detail of leaf blade in *h* with mined circlets removed for incorporation as elements of larval cases. *j*, Serpentine leaf mine, probably of Agromyzidae (Diptera), on *Aesculus* sp. (Hippocastanaceae); UWBM 94134, loc. B3389, Princeton; plant host identified by W. Wehr; DT41?. *k*, Detail of leaf mined region in *j*, showing avoidance of secondary venation. *l*, Probable shield-bearer leaf mines similar to *Antispila* (Lepidoptera: Heliozelidae), on *Comptonia columbiana* Dawson (Myricaceae); UWBM 36831, loc. B4131, Republic; plant host identified by J. Wolfe; DT38. *m*, Detail of leaf mine at upper-right of *l*, exhibiting ellipsoidal mine prior to excision of mined disc from leaf blade (note unsevered vein at arrow). *n*, Detail of leaf mine at upper-left of *l*, exhibiting two ellipsoidal mines after excision of mined area from leaf blade.



be provided in a study in preparation. That study will provide extensive illustration and complete description of available plant damage, documentation of abundant and highly stereotyped insect damage on particular plant hosts, and additional discussion of associations between insects and land plants at Republic. Additionally, that follow-up study will document the intensity and spectrum of herbivore damage on an anthropogenically unbiased sample of the flora, collected in 1997, that will include frequency of attack levels and amount of herbivorized leaf area, partitioned by plant-host taxa and insect functional feeding group. A preliminary report was provided by Palmer et al. (1998) and a categorization of known damage types and their degrees of inferred host specificities are listed in Table 1. The insect damage listed in Table 1 is an ongoing update of previous studies (Wilf and Labandeira, 1999; Labandeira et al., 2002). It includes new, diagnosable associations found at Republic but excludes previously recognized types that have not been recognized there.

## Galling

### Introduction

Galls are three-dimensional structures consisting generally of dense, often hardened, response tissue induced to growth by an insect occupant. Their preservation as fossils rarely reveals the histological detail necessary for assignment to a particular lower-level insect taxon (Larew, 1986, 1992; but see Labandeira and Phillips, 1996b). By contrast, leaf mines are two-dimensional features

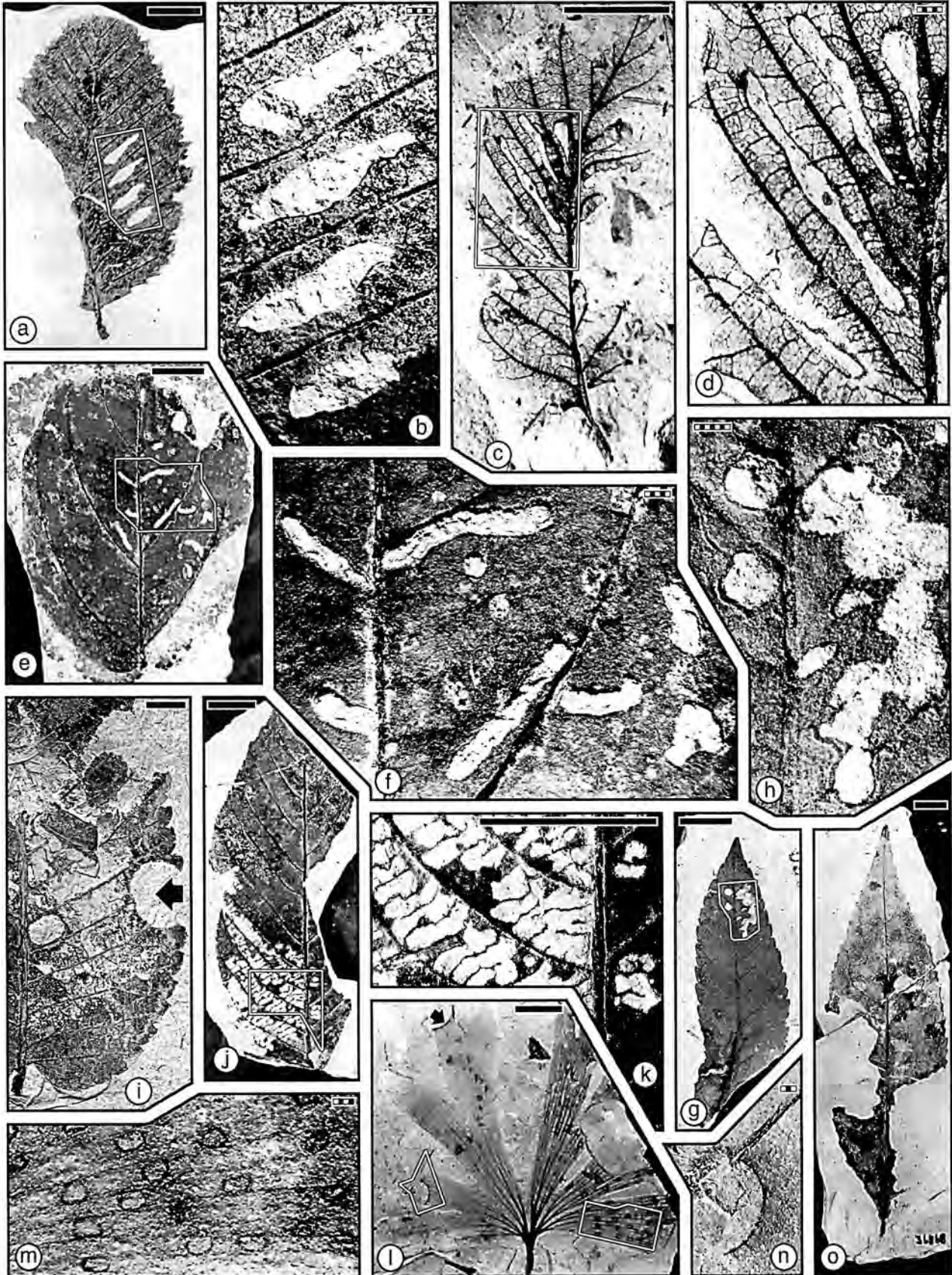
that present considerable histologic detail in compression fossils when preservation is good to excellent. The external size, shape, and surface texture of fossil galls, in conjunction with their location on plant organs, can be helpful in revealing the identity of the galler, sometimes to the family level (Scott et al., 1994) and occasionally to the generic level (Möhn, 1960; Gagné, 1968; Lewis 1985). Because of this taphonomic restriction, it is often the case that only broad generalizations can be proposed regarding the association of fossil plant lineages and their insect gallers. The best cases in the fossil record are Neogene insect galls resolvable to the generic level and occurring on known plant-host genera (Mädler, 1936; Lewis, 1985; Waggoner and Poteet, 1996). The following examples attest to the general absence of taxonomic resolution for insect galling.

### *Cecidomyiidae* (Gall Midges)

Cecidomyiidae, or gall midges, are an economically important, cosmopolitan lineage of nematocerosous Diptera consisting of approximately 5,000 species (Gagné, 1994). Gall midge larvae are closely associated with plants, generally as gallers or other endophytic consumers of various plant tissues. Feeding is overwhelmingly or entirely accomplished by the larva, which is a sap feeder that predigests and liquefies plant tissues by salivary secretions. Larvae are legless, less than 0.5 cm long and, in gall-inhabiting forms, occur in a spheroidal or irregularly shaped cavity surrounded by protein- and lipid-rich, plant tissues that proliferate as an inner layer of the gall. This

