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Preliminary assessment of insect herbivory across the Cretaceous-Tertiary boundary: Major extinction and minimum rebound

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ABSTRACT

Forty-nine insect damage types morphologically characterize plant-insect associations spanning a 136 m composite boundary interval from the uppermost Cretaceous Hell Creek Formation to the lowest Paleocene Fort Union Formation. The time duration of this interval is ~2.2 m.y., 1.4 m.y. of which is latest Cretaceous. These data originate from 80 localities from the Williston Basin of southwestern North Dakota and are allocated to four assemblage zones consisting of 385 megafloral morphotypes of bryophytes, ferns, conifers, cycads, *Ginkgo*, monocots, and 333 dicots.

All 49 foliar damage types were produced by external foliage feeding, mining, galling, and piercing and sucking insects, each of which was assigned one of the following host specificity levels: generalized, intermediate, or specialized. A distinctive pattern emerged when these damage types were plotted stratigraphically: of the 22 damage types that survive the Cretaceous-Tertiary boundary (K-T), 55% are generalized; of the 15 damage types that are extinguished immediately below the boundary, all are specialized or intermediate, as are the 12 damage types that disappear in stepped fashion somewhat before the boundary. Within this interval only two damage types are unique to the Fort Union Formation, occurring during the lowest Paleocene. These data indicate that highly and moderately specialized associations were preferentially culled at the K-T boundary, disproportionately enriching early Paleocene floras in generalized herbivores as dominant colonizers. These data are local, and the Signor-Lipps effect may partially obscure the true pattern, thus restricting extrapolation to the Western Interior of North America. Nevertheless, (1) the selective extinction of specialist herbivores at the boundary, (2) the absence of significant evidence for immigrant colonization, (3) the prolonged occurrence of species-depauperate floras during the Paleocene, and (4) the high percentage of last occurrences at and not before the boundary, despite the Signor-Lipps effect, suggest a role for end-Cretaceous abiotic perturbation and consequent biotic response in the evolution of modern plant and insect associations.

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INTRODUCTION

The major biotic extinction at the end of the Mesozoic was a profound event that shaped the trajectory of life during the past 65.5 m.y. This event, the Cretaceous-Tertiary (K-T) boundary, primarily has been documented in the marine realm, although finely resolved patterns of extinction and survival have been extended to the terrestrial record. Marine organisms that are identified with the end-Cretaceous event include planktonic foraminifera (Norris, 1991; D'Hondt and Zachos, 1998), ammonites (Ward, 1995), rudistid bivalves and other marine molluscs (Kauffman, 1984; Hansen et al., 1993), cartilaginous fish (Hoganson and Murphy, 1999), and large marine reptiles. Prominent continental lineages that perished at the boundary include some freshwater mollusks (Hartman, 1999), all dinosaurs (Sereno, 1999), pterosaurs and most champosaurs (Pearson et al., 1999), many lineages of birds (Chatterjee, 1997), and a broad spectrum of mammals (Hunter and Archibald, 1999). However the fates of the two most diverse clades of terrestrial macroscopic organisms—vascular plants and insects—have only been tentatively investigated, with opposite results. Although it was once thought that plant lineages were relatively immune from the K-T extinction (Hickey, 1981; Tschudy, 1984; Briggs, 1991; Hughes, 1994), current evidence from much greater sampling indicates a major extirpation of lineages, at least regionally in North America (Wolfe and Upchurch, 1987; Boulter et al., 1988; Johnson, 1989; Johnson and Hickey, 1990; Lupia, 1999; Sweet et al., 1999). Recent estimates of vascular plant extinction for the Western Interior of North America are ~70% for all megafloral morphotypes, and 20%–31% for taxonomically coarser palynomorph form genera (Hotton, 1984; Johnson, 1992, 1999; Nichols and Johnson, 1999).

Insect diversity, by contrast, has been analyzed only at the coarser family level by several authors (Whalley, 1987; Dmitriev and Zherikhin, 1988; Rasnitsyn, 1988; Jarzembowski, 1989; Labandeira, 1992; Labandeira and Sepkoski, 1993; Jarzembowski and Ross, 1993), who concluded that there was no significant decline of diversity above background levels. Nevertheless other anecdotal observations indicate that Late Cretaceous extinctions are detectable at the genus level for groups as varied as aphidoid Homoptera (Heie and Pike, 1992), scarabaeoid beetles (Scholtz and Chown, 1995; see also Chin and Gill, 1996), and perhaps weevils (Kuschel et al., 1994). By contrast, these observations differ from evidence for long-term persistence of well-defined lineages since the mid-Cretaceous, including flies (Rayner and Waters, 1990; Borkent, 1995), leaf-mining moths (Kozlov, 1988; Labandeira et al., 1994; Powell et al., 1999), pollinivorous bees (Michener and Grimaldi, 1988), and phytophagous beetles (Farrell, 1998; Windsor et al., 1999). Case studies have documented the geochronologically shorter-term persistence of intricate associations such as bees and Malpighiaceae since the late Paleocene (Taylor and Crepet, 1987), aphids and barberry since the middle Eocene (Moran, 1989), domatia-inhabiting mites and their plant associates from the late Eocene (O'Dowd et al., 1991), and leaf-mining moths and oak associations that are traceable to the late Miocene (Opler, 1973, 1974). This latter pattern of insect resiliency and immunity from extinction also is consistent with various examinations of the response of beetles to Pleistocene climatic change, which responded by biogeographical shifts rather than in situ extinction (Matthews, 1979; Coope, 1995). Studies of the terminal Pleistocene indicate that beetles—the principal taxonomic component of insect faunas—were highly immune from major environmental perturbation, unlike the very disparate pattern for the heightened extinction of vertebrates (Graham, 1986; Martin, 1986). Obvious questions issuing from these data and hypotheses include an assessment of the types of fossil data from which these varying conclusions regarding extinction are derived (e.g., Poinar et al., 1999), and more important, formulating analyses of more refined taxonomic data to test the universality of these conclusions.

To date, the predominant approach for analysis of the fossil plant and insect records across the stratigraphically narrow confines of the K-T boundary has been temporal extrapolation by examination of larger scale diversity patterns based on body-fossil occurrences. These occurrences have been documented from well-preserved and often diverse floras (Niklas et al., 1980; Niklas, 1988) and insect faunas (Ponomarenko, 1988; Rasnitsyn, 1988; Wootton, 1990; Labandeira and Sepkoski, 1993; Jarzembowski and Ross, 1993). There has been a shift, particularly in North America, toward assessment of species-level floral diversity typically from basins that are stratigraphically and geochronologically well defined (Johnson et al., 1989; Johnson, 1992). However, such a targeted and taxonomically detailed approach is unavailable for insects because of the worldwide absence of informative and continuous body-fossil sequences across the K-T boundary (Labandeira et al., 1999). Only several Late Cretaceous insect-bearing Lagerstätten are known (exceptionally preserved deposits), notably amber-bearing strata from the probable Cenomanian of Alaska (Langenheim et al., 1960), Turonian to Campanian of New Jersey (Grogan and Szadziewski, 1988; Grimaldi, 1996), the Santonian to Campanian of the Taimyr Peninsula in northern Russia (Zherikhin and Sukacheva, 1973; Botosaneanu and Wichard, 1983), and the Campanian of Alberta (McAlpine and Martin, 1969; Brown and Pike, 1990; Heie and Pike, 1992). No relevant latest Cretaceous (Maastrichtian) or earliest Paleocene (Danian) insect deposits are documented anywhere with significant diversity (Poinar, 1992; Pike, 1993; Ponomarenko, 1995). In addition, relevant insect compression deposits are limited to the mid-Cretaceous, such as those from the Cenomanian at Orapa, Botswana (Rayner and Waters, 1990), and the Czech Republic (Fritsch, 1882, 1901), or those from the Turonian of Russia (Rasnitsyn, 1988), matched in the Paleocene by the earliest significant occurrence from the Fur Formation of the Paleocene to Eocene boundary in Denmark (Andersen, 1998; Rust, 1998), ~9.5 m.y. after the K-T event.

Because of this absence of body fossils for detecting local insect diversity anywhere across the boundary, we have used proxy data based on plant-insect associations. Our data originate from relatively continuous sequences of well-preserved foliar material across the latest Cretaceous to earliest Paleocene boundary in the Williston Basin of southwestern North Dakota. These data record patterns of plant-host use by diverse insect herbivore species, providing a detailed pattern of insect ecological diversity across an important extinction event. Notably, such data would still be valuable even if there were a continuous insect body-fossil record at this boundary, because damage-type spectra would reveal patterns of herbivore colonization of plant hosts that are difficult to unravel from the body-fossil record alone. This fine-scale approach and type of analysis for changing herbivory patterns within geochronologically short intervals has been used for the late Paleocene to early Eocene warming interval in the greater Green River Basin (Wilf and Labandeira, 1999; Coley, 1999), which demonstrated robust correlations among paleoclimate, floral turnover, and associated insect herbivory patterns. An analysis resulting from an expanded data set stemming from the current authors' research on the K-T boundary of the Williston Basin has been reported (Labandeira et al., 2002).

WILLISTON BASIN IN SOUTHWESTERN NORTH DAKOTA

Megafloras from a composite 136 m of stratigraphic section in Upper Cretaceous and lower Paleocene exposures near Marmarth, southwestern North Dakota, have been collected since 1981 and have been studied for floristic change through the K-T boundary (Belt et al., 1984; Johnson et al., 1989; Johnson and Hickey, 1990; Johnson, 1992, 1996). This sequence is paleomagnetically well calibrated (Cande and Kent, 1995; Johnson et al., 1990; Lund and Hartman, 1999; Obradovich and Hicks, 1999; Hicks et al., this volume) and increasingly is being linked to isotope records (Stott and Kennett, 1990; Arens and Jahren, 2000; Hicks et al., 1999) and foliar physiognomy (Johnson and Hickey, 1990; Johnson and Wilf, 1996) for paleoclimatic inferences. Currently 171 localities are included for this interval, representing ~25 500 specimens located principally at the Denver Museum of Nature & Science in Colorado and the Yale Peabody Museum in New Haven, Connecticut. A minor collection is present at the National Museum of Natural History in Washington, D.C.

General geological and paleoenvironmental context

The southwestern Williston Basin of the northern Great Plains consists of badlands exposures along the north-flowing Little Missouri River. These outcrops are prominent where the Little Missouri River has cut down into the northeastern flank of the northwest- to southeast-trending Cedar Creek anticline, which structurally separates the Powder River Basin of easternmost Montana from the Williston Basin of southwestern North Dakota. Progressively younger deposits are exposed toward the northeast, corresponding to the onset of transgression for the Cannonball Seaway during the early Paleocene. Deposition during the latest Maastrichtian to early Paleocene was apparently continuous, initially consisting of fluvial, lignite-poor deposits of the uppermost Colgate Member of the Fox Hills Formation and throughout the Hell Creek Formation, followed by fluviodeltaic and lignite-rich strata of the superjacent Lower Ludlow Member of the Fort Union Formation (Johnson, 1992).

The investigated late Maastrichtian section within the Williston Basin consists of a 91 m composite sequence of horizontal mudstone beds interspersed among lenticular and often argillaceous sandstone. This interval corresponds to ~1.4 m.y. (Hicks et al., this volume) and represents a flood-plain environment, as evidenced by pedogenic features such as root traces, slickenslides, and leached horizons typical of paleosols. These strata are modified by channel deposits that include lateral accretion units, cross-bedded sandstones, and planar, laminated mudstones that are considered to represent varied fluvial environments. The floras examined from this interval originate sporadically from outcrops ranging from the uppermost Fox Hills Formation below to the top of the Hell Creek Formation above, including in places as much as 3 m of the bottommost Fort Union Formation, where the K-T boundary is defined palynologically as the disappearance of the *Wodehouseia spinata* assemblage zone (Nichols et al., 1982; but see Sweet et al., 1999). Consequently, this places the K-T boundary from the top contact of the Hell Creek Formation to within the lower 3 m of the Fort Union Formation, depending on location. This boundary regionally coincides with an iridium anomaly (Alvarez et al., 1980) and is associated with shocked quartz (Bohor et al., 1987; Izett, 1990), indicating an extraterrestrial impact (Alvarez, 1997). Iridium anomalies have been found at two sites within the Williston Basin study area (Johnson et al., 1989; Nichols et al., 2000).

The lower Ludlow Member of the Fort Union Formation represents an increase in deltaic sedimentation, indicated by a greater proportion of mudstone units, lignite beds, and planar to lenticular sandstone bodies. These examined strata, corresponding an ~0.8 m.y. interval (Hicks et al., this volume), have been interpreted as ponds, backswamp deposits, crevasse splays, and interspersed meandering channels. Floras from ~44 m of this sequence above the K-T boundary and below the first marine bed that represents a transgressive event during Torrejonian time have been scrutinized. The weathering profile of the Fort Union Formation is generally better developed, supporting distinctive modern vegetation, when compared to strata of the more stark landforms of the subjacent Hell Creek Formation.

The ~2.2 m.y. represented by the Hell Creek to Fort Union succession are characterized by dramatic paleoenvironmental changes involving prolonged, ambient trends and short-term consequences of the K-T event. The geochemical and plant physiognomic data that are the source data for these trends are correlated to a known paleomagnetic chronology (Johnson et al., 1990; Hicks et al., this volume) and inserted into a vertebrate (Pearson, 1992; Pearson et al., this volume) and marine invertebrate (Gill and Cobban, 1973) record. During the earlier Maastrichtian time of this interval, mean annual temperature was 10–15 °C, followed by rapid thermal fluctuation, and then an increase to 15–19 °C during the latest Maastrichtian (Johnson and Hickey, 1990; Johnson and Wilf, 1996), a pattern corroborated by data from Antarctica (Stott and Kennett, 1990). At or immediately below the K-T boundary, there was a sharp decrease in mean annual temperature to 7–12 °C, continuing into earliest Danian time and residing at that level for the balance of the sampled interval. By comparison to the late Maastrichtian, early Paleocene precipitation increased, as probably did the mean annual range of temperature, causing biologically significant freezing winters. The Paleocene trend of relatively cool temperatures and increased precipitation persisted, with short but occasional deviations (Ellis and Johnson 1999), until the thermal maximum of the latest Paleocene to early Eocene transition (Wilf, 2000; Wing et al., 2000).

Plant hosts

Megafloras of latest Cretaceous and earliest Paleocene age have been collected for more than 100 yr from the northern Great Plains (Newberry, 1863, 1898; Lesquereux, 1874, 1878; Ward, 1887; Dorf, 1940, 1942; Brown, 1962). However, only recently has major progress been made to resolve a historically chaotic taxonomy based on the practice of assignment of Linnean names from the overall resemblance of fossil leaves to modern taxa (Upchurch and Dilcher, 1990). By establishing additional megafloral localities and relocation of older sites that are sources of known repository collections, an expanded database of 60 000 fossil leaf specimens are now known from 8 major study areas of the northern Great Plains (Johnson and Hickey, 1990). Of these study sites, the succession near Marmarth in the Williston Basin of South Dakota is the richest taxonomically (385 morphotypes) and the most heavily sampled (25 400 specimens), originating from 171 current localities (Johnson, 1999). These floras are overwhelmingly dominated by dicotyledonous angiosperms, but also include bryophytes, pteridophytes, cycads, gingkophytes, conifers, and monocotyledonous angiosperms. Currently, 385 distinctive megafloral morphotypes have been identified, 333 of which are dicotyledonous angiosperms, with links to Linnean taxa ranging in resolution from the ordinal to species rank. On the basis of stratal distributions of megafloral occurrences, this Hell Creek to Fort Union sequence was subdivided into five assemblage zones: HCI, HCII, HCIII, FU0, and FUI, from oldest to youngest; in addition, HCI and HCII were each further subdivided into two subzones (Johnson, 1989; Johnson et al., 1989; see Johnson et al., this volume). The section in the Marmarth area is the most intensely collected megafloral interval representing the K-T boundary.