**Figure 5, facing page.** Examples of external foliage feeding. Scales: solid bars indicate 1 cm; and each unit on striped bars indicates 0.1 cm. DT in caption refers to damage types listed in Table 1. See caption to Figure 3 for museum acronyms. *a*, Center feeding on *Betula leopoldae* Wolfe & Wehr (Betulaceae) with serially deployed, interveinal feeding holes; UWBM 94270, loc. A0307, Republic; plant host identified by J. Wolfe; DT63. *b*, Enlargement of insect-damaged region in *a*. *c*, Center feeding on an undetermined dicot, with similar, serially deployed, interveinal feeding holes as in *a*; SR 95-31-1, loc. B4131, Republic (Stonerose); DT63. *d*, Enlargement of insect-damaged region in *c*. *e*, Probable chrysomelid (Coleoptera) center feeding on *Alnus parvifolia* (Berry) Wolfe & Wehr (Betulaceae); UWBM 95725, loc. B4131, Republic; plant host identified by W. Wehr; DT8. *f*, Magnification of elongate feeding traces in *e*. *g*, Probable curculionid (Coleoptera) feeding on *Rhus malloryi* Wolfe & Wehr (Anacardiaceae); UWBM 76456, loc. A0307, Republic; plant host identified by C. Labandeira; DT5. *h*, Detail of feeding damage in *g*. *i*, Megachilid (Hymenoptera) margin feeding on an *Ulmus* sp. (Ulmaceae); UWBM 95726, loc. B4131, Republic; plant host identified by W. Wehr; DT12 (individual excision site indicated by arrow). *j*, Interveinal skeletonization of *Aesculus* sp. (Hippocastanaceae); UWBM 40229, loc. B3389, Princeton; DT16. *k*, Detail of feeding damage in *j*. *l*, Megachilid (Hymenoptera) margin feeding (arrow) and ovipositional damage on *Ginkgo* sp. (Ginkgoaceae); UWBM 77597, loc. B5757, McAbee; plant host identified by C. Labandeira; DT12, 54. *m*, Enlargement of probable ovipositional damage on right side of *l*. *n*, Enlargement of excision of blade margin on left side of *l*. *o*, Extensive margin feeding on *Gordonia* sp. (Theaceae); UWBM 36868, loc. B4131, Republic; plant host identified by J. Wolfe; DT12, 14.





specialized, parenchymatous tissue, known as nutritive tissue, is the food source of the larvae, and frequently it is surrounded toward the outside by cornified or otherwise hardened external tissues that provide shape and structure to the gall. In some instances, gall midge larvae occupy a gall for as long as two years, spending most of their lives in diapause (Gagné, 1989). More frequently, however, gall midges inhabit galls only for several days to a few weeks or months to complete the larval phase of their life cycle. This is followed by a short pupal stage, either within the larval chamber or outside the gall. Adult gall midges are small, delicate flies that typically do not feed. They have an ephemeral existence, sufficient for mating and subsequent oviposition of eggs into the tissues of an appropriate host.

Not all gall midges occur as occupants of foliar, stem, bud, or root galls. Some species are stem borers, others occur gregariously in leaf rolls, and some even occur as parasitic visitors (inquilines) in other cecidomyiid galls. Primitive gall midge lineages are not gall makers, but feed on fungi (Foote, 1991a), similar to members of the related families Mycetophilidae and Sciaridae. The most derived and diverse lineage of gall midges is characterized by the galling life-habit, and it occurs on virtually all major groups of land plants, including ferns, conifers, gnetaleans, and dicotyledonous and monocotyledonous angiosperms (Docters van Leeuwen-Reijnvaan and Docters van Leeuwen, 1926; Gagné, 1989; Roskam, 1992). Most gall midges are monophagous, consuming one host species, or

oligophagous, consuming a few related host species; a few are polyphagous, galling unrelated plant hosts (Gagné, 1989, 1994). However, polyphagous gall midges usually cause simple tissue swellings and do not produce conspicuous, complex galls.

Five examples of probable gall midge galls are illustrated in Figure 3. The elongate midrib gall occurring on *Gordonia* (Theaceae; Fig. 3e-f) is structurally consistent with induction by a gall midge. It resembles an immature gall of *Dasineura tumidosae* Felt on *Fraxinus*, the ash midrib gall (Beutenmüller, 1904; Gagné, 1989). Modern gall midges are known to form similar midrib galls on the related theaceous genus, *Eurya*, in Sumatra (Docters van Leeuwen-Reijnvaan and Docters van Leeuwen, 1926), although the *Gordonia* gall is similar to the modern *Resseliella tulipiferae* (Osten Sacken) on the tuliptree *Liriodendron tulipifera* L. (Magnoliaceae; Gagné, 1989, fig. 335). In North America and Eurasia, modern species of several other genera of gall midges, including *Blaesodiplosis*, *Dasineura*, *Janetiella*, *Lasioptera*, *Macrodiplosis*, and *Polystepha* regularly induce similar linear galls on leaf midribs or major secondary veins in a variety of dicotyledonous angiosperms (Kolomoets et al., 1989; Gagné, 1989). In the tropical and temperate regions of Asia, members of the Theaceae, including *Camellia*, *Gordonia*, *Eurya*, and *Thea* are galled extensively by thrips, aphids, psyllids, and tenthrinids (Houard, 1923; Docters van Leeuwen-Reijnvaan and Docters van Leeuwen, 1926). Like *Gordonia*, the plant host of the spheroidal midrib gall documented in Figure 3g-h is unknown. The

**Figure 6, facing page.** Examples of bud boring, external foliage feeding, and ovipositional damage. Scales: solid bars indicate 1 cm; and each unit on striped bars indicates 0.1 cm. DT in caption refers to damage types listed in Table 1. See caption to Figure 3 for museum acronyms. *a*, Bud boring by an endopterygote larva on *Maeginitia gracilis* (Lesquereux) (Platanaceae); UWBM 76885, loc. B1540, Republic; plant host identified by J. Wolfe; DT6. *b*, Detail of bud boring in *a*. *c*, Bud boring by an endopterygote larva on *Ulmus* sp. (Ulmaceae); UWBM 77329, loc. B4131, Republic; plant host identified by W. Wehr; DT6. *d*, Detail of bud boring in *c*. *e*, *Coleophora* (Lepidoptera: Coleophoridae) casebearer damage on an unidentified dicot; UWBM 77608, loc. B4131, Republic; DT66. *f*, Detail of coleophorid damage in *e*, showing several cigar-shaped larval cases (arrows indicate cases with arcuate shape in profile view). *g*, Free feeding on an unidentified dicot; UWBM 54828b, loc. B4131, Republic; DT26. *h*, Possible Pyralidae (Lepidoptera) center feeding along the medial midrib of *Sassafras hesperia* Berry (Lauraceae); UWBM 54805, loc. B4131, Republic; plant host identified by W. Wehr; DT50. *i*, Enlargement of center feeding damage in *h*. *j*, *Altica* sp. (Coleoptera: Chrysomelidae) oviposition sites on *Alnus parvifolia* (Berry) Wolfe & Wehr (Betulaceae); UWBM 57187, loc. A0307, Republic; plant host identified by W. Wehr; DT54. *k*, Detail of crescentic oviposition tracks in *j*. *l*, *Altica* (Coleoptera: Chrysomelidae) oviposition sites on "*Paracrataegus*" sp. (Rosaceae); UWBM 94017, loc. B5751, McAbee; plant host identified by W. Wehr; DT54. *m*, External foliage feeding on an undetermined fern; UWBM 77764, loc. A0307B, Republic; DT12, 14. *n*, Magnification of cusped excavations, indicated by arrows, from margin feeding in *m*. *o*, Hole- and margin-feeding on *Alnus parvifolia* (Berry) Wolfe & Wehr (Betulaceae); UWBM 77133, loc. 0307, Republic; plant host identified by W. Wehr; DT12, 15, 63. *p*, Detail of margin feeding in *o*, showing reaction rim (left arrow) and flap of necrotic tissue (right arrow) along the outer margin of the reaction rim.