The stratigraphically lowest zone, subzone HCIa, is dominated by "*Dryophyllum*" *subfalcatum*, *Leepierceia preartocarpoides*, "*Vitis*" *stantonii*, and "*Celastrus*" *taurenensis*. Above this is subzone Ib, characterized by small-leafed taxa that are dominant (Johnson and Hickey, 1990). Subzone IIa is dominated by "*Dryophyllum*" *subfalcatum* and subordinately by *Erlingdorfia montana*, whereas subzone IIb contains "*Vitis*" *stantonii* and subordinately "*Dryophyllum*" *subfalcatum*. In contrast, zone III is dominated by *Marmarthia trivialis* and *Platanites marginata*, but also harbors an abundant palm and varied lauralean taxa. Above zone III is the lowermost 1.4 m of the Fort Union Formation, Cretaceous in age, which has not yielded significant megafloral material but is represented by a diverse palynoflora up to the iridium anomaly. This interval has been assigned to zone FU0 (Johnson, this volume). The earliest Paleocene megafloral zone FUI is a distinctive assemblage of species that are rare or absent in the underlying Cretaceous. Dominants, in decreasing order of abundance, are "*Populus*" *nebrascensis*, "*Cocculus*" *flabella*, *Dicotylophyllum anomalum*, *Quereuxia angulata*, *Platanus raynoldsii*, *Paranymphaea crassifolia*, and *Limnobiophyllum scutatum*. The taxodiaceous conifers *Glyptostrobus europaeus* and *Metasequoia occidentalis* are minor components. The extinction of taxa between the HCIII and FUI assemblage zones ranges from ~20% to 31% for pollen and spore form-taxa, and 70% for megafloral morphotypes. This abrupt turnover corresponds to a distinctive facies change, discussed here, and is linked to poorly drained soils and meandering channels in a flood-plain environment replete with swamps, ponds, and straight to meandering deltaic river channels. Recent analyses of lowermost Fort Union floras indicate that taxa from wetland mire deposits preferentially survived the terminal Cretaceous event and formed many of the dominant elements in early Paleocene plant communities from the Williston Basin and elsewhere in the Western Interior (Gemmill and Johnson, 1997; Johnson, 1999).

Insect herbivores

Only five undetermined insect body fossils have been found throughout the examined Hell Creek and Fort Union succession, compared to more than 7000 analyzed leaf fossils. This renders body-fossil evidence of negligible consequence for understanding the dynamics of insects at the end-Cretaceous event. Because an excellent megafloral record is present throughout this interval in the Williston Basin, a unique opportunity exists for the examination of insect-mediated damage to assess the response, or lack thereof, of insect herbivores to the K-T event. Thus, this rich leaf record permits the examination of only the herbivore fraction of the total insect biota during this interval. Herbivorous taxa nevertheless constitute approximately half to somewhat more than half of all insect species (Strong et al., 1984; Wilson, 1992), a percentage that is likely to increase because of the disproportionately greater number of described insect herbivore species over nonherbivorous ones (Erwin and Scott, 1980). Such a percentage was probably true for the Late Cretaceous and Paleogene, based on the presence of a similar proportion of herbivore versus nonherbivore insect families during this interval (from Labandeira, 1994), and investigations that many major herbivore lineages have relatively deep Cretaceous or even earlier roots (Jarzembowski, 1990; Labandeira et al., 1994; Farrell, 1998). The selection of the herbivore component of the insect fauna has an additional consequence in that consumers of primary production are typically several times more abundant as individuals than the superjacent trophic level of predators (Price, 1997). Consequently, the herbivore component of the regional insect fauna is a more ubiquitous and ecologically sensitive indicator of their trophically dependent plant hosts and associated environmental perturbation than more generalist and less abundant insect predators or the more degraded fossil record of parasitoids or parasites (Labandeira, 2002a). This approach spotlights the value of trace-fossil data in assessing ecological diversity trends across intervals of major environmental perturbation.

Insect herbivores are so taxonomically diverse and ecologically pervasive that they can be characterized by the mode in which they consume plants. The functional feeding group approach is a classification of the basic ways that insects access plant tissue, and include surface fluid feeders, seed predators, borers, and spore or pollen consumers, all which have an informative fossil history that is linked to the body-fossil records of both plants and insects (Labandeira, 1998a, 2002b). However, four important functional feeding groups—external foliage feeding, leaf mining, galling, and piercing and sucking—are abundantly documented in foliar material for many deposits from the Late Pennsylvanian to the Pleistocene, where preservation is good (Chaloner et al., 1991; Scott et al., 1992) and are represented by a rich fossil record (Labandeira, 2002b). In fine-grained clastic deposits minimally affected by postdepositional diagenetic alteration, foliar material can reveal significant detail of insect-mediated damage, including bite marks from external feeders (Stephenson, 1992; Beck and Labandeira, 1998), frass trail detail of leaf miners (Kozlov, 1988; Labandeira et al., 1994), and occasionally gross structure of three-dimensional galls (Stephenson, 1992; Larew, 1992; Waggoner and Poteet, 1996). Each of these four functional feeding groups can be subdivided into categories; e.g., external foliage feeding comprises margin feeding, hole feeding, skeletonization, and special types such as bud feeding and free feeding (Becker, 1938; Kuroko, 1960; Wong and Melvin, 1976; Coulson and Witter, 1984; Kazakova, 1985; Selman, 1988; Heron and Borowiec, 1997; Heron, 1999; Togashi, 1999). These subcategories, in turn, can be objectively categorized into damage types that are the basic recognizable and irreducible units of insect-mediated damage. Thus all insect consumption or alteration of foliar tissue can be classified into discrete morphotypes, each of which represents a distinctive and diagnosable category of plant damage based on size, shape, position, or modified tissue-associated attributes. These damage morphotypes are temporally recurring, identifiable features that are present on individual leaf specimens, often specific to plant taxa or lineages, that are present within a flora or a vertical succession of floras.

METHODS

General procedure

The procedure for determining the temporal patterns of plant-insect associations across the K-T boundary was divided into four phases. The first was taxonomic morphotype identification of each megafloral specimen (Johnson, this volume); the second was a subsequent characterization of each fossil leaf according to an insect damage type, if any (Appendix 1). Third, after assignment of each leaf specimen to a plant morphotype—infrequently listed as unidentifiable if key diagnostic features were missing—specimen numbers were assigned as an identification for each specimen. Last, these data were plotted graphically (Figs. 1 and 2). For each examined flora of the K-T succession, four types of information were recorded for each specimen: locality number, specimen number, plant host morphotype, and leaf damage type, if any. Figure 1 provides a trivariate grid expressing (1) the presence and/or absence data of damage types, (2) locality with reference to the K-T boundary and the Hell Creek–Fort Union contact, and (3) the degree of host specificity discussed below. These raw data were converted to stratigraphic ranges in Figure 2, retaining the same threefold categorization of host specificity. These ranges, like their plant host taxa (Johnson et al., 1989), necessarily decay away from the K-T boundary and terminate at the beginning and end of the studied section because occurrences were not recorded beyond the confines of the Hell Creek Formation and the Ludlow Member of the Fort Union Formation. Data for each of the 80 localities, including 5178 total Cretaceous leaves (72.9%) and 1917 Paleocene leaves (27.1%), were examined and tabulated for insect damage and assigned to one of the four megafloral assemblage zones.

Plant-host morphotypes. Examination and identification of plant hosts from the K-T succession of the Williston Basin is based on the leaf morphotype system described by Johnson (1989), which borrows the terminology of Hickey (1973, 1979). This system of identification was updated and elaborated by the Leaf Architecture Working Group (1999), using leaf architectural, venational, margin-associated and other characters for elucidating Late Cretaceous and Paleogene vascular plant taxa. The motivation for establishing a seemingly parallel system to that of traditional Linnean nomenclature was the difficulty of unambiguously recognizing fossil leaves that were assigned on superficial similarities to modern leaves, rather than circumscription by objective, commonly understood, and taxonomically significant characters (Upchurch and Dilcher, 1990). Although this system is methodologically independent of previous

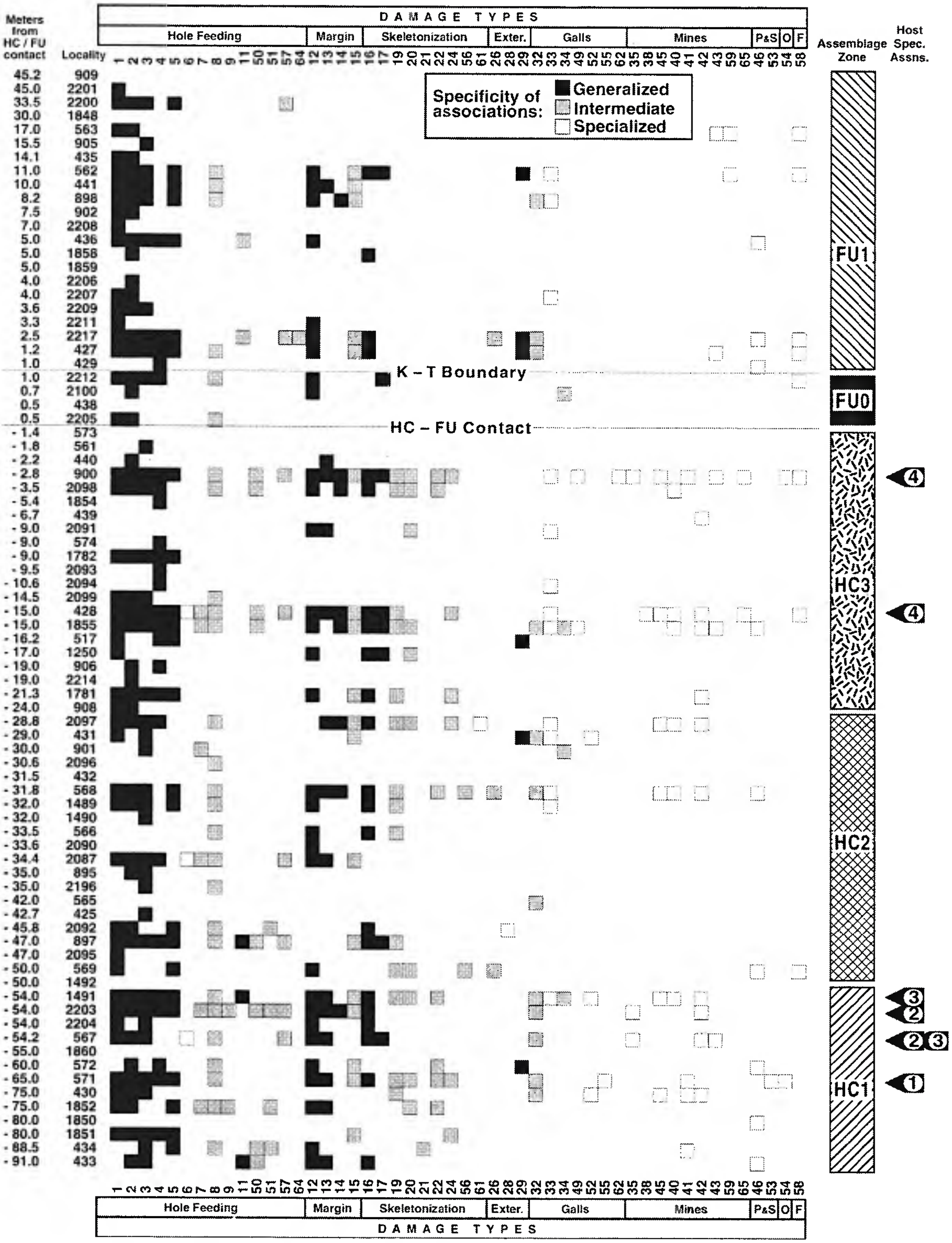


Figure 1. Matrix of damage types and inferred host specificity throughout all examined floras of upper Hell Creek (HC) to lower Fort Union (FU) formational succession in Williston Basin. Vertical stratigraphic elevations are with respect to Hell Creek–Fort Union formational contact, often not coincident with Cretaceous-Tertiary (K-T) boundary. Numbers in arrows at right refer to four host-specific associations detailed in text and in Table 1. Abbreviations: exter. = special external feeding; p&s = piercing and sucking; o = oviposition, and f = fungal damage.

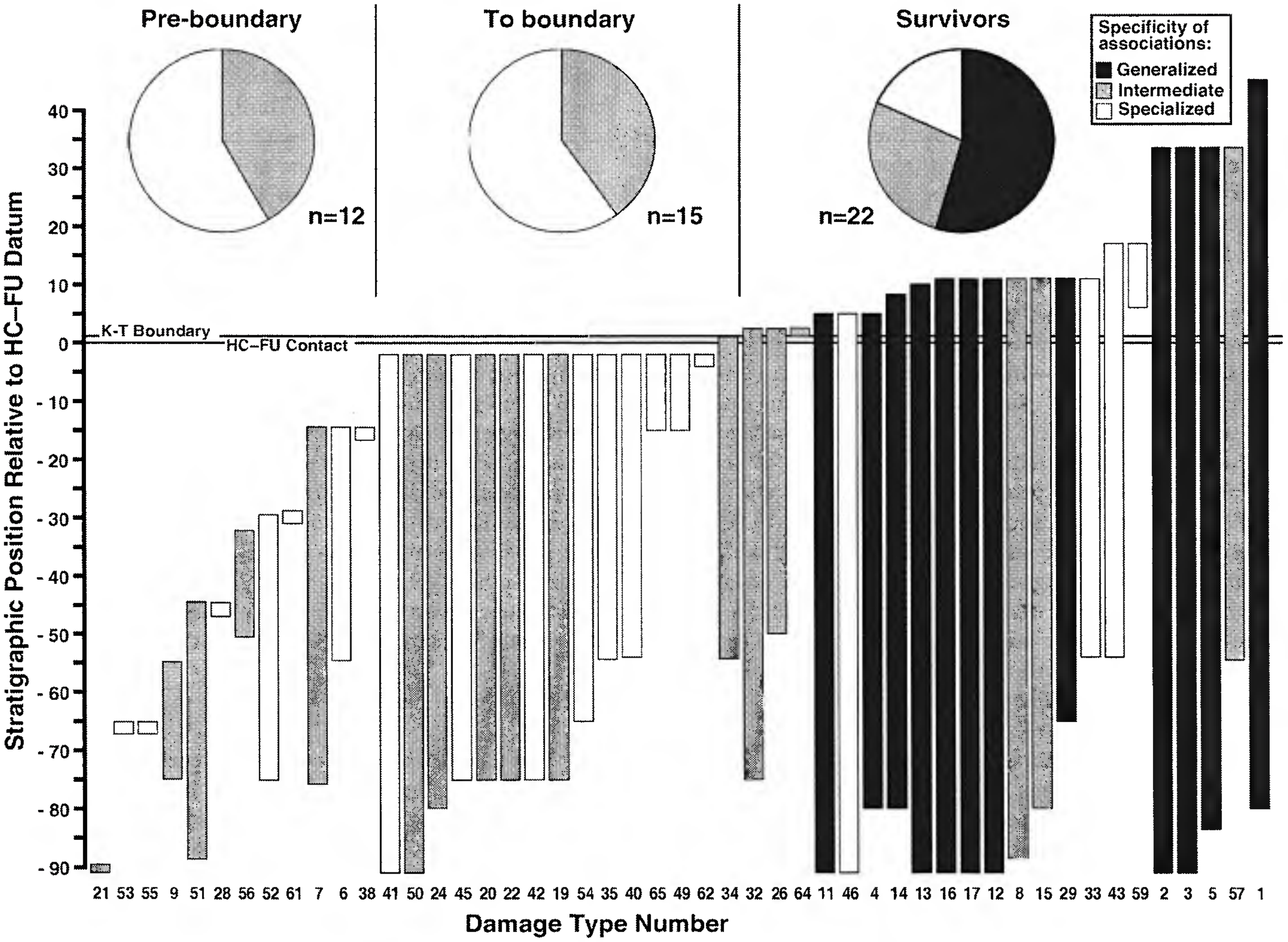


Figure 2. Summary of Figure 1, expressed as temporal ranges calibrated to standardized stratigraphic scale relative to Hell Creek–Fort Union (HC–FU) formational contact. Damage types are partitioned into three cohorts—namely those that disappear before boundary (preboundary), those that are extinguished at boundary (to boundary), and those that cross boundary (survivors). Proportions of generalized (black), intermediate (dark gray), and specialized (light gray) associations are provided for each cohort, indicating differential extinction of specialized associations before boundary and selectivity for plant host generalists among surviving taxa. K-T, Cretaceous-Tertiary.