**Table 1. The forty-one insect damage-types known to be represented in the Republic Flora, both described in this study and from documented but unpublished material. Host specificity numbers refer to generalist (1), intermediate (2), and specialized (3) degrees of host-plant dependence (Wilf and Labandeira, 1999).**

Damage Type	Category	Physical Description	Host Specificity
1	HOLE FEEDING	Small (<1 mm)	1
2	HOLE FEEDING	Medium (1 to 5 mm)	1
3	HOLE FEEDING	Medium (1 to 5 mm), polylobate	1
4	HOLE FEEDING	Large (> 5 mm)	1
5	HOLE FEEDING	Large (> 5 mm), polylobate	1
6	HOLE FEEDING	Bud feeding	3
7	HOLE FEEDING	Curvilinear	2
8	HOLE FEEDING	Elongated slot (length > 2.5 width)	2
9	HOLE FEEDING	Polymorphic, generally ellipses (>2 mm)	2
50	HOLE FEEDING	Adjacent to midvein	2
57	HOLE FEEDING	Small (< 3 mm longest dimension), reniform to ovoidal, at primary vein angles	2
60	HOLE FEEDING	Elongate slots parallel to tertiary venation	3
63	HOLE FEEDING	Large, intersecondary areas consumed	1
64	HOLE FEEDING	Repeated, circular, interveinal holes adjacent leaf margin	2
65	HOLE FEEDING	Comma-shaped to curved-elongate holes clustered toward leaf margin	3
12	MARGIN FEEDING	Generalized, cusped	1
13	MARGIN FEEDING	Leaf apex	1
14	MARGIN FEEDING	To primary vein	1
15	MARGIN FEEDING	Trenched or otherwise deeply incised	2
16	SKELETONIZATION	General, reaction rim weakly developed	1
19	SKELETONIZATION	Broad, with rectangular pattern	2
21	SKELETONIZATION	Highest order of venation removed	2
22	SKELETONIZATION	Linear pattern	2
24	SKELETONIZATION	Ovoidal, adjacent to midvein	2
56	SKELETONIZATION	In basal angle formed by primary and secondary veins	2
26	EXTERNAL-SPECIAL	Free feeding	2
29	EXTERNAL-SPECIAL	Window feeding, generalized	1
32	GALLING	On nonveinal part of leaf	2
33	GALLING	On primary vein; spheroidal	3
67	GALLING	On primary vein; elongate—elliptical to lenticular	3
34	GALLING	On secondary vein	2
55	GALLING	Petiolar (or stem) galls	3
35	MINING	Blotch, with a central chamber	3
38	MINING	Circular to elliptical, with or without case	3
66	MINING	Small, circular, mined areas with elongate coleophorid cases	3
39	MINING	Confined between closely spaced secondaries, frass particulate	3
41	MINING	Serpentine A; long, undulatory, frass particulate	3
43	MINING	Serpentine C; short, solid frass trail	3
46	PIERCING & SUCKING	Small scale or puncture (<2 mm), circular depression	3
54	OVIPOSITION	Scars in arcuate rows, en echelon	3
58	FUNGAL DAMAGE	Ovoid to polylobate fungal blotches	

modern plant genus *Cornus* (dogwood) does bear similar midrib galls, particularly those made by *Craneiobia corni* (Giraud) and *Lasioptera corni* Felt (Gosev and Rimsky-Korsakov, 1951; Skuhřavá et al., 1984; Gagné, 1989; Kolomoets et al., 1989).

The following three galls are found on extinct plant host genera that belong to modern families. The first, an ovoidal stem gall approximately 1.3 cm in diameter (Fig. 3a–b), is on the rosaceous "*Paraprunus*," an early relative of the modern, wide-ranging, Holarctic genus *Prunus* (Wehr and Hopkins, 1994; Wehr, 1995). Similar ovoidal stem galls occurring on modern rosaceous plants include "variable, oval or fusiform twig galls on wild black cherry, *P[runus]. serotina*" (Felt, 1917, p. 150), and a remarkably similar "ovoid outgrowth of [a] stem, simulating [a] swollen bud" on *Spiraea* (Gagné, 1994), described and discussed by Tavares (1918) and Houard (1933). The following galls occur on midribs and have a pyriform to lenticular shape. The first of these is on the plant host *Tsukada davidifolia* Wolfe & Wehr (Fig. 3i–j), a member of the warm-temperate Davidiaceae, closely related to or confamilial with the Cornaceae (Cronquist, 1981; Heywood, 1993; Judd et al., 1999). This specimen bears an ovoidal, multiloculate midrib gall, of which several spheroidal exit holes can be identified along the gall margin in Figure 3j. No known galls have been documented from the only extant representative of this lineage, *Davidia involucrata* Baillon (Chinese dovetree), from southwestern China.

The third extinct genus, *Plafkeria*, is a member of the Tiliaceae, a diverse family of tropical to temperate, cosmopolitan trees and shrubs. Modern Tiliaceae comprise about 41 genera (Heywood, 1993) that harbor an elevated spectrum of insect gallers (Docters van Leeuwen-Reijnvaan and Docters van Leeuwen, 1926; Mani, 1964). Although the ovoidal midrib gall of *Plafkeria* (Fig. 3k–l) is featureless, similarly shaped midrib galls have been documented on modern tiliaceous genera, including *Grewia* (Docters van Leeuwen-Reijnvaan and Docters van Leeuwen, 1926), *Heliocarpus* (Möhn, 1964; Gagné, 1994), *Luehea* (Tavares, 1914; Houard, 1933; Gagné, 1994), *Pentace* (Burmese mahogany; Docters van Leeuwen-Reijnvaan and Docters van Leeuwen, 1926), and *Tilia* (linden; Mani, 1964; Felt, 1965; Kolomoets et al., 1989; Zerova et al., 1991; Alford, 1991). As most cecidomyiid gallers of plants are mono- or oligophagous, it

is probable that the extinction of "*Paraprunus*," *Tsukada*, and *Plafkeria* also resulted in the demise of their associated gall midges. It remains possible, however, that there was lateral host transfer onto a related or otherwise similar extant genus or, alternatively, they survived via anagenetic evolution onto a descendant species.

#### *Cynipidae* (Gall Wasps)

Cynipids, commonly known as gall wasps, are some of the most conspicuous of gall making insects, principally because of the colorful, spheroidal, almost golfball-sized galls that they produce on oaks in Eurasia and North America. Gall formation in gall wasps commences after the larva has hatched and secreted salivary substances that induce atypical tissue proliferation by the host plant, and not at the time of oviposition as in the case of other gall-forming Hymenoptera, such as sawflies. Cynipid galls exhibit considerable diversity in shape, size, texture, and tissue hardness; in fact, many biological species are recognized by the distinctive form and location of their galls (Redfern and Askew, 1992). Gall wasp larvae are characteristically robust and wormlike, possess pronounced mandibles, and generally a single larva inhabits a cavity within each gall. Pupation occurs inside the gall. Adults are ephemeral, small- to rarely medium-sized wasps that do not feed but may imbibe exudates such as nectar or honeydew (Gauld and Bolton, 1988).

The life-habits characterizing taxonomic subdivisions of gall wasps parallel those of gall midges since the most derived subgroup bears the galling habit. More primitive lineages are nongalling forms. In the case of cynipids, the basal groups usually are endoparasitoids that develop within endopterygote larvae or inquilines occurring in other cynipid galls (Ronquist, 1995). The highly derived subfamily Cynipinae, or gall wasps proper, consists of about 1,000 described species worldwide (Gauld and Bolton, 1988), although their suspected diversity is several times that number. Approximately 86 percent of all cynipids that gall plants have Fagaceae as hosts, especially oak (*Quercus*; Drooz, 1985). Other plant families that are attacked with much less frequency are Asteraceae, Lamiaceae, Rosaceae (especially rose, *Rosa*), and a few species are known to produce galls on Sapindaceae such as maple (*Acer*; Askew,

1984). Virtually all species are host-specific at the level of the plant species or genus (Gauld and Bolton, 1988), although some species occur on unrelated, alternate hosts for the asexual and sexual phases of their life-cycle.