Linnean assignments, it allows fossil leaves to be allocated to a distinctive morphotype that eventually can be upgraded to a formally described Linnean binomial once sufficient, diagnostic, and commonly understood characters are assembled from a representative suite of well-preserved material. Unlike the Linnean system, which requires a permanently designated holotype, holomorphotypes can be updated periodically as better material becomes available, providing for a reference specimen that displays more exacting criteria for eventual taxonomic placement. We acknowledge the possibility that some of these morphotypes may be taxonomically split and others amalgamated, but such reassignments would be done at low taxonomic rank and would not significantly alter our results. Although only 18% of the K-T flora has been formally and convincingly described at the species level (Johnson, 1996, 1999), it is expected that the entire flora will be converted to Linnean taxa as the quality of the morphotype reference collection is improved.

Insect damage types

A system of foliar damage types was developed by Wilf and Labandeira (1999), later elaborated (Wilf et al., 2001), explicitly to categorize recognizable insect modification of leaves in the fossil record. The initial leaf damage spectrum of 41 types, used in a study of late Paleocene to early Eocene insect herbivory of the greater Green River Basin of Wilf and Labandeira (1999), has been updated and consists of 49 damage types documented in this study. Damage type hereafter will be abbreviated DT when referring to a discussed example. An additional 16 K-T damage morphotypes not found in the previous study have been added, and 7 from the Green River list are absent in this study, resulting in a total of 49 recognizable categories for the Hell Creek to lower Fort Union succession that serves as the basis for the current study (Appendix 1). Each insect damage type from the Late Cretaceous to the early Eocene has been assigned a linked reference specimen for comparison purposes; the number of damage morphotypes is expected to increase and be replaced as better preserved and additional foliar material is examined.

These herbivore damage types can additionally be partitioned from specialized to generalized, based on knowledge of plant host specificities of modern descendants or ecologically analogous taxa, following Wilf and Labandeira (1999). Generalized associations, such as most hole feeding and margin feeding, are designated 1 (see Bernays and Chapman, 1994), whereas highly specialized associations such as leaf mines (Spencer, 1990; Hespenheide, 1991; Connor and Taverner, 1997), piercing and sucking damage (Patch, 1938; Deckle, 1965; Dixon, 1998), and galls (Gagné, 1989; Yukawa and Uechi, 1999) are assigned a 3. An intermediate assignment of 2 is given to types of damage whose modern analogs typically are not deemed either monophagously specialized or polyphagously generalized. It should be stressed that multiple, unrelated insect taxa can produce the same generalized insect damage patterns, or alternatively, the same insect species can produce different damage patterns, the latter mostly as a consequence of instar-related feeding differentiation in holometabolous insects (Buzzi, 1975). Specialized damage types, such as leaf mines, scale insect scars, and highly stereotyped hole feeding are typically synonymous with single plant-host and insect-herbivore associations, whereas intermediate associations have much less host specificity. Based on a prolific, mostly agriculturally based literature of modern plant-insect associations (summarized in Packard, 1889; Houard, 1909a, 1909b; Hering, 1951, 1967; Zerova et al., 1988, 1991; Kolomoets et al., 1989; Johnson and Lyon, 1991; Alford, 1991; and numerous other sources), generalized, intermediate, and specialized damage patterns typically can be recognized. We have taken a conservative approach, opting to characterize a damage type as specialized only if supported by widespread extant ecological observations, supplemented with patterns of host use in the investigated K-T interval. We recognize the probable inclusion of some specialist feeders possessing nondiagnostic consumption patterns within the generalized damage types of external foliage feeding. However, this inclusion would bias our results against a conclusion that recognizes the extinction of host specialists at the end of the Cretaceous.

We have established four explicit criteria by which we have based our determinations of foliar herbivory (Labandeira, 1998b), as opposed to abiotically mediated damage (Katerman, 1990; Vincent, 1990). The first criterion is presence of plant-reaction tissue adjacent to or otherwise surrounding the damaged area, including thickened callus, intervening necrotic tissue, or an encircling reaction zone some distance away (Beck and Labandeira, 1998). Second, we have used microscopic details of the damaged tissue margin, such as veinal stringers (Kazikova, 1985) or minute, cuspate tissue flaps (Gangwere, 1966) indicative of chewing activity. Third, we have noted stereotypy of the plant host damage in terms of overall pattern, position on the leaf, and size and shape of the individual damage elements (e.g., Kile, 1974; Heron and Borowiec, 1997; Heron, 1999). Last, we have noted the presence of host specificity patterns for all damage types, which would be highly atypical if the causative agent were abiotic. Single or various combinations of these four criteria in almost all instances were sufficient to separate insect-mediated from other damage, although the recognition of fungal damage (Dilcher, 1965; Sinclair et al., 1987) presented special problems in some instances. An additional complication was detection of normally delicate damage types that occur in coarser grained deposits, where the threshold of preservational detail is higher. Thus coarser sandy deposits frequently lack detail of delicate insect damage such as small leaf mines or piercing and sucking punctures that would be evident in finer grained depositional facies: in such instances, where damage was preservationally marginal but could not be documented convincingly, they were not included as data.

RESULTS

Four major results characterize this preliminary analysis of the K-T succession from the Williston Basin: (1) the greatest diversity of insect damage types so far examined explicitly from any fossil flora; (2) the occurrence of ~15 unique, host-specialized associations within the Cretaceous portion of the succession, four of which are detailed in herein (Table 1); (3) the extirpation of many associations by the K-T event, particularly specialist ones, and the subsequent preferential enrichment of generalist herbivores; and (4) the lack of a recovery phase of plant and/or insect associations during the sampled early Paleocene.

Plant host and damage-type diversity and abundance

Currently 49 diagnosable plant-insect associations have been recovered from the Hell Creek to Fort Union boundary succession of the Williston Basin. Some are abundant, particularly generalized types, but there are also some intermediate and specialized damage types; others are rare, mostly specialized damage types (Appendix 1). Based on functional feeding groups, these damage types are represented as 30 for external foliage feeding, 7 for galling, 9 for mining, 2 for piercing and sucking, and 2 extraneous types (oviposition and undifferentiated fungal damage), the latter of which was noted but not included in our analyses. We were unable to find pollen- or nectar-related activities on preserved but relatively rare flowers, although their presence in the Late Cretaceous is provided by other types of well-preserved deposits and inferences from body fossils (Crepet and Friis, 1987; Schlüter 1987; Willemstein, 1987). Nevertheless, the recorded damage types represent a broad spectrum of herbivore associations that are similar to those from extant warm-temperate to subtropical floras. Several of the plant host and insect herbivore associations are spatially and temporally unique for the fossil record, and some have been reported previously (Lang, 1996). Four selected examples are discussed here, representing the external foliage feeding, galling, piercing and sucking, and leaf-mining functional feeding groups.

A total of 7095 fossil leaves were examined for this study, 5178 of which occur in the Hell Creek Formation and represent 54 localities, and 1917 of which occur in the Fort Union Formation and represent 26 localities. Of these specimens, ~62% originate from 12 deposits with greatest leaf abundances and are distributed rather evenly throughout the K-T interval (Table 2). These 12 floras contain 8–25 damage types, although one with the least number of specimens of these is anomalously low, with 5 damage types. Of the 80 floras, 9 lacked any indication of insect-mediated damage (Fig. 1), and 18 contained only one damage type. However, there is a monotonic increase in specimens per locality from several to 135 specimens, culminating in the tally provided in Table 2. We inventoried the entire relevant collection from the K-T boundary of the Williston Basin housed at the Denver Museum of Nature & Science (as of December 2000). A subsequent analytical study has examined 6500 additional specimens inventoried at the Peabody Museum of Yale University (Labandeira et al., 2002).

With the exception of bryophytes and sphenopsids, all major taxa of plants occurring within the studied interval display evidence of interactions with insect herbivores. Several fern species (Fig. 3, A and B) and the conifer *Metasequoia* exhibit cuspate margin feeding and ovoidal hole feeding (DT 12 and DT 2, respectively), but the incidence of attack is rare. Ginkgophytes, represented by *Ginkgo adiantoides,* bear generalized skeletonization (DT 16) similar to that described by Hase (1955) (Fig. 3E), a less incised version of cuspate margin feeding (DT 12), and characteristic slot-hole feeding (DT 8) comparable to those of monocots (Selman, 1988). Cycads, present as *Nilssonia yukonensis,* are characterized by generalized window feeding (DT 29) (Fig. 3, C and D), reminiscent of modern feeding damage by the basal chrysomelid beetle *Aulacoscelis* on *Zamia fairchildiana* in Panamá and Costa Rica (Windsor et al., 1999; Cox and Windsor, 1999). No specialized associations (level 3) were found in nonangiospermous plants. Monocotyledonous angiosperms, principally the ginger *Zingiberopsis attenuata,* exhibited slot feeding (DT 8) and strip feeding inclined or perpendicular to venation (DT 28) (Fig. 3, F and G), characteristic of some extant hispine beetles (Strong, 1977; Wilf et al., 2000). A few nymphaealean and indeterminate monocots

TABLE 1. FOUR SELECTED HOST-SPECIFIC ASSOCIATIONS FROM THE HELL CREEK FORMATION, WILLISTON BASIN OF NORTH DAKOTA

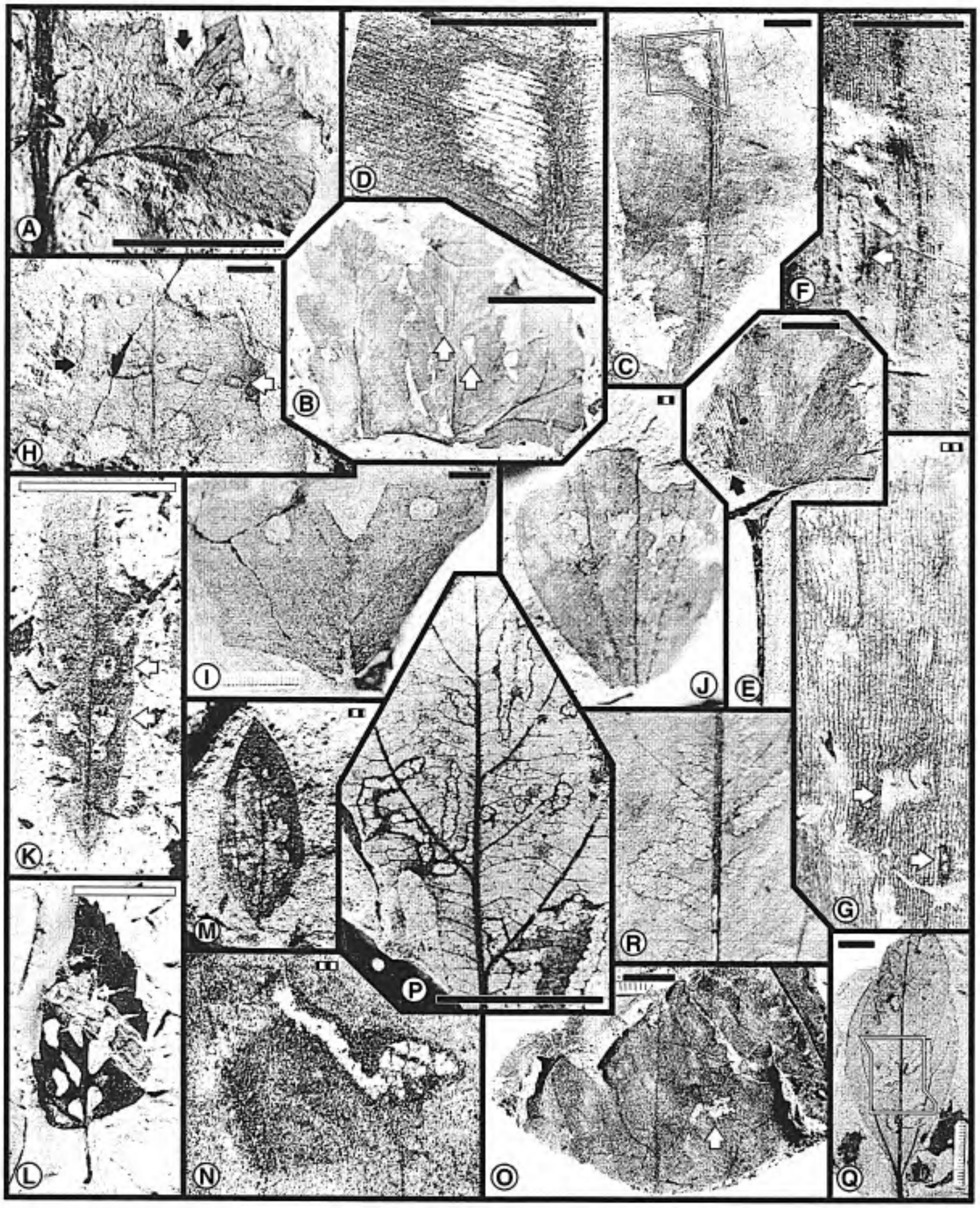
DMNH localities and Hell Creek–Fort Union datum horizon (m)	Plant host and morphotype	Damage type	Functional feeding group	Text figure
900 (−2.8 m) 428 (−15.0 m)	*Marmarthia pearsonii* (Laurales) (HC161)	DT 45	Leaf miner	12
567 (−54.0 m) 1491 (−54.2 m)	Undescribed dicot (HC135)	DT 33	Galler	11
567 (−54.0 m) 2203 (−54.2 m)	Undescribed dicot (Urticales) (HC81)	DT 57	External foliage feeder	10
571 (−65.0 m)	*Erlingdorfia montana* (Platanaceae) (HC57 + HC64)	DT 53	Piercer-and-sucker	9

Note: DMNH—Denver Museum of Nature & Science.

TABLE 2. LOCALITIES WITH THE GREATEST NUMBER OF EXAMINED LEAF SPECIMENS

DMNH locality	Stratigraphic elevation to Hell Creek–Fort Union contact (m)	Number of specimens examined	Number of damage types
428	−15.0	836	20
900	−2.8	560	25
2217	+2.5	436	14
2203	−54.0	413	14
567	−54.2	396	11
2087	−34.4	378	8
571	−65.0	296	18
2097	−28.8	268	13
2200	+33.5	258	5
1491	−54.0	203	17
898	+8.2	187	10
427	+1.2	177	12
		4408	

Note: DMNH—Denver Museum of Nature & Science.



displayed rare hole feeding and two mines, although palms evidently do not show any evidence of herbivory. Dicotyledonous angiosperms, by contrast, collectively displayed virtually all of the 49 damage types described in Appendix I. Included in this broad spectrum of insect-mediated damage is margin feeding (Fig. 4), hole feeding associated with leaf laminae (Fig. 3, B, F, G, and L), and primary veins (Fig. 5), of which characteristic slot-feeding by chrysomeloid beetles (Fig. 6) and skeletonization along primary veins indicative of leaf rollers or tiers (Fig. 7, A–N) or other external feeders (Fig. 3, M-R; Fig. 7, O and P), are very distinctive. In addition, various types of primary-vein petiolar and leaf-blade galls (Fig. 8, A–F), serpentine and

←

Figure 3. External feeding damage to nondicotyledonous plants; bud feeding, stereotyped hole feeding, and serpentine skeletonization from floras of Hell Creek Formation. A: Cuspate margin feeding (arrow) on unidentified filicalean fern (locality [loc.] 2087, DMNH-19962; HC241, DT 12). B: Medium hole feeding (arrows) on unidentified filicalean fern (loc. 2087, DMNH-19927b; HC241, DT 2). C: Skeletonization or surface feeding on *Nilssonia yukonensis* (Cycadales) (loc. 571, DMNH-7128; HC164, DT 16, 24). D: Detail of damage in C, exhibiting continuity of secondary venation and surrounding darker reaction rim. E: Generalized skeletonization on *Ginkgo adiantoides* (Ginkgoaceae) (loc. 568, DMNH-19979; HC114, DT 16). F: Slot hole feeding (*Cephaloleichnites*) on *Zingiberopsis attenuata* (Zingiberaceae) (loc. 2092, DMNH-19959; HC196, DT 8) (Wilf et al., 2000). G: Hole feeding and skeletonization on *Zingiberopsis attenuata* (Zingiberaceae), showing reaction rims (arrows) and continuity of secondary venation through damaged area (loc. 2092, DMNH-19957; HC36, DT 26). H: Medium polylobate hole feeding (bud feeding?) occurring approximately symmetrical on each side of midvein of unidentified dicot (loc. 900, DMNH-7240; HC-UNID, DT 3, DT 17, ?DT 6). I. Bud feeding on *Liriodendrites bradacii* (Magnoliales) (loc. 428, DMNH-20066; HC166, DT 6). J: Probable bud feeding on immature leaf of "*Cinnamomum*" *lineafolia* (Trochodendrales) (loc. 567, DMNH-19950; HC92, DT 6). K: Probable bud feeding, indicated by two arrows, on *Humulus* sp. (Cannabinaceae) (loc. 2087, DMNH-19972; HC243, DT 6). L: Polylobate hole feeding on unidentified species of Ulmaceae (loc. 2098, DMNH-20017; HC224, DT 3). M: Skeletonization of very small, immature leaf of "*Cinnamomum*" *lineafolia* (Trochodendrales) (loc. 567, DMNH-19358; HC92, DT 1). N: Serpentine skeletonization, possibly terminal phase of leaf mine (?), on *Liriodendrites bradacii* (Magnoliales) (loc. 900, DMNH-7317; HC166, DT 20). O: Serpentine skeletonization of unidentified dicot (loc. 1855; DMNH-20003a; HC254, DT 20). P: Curvilinear skeletonization on *Erlingdorfia montana* (Platanaceae) (loc. 1250, DMNH-19997; HC57, DT 20). Q: Curvilinear skeletonization associated with midvein of *Marmarthia pearsonii* (Laurales) (loc. 900, DMNH-7713; HC162, DT 20). R: Detail in Q showing feeding path and affected venation. Solid scale bars = 1.0 cm, except in G and J, where striped bars = 0.1 cm.

blotch miners (Figs. 8, G-M), piercing and sucking (Fig. 9), rare bud feeding (Fig. 3, H–K), and oviposition (Fig. 8, N and O) are also present. All major subclasses of dicots (sensu Cronquist, 1981) were herbivorized, except for Caryophyllidae and Asteridae, which were very rare in the flora; the most intensively herbivorized subclasses were Magnoliidae, especially Laurales, and Hamamelidae, particularly Platanaceae, Cercidiphyllaceae, Trochodendraceae, and Urticales.

Host specific associations

In assemblage zone HCI, at Denver Museum of Nature & Science (DMNH) locality 571, located −65.0 m from the HC-FU datum, *Erlingdorfia montana* (Brown) Johnson, a trifoliately compound member of the Platanaceae (leaf morphotype HC57), exhibits large, circular to subtly ovoidal structures 5–9.5 mm in diameter that always are situated on or adjacent to primary veins (Fig. 9). This host-specific association (DT 53) is known only from one locality that has yielded 32 instances of damage, representing a highly variable number of circular structures per leaf, including 7 on a single specimen (Fig. 9, A and B), 4 on another specimen (Fig. 9, C and D), 3 on 2 specimens, 2 on 3 specimens (Fig. 9, E, F, I, M, P), and 1 on 10 specimens (Fig. 9, G, H, N, O). In several specimens, prominent areas of discolored foliar tissue surround each or a group of these circular structures (Fig. 9, A, G, J, O, L), interpreted as a reaction response similar to chlorotic zones surrounding extensive scale infestations in modern Platanaceae (Wheeler, 1980). These circular structures lack fusain or other indication of thickened tissue, such as hyperrelief or hyporelief depression, into the matrix that would suggest a gall. We attribute these structures to scale insects (Hemiptera: Coccoidea); they are similar in size, shape, and plant host position to extant members of the Coccidae (common scale insects) that commonly occur on broadleaved dicots (Comstock, 1916; Deckle, 1965; Williams and Kosztarab, 1972). Modern Platanaceae are heavily attacked by a broad spectrum of insects (Smith, 1944; Brown and Eads, 1965; Filer et al., 1977; Thompson and Solomon, 1986; Klausnitzer, 1988; Halperin, 1990), and prominently include piercing and sucking forms such as coccids (Wunn, 1925; McConnell and Davidson, 1959; Murakami, 1970), leafhoppers (Brown and Eads, 1965; McClure, 1974), and lacebugs (Maceljski and Balarin, 1972; Rogers et al., 1982). Although the scale damage on *Erlingdorfia* is large by modern standards, it is well within the size range of some extant Margarodidae, some tropical species of which reach 40 mm in diameter (Essig, 1926; Carver et al., 1991), and Coccidae such as *Eulecanium caryae,* which occurs on hickory and occasionally on *Platanus occidentalis* (Williams and Kosztarab, 1972; Johnson and Lyons, 1991), reaching a maximum diameter of 15 mm. Notably these fossil scales cluster exclusively on primary veins—a habit that is present in many piercing and sucking folivorous insects that insert their stylets into more nutritionally rewarding vascular tissue rather than intervening epidermis and parenchyma (Sanders, 1905; Dodge, 1943; Wakgari and Giliomee, 1998). Koteja (1985) and Foldi (1997) discussed the colonization of angiosperms by scale insects during the Late Cretaceous and their resemblance to many modern forms.

A second example, this time an intermediate-specialized association, originates from zone HCI, occurring at DMNH localities 567 and 2203, at −54.2 and −54.0 m, respectively, from the HC-FU datum. Two externally feeding damage types are evident in this host: very common DT 57 consisting of triangular to ovoidal to reniform hole feeding in angles subtended by primary and secondary veins (Fig. 10), and uncommon DT 50 consisting of circular feeding along primary veins (Fig. 10, I). These two types of damage, while delicate and distinct, were probably caused by different insects. Occasional slot feeding of DT 8 also has been noted, although this feeding mode undoubtedly was caused by a species of a chrysomelid beetle or even a weevil. Hundreds of individual damage traces (DT 57) have been observed from these two floras, occurring almost exclusively on the five-lobed, serrately margined herbaceous leaf probably representing an undescribed species of

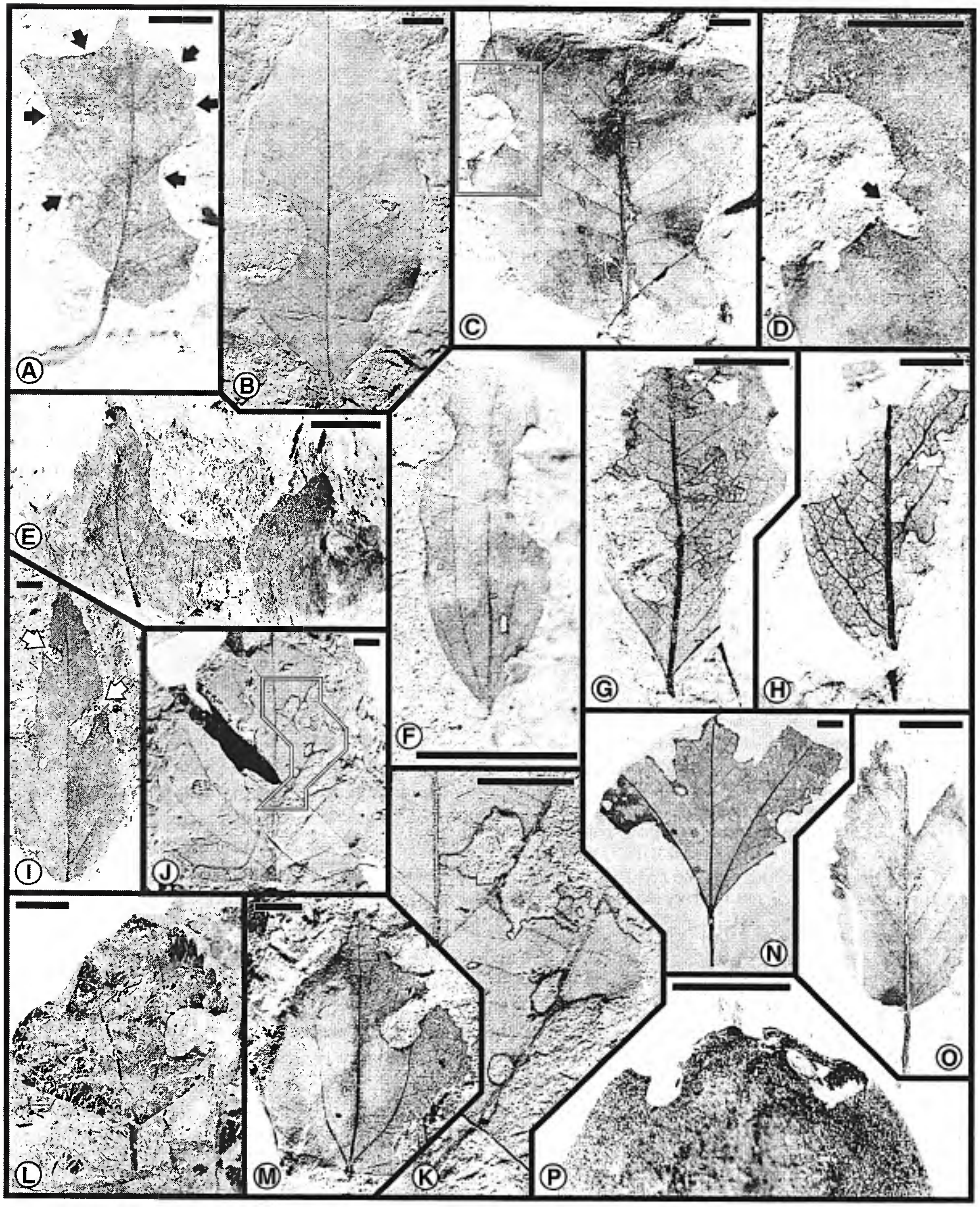


Figure 4. Varied types of insect margin feeding from Hell Creek (A-D, F, G, K-P) and Fort Union (E, J) Formations. A: Cuspate margin feeding on unidentified dicot (locality [loc.] 2091, DMNH-20058; HC-UNID, DT 12), resembling that of extant megachilid bees. Arrows indicate separate events of leaf-margin excision. B: Cuspate margin feeding on unidentified dicot (loc. 2091, DMNH-19722; HC285, DT 12). C: Cuspate and secondarily trenched margin feeding on undetermined magnoliid dicot (loc. 2091, DMNH-18874; HC66, DT 12, DT 15). D: Detail of cuspate excision in C; arrow indicating a secondary feeding event. E: Cuspate margin feeding on leaf fragment of *Dicotylophyllum anomalum,* unidentified dicot (loc. 898, DMNH-20048; FU29, DT 4, DT 14). F: Cuspate margin feeding on immature leaf of *Erlingdorfia montana* (Platanaceae) (loc. 568, DMNH-20074; HC64, DT 12). G: Margin feeding to midrib in "*Dryophyllum*" *subfalcatum,* unidentified dicot (loc. 2097, DMNH-19986; HC49, DT 14). H: Margin feeding to midrib and hole feeding in unidentified dicot "*Dryophyllum*" *subfalcatum* (loc. 2097, DMNH-19988; HC49, DT 3, DT 14). I: Trenched margin feeding on undescribed platanaceous leaf (loc. 900, DMNH-20025; HC329, DT 15). J: Varied margin feeding and hole feeding on *Pterospermites cordata* (Dilleniidae) (loc. 898, DMNH-20052; FU61, DT 2, DT 3, DT 14, DT 15). K: Detail in J, showing extent of damage. L: Trenched margin feeding on *Cercidiphyllum ellipticum* (Cercidiphyllaceae) (loc. 2087, DMNH-19967; HC212, DT 15). M: Another example of trenched margin feeding on *Cercidiphyllum ellipticum* (Cercidiphyllaceae) (loc. 1491, DMNH-19073; HC212, DT 15). N: Extensive cuspate, apical, and primary-vein associated margin feeding and hole feeding on *Erlingdorfia montana* (Platanaceae) (loc. 567, YPM-6148; HC57, DT 3, DT 12, DT 13, DT 14). O: Margin feeding associated with primary vein of unidentified ulmaceous dicot (loc. 2098, DMNH-20018; HC36, DT 14). P: Apex of unknown dicot exhibiting trenched margin feeding and medium hole feeding (loc. 1491, DMNH-18887; HC135, DT 2, DT 15). Solid scale bar = 1.0 cm.