The probable cynipid gall illustrated in Figure 3c-d is an hemispheroidal foliar gall on *Acer* sp., approximately 1 cm in diameter. Based on size, shape, foliar location, and plant host, this gall resembles modern galls made by *Pediaspis* gall wasps (Gosev and Rimsky-Korsakov, 1951, fig. 177; Zerova et al., 1988, pl. 15, fig. 6a) of the tribe Pediaspidini. This taxonomically isolated and monotypic lineage currently consists of only two or three known species from Europe that gall only *Acer* hosts (Folliot, 1964; Askew, 1984). If this attribution is correct, it may be the oldest record of a cynipid gall on a modern genus of plant. A Cretaceous gall was described by Lesquereux (1892) and Berry (1923) from the Cenomanian Dakota Formation as an "oak gall" (Scott et al., 1994). Scott et al. (1994) presented additional evidence for cynipid galls from the Dakota Formation (their gall types 8 and 9). From slightly earlier Albian deposits in Maryland, Hickey and Doyle (1977) briefly mentioned foliar galls on "*Sassafras*," which Larew (1992) considered as complex spangle galls resembling those produced by modern cynipids on oaks. However, these Cretaceous galls occur on plant hosts that cannot be identified as modern genera.

## Leaf Rolling

### Introduction

Leaf rolls are difficult to detect in the fossil record principally because insect-mediated leaf curling is similar to other types of leaf manipulation by insects, or simply from physical trauma. In many instances, leaf rolls grade imperceptibly into galls, as the leaf-roll occupant begins to feed extensively on foliar tissue and a galling response is elicited subsequently from the host plant. Leaf rolls are relatively uncommon in the fossil record but are best recognized by elongate fields of skeletonization on a leaf that indicate leaf folding and consumption of surface tissues.

### *Pemphigidae* (Plantlice)

Pemphigids are aphid-like insects, commonly referred to as plantlice or woolly aphids. Like most aphids and their relatives, pemphigids alternate

their life cycles between hosts and reproduce sexually and asexually through parthenogenesis (Wool, 1984; Dolling, 1991; Whitham, 1992). Adult, normal-sized females lay one, large, overwintering egg on the primary host, usually a dicotyledonous tree or shrub. This egg hatches during the spring, resulting in offspring that lack mouthparts and, although undergoing four typical molts, remain dwarfed and wingless. Adult females of this population reproduce parthenogenetically and give live birth to both sexes. Of these hatchlings, winged females fly to an alternate host, such as a perennial grass, when the primary woody host is dormant. During the summer, this alternate host provides a substrate for winged females to produce offspring of both sexes parthenogenetically. After a few generations, usually during the spring, some members of their offspring eventually fly to the primary host, mate, lay their eggs, and renew the cycle.

Pemphigids of the subfamily Eriosomatinae occur on elms (*Ulmus*) as their primary host (Schuh and Mote, 1948; Meyer, 1987; Foster and Northcutt, 1994), on which they produce a variety of distinctive leaf rolls and leaf galls (Patch, 1910; Hoffmann, 1942; Zerova et al., 1991). Frequently the midribs or petioles of individual leaves are abnormally bent or otherwise misshaped in the process of leaf rolling and galling (Parks, 1936; Baldwin, 1952, fig. 23; Redfern and Askew, 1992). This characteristic deformation is conspicuously displayed by pemphigids on elm (*Ulmus*) and also on the unrelated poplar or cottonwood (*Populus*; Mädler, 1936; Harper, 1966; Alford, 1991; Redfern and Askew, 1992). The leaf roll shown in Figure 3m-n is typical of pemphigid leaf rollers, consisting of a deformed midrib that is surrounded by overlapping regions of the leaf blade.

## Leaf Mining

### Introduction

Of all plant-insect interactions encountered in the fossil record, leaf mining has the greatest potential for identification of an insect herbivore to a lower taxonomic level. Frequently, fossil leaf mines have been assigned to insect families, subfamilies, and genera (Hering, 1930; Freeman, 1965; Opler, 1973, 1982; Labandeira et al., 1994; Jarzembowski, 1995). This heightened reliance in taxonomic assignment is attributable to the highly stereotyped nature of leaf mine damage in modern taxa (Needham et al., 1928; Hering, 1951). Several

features — the location of oviposition, mine, and emergence sites; the consistency, continuity, and pattern of the frass trail; and the size, shape and disposition of frass in the terminal emergence chamber — are highly diagnostic of modern leaf mining taxa. When plant hosts identifiable to a family (or especially a modern genus) contain distinctive leaf mines, there is considerable promise for addressing the macroevolutionary history of modern, often coevolved, plant-insect associations (Opler, 1973, 1974; Labandeira et al., 1994, 2002). One of these is an example of high taxonomic resolution of plant host and its leaf miner, *Stigmella* (Lepidoptera, Nepticulidae) on the rosaceous *Sorbus* (mountain ash), that is very similar to an association on an extant European species of *Sorbus*.

#### *Nepticulidae (Nepticulid Leaf Miners)*

The highly specialized, leaf mining, lepidopteran family Nepticulidae possesses larvae that dominantly occur within leaf mesophyll or epidermis, and rarely in buds, the bark of twigs, or epidermal tissues of fruit (Davis, 1987a, 1998). A few species are twig gallers. The larva emerges from a flat, surface-attached egg, initially bores into the host, and immediately initiates a threadlike, serpentine to linear mine characterized by a continuous median frass trail (Davis, 1987a, 1998). The mine subsequently enlarges upon each successive instar, becoming an enlarged blotch in some species. It is always characterized by an intermittently broken, sometimes bead-like, frass trail. Pupation occurs in a lenticular cocoon outside the mine.

The Nepticulidae is a primitive, cosmopolitan group of leaf miners consisting of 11 genera and approximately 800 described species, of which 100 occur in North America (Johansson et al., 1990; Davis, 1998). Its fossil record extends to the mid Cretaceous (Labandeira et al., 1994) and possibly to the Jurassic-Cretaceous boundary of northeastern Australia, on the seed fern *Pachipteris* (Rozeffelds, 1988). The hosts of nepticulids comprise approximately 20 families of woody dicotyledonous angiosperms, particularly the subclasses Hamamelidae, Rosidae, and Dilleniidae (Wilkinson and Scoble, 1979; Nieuwerkerken, 1986). Only a few species are of substantial economic importance. Examples include: species of *Obrussa* that bore into the petioles, buds, and samaras of maples; and cotton, which is attacked by a species of *Stigmella* (Davis, 1987a).

The nepticulid mine in Figure 4a–b represents an unknown species owing to the absence of a preserved frass trail. Its ontogenetic pattern, size, and shape, however, suggest that it is a *Stigmella*. Two additional and complete nepticulid mines are shown in Figure 4e, one on each side of the midrib of a leaf closely related to the modern rosaceous tree, *Sorbus* (mountain ash). These mines show an initial serpentine phase detailed in Figure 4f, followed by a blotch phase enlarged in Figure 4g. Both mines on this leaf were made by the same nepticulid species. They are virtually identical to species of modern *Stigmella* that mine *Sorbus acuparia* L. in central and northern Europe (Sorhagen, 1919; Nieuwerkerken, 1986), particularly *Stigmella nylandriella* Tengström and *S. magdalenae* Klimesch (Borkowski, 1969, fig. 19; 1994, fig. 68; Schoorl et al., 1985, figs. 67, 68; Gustafson, 1985, figs. 10H and 11A). A particularly striking similarity between the fossil and extant mines is a very thin, threadlike, central frass trail within a relatively expansive late instar portion of the mine or a beginning portion of the terminal chamber (Fig. 4g).

#### *Heliozelidae (Shield Bearers)*

The Heliozelidae is an inconspicuous, cosmopolitan family of 12 genera and somewhat over 100 species of incurvarioid Lepidoptera possessing leaf mining larvae, commonly known as shield bearers (Gerasimov, 1952; Scoble, 1992; Davis, 1998). As adults, females insert eggs into host-specific plant tissue, from which newly hatched larvae target a particular leaf tissue and become serpentine miners. After a few instars, shield bearer larvae become full-depth blotch miners, often obliterating the previously made serpentine mine (Davis, 1987b). Within this blotch mine, the last larval instar constructs an oval to ellipsoidal case by cutting the upper and lower surfaces of a leaf and attaching the two ovoidal or circular plates of epidermal tissue with silk (Dziurzynski, 1958; Kuroko, 1961; Brown and Eads, 1969; Emmet, 1973). While enclosed in this disk-shaped “shield,” the larva does not feed and forms a cocoon, in which pupation occurs, usually during winter in temperate regions (Davis, 1987b).