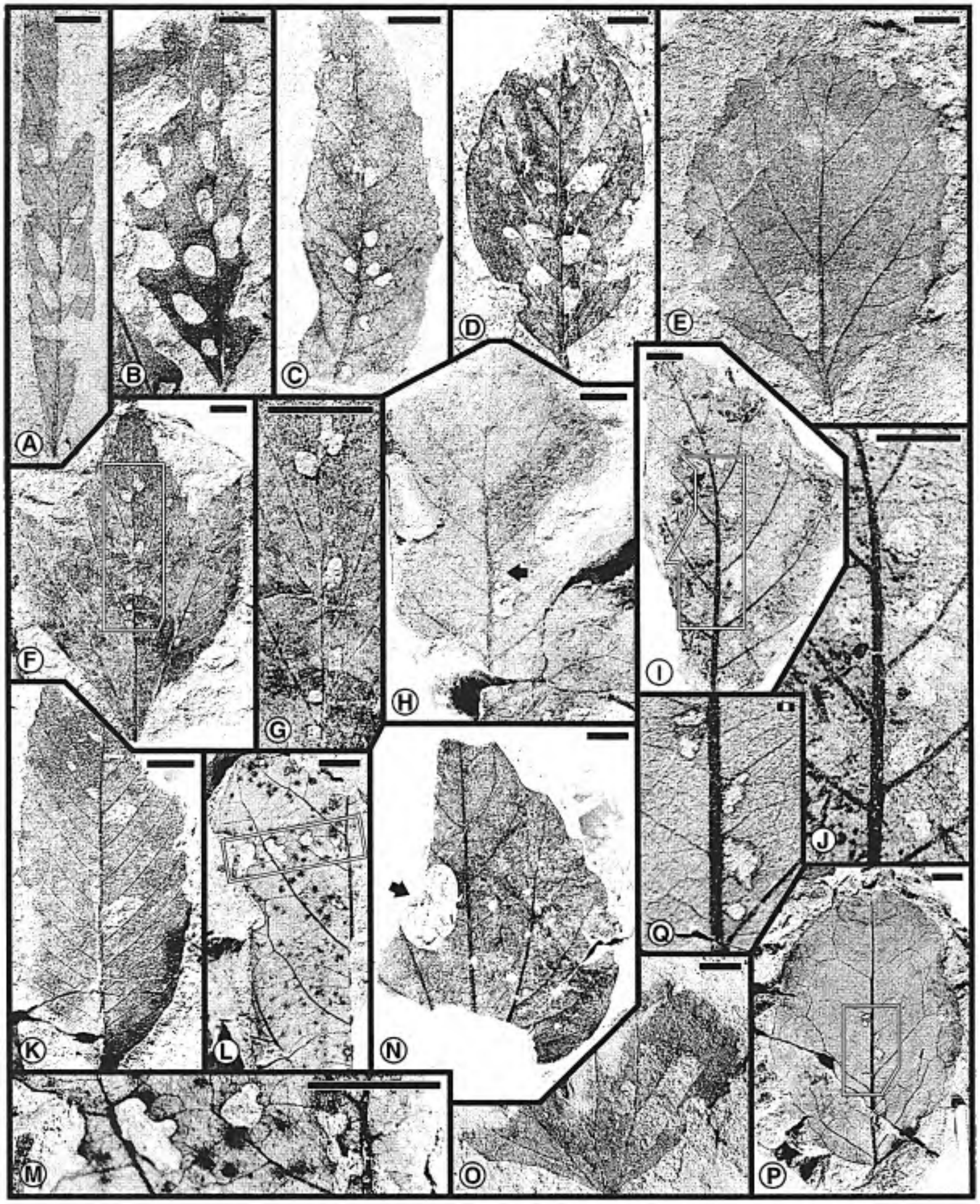


Figure 5. Examples from floras of Hell Creek Formation of mostly hole feeding and skeletonization associated with primary veins. A: Midvein-associated hole feeding on "*Dryophyllum*" *tennesseensis* (Magnoliidae) (locality [loc.] 428, DMNH-20063; HC44, DT 50). B: Extensive hole feeding and margin feeding between secondary veins on unidentified dicot (loc. 900, DMNH-7595; HC?330, DT 2, DT 14). C: Midvein-associated hole feeding on "*Dryophyllum*" *subfalcatum,* undetermined dicot (loc. 433, DMNH-13196; HC49, DT 50). D: Medium and large polylobate hole feeding on unidentified dicot (loc. 1489, DMNH-19977; HC254, DT 3, DT 5). E: Hole feeding at basal vein angles of *Grewiopsis saportana* (Platanaceae) (loc. 428, DMNH-6722; HC2, DT 57). F: Hole feeding adjacent to central primary vein on *Erlingdorfia montana* (Platanaceae) (loc. 1855, DMNH-20010; HC57, DT 50). G: Detail of hole feeding illustrated in F. H: Small and medium sized hole feeding adjacent midvein of lauralean dicot, indicated by arrow (loc. 428, DMNH-20059; HC199, DT 24, DT 39). 1: Midvein associated hole feeding on unidentified dicot (loc. 428, DMNH 6789; HC-UNID, DT 50). J: Detail of damage adjacent to midvein in 1, showing ovoidal and polylobate hole feeding. K: Removal of intersecondary areas by hole feeder on "*Rhamnus*" *cleburni* (Rhamnaceae) (loc. 2088, DMNH-19958; HC62, DT 63). L: Medium sized, polylobate hole feeding and margin feeding on *Bisonia niemi* (Lauraceae) (loc. 1781, DMNH-19991; HC200, DT 3). M: Detail of damage in L, perhaps showing secondary fungal infection in blackened necrotic areas. N: Large and small hole feeding on *Marmarthia trivialis* (Laurales) (loc. 1781, DMNH-19992; HC105, DT 5). O: Skeletonization of intersecondary vein areas on *Platanites marginata* (Platanaceae) (loc. 428, DMNH-7431; HC106, DT 16, DT 19). P: Midrib-associated ovoidal skeletonization of unidentified magnoliid dicot (loc. 900, DMNH-7184; HC43, DT 24). Q: Detail of skeletonization in P, showing thick reaction rims. Scale bars: solid = 1.0 cm, except in Q, where striped bar = 0.1 cm.

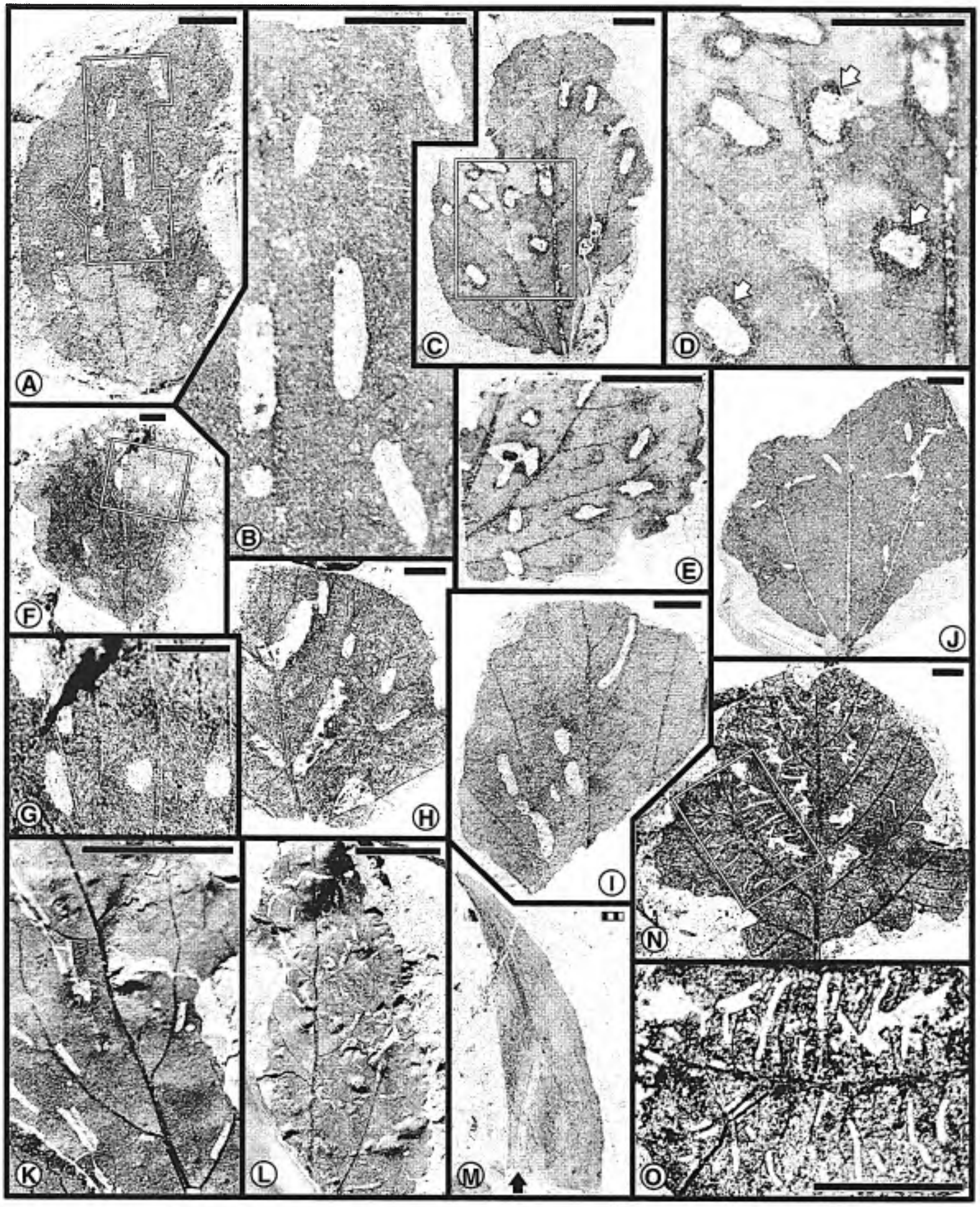


Figure 6. Examples of hole-feeding damage from floras of Hell Creek Formation, deployed principally as slots parallel to major venation. A: Slot hole feeding (top) and rectangular skeletonization (bottom) on *Marmarthia trivialis* (Laurales) (locality [loc.] 428, DMNH-20065; HC105, DT 8, DT 19). B: Detail of slot hole feeding in B. C. Slot hole feeding on *Marmarthia trivialis* (Laurales) with exceptionally thick reaction rims (loc. 428, DMNH-7495; HC105, DT 8). D: Detail of slot hole feeding in C; arrows indicate well-developed reaction rims. E: Slot and medium hole feeding on platanaceous leaf fragment, similar to C (loc. 434, DMNH-18651; HC209, DT 3). F: Medium, ovoidal hole feeding on *Platanites marginata* (Platanaceae) (loc. 906, DMNH-19995; HC106, DT 2, DT 8). G: Detail of hole feeding in F, showing avoidance of primary veins. H: Slot and large polylobate hole feeding on undetermined platanaceous leaf (loc. 897, DMNH-19955; HC98, DT 4, DT 8, DT 57). I: Slot and possible polylobate hole feeding on *Marmarthia trivialis* (Laurales) (loc. 428, DMNH-13617; HC105, DT 8). J: Another example of elongate slot hole feeding on *Marmarthia trivialis* (Laurales) (loc. 428, DMNH-6850; HC105, DT 8). K: Slot hole feeding on cercidiphyllaceous leaf fragment (loc. 2203, DMNH-19611; HC229, DT 8). L: Example of slot hole feeding on cercidiphyllaceous leaf (loc. 2203, DMNH-19550; HC229, DT 8). M: Elongate slot on unidentified dicot (loc. 567, DMNH-19386; HC131, DT 8), indicated by arrow. N: Linear and polylobate slot hole feeding parallel to tertiary venation of platanaceous leaf (loc. 434, DMNH-18659; HC209, DT 51, DT 60). O: Detail of distinctive feeding damage in N showing linear and anastomosing slots. Solid scale bars = 1.0 cm, except in M, where striped bar = 0.1 cm.

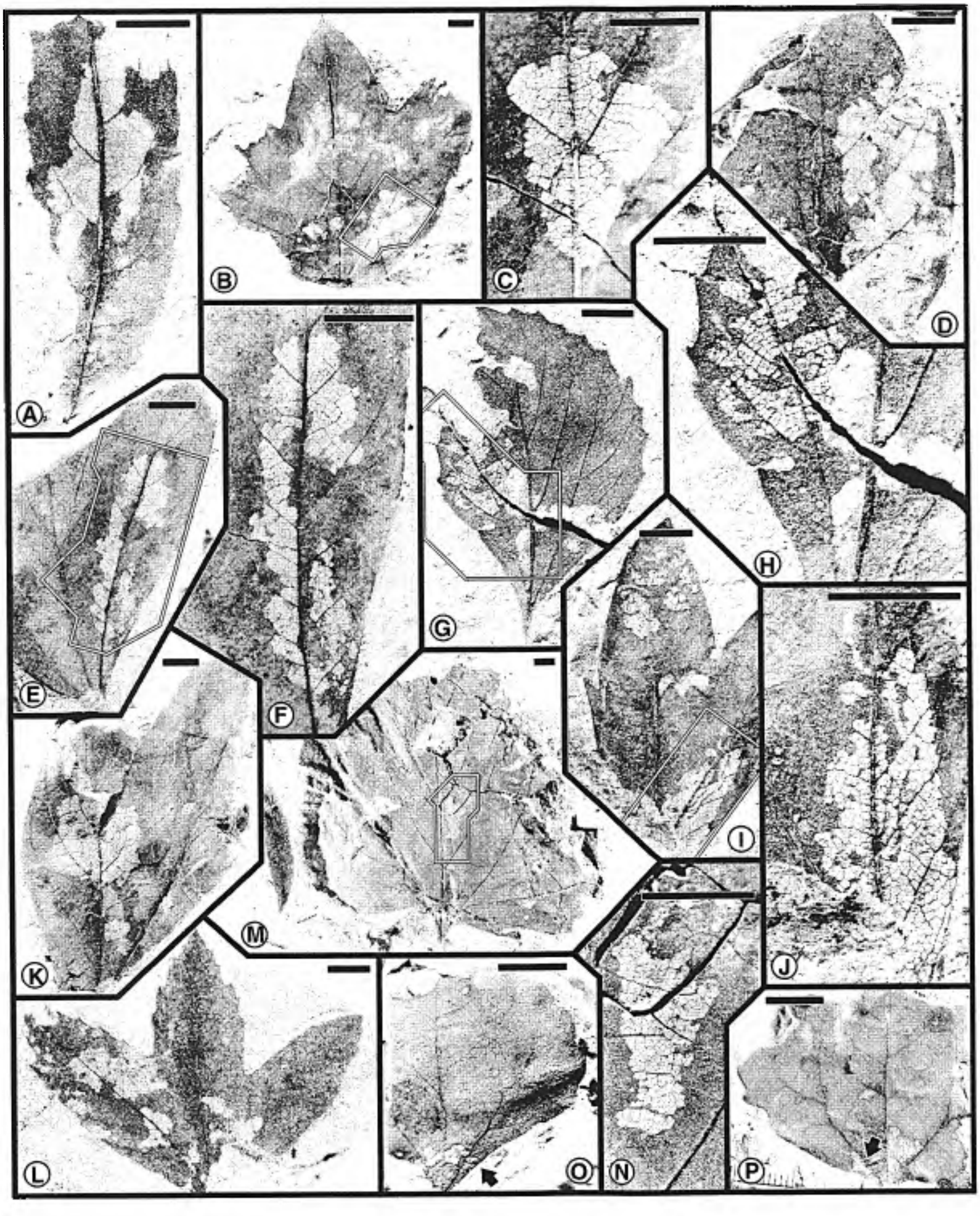


Figure 7. Leaves from floras of Hell Creek Formation, exhibiting elongate skeletonization along primary veins, suggesting folivory by leaf rollers or tiers. A: Rectangular skeletonization oriented obliquely on midrib of unidentified dicot (locality [loc.] 571, DMNH-7646; HC49, DT 19). B: Primary-vein associated skeletonization on *Erlingdorfia montana* (Platanaceae) (loc. 571, DMNH-18835; HC57, DT 16). C: Detail of skeletonized region in B, showing venational meshwork. D: Rectangular skeletonization parallel to midrib and leaf margin of unidentified dicot (loc. 1781, DMNH-19993a; HC-UNID, DT 19). E: Rectangular skeletonization associated with primary vein of *Erlingdorfia montana* (Platanaceae) (loc. 568, DMNH-20074; HC64, DT 19). F: Detail of skeletonization in E, displaying venational network. G: Skeletonization and medium hole feeding on unidentified dicot (loc. 571, DMNH-18881; HC-UNID, DT 2, DT 16). H: Detail in G, exhibiting tertiary venation at upper left and hole feeding at lower right. I: Skeletonization on lobe apex of *Erlingdorfia montana* (Platanaceae) leaf (loc. 571, DMNH-11014; HC57, DT 19). J: Detail of skeletonization associated with primary vein in I. K: Symmetrical skeletonization along primary vein of *Erlingdorfia montana* (Platanaceae) leaf (loc. 571, DMNH-11013; HC64, DT 19). L: Obliquely oriented skeletonization along primary vein of *Erlingdorfia montana* (Platanaceae) (loc. 568, DMNH-6256; HC57, DT 19). M: Elongate skeletonization parallel to midrib of undetermined platanaceous leaf (loc. 571, DMNH-8564; HC99, DT 16). N: Detail in M, illustrating tertiary and quaternary veinal network. O: Skeletonization of basal region of *Cercidiphyllum ellipticum* (Cercidiphyllaceae) leaf (loc. 1491, DMNH-19070; HC212, DT 20). P: Skeletonization of basal leaf region of *Trochodendroides nebrascensis* (Trochodendrales) leaf (loc. 569, DMNH-8490; HC103, DT 20). Solid scale bars = 1.0 mm.

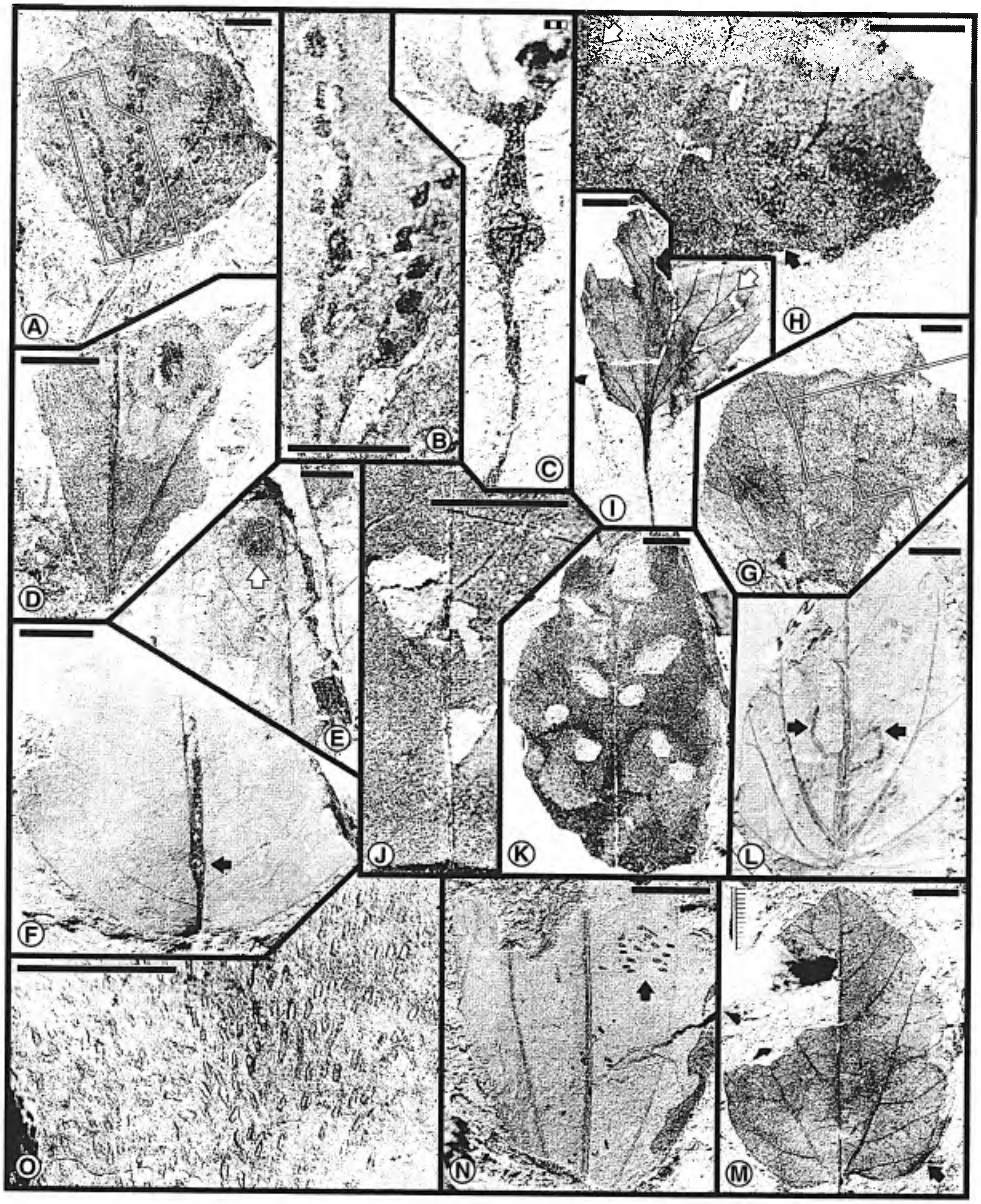


Figure 8. Examples of galls, blotch and linear leaf mines, and oviposition from floras of Hell Creek (A–K, M–O) and Fort Union (L) Formations. A: Galls on primary veins of *Trochodendroides nebrascensis* (Trochodendrales) (locality [loc.] 1489, DMNH-19976; HC103, DT 33). B: Detail of two gall-bearing veins in A; 34 galls have been recorded from this leaf. C: Petiolar gall on unidentified dicot (loc. 571, DMNH-18876; HC-UNID, DT 55). D: Gall on lamina of *Marmarthia pearsonii* (Laurales) showing reaction rim at some distance from gall core (loc. 900, DMNH-7210; HC162, DT 49). E: Large, fusain-containing gall on unidentified dicot (loc. 900, DMNH-7606; HC-UNID, DT 62). F: Incipient midrib gall (arrow) on unidentified magnoliid dicot (loc. 2091, DMNH-20011; HC43, DT 33). G: Blotch leaf mine on *Grewiopsis saportana* (Platanaceae) leaf (loc. 428, DMNH-20061; HC2, DT 35). H: Detail in G, showing tissue disruption and frass trail delineated by arrows. I: Serpentine skeletonized region on magnoliid (?Laurales) dicot, indicated by white arrow, probably representing leaf miner due to increase in damage width (loc. 2097, DMNH-19984; HC32, DT 61). J: Possible blotch mines in primary vein angles of *Erlingdorfia montana* (Platanaceae) (loc. 897, DMNH-19952; HC57, ?DT 57). K: Probable blotch mines on unidentified dicot (loc. 900; DMNH-7238; HC-UNID, DT 19); holes may represent pupation chambers with exfoliated epidermal tissue. L: Two distinctive, linear leaf mines with expansive terminal chambers (arrows) on each side of midrib of *Paranymphaea crassifolia* (?Nympheales) leaf (loc. 563, DMNH-20055; FU1, DT 59). M: Linear leaf mine along margin of "*Ficus*" *planicostata* (Laurales) (loc. 900, DMNH-7506; HC4, DT 41). N: Linearly oriented oviposition scars on *Marmarthia pearsonii* (Laurales) (loc. 900, DMNH-7265; HC162, DT 54). O: Radially oriented oviposition scars on *Erlingdorfia montana* (Platanaceae) (loc. 571, DMNH-11007; HC57, DT 54). Solid scale bars = 1.0 cm, except in C, where striped scale bar = 0.1 cm.

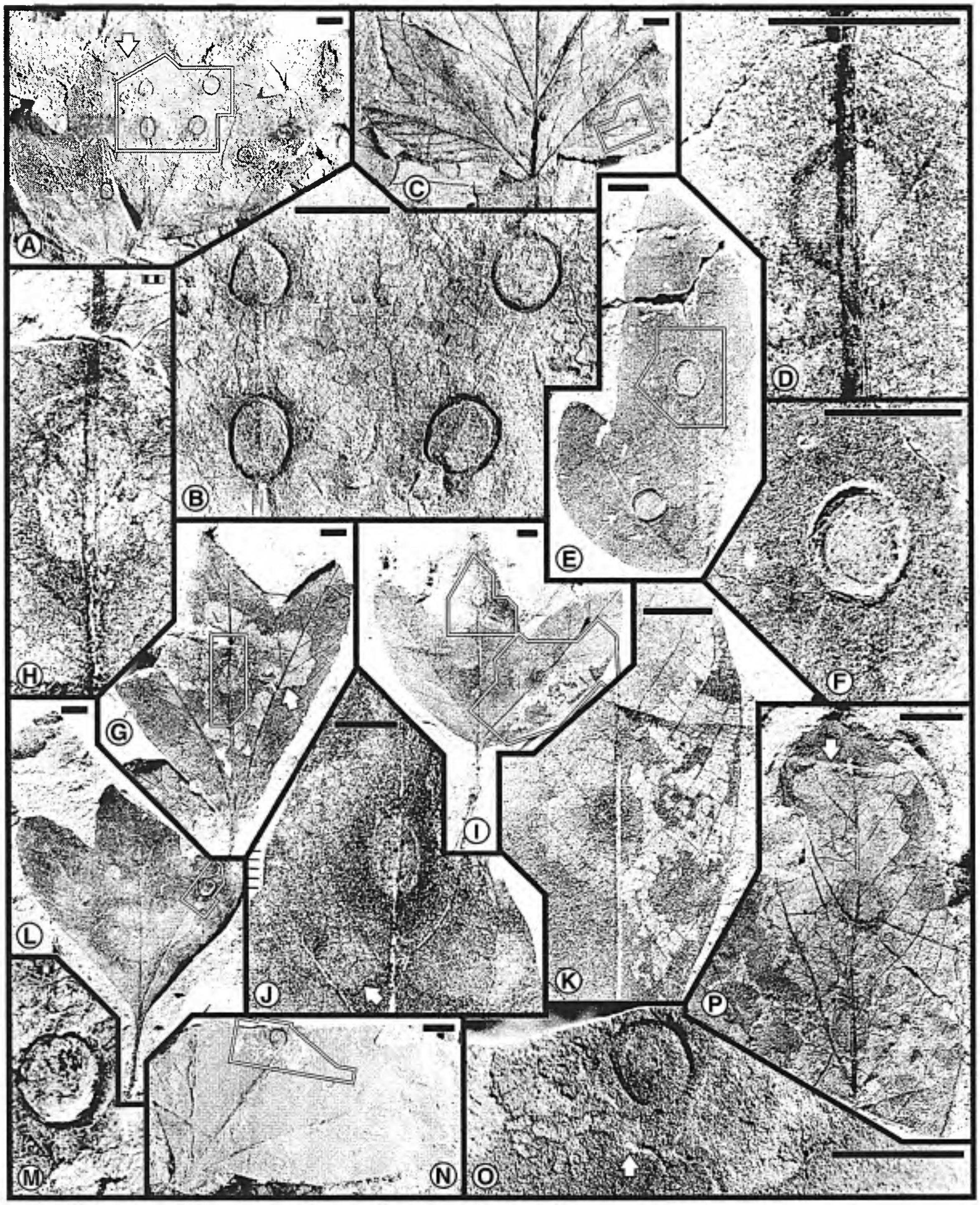


Figure 9. Host-specific association between a platanaceous host, *Erlingdorfia montana,* and a coccoid scale (Hemiptera), from Hell Creek Formation. All specimens originate from locality 571, represent damage type 53, and are found only on primary veins of compound leaf representing morphotypes HC57 (median leaves) and HC64 (lateral leaves) of *Erlingdorfia montana* (Platanaceae). A: Seven scales on simple leaf (DMNH-18829b), showing tissue imprints typical of pit scales. Note lighter hued region surrounding scales, indicating plant host-tissue response. B: Magnified detail of A, showing occurrence of four scales on two primary veins. C: Four scales on compound leaf (DMNH-18830). D: Enlargement of portion of right leaflet in C, showing scale and apparently unaffected primary vein. E: Two scales on leaf fragment, showing craterlike structure (DMNH-8587) representing opposite leaf surface to that of B. F: Detail of upper scale in E, showing well-developed rim. G: Portion of compound leaf showing central scale and associated zone of probable necrotic tissue; white arrow delineates boundary with unaffected tissue (DMNH-18836a). H: Magnified area in G, showing scale and unaffected primary vein. I: Simple leaf showing two scales (DMNH-11002). J: Detail of upper scale in I, revealing concentric ring within scale and enveloping necrotic zone (white arrow). K: Detail of lower right scale in I, showing associated necrotic zone and perhaps resulting in limited skeletonization. L: Leaf with two scales (DMNH-7641). M: Magnification of scale in L, showing structure. N: Scale on simple leaf (DMNH-6282). O: Detail of scale in N, revealing necrotic zone (white arrow) that apparently includes digitate skeletonization. P: Two scales on leaf lobe, displaying extensive necrotic zone defined by conspicuous margin (white arrow). Solid scale bar = 1.0 cm.

Figure 10. Host-specific association between an undescribed species of Urticales and an external foliage feeder, probably a weevil (Curculionidae) or leaf beetle (Chrysomelidae). This feeding pattern on leaf morphotype HC81 is characterized by damage type 57 and to lesser extent DT 50, consisting of triangular to ovoidal hole feeding in primary vein angles; one example of DT 12 is provided in J. This association occurs only at localities 567 and 2203. A: Almost complete, quinquepartite leaf with hole feeding at major vein angles (locality [loc.] 567, YPM-6703) B: Another relatively complete, quinquepartite, leaf with vein-angle hole feeding (loc. 567, YPM-6661). C: Tripartite leaf with damage (loc. 2203, DMNH-19206). D: Undivided leaf with margin serrations and vein-angle hole feeding (loc. 567, YPM-6661). E: Tripartite leaf with extensive hole feeding at basal vein angles (loc. 2203, DMNH-19539) F: Magnified region in E, showing vein-angle hole feeding amid mineralized epidermal structures on foliar surface, expressed as round dots. These features probably represent the silicified bases of stinging hairs. G: Closeup of E, showing juxtaposition of hole feeding and silicified structures. H: Lobe of leaf showing extensive vein-angle hole feeding (loc. 2203, DMNH-19549). I: Enlargement of region in H, illustrating consumption of nonvascular foliar tissue, including epidermis rich in presumptive stinging hair bases. J: Cuspate margin feeding (DT12), showing indiscriminate consumption of silica-containing foliar tissue (loc. 2203, DMNH-19585). Arrows point to individual feeding events revealed by crescentic margins. K: Extensive interveinal hole feeding and margin feeding (arrow) (loc. 2203, DMNH-19597). L: Closeup of region in K, showing avoidance of vascular tissue but consumption of silica-bearing intervening tissue. M: Vein-angle hole feeding on leaf lobe with extensive siliceous structures (loc. 2203, DMNH-19592). Solid scale bars = 1.0 cm; striped scale bars = 0.1 cm.

Urticales, and corresponding to leaf morphotype HC81. Although this damage type is structurally indistinguishable from that of several other leaf taxa in younger floras (Fig. 1), it is highly specific to HC81 at these two localities based on a survey of 809 leaf specimens. The sole exception is a HC228 leaf from locality 2203, which also is placed in the Urticales, the same order as HC81 (Cronquist, 1981). Lastly, an extremely small, linear leaf mine has been recorded in one specimin (DMNH 19619, not shown) that is consistent with a sap-feeding agromyzid miner occurring on such extant urticalean species as common nettle *Urtica dioica* L. and hemp *Cannabis sativa* L. from North America and Eurasia (Hering, 1932; Spencer, 1976, 1990).