Most heliozelids are mesophyll feeders that form blotch mines on leaves, petioles, and twigs (Scoble, 1992). In some species these mines are initially transformed into galls (Needham et al., 1928), providing nutritive tissue for larval consumption. Although only one heliozelid is known as a serious pest — the resplendent shield

bearer, *Coptodisca splendoriferella* Clemens, on apple (Snodgrass, 1922; Needham et al., 1928) — records from North America indicate that twelve plant host families are mined by heliozelids, including Betulaceae, Cornaceae, Ericaceae, Rosaceae, Salicaceae, and Vitaceae (Hering, 1951; Brown and Eads, 1969; Davis, 1987b). Three probable mines (Fig. 4l–n) occur on *Comptonia* (Myricaceae), a host not known for modern heliozelids in North America. These three ellipsoidal mines, however, have an average major axis length of 5.3 mm and a minor axis width of 2.9 mm. The measurements are of identical aspect ratio, but slightly larger than *Antispila petryi* Martini on *Cornus sanguinea* L. in Poland (Dziurzynski, 1958), and of similar aspect ratio, but somewhat larger than six species of *Antispila* on cornaceous and vitaceous hosts in Japan (Kuroko, 1961). An interesting aspect is that one mine exhibits an epidermis that had been perforated by the larva (Fig. 4m) but remains attached to the leaf blade by a secondary vein; by contrast, two ellipsoidal leaf cases have been freed from older, adjacent mines on the opposite side of the midrib (Fig. 4n). Other types of damage for which these circular excisions can be mistaken include the related Incurvariidae (discussed below) and the circular holes that are cut by some lepidopterans, such as Hesperidae, for formation of chrysalises (Bondar, 1913).

#### *Incurvariidae (Fairy Moths)*

The Incurvariidae, or fairy moths, is a widespread family of about 11 genera and 100–300 species whose center of diversity is Australia (Heath, 1976; Davis, 1987c, 1998; Scoble, 1992). Adults are drably colored, small moths, females of which oviposit in tissue on the undersides of leaves (Davis, 1987c). First instar larvae typically are blotch leaf miners. At the end of the first instar, larvae cut circular or broadly ovoidal discs of lower and upper epidermis from their mine, which they connect with silken threads (Dziurzynski, 1958; Parra and Ibarra-Vidal, 1994). During subsequent instars, the larva drags its case onto a leaf surface, relocating it to an unconsumed region of the same leaf or onto an adjacent leaf. The larva then successively adds somewhat larger discs of leaf epidermis on both sides of its sandwiched case (Ross, 1962) after it has skeletonized or surface fed on the fresh leaf substrate in a circular to ovoidal ring paralleling the margin of the current case (Brown and Eads, 1965a). Up to five or more pairs of cases, one per instar, are associated with incurvariid

larvae prior to pupation. After termination feeding in the last larval instar, a circular to elliptical final case is excised that often is perfectly rounded, displaying sharp margins, and lacking of any apparent damage to the surrounding leaf tissue, thus appearing as a “shot hole” (Lundblad, 1927; Jensen, 1932; Saalas, 1935; Brown and Eads, 1965a). These excised cases are circular to broadly ovoidal and highly rounded (Herrick, 1923; Hering, 1951; Dziurzynski, 1958; Davis, 1972; Johnson and Lyon, 1991). Excellent discussions of incurvariid larval life-habits are provided by Saalas (1935), Dziurzynski (1958), Ross (1962), Brown and Eads (1965a), and Davis (1998).

Globally, incurvariids mine several major plant families, including Betulaceae, Cornaceae, Ericaceae, Fabaceae, Fagaceae, Myrtaceae, Rosaceae, and Proteaceae (Nielsen, 1982; Scoble, 1992). However, the species that has attained pest status in North America, *Paraclemensia acerifoliella* (Fitch), is one of the few incurvariids that attacks maple (Aceraceae) as its primary host (Herrick, 1923; Ross, 1962; Nielsen, 1982). A probable example of incurvariid damage from Republic involves two circular holes on *Aucuba* (Cornaceae; Fig. 4h). These circular excavations occur on a rather thick, featureless, and once thick leaf, bear sharp edges, and measure 0.8 mm in diameter — attributes that are consistent with patterns of modern incurvariid damage (Saalas, 1935; Dziurzynski, 1958; Davis, 1972, 1974). Incurvariid larvae are known to mine Cornaceae, particularly the dogwoods *Cornus* and *Swida* (Dziurzynski, 1958; Heath, 1976; Bruun, 1988), although the subtropical genus, *Aucuba*, currently is not known to harbor incurvariid miners. Native species of *Aucuba* occur in central and eastern Asia, whereas cultivated varieties of *Aucuba*, also known as Japanese laurel, now are cosmopolitan. The only other examples of probable incurvariid damage in the fossil record include penecontemp-oraneous, circular leaf mines occurring on the leaf margins of *Laurophyllum* (Schaarschmidt, 1992, fig. 34) from Messel, near Darmstadt in Germany, and a specimen of *Macginitiea wyomingensis*, with leaf mines remarkably similar to extant *Paraclemensia*, from the Green River Formation of Utah (Labandeira 1998b).

#### *Gracillariidae (Blotch Leaf Miners)*

The gracillariids, also known as blotch leaf miners, are the most diverse clade of plant mining Lepidoptera, representing minimally 2,000 known



species within about 75 genera. The diversity of this group in the tropics, however, is barely known (Davis, 1987d; Davis and Robinson, 1998). Species of gracillariids have 4–11 larval instars (Kumata, 1978) that are subdivided into two major phases of hypermetamorphic larvae, which have distinct life-habits that are differentiated morphologically. The first phase, occurring after hatching, is a sap feeding stage in which a flat, legless larva becomes a serpentine or shallow-blotch miner. The larva of this stage possesses highly specialized mouthparts and lacks a spinneret. The second phase is a tissue feeding or silk spinning stage characterized by a larva with a more cylindrical body, frequently with functional legs, and bearing generalized, spinneret-bearing mouthparts. These mouthparts are important for feeding or spinning in a deeper blotch mine that sometimes serves as a pupal chamber (Davis, 1987d; Davis and Robinson, 1998). The larval mine of gracillariids is distinctive, consisting of an initial slender, serpentine phase, usually followed by a blotch mine wherein pupation may occur. The frass within the serpentine part of the mine is deposited medially, frequently as a sinusoidal to increasingly tightly undulating, bolus stream. The combination of a linear to blotch leaf mine geometry, patterns of frass deposition, and location of the leaf mine are highly diagnostic of the Gracillariidae (Labandeira et al., 1994).

As a leaf mining family of the most successful lineage of Lepidoptera, the Ditrysia, gracillariids achieve their success by occurring on diverse plant hosts and by an ability to exploit a variety of tissue types endophytically, including leaf mesophyll and epidermis, bark cambium, seed parenchyma, and fruit epidermal tissues. Gracillariids occur on diverse plant hosts, especially on woody dicotyledonous trees such as Betulaceae, Fabaceae, Fagaceae, Rosaceae, and Salicaceae, but they also occur on herbaceous taxa in the Ericaceae and Asteraceae. Several gracillariid species have achieved pest status on crops such as apple and azalea, and many species occur on various oaks that have significant fossil records (Opler, 1974; Opler and Davis, 1981). The illustrated gracillariid mine (Fig. 4c–d) exhibits an initial, apparently continuous frass trail, followed by an undulatory frass trail in later instars. The host is unknown.

#### *Coleophoridae (Casebearers)*

The Coleophoridae is a cosmopolitan family of gelechioid Lepidoptera comprised of 13 genera and approximately 1,050 species, 145 of which occur in

North America (Stehr, 1987b; Scoble, 1992; Hodges, 1998). The subfamily Coleophorinae consists of leaf miners and seed predators, of which *Coleophora* is the most speciose genus. Members of Coleophoridae are typically known as casebearers for their characteristic cigar- or pistol-shaped, portable larval cases. Early instars of all species are miners within the leaf, and lack larval cases. By contrast, later instars of most species are external leaf miners whose bodies are concealed in portable cases on leaf surfaces. As casebearers, larvae are window feeders or rarely hole feeders when the entire leaf blade is locally consumed (Keller, 1917; Feehan, 1996; Emmett, 1997). In these instars, cases are constructed from leaf fragments, frass, and silk and are perched on the leaf surface, frequently adjacent to the primary veins, from which the anterior part of the larva descends into the host leaf to feed on preferred tissues (Briggs, 1905; Gillespie, 1932; Stehr, 1987b). Because of the variety in shape and composition of larval cases made by coleophorids, species of *Coleophora* often can be determined from their case morphology alone (Stehr, 1987b). Notably, there are also distinctive sizes and shapes of cases for an instar series in several well-documented casebearers (Snodgrass, 1922; Raske, 1976).

Coleophorids are found on economically important, woody, dicotyledonous plants (Fal'kovich, 1997), including Pinaceae (Johnson and Lyon, 1991), Anacardiaceae (Herrick, 1909), Betulaceae (Salman, 1929; Gillespie, 1932), Ericaceae (Kumata and Nakatani, 1995), Rosaceae (Gould, 1931; Oku, 1965), and Ulmaceae (Oku, 1965). Notable examples of pest species include the larch casebearer (*C. laricella* Hübner), the pistol casebearer (*C. malivorella* Riley) on apple, and the cigar casebearer (*C. serratella* [L.]) on birch. The specimens documented in Figure 6e–f may occur on a rosaceous host, a common family of plants attacked by coleophorids. An additional specimen of several casebearers on the same host is unfigured. However, the curvilinear shape and smooth-walled exterior of these probably third instar cases more closely resemble species found on modern hosts, such as *Betula* (Raske, 1976) and various species of Juglandaceae, especially hickory (*Carya*; Gill, 1917; Johnson and Lyon, 1991).

#### *Agromyzidae (Leafminer Flies)*

Unlike the five preceding moth groups, members of the Agromyzidae are true flies, although they are one of the few lineages of acalyptrate

Diptera that are leaf miners. Agromyzid larvae are almost always associated with live plants, with the vast majority of species being miners of leaf tissues, although cambium miners, root miners, and seed feeders are also known (Foote, 1991b). The mining larva is a sap feeding maggot with mouthhook-bearing, modified mouthparts occurring on the apex of a retractile head region. Agromyzid leaf mines are variable in shape and may be linear, serpentine, star-shaped, or blotch-like (Hering, 1951). Agromyzid species can be diagnosed informally by the tissue consumed, such as palisade parenchyma, spongy parenchyma, epidermis, and its location on the leaf, namely on the top or underside of the leaf, or whether it is proximal to the midrib or leaf margin. Frass deposition is either continuous in earlier mines, or as small, liner films in subsequent mines (Hering, 1951; Stegmaier, 1967). Typically there are only a few instars; pupation usually occurs outside the mine, amid ground litter (Spencer, 1987).

Agromyzids are one of the most diverse groups of leaf miners, with 2,500 recognized species in 31 genera (Spencer, 1990), although the total number of species may approach 4,000. Polyphagy is uncommon in the group (16% of species); oligophagy and monophagy overwhelmingly characterize most subgroups (Spencer, 1987). In an exhaustive study, Spencer (1990) found that agromyzids mine almost all major land plant groups, including mosses, horsetails, ferns, conifers, and dicotyledonous and monocotyledonous angiosperms. He concluded that there are several origins of associations between agromyzids and their host plants, including the sequential evolution postulated by Ehrlich and Raven (1964), as well as opportunistic colonization of plant families bearing similarities in biochemistry but not related phylogenetically. He found limited evidence for a pattern indicating that the most primitive agromyzid endophages also occur on primitive plant hosts. In Figure 4j-k, an agromyzid leaf mine occurs on the buckeye *Aesculus* (Hippocastanaceae), a family of plants for which no known agromyzid is currently documented (Spencer, 1973, 1990).

## External Foliage Feeding

### Introduction

The taxonomic affinities of insects responsible for external foliage feeding are among the most difficult of plant-insect interaction types to pin

down in the fossil record. Because of the inordinate diversity of larval and adult phytophagous mandibulate insects on a similar, near-limitless spectrum of broadleaved plant hosts, there has been continual reinvention of the same feeding strategy among unrelated insect lineages and among conspecific immatures and adults. Consequently, insect groups as unrelated as Orthoptera, Phasmatodea, Coleoptera, Lepidoptera, and Hymenoptera often display the same type of plant damage. In some instances, highly stereotyped behaviors of external feeding, idiosyncrasies of plant host preference, or distinctive patterns based on tissue type and location, can reveal the responsible herbivores at lower taxonomic levels. An example of multiply implicated taxa is damage shown in Figure 6h-i along the midrib of *Sassafras* (Lauraceae). The feeding marks suspiciously resemble pyralid (Lepidoptera) damage on modern pecan (*Carya*; Gill, 1917, pl. 1, fig. 5; Leiby, 1925, fig. 6), although there are other lepidopteran possibilities, such as coleophorid and gelechiid damage (Gill, 1917; Leiby, 1925; Wagner, 1998, personal communication). Other damage illustrated in Figures 5a-d, o and 6g, o-p cannot be attributed to any particular insect lineage, even at the ordinal level.

### *Chrysomelidae* (Leaf Beetles)

Chrysomelids, commonly known as leaf beetles, involve an extremely diverse, cosmopolitan lineage of almost entirely phytophagous Coleoptera. They have a varied body form, but often they are dorso-ventrally flattened and brightly colored (Lawrence and Britton, 1994). Chrysomelids occur in virtually every habitat in which land plants are present (Lawson, 1991). The adults feed externally and the larvae are either external or internal feeders on diverse plant organs and structures, including roots, herbaceous stems, leaves, leaf and flower buds, flowers, fruit, seeds, and pollen (Lawrence and Britton, 1994). Traditionally, chrysomelids have been taxonomically subdivided into approximately 16 to 18 subfamilies, although some of the evolutionary distinctiveness of these subgroups is doubtful. Chrysomelid larvae that feed on the mesophyll and epidermis of leaves commonly are margin feeders, hole feeders, skeletonizers or window feeders. Some hole feeders create elongate, parallel-sided damage consisting of separate but confluent feeding holes arranged into a linear or subtly meandering slot (Wellhouse, 1922; Rose and Lindquist, 1982; Andrade, 1984; McGiffen and Neunzig, 1985; Heron

and Borowiec, 1997). By contrast, the subfamily Alticinae, known as flea beetles, is a widespread group of external feeders on foliage whose adults produce a distinctive pattern of holes that are small to medium in size, elongate to rounded in shape, and occur within the intersecondary regions of the leaf blade (Fig. 5g-h) on both herbaceous plants and arborescent broadleaved trees (Woods, 1917; Becker, 1938; Bartkowska, 1975; Virkki, 1980; McGiffen and Neunzig, 1985). Many larvae that feed on leaves commonly skeletonize or window-feed on mesophyll (Rose and Lindquist, 1982).