The insect consumption of herbaceous HC81 provides an important occurrence in the early history of angiosperm antiherbivore defense. Under high magnification, the foliar surfaces of this taxon contains abundant, evenly spaced structures that may be calcium carbonate cystoliths in the hypodermis or more likely the silicified epidermal bases of stinging hairs (Thurston, 1974; Cronquist, 1981), features of which are amber in color and texture (Fig. 10E–10M). This leaf species only occurs in two localities and is similar to at least a few modern genera of Urticaceae (L. Hickey, 2001, personal commun.), although floral features are not present for confident assignment to any extant or extinct genus within this family. Likely herbivore coandidates, especially for DT 57, are leaf beetles of the Chrysomelidae (Essig, 1926; Jolivet and Hawkeswood, 1995; Konstantinov and Vandenberg, 1996), and less likely lepidopteran caterpillars such as members of the Pyralidae and Noctuidae (Forbes, 1923, 1960). Several modern insect taxa produce similar hole damage on native nettle, *Urtica dioica* L., including leaf beetles, weevils, and lepidopteran caterpillars (Bredemann, 1959; Carter and Hargreaves, 1986; Alford, 1991; Amelung, 1995). Implicit in this fossil association is herbivore avoidance from foliage laden with mineralic compounds, suggesting an association at 66.0 Ma similar to that of some pests on Urticaceae today, and perhaps to the deterrent effect that grass phytoliths have on extant graminivorous insects (Dravé and Laugé, 1978; Bernays and Barbehenn, 1987; Köhler et al., 2000).

The third host-specific association originates from DMNH localities 1491 and 567, situated −54.0 and −54.2 m, respectively, below the HC-FU contact, within assemblage zone HCI. This association consists of 588 galls that are thick, circular, and characteristically range from 0.5 to 3.0 mm in diameter, although the overwhelming majority are 0.75–1.25 mm in diameter (Fig. 11). They occur exclusively on the primary veins of an unassigned dicot (HC135) at both localities. These galls, assigned to DT 33, occasionally occur in clusters and are linked by necrotic foliar tissue within denser gall patches (Fig. 11, K, L, N). There is indication of a central chamber or possibly multiple chambers, revealed by the frequent presence of a central, craterlike depression. This depression is of intermediate hue between unaltered leaf and the surrounding rock matrix, indicating that there has been incomplete modification of tissue and not complete removal of the leaf that would be expected from a hole feeder (Fig. 11, B, E, J). Thus the surrounding ring of dark, thickened material is interpreted as the walls of a gall; some specimens also have an encircling zone of apparently necrotic tissue (Fig. 11, F and G). In a few instances, a light colored ovoidal structure within the gall may represent an emergence hole (Fig. 11, E and J), although in other cases differently shaped and positioned holes are interpreted as parasitoid damage or herbivory by an external feeder subsequent to gall formation (Fig. 11F). Although this association is host specific at this locality, galls of this general type occur on other plant hosts in other localities. However, this host is the only intensely galled plant within this local flora, and patterns of gall abundance, location on veinal tissue, and uniformity of size and shape among galls strongly indicate the singular targeting of this plant. This gall resembles simple dipteran galls of the family Cecidomyiidae (gall midges) that currently occur in taxonomic profusion on diverse dicotyledonous angiosperms (Gagné, 1989, 1994). The presence of gallers on this plant host is not unexpected; there is an extensive Late Cretaceous gall record on dicotyledonous angiosperms (Stephenson, 1992; Larew, 1992; Scott et al., 1994; Lang, 1996; Labandeira, 1998c).

The fourth specialized association is a lepidopteran leaf miner assigned to the family Gracillariidae, occurring on leaves of the dicot *Marmarthia pearsoni* Johnson (1996), a member of the Laurales and assigned to leaf morphotype HC162 (Fig. 12). These mines were illustrated by Lang (1996), are referable to DT 45, and occur in assemblage zone HCIII from DMNH localities 428 and 900, −15.0 and −2.8 m, respectively, from the HC-FU formational contact. Although this plant host occurred in other localities in zone HCIII, most of these deposits consist of a coarser grained, sandy matrix that probably precludes recognizable preservation. Five well-preserved and complete examples are known of this leaf mine (Fig. 12, A–E, H–L), characterized by a definable, circular oviposition site, followed by a serpentine phase representing an initial threadlike, coiled mine, followed by subsequent instar width increases that assumes a more linear trajectory, and terminating in a more expansive, elongate to ovoidal chamber. These mines were made by a minute, flattened larva that produced a median, initially linear but subsequently tightly undulatory frass trail of solid fecal material (Fig. 12, E and L). Judging from the particulate nature of the frass trail, this miner was a whole-cell feeder consuming either palisade or spongy mesophyll tissue. The mines were highly constrained by primary and secondary venation and occur between the median and lateral primary veins and rarely along the leaf margin. The prepupal instar stage occasionally crosses primary veins. A total of 31 mines, many aborted or otherwise incomplete, have been documented on 21 individuals of the plant host *M. pearsoni.* Three of these mines originate from DMNH locality 428 (Fig. 12, M–O).

Almost all modern genera of Lauraceae, particularly *Actinodaphne, Cinnamomum, Laurus, Lindera, Litsea, Parabenzoin,*

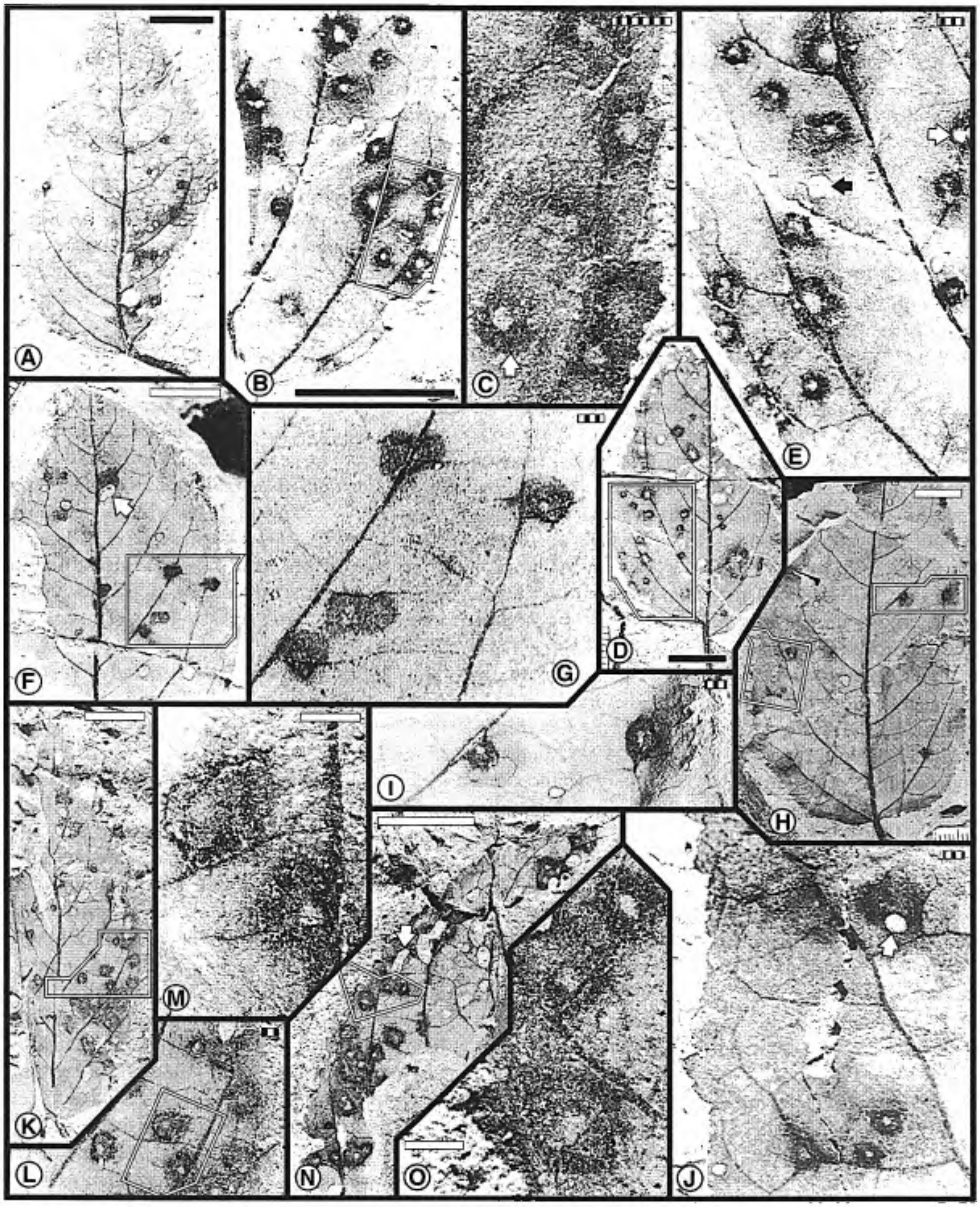


Figure 11. Small, cecidomyiid-type, cratered galls on primary veins of morphotype HC135, an unassigned dicotyledonous angiosperm from Hell Creek Formation. This host-specific association (DT 33) occurs only in localities 567 and especially 1491, latter of which supplied all illustrated examples. A: Typical example with several galls interspersed among more numerous examples of small hole feeding (DMNH-18895b). B: Extensively galled leaf fragment showing veinal association and modest variation in gall size (DMNH-19059) C: Enlargement of region in B showing five galls, each possessing pronounced fusanized rim (arrow) surrounding central depression. D: Leaf with galls and hole feeding (DMNH-18919). E: Magnified region in D illustrating random, vein-associated distribution of galls. F: Leaf with 10 galls, one of which has been partly consumed secondarily by hole feeder (arrow) after gall formation (DMNH-18894). G: Magnified region in F demonstrating absence of central cratered structures. H: Leaf with ~10 galls (DMNH-19728). I: Detail of two galls in H, with surrounding altered tissue. J: Detail of four galls, one apparently bearing emergence hole (arrow). K: Leaf with hole feeding and cluster of galls (DMNH-18914). L: Enlargement of gall cluster in K, showing central depressions and intervening altered tissue. M: Enlargement of two galls in L, illustrating outer gall wall and central cavity. N: Leaf fragment bearing cluster of galls and various hole feeding (DMNH-19040). O: Detail of three galls in N, showing outer wall, central depression, and relationship to major venation. Solid scale bars = 1.0 cm; striped scale bars = 0.1 cm.

Figure 12. Host-specific association between *Marmarthia pearsonii* (Laurales) and a gracillariid leaf miner (Lepidoptera), from the uppermost Hell Creek Formation. This highly stereotyped damage type, DT 45, is a serpentine mine typically with initial coiled phase, subsequent curvilinear trajectory, and modestly expanded terminal chamber. It occurs exclusively on plant host HC162 at localities 900 and 428. A: Near-complete leaf mine following primary venation of *M. pearsonii* leaf (locality [loc.] 900, DMNH-7313). B: Enlargement of A, with dark colored, medial frass trail detectable at upper left corner, along primary vein. C: Complete leaf mine with terminal chamber at upper right (loc. 900, DMNH-7263). D: Enlargement of latter serpentine phase and terminal chamber of leaf mine in C. E: Closeup of terminal chamber displaying dark frass trail (top arrow) and chamber edge (bottom arrow). F: Fragment of leaf portion of leaf mine; note coiled early phase (loc. 900, DMNH-7199). G: Closeup of mine in F. H: Complete leaf mine bounded by median and lateral primary veins of plant host, typical for this species (loc. 900, DMNH-20023). I: Detail of mine in H, showing median frass trail at upper left. J: Three aborted leaf mines, two of which have coiled initial phase (loc. 900, DMNH-7325). K: Complete leaf mine with extensive terminal chamber illustrating frass trail (loc. 900, DMNH-7264). L: Enlargement of terminal mine chamber in K, showing path of undulatory frass trail, indicated by white arrows. M: Two aborted leaf mines with coiled initial phases (loc. 428, DMNH-7498). N: Enlargement of leaf mine at upper left in M, showing coiled (darkened) initial phase. O: Enlargement of leaf mine at lower right in M, revealing coiled (darkened) initial phase, and subsequent curvilinear phase along median primary and branching secondary veins (arrow). P: Two adjacent leaf mines aborted early in development (loc. 900, DMNH-7313). Scale bars = 1.0 cm; striped scale bars = 0.1 cm.

Persea, Sassafras, and *Umbellaria,* collectively are hosts to several genera of gracillariid leaf miners, namely species of *Acrocercops, Caloptila, Gracillaria, Lithocolletis,* and *Phyllocnistis* (Fletcher, 1920, 1933; Needham et al., 1928; Hering, 1967; Kumata, 1982; Kumata et al., 1988; Yuan and Robinson, 1993), contrary to the undocumented statement of Grimaldi (1999). These modern and latest Maastrichtian associations variously represent an old relationship between lauralean and gracillariid taxa that extends back to the early Maastrichtian of northern Wyoming (Labandeira et al., 1995; Lang, 1996), Turonian of eastern Kazakhstan (Kozlov, 1988), the earliest Cenomanian of Kansas and Nebraska (Labandeira et al., 1994; Futuyma and Mitter, 1996; Kristensen, 1997; Powell et al., 1999), and undoubtedly into the late Early Cretaceous. Several other lineages of Lepidoptera and other leaf-mining insect clades have been documented in middle and Late Cretaceous floras (Skalski, 1979; Stephenson, 1992; Labandeira et al., 1994; Lang, 1996), indicating a radiation of the leaf-mining habit by multiple lineages onto dicotyledonous hosts. The apparent extinction of *M. pearsoni* immediately before or at the K–T boundary indicates that this herbivore specialist also succumbed, although other lauraceous host lineages and their gracillariid herbivores persisted to the present.

Other host-specific associations occur, such as insect damage on the ginger *Zingiberopsis* (Zingiberaceae) (Hickey and Peterson, 1978), that are identical to modern descendant lineages of certain hispine beetles (Strong, 1977, 1984) described by Wilf et al. (2000). Additional associations include stereotyped skeletonization, such as a serpentine form occurring on the unidentified dicot HC254 (Fig. 3, Q and R), and a rectangular-elongate type found on the platanacean taxon *Erlingdorfia montana,* probably representing a leaf roller (Fig. 7, A–F, I–L). All insect damage from this K-T sequence will be qualitatively and quantitatively detailed in a forthcoming monograph.

Extinction at the boundary

These and most of the other host-specific associations occurring in Hell Creek strata do not survive the end of the Cretaceous (Fig. 2), resulting in an overall major decrease of damage types for the early Paleocene (Lang, 1996). Of the 22 damage types that remain in strata of the earliest Paleocene Fort Union Formation, 55% are generalized associations (level 1), such as nonstereotyped hole feeding, margin feeding, and some types of skeletonization. Six less generalized, moderately specific associations (level 2) survive the boundary and are more stereotyped forms of external foliage feeding. Only four highly specific associations, assigned to level 3, survive the boundary. They are two leaf mines, a gall, and a type of piercing and sucking puncture. Only two highly specific associations have been documented from earliest Paleocene deposits that do not occur previously in Hell Creek strata.