Two examples of external feeding by leaf beetles are provided in Figure 5, including probable adult (e-f) and larval (j-k) damage. The adult damage is characterized by linear to gently meandering feeding tracks, approximately 1 mm wide and up to 8 mm long, occurring in the interveinal region of the blade and often constrained by secondary veins. This damage pattern is nearly identical to that of adult *Fidia longipes* Melsheimer, an external feeder on grape (*Vitis*) leaves (Isely, 1930; McGiffen and Neunzig, 1985). Other adult phytophagous beetles form linear to curvilinear slot-like channels on dicotyledonous leaves, such as some species of the longhorn beetle *Oberia* on cottonwood (Morris et al., 1975) and the tortoise beetle *Cassida* on Amaranthaceae (Heron and Borowiec, 1997). The latter damage (Fig. 5j-k) is more broadly displayed among many taxa of extant leaf beetles, and it is typical of certain chrysomelid larvae that intensively skeletonize or surface-feed on epidermal and mesophyll tissue delimited by secondary and tertiary venation (Alford, 1991; Johnson and Lyon, 1991). Common leaf beetles producing similar damage are *Pyrrhalta* on elm and *Plagioderia* on willows (Becker 1938; Baker, 1972; Johnson and Lyon, 1991).

#### *Curculionidae (Weevils)*

The Curculionidae, or weevils, is the most speciose family of insects, consisting of approximately 60,000 known species that are dominantly associated with land plants (Crowson, 1981). Weevils are a cosmopolitan group whose larvae variously bore, mine, gall, and externally feed on all organs and most tissues of land plants (Anderson, 1991). Adult weevils are heavily sclerotized, robust in shape, clothed in scales or bristles, and variously bear a prolongation of the anterior head region into a distinctive rostrum. This rostrum is used for boring into plant tissue, either by excavating

cavities for oviposition (Howden, 1995; Anderson, 1995) or by feeding on plant tissue. Foliar feeding patterns of externally feeding weevils are highly variable, ranging from lenticular, ovoidal, ellipsoidal to irregularly elongate feeding excavations that puncture the entire leaf blade (Burns and Gibson, 1968) to surface feeding on epidermal and deep mesophyll tissue with noticeable damage confined to the upper or lower leaf surface (Grandi, 1933; Servadai, 1933). Adult weevils are generally external feeders on leaves; less commonly they are concealed tissue feeders on wood, pollen, or fungi.

Because of the spectacular diversity of weevils and the largely undocumented modern fauna, it is difficult to assign the damage on the sumac (*Rhus malloryi* Wolfe & Wehr, Anacardiaceae; Fig. 5g-h) to any subordinate curculionid taxon. Modern *Rhus* is attacked by various species of weevils in Eurasia (Gosev and Rinsky-Korsakov, 1951; Furth, 1985) and North America (Howden et al., 1951).

#### *Megachilidae (Leafcutting Bees)*

Megachilid bees, also known as leafcutting bees, are a cosmopolitan group of metallic black- or bluish-colored, long-tongued bees that lack complex social organization. They generally nest in existing burrows or hollows in soil or rock substrates, or they construct nests within the tissues or on the surfaces of plants (Gauld and Bolton, 1988). These nests are constructed from diverse building materials, often soil particles such as small pebbles, or plant products that include resin, wood fragments, and leaves (McGinley, 1987). One representative and globally widespread genus is *Megachile*, which detaches arcuate pieces of leaves, often in succession, along the margins of leaf blades. These circular leaf blade fragments are subsequently used in the construction of nests that are provisioned with a paste of masticated pollen (Alford, 1991; Maeta, 1999). The damage that leafcutting bees inflict on plants is highly stereotyped. Frequently, particular plant species are targeted, such as *Rosa* (rose). In rare instances the semicircular, leaf-margin notches of megachilid bees resemble the work of New World leafcutting ants, such as *Atta*.

In addition to the more intensely collected and younger Florissant Biota, where megachilid body fossils and plant damage co-occur (Cockerell, 1908, 1910), three middle Eocene floras of North America also exhibit evidence of plants damaged

by megachilid bees. Included are the Mississippi Embayment (Berry, 1931; Brooks, 1955; Johnston, 1993), Green River Formation in the Piceance Basin of Colorado (Labandeira, personal observation), and Republic (Lewis, 1992, 1994). In addition to the *Prunus* leaf previously discussed by Lewis (1992, 1994), a large *Ulmus* leaf and *Ginkgo* (Fig. 5i, l, n) now are documented as probable megachilid hosts. Interestingly, this is the first documentation of fossil *Ginkgo* as a substrate for megachilid bees, even though several studies (Hase, 1955; Tulecke and Colavito, 1966; Wheeler, 1975) support the presence of an herbivore fauna, albeit sparse, on modern *Ginkgo biloba* L. These and other recent studies have not mentioned modern *Ginkgo* leaves as a source of building material for leafcutting bees. It is possible that the unidentified fern in Figure 6m-n may bear megachilid chew marks, although another external foliage feeder is more probable. Many other insects produce arcuate excisions on leaf margins, including larval sawflies (Pieronek, 1979), larval lepidopterans (Essig, 1926), and adult and larval beetles (Kile, 1974; Drooz, 1985), all of which are virtually impossible to assign because this feeding damage has margins that are uniformly cusped, sharp, and entire.

### Bud Feeding

Two examples of bud feeding are documented in Figure 6. The first example (a-b) is from the extinct platanaceous genus *Macginitiea*, a distant relative of modern *Platanus*, species of which include the American (*Platanus occidentalis* L.) and Californian (*P. racemosa* Nuttall) sycamores. This damage is characterized by three pairs of shot-holes, each pair characterized by a near-perfect circular hole laterally adjacent a primary vein. This highly stereotyped pattern suggests that a feeding larva consumed leaf tissue through an unfurled, palmate leaf as it lay pleated within the bud. Inspection of the considerable literature on modern insect damage on *Platanus* (e.g., Brown and Eads, 1965b; Filer et al., 1977; Thompson and Solomon, 1986; Halperin, 1990) has failed to pinpoint a modern lineage of bud feeders at the level of family or genus that could be responsible for this damage. The second example (Fig. 6c-d) is a pinnate leaf of *Ulmus*, which has a symmetric pattern of tissue damage on either side of the basal region of the midrib. Unlike the accordion pattern of leaf folding for palmate leaves, most pinnate leaves fold in half within the bud, along the

midrib, such that a potential insect bud feeder will inflict a bilaterally symmetrical pattern of damage noticeable upon leaf emergence from the bud. As for *Macginitiea* discussed above, there are few diagnostic clues for elucidating a culprit.

Insect bud feeding occurs on most modern angiosperms and the feeders include representatives from the Coleoptera (e.g., Buprestidae, Chrysomelidae, Curculionidae), Lepidoptera (e.g., Tortricidae, Gelechiidae, Plutellidae, Pyralidae, Noctuidae), Hymenoptera (e.g., Tenthredinidae, Argidae, Cimbicidae), and other endopterygote groups (Hill, 1952; Sandved and Prance, 1985, p. 182; Stehr, 1987a, 1991). For now, the highest level of taxonomic resolution attainable for these bud feeders is that they were larval endopterygote insects. Bud feeding is rarely encountered in the fossil record of plant-insect interactions. Other documented examples are: a sequence of shot holes inclined 45° to the midrib in a specimen of *Castanea* (chestnut) from the lower Pliocene of Germany (Berger, 1953); two symmetrical holes on the magnolalean dicot *Liriodendrites*, from the Hell Creek Formation of North Dakota (Labandeira et al., 2002); ovoid excavations arranged symmetrically on both sides of a midrib on an unidentified angiosperm of late Cretaceous age from the Ripley Formation of Tennessee (Scott et al., 1992); and seven elongate shot holes arranged in register on an expanded frond of the coryphoid palm *Washingtonites*, from the late Cretaceous of Wyoming (Labandeira et al., 1995).