Of the 14 Cretaceous associations that are extinguished at the boundary, 6 are intermediate, 8 are highly specialized, and none are generalized. Of the 13 associations that disappear prior to but not at the boundary, 8 are plant host specialists, 5 are intermediate, and none are generalized, possibly indicating that highly host-specialized associations were declining before the terminal Cretaceous effect. Nevertheless, this geochronologically stepped pattern could be a sampling artifact, suggesting that preboundary associations may extend closer to the boundary if there were greater sampling effort in floras proximal to the HC-FU datum. However, many floras that occur throughout the 136 m interval across the boundary are highly sampled and occur throughout the entire interval (Table 2), and include DMNH locality 900, which is −2.8 m below the HC-FU contact and contains the second-most abundant number of specimens, thus making it unlikely that the pattern is only an artifact of collection strategy, which would be predicted by the Signor-Lipps effect (Signor and Lipps, 1982). However, a possible taphonomic explanation for the pattern remains, in which depositional conditions were inhospitable for preservation of floras proximal to the boundary that would extend upward damage-type ranges. Although one or any these alternatives explains the data, an objective reading of the pattern indicates that a pronounced extinction of intermediate and highly specialized associations occurred at or before the boundary, preferentially enriching the earliest Paleocene survivors in generalized herbivore taxa. Note also that the generalist category probably subsumes additional, unrecognized, host-specific plant damage that would bias against our conclusion for an extinction of host specialists at the boundary.

Lack of a recovery phase

The post-Cretaceous insect herbivore fauna, as judged from plant-related damage spectra, was not accompanied by significant immigration of new extrabasinal associations. Currently only two early Paleocene associations can be attributed to an immigrant or previously unsampled taxon, one of which is a specialized leaf miner. This suggests that the earlier extinction event at the K-T boundary was not accompanied by a short-term rebound phase to previous levels of plant-insect associations, at least on the order of tens to hundreds of thousands of years. Thus the earliest 0.8 m.y. of the Paleocene indicates depauperate levels of plant-insect associations. Additional research is needed to determine whether the 1.4 m.y. of latest Cretaceous levels of plant-insect associations reached a comparable level during the early Eocene, ~11.0 m.y. later (Wilf and Labandeira, 1999). Undoubtedly the extirpation of associations at the K-T boundary is tied to the extinction of their plant hosts as a consequence of broader ecosystem collapse at the terminal Cretaceous. However, this plant extinction did not result in an "across the board" reduction in insect associations: it preferentially affected specialized over generalized associations and also considerably curtailed the number of associations on early Paleocene survivors when compared to their latest Cretaceous conspecifics.

DISCUSSION

Three larger scale implications result from our study of regional patterns of insect herbivore diversity across the K-T boundary. First is the broader temporal context in comparison to what is known of herbivore damage trends during the Late Cretaceous and Paleocene. Second is whether our K-T boundary patterns can be explained by the biogeographical restriction of the study site and the consequent immigration of insect herbivores outside of the Williston Basin. Third is the increasing importance of insect trace-fossil data for resolving temporal trends of insect history that are not addressable by largely unavailable body-fossil data.

Larger temporal context

Judging from descriptions of insect-mediated damage (Kozlov, 1988; Lang, 1996; Stephenson, 1992; Labandeira et al., 1994, 1995), Late Cretaceous floras from the Northern Hemisphere have a comparatively elevated level of associations, characterized by a diverse spectrum of external foliage feeding, mining, galling, piercing and sucking, and oviposition damage types. This is in contrast to our preliminary survey of early Paleocene floras from the Western Interior, which lack generally the higher diversity and host specificity of associations. However, examination of insect associations for most Paleocene floras are incomplete when compared to those of the Late Cretaceous, latest Paleocene, or Eocene. Additional study of other North American Paleocene floras will be required for confirmation of this apparent trend of depauperate associational diversity. The recent documentation of an early Paleocene flora with atypical taxa indicating a warming event (Ellis and Johnson, 1999) indicates rare periodic incursions of thermophilic vegetation, possibly accompanied by distinctive herbivores. Such events would presage the warming trend that occurred during the latest Paleocene to early Eocene that was trophically connected to an increase in herbivore intensity and diversity (Wilf and Labandeira, 1999; Wilf et al., 2001). This level of herbivory continued into the later Eocene as well (Lang et al., 1995; Palmer et al., 1998; Wilf et al., 2001).

The persistence of diverse types of Late Cretaceous insect damage at elevated levels in North America currently is based on a few examined floras, principally documented from the early Cenomanian Dakota flora (98 Ma), the early Maastrichtian Meeteetsee flora (72 Ma), the middle Maastrichtian Ripley flora (ca. 68 Ma), and the late Maastrichtian Hell Creek flora (67.0 Ma) (Stephenson, 1992; Labandeira et al., 1994, 1995; Labandeira, 1998c; Lang, 1996). Herbivory in these floras variously affected all major vascular plant groups; i.e., ferns, conifers, cycadophytes, gingkophytes, monocots, and dicots. Of particular importance is the presence of extensive herbivory on herbaceous angiosperms, particularly in DMNH localities 2203 and 567 of zone HCIb. The meadow-like plants of these assemblages, consisting of low-statured and nonarborescent plants with highly lobed and dissected leaves, is also found in the early Maastrichtian Meeteetsee flora of north-central Wyoming (Wing et al., 1993; Labandeira et al., 1995), although there are few to no cooccurring lower level taxa. Undoubtedly this angiospermous life habit had earlier antecedents. Notably this Hell Creek assemblage includes the earliest megafloral representatives of the Rosaceae (HC80) and Urticales (HC81, HC229), both which harbored leaf miners (Labandeira, personal observation) and various external feeders. This colonization of herbaceous plants is complemented by observations of a variety of charcoalified floral remains from the Turonian to Santonian coastal plain sequence of eastern North America; relatively advanced plant-insect pollination mutualisms were already deployed on a diverse, lowland flora, but of woody dicotyledonous angiosperms (Crepet and Friis, 1987; Crepet and Nixon, 1996, 1998; but see Friis, 1984).

Biogeographical and ecological considerations

The demise of many of these Late Cretaceous associations essentially reset the plant-insect associational clock for the Paleogene. Thus many modern associations in the Western Interior either reevolved or possibly accumulated as immigrant herbivores colonized floras that became progressively diverse and more thermophilic during the Paleocene to Eocene transition. These two processes are demonstrated by the autochthonous radiation of Paleocene mammals (Alroy, 1999) as well as immigration of taxa from Asia during the later Paleocene (Beard, 1998). The Paleogene history of seed plants is also well documented (Manchester, 1999) and indicates that interchange of most dicotyledonous angiosperms across the Beringian or northern European land bridges did not occur until late in the Paleocene or early Eocene, although taxa such as *Nordenskioldia, Platanites,* and *Quereuxia* had earlier dispersal trajectories (Manchester, 1999). It is most likely that dispersal from Asia or Europe to North America had little effect on the character of earlier Paleocene insect herbivores, particularly because the dominant source of earliest Paleocene floras in the Williston Basin was local or regional mire-associated taxa of the latest Cretaceous (Johnson, 1999) that lacked post-Cretaceous taxonomic affinities to coeval Eurasian taxa.

Studies of modern specialist herbivorous insects and their plant hosts strongly suggest that differentiation of an ancestral species into populations that exhibit novel plant host preferences can be rapid (Jaenike, 1990). A classic example is the morphological partitioning during the past 60 yr of the soapberry bug, *Jadera haematoloma,* into three populations with distinctive beak lengths for exploiting different species of soapberry seeds (Carroll and Boyd, 1992; Bernays and Chapman, 1994). This indicates that such segregation can be a rapid process that leads to eventual species-level differentiation. A different approach has documented the extensive, species-level radiation of the weevil genus *Miocalles* onto varied plant hosts on Rapa Island during the past 10^5 yr (Paulay, 1985). These and other examples indicate that there is a significant potential for rapid evolution of herbivore colonization of novel, albeit often phylogenetically related, plants at ecological time scales (Schoonhoven et al., 1998; but see Piegler, 1986).

Our observations that largely document an absence of new associations during the 0.8 m.y. interval after the K-T event seem paradoxical. This is particularly so, given studies establishing the rapidity of host colonization by some modern herbivorous insects and the virtual absence of decreases in damage types during the late Paleocene to early Eocene warming event (Wilf and Labandeira, 1999). However, if the K-T reduction of the local insect herbivore fauna was sufficiently severe and persisted millions of years into the early Paleocene, there would have been minimal diversity of species constituting the pool for establishing plant-insect associations. Accordingly, depressed levels of earliest Paleocene plant-insect associations would have been attributable not only to the presence of a depauperate regional flora, but more important, to decimation of those insect lineages that would have been available as potential plant consumers. Thus the repertoire of present-day plant-insect associations likely is a mixture of older Mesozoic colonizations of plants (Zwölfer, 1978; Rohr et al., 1984; Thien et al., 1985; Michener and Grimaldi, 1988; Genise, 1995; Labandeira, 1998a), perhaps including such examples as the specialized leaf miners on Cenomanian Platanaceae (Labandeira et al., 1994; also see Becerra, 1997), and external foliage feeding on Maastrichtian Zingiberaceae (Wilf et al., 2000) and more recent and abundant, Paleogene originations. If correct, this temporally bimodal distribution of associations ultimately resulted from major environmental disruption and ecosystem replacement (Coley, 1998; McIver, 1999) of herbivore assemblages at the end of the Cretaceous.

The effects of extensive plant and insect herbivore extinction at the K-T boundary must have had dramatic consequences that trophically cascaded upward, affecting consumers of herbivorous insects. The superjacent trophic levels of parasites, parasitoids, and predators likely were affected dramatically by a decreased food resource base (Labandeira, 2002a). This inference would affect host-dependent parasitoids and parasites the most, because insect predators that dispatch their victims immediately are typically dietary generalists (Price, 1997). This prediction would be difficult to test, however, as sufficiently diverse body-fossil deposits proximal to the K-T boundary are unknown, and therefore appropriate before and after comparisons are unavailable. The expectation is that parasite and parasitoid diversity also suffered a major decline during the earliest Paleocene and, subsequently, reestablished newfound associations on insect hosts, approximately in tandem with the plants and herbivorous insects constituting the subjacent levels of the trophic pyramid.

Value of body-fossil versus trace-fossil data

The spatial and temporal context of this study represents a few orders of magnitude greater resolution than earlier comprehensive but qualitatively coarser grained studies of insect diversity that were based on global compendia for a 410 m.y. fossil record (Dmitriev and Zherikhin, 1988; Labandeira and Sepkoski, 1993; Jarzembowski and Ross, 1996). The relevant outcrop area within the Williston Basin represents ~0.00025 that of available terrestrial outcrop worldwide, and the 2.2 m.y. interval is ~0.005 that of the total duration of the fossil insect record. Equally important is the source of our data: we have chosen the fossil record of insect-plant associations, characterized as damage types, rather than insect body fossils evaluated at the family level. Although the insect body-fossil record is taxonomically better than previously thought (Labandeira and Sepkoski, 1993; Labandeira, 1994), it represents a series of mostly exceptionally preserved deposits that are sporadically deployed in time and space but are typically absent at important, stratigraphically confined intervals of major theoretical interest. Because of a dominantly Lagerstätten-driven record of insect occurrences, it is necessary to employ proxy data—in this case the parallel fossil record of insect damage on plants—for evaluating insect diversity across stratigraphically focused successions where insect body fossils are effectively absent but plant deposits are comparatively plentiful.

Insect herbivory patterns on fossil plant hosts are valuable for chronicling phenomena such as mass extinctions, major environmental perturbation, and the evolutionary radiations between insect and plant taxa. This is because insect-modified foliar material from the fossil record provides crucial ecological data that otherwise are unavailable from insect bodies or from pristine leaves. This approach has been underappreciated in part because the historical concern of paleoentomology has been description of body fossils from selected Lagerstätten of high preservational quality. Our study demonstrates that detailed examination of the plant-insect associational record can supply robust data for testing hypotheses (Labandeira, 2002b)—such as the response of insects to the K-T event—that otherwise would be unavailable if the only recourse was study of body fossils. In addition, for many important phytophagous taxa, the fossil record of insect-mediated plant damage reveals considerably more detail about their ecologic and even evolutionary history than the parallel body-fossil record. One example of this is the record of Cretaceous lepidopteran leaf mines (Powell et al., 1999), which provides considerably more natural historical and taxonomic insight than their corresponding depauperate record of body fossils, including those found in amber.

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APPENDIX. INSECT DAMAGE TYPES (DT)

Damage Type	Category	Physical Description	Host Specificity
1	HOLE FEEDING	Small, (<1 mm)	1
2	HOLE FEEDING	Medium (1–5 mm)	1
3	HOLE FEEDING	Medium (1–5 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
11	HOLE FEEDING	Thick rim of necrotic tissue	1
50	HOLE FEEDING	Adjoining midvein	2
51	HOLE FEEDING	Slots overlapping into enlarged central area and those associated by pattern	2
57	HOLE FEEDING	Pattern associated with divergence point of secondary from primary veins	2
64	HOLE FEEDING	Series of medium (<5 mm) circular holes in a margin-associated pattern	2
12	MARGIN FEEDING	Generalized, cuspate	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
17	SKELETONIZATION	General, reaction rim well developed	1
19	SKELETONIZATION	Broad, with rectangular pattern	2
20	SKELETONIZATION	Curvilinear	2
21	SKELETONIZATION	Highest order of venation removed	2
22	SKELETONIZATION	Linear pattern	2
24	SKELETONIZATION	Ovoidal, adjacent to midvein	2
56	SKELETONIZATION	At leaf base between primary veins	2
61	SKELETONIZATION	Adjoins and exactly follows primary and secondary veins, increasing in size	3
26	EXTERNAL-SPECIAL	Free feeding	2
28	EXTERNAL-SPECIAL	Strip feeding between secondary veins; *Cephaloleichnites strongi*	3
29	EXTERNAL-SPECIAL	Window feeding, generalized	1
32	GALLING	On nonveinal part of leaf	2
33	GALLING	On primary vein	3
34	GALLING	On secondary vein	2
49	GALLING	Large (core > 3 mm), with distinctive reaction rim at some distance	3
52	GALLING	Relatively large (>3 mm), with woody and radiating partitions	3
55	GALLING	On petiole	3
62	GALLING	Large, (~5 to 10 mm diameter), flat, "pock-marked," alternating light/dark areas	3
35	MINING	Blotch, with a central chamber	3
38	MINING	Circular, with case	3
40	MINING	Semilinear, reaction rim present; frass is solid, thick and 3-D; terminal chamber	3
41	MINING	Serpentine A: long, undulatory, frass particulate	3
42	MINING	Serpentine B: medium, width rapidly increasing, irregular margin	3
43	MINING	Serpentine C: short, solid frass trail	3
45	MINING	Serpentine E: medium length, margin irregular, well-developed terminal chamber	3
59	MINING	Initially adjacent to secondary vein, then primary; thin and with minimal width increase; terminating into a 5–10 mm ovoidal/elliposoidal terminal chamber	
65	MINING	Large (>30 mm length), linear, blotchlike, with rapidly expanding width	3
46	PIERCING & SUCKING	Small scale or puncture (<2 mm), circular depression	3
53	PIERCING & SUCKING	Large scale (>4 mm), on primary veins (e.g., *Erlingdorfia*)	3
54	OVIPOSITION	Scars in arcuate rows, en echelon	3
58	FUNGAL DAMAGE	Ovoid to polylobate fungal blotches	n/a

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