### Oviposition

The middle Eocene floras of Republic and MacAbee contain several host-plant species that bear highly stereotyped damage interpreted as oviposition sites. This damage consists of rows of separate, equal-sized, lenticular scars that are arranged into semicircular arcs. These arcs may be single (Fig. 5l) or deployed as a series of multiple, subparallel to obliquely intersecting crescentic rows (Fig. 6f-l). Similar foliar structures have been documented for the mid Cretaceous of the Czech Republic on an unknown angiosperm (Hellmund and Hellmund, 1996a, figs. 18, 19) and the late Cretaceous of North Dakota on platanaceous and lauraceous hosts (Labandeira et al., 2002, fig. 8n-o). From approximately contemporaneous, middle Eocene deposits, the same ovipositional pattern has been recorded on unknown hosts from the Messel Flora of Germany (Schaarschmidt, 1992,

fig. 78) and the Tallahatta Flora of the Mississippi Embayment (Johnston, 1993, pl. 1, fig. 4).

More recent occurrences have been documented on *Alnus* and lauraceous genera from the lower Oligocene Hammerunterwiesenthal Flora of Germany (Hellmund and Hellmund, 1998), on *Alnus* from the John Day Flora of Oregon (Lewis and Carroll, 1992, fig. 2), and on additional hosts from a variety of angiosperm families from several other localities (Hellmund and Hellmund, 1996a, 1996b). At Republic, this distinctive damage occurs on *Alnus* (Fig. 6j-k), *Betula*, aff. *Crataegus*, *Paracrataegus* (Fig. 6l), *Sorbus* (Rosaceae), an undetermined genus of Lauraceae, and approximately 10 other specimens of unknown dicots; at MacAbee it occurs on *Ginkgo* (Ginkgoaceae; Fig. 5l-m). These ovipositional traces have been attributed to alticine chrysomelid damage (Lewis and Carroll, 1991, 1992; Lewis, 1992), namely *Altica*, species of which occur today on *Alnus* (Woods, 1917; Barstow and Gittins, 1971) and on *Crataegus* (Wellhouse, 1922). Chrysomelid beetles such as *Altica* do oviposit egg clusters or, less frequently, distinguishable rows of closely spaced eggs on the leaf surfaces of their host plants (Woods 1917, 1918; Barstow and Gittins, 1971; De Swarte and Balsbaugh, 1973). However, the expansive pattern of en echelon rows observed in the fossils is not characteristic of modern alticine chrysomelids. Chrysomelid beetles more typically deposit compact clusters of tightly packed eggs on leaf surfaces and not within mesophyll tissue, frequently adjacent to primary veins (Lesne, 1893; Woods, 1918; Buzzi, 1976). Consequently, the formation of callus tissue around each scar would not be expected; rather, scar tissue would result from endophytic egg insertion by an insect with a robust, slicing ovipositor.

The occurrence of these semicircular arcs of ovipositional scars on at least five unrelated angiosperm families in the Pacific Northwest is more consistent with that of certain coenagrionid damselflies. There exists modern ecologic documentation (Schiemenz, 1953; Jurzitza, 1974; Grunert, 1995) for this group as well as a fossil record of plant damage extending to middle Triassic horsetail stems (Grauvogel-Stamm and Kelber, 1996). Coenagrionid damselflies insert their eggs into the tissues of submergent and emergent hydric plants. They also oviposit into mesic plants adjacent to freshwater bodies, apparently selecting leaves on the basis of availability rather than trophic dependency, particularly since all dragonflies are pursuit predators. Their pattern of oviposition consists of more-or-less widely spaced

ovipositional scars ranging from a zig-zag pattern along a continuous and unidirectional axis, to linear rows, to more often crescentic arcs that are concentric and slightly overlapping (Wesenburg-Lund, 1913a, 1913b; Grunert, 1995; Hellmund and Hellmund, 1998).

## PROSPECTS FOR FUTURE WORK

This study, to be supplemented by work in progress, is an attempt to provide an historical dimension toward an understanding of the evolutionary history of modern plant-insect associations. There is a gathering realization that appreciation of how plants and their insect herbivores enter into loose to highly coevolved associations requires a dual approach involving study of modern, often complex, interrelationships in conjunction with the fossil record of responses to major historical changes (Labandeira, 2002). This complementary combination of evolutionary biology and paleobiology has the potential for using fossil data to record how the two most diverse terrestrial groups have interacted to generate the bulk of the world's species. Several issues can help illuminate this macroevolutionary record.

One issue is the geography of plant-insect associations among the three, major, middle Eocene floral regions for which there is abundant and well-preserved data. These localities are: the Pacific Northwest, which contains localized graben-fill floras such as Republic; the extensive lacustrine floras of the Green River lake system in Colorado, Utah, and Wyoming; and the coastal floras of the Mississippi Embayment, especially those in Arkansas and Tennessee. Examination of middle Eocene plant-insect associations across this North American landscape could be informative about the early differentiation of associations that occur today in eastern and western parts of the continent. Dicotyledonous taxa such as *Aesculus* (Hippocastanaceae), *Myrica* (Myricaceae), *Platanus* (Platanaceae), and *Sorbus* (Rosaceae) have species with centers of distribution on either side of the continent and are separated by major absences in the center. These disjunct distributions could be ancient ones that commenced with gradual thermal cooling and aridification during the later Eocene or perhaps earlier and continuing to the present. Insect plant-damage types can be compared among these middle Eocene regions, the Recent, and intervening floras, to examine the evolution of component communities — a host-plant species (or lineage) and all of its trophi-

cally dependent organisms – for an assessment of persistence or turnover in insect herbivore types (Root, 1973; Futuyma and Mitter, 1996). For example, highly herbivorized ancestral species of a lineage from the earlier Cenozoic may have undergone subsequent population bottlenecks with attendant range contraction. Such hypothetical events would result in a significant diminution of the component herbivore community on geologically younger species of this lineage. This pattern also may be reflected in a major deficit of insect herbivores on extant descendant species.

Another related issue is whether host-shifts, extinction, or long-term persistence is the norm for insect associations on Cenozoic plants. A current example is the presence of a *Paraclemensia*-type leaf mine on a *Macginitiea wyomingensis* Lesquereaux (Manchester) leaf, an extinct genus of platanaceous tree related to modern sycamores, from the Green River Formation of Colorado (Labandeira 1998b). *Paraclemensia* today overwhelmingly colonizes *Acer* (maple), although it occasionally will attack *Fagus* (beech) and *Betula* (birch) if they are adjacent to infested maple trees (Johnson and Lyon, 1991; Zhang, 1994). These observations suggest that the colonization of *Macginitiea* by a *Paraclemensia*-type leaf miner ended either by extirpation of the herbivore approximately coincident with extinction of the plant-host, or alternatively lateral transfer on maple attributable to architectural or phytochemical similarities. Ideally, a spatio-temporal matrix of fossil plant-host and insect herbivore associates in North America could reveal the macroevolutionary tempo and past autecological shifts for many plant-insect associations.

## CONCLUSIONS

A preliminary inventory of insect damage occurring on plant hosts of the Republic and other coeval floras of the Pacific Northwest indicates that an impressive variety of plant-insect associations was present at approximately 48 Ma. Many of these interactions were nonspecific and represent opportunistic consumption of foliar tissue by polyphagous insects. Other interactions, particularly leaf miners and galls, probably represent highly dependent, perhaps coevolved associations with plants. While additional paleobiological and neobiological research is needed to ascertain whether these coevolved associations have been maintained in host plant and herbivore lineages to

the present, data from the middle Eocene nevertheless demonstrate that associations identifiable at the generic level were present.

There has been minimal exploitation of the fossil record for answering fundamental questions regarding the macroevolutionary history and paleobiology of modern plant-insect associations. Two of these issues can be addressed by the middle Eocene floras of the Pacific Northwest. First, there is evidence that at least some modern plant-insect associations are evolutionarily conservative, in which the earliest known host occurrences harbored essentially the same herbivore associates as their modern descendants. Second, there is limited evidence for geographically based, differential extinction of insect herbivores on host plant lineages that currently occur elsewhere in eastern North America or eastern Asia. The rich fossil record of plant-insect interactions from middle Eocene floras of the Pacific Northwest, integrated with other well-preserved and abundant fossil floras, will provide critical temporal data for addressing these and other salient issues regarding the evolutionary biology of Cenozoic plants and their insect associates.

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