

Insect Outbreaks Revisited

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13

Evidence for Outbreaks from the Fossil Record of Insect Herbivory

Conrad C. Labandeira

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13.1 Introduction

The topic of insect outbreaks is virtually nonexistent in the paleoecological literature of plant–insect associations. Of the few examples explicitly studied to date, all are of Holocene age and occurred within the past 11 000 years, after the great megafaunal mass extinctions of the Americas and Eurasia. Evidence for these subfossil insect outbreaks largely is confined to North America and involves evidence for unusually high levels of plant consumption by insects in forest ecosystems. Some of the best examples consist of evidence for multiple rounds of elevated herbivory by two species of lepidopteran larvae in subfossil pollen floras affecting conifer and woody dicot hosts in Eastern Deciduous Forest or in related, ecologically nonanalog communities. These Holocene outbreak studies are extensions of modern plant–insect associational dynamics to the subfossil record. Such shallow-time studies involve prominent insect herbivores that periodically express outbreaks on modern tree hosts (Johnson and Lyons 1991, Metcalf and Metcalf 1993). By contrast, examination of older events provide better understanding of how insect outbreaks may have originated and occurred in floras and plant communities that lack ecologic parallels in the modern world. Very little is known about the earlier, pre-Holocene record of insect outbreaks extending to the rest of the Cenozoic, the Mesozoic, and even the mid- to late Paleozoic when insect herbivory initially was launched on land (Labandeira 2006a, 2006b). Pre-Holocene examples of insect outbreaks historically have not been a concern of paleobotanists, paleoentomologists, or, except lately, even investigators of fossil plant–insect associations. However, there are examples of unusually elevated levels of insect herbivory in the older fossil record that targeted particular plant hosts, often at the species level, but also consumption of groups of closely related species within encompassing host taxa. These examples of elevated insect host specificity on particular hosts have rarely been termed “insect outbreaks” in the paleobiological literature, although now would be the time to address the issue and ascertain the similarities that these intriguing examples have to modern insect outbreak phenomena.

In this chapter, I will discuss initially Holocene events, referred to as “shallow-time” examples of insect outbreaks, followed by four more extensive examples of earlier, “deep-time” outbreaks. Then I will provide an operational definition of how insect outbreaks may be detected in the fossil record. I will end the chapter in discussing the paleobiological and macroevolutionary significance of outbreak phenomena for both plant hosts and their insect herbivores. It is the hope that this discussion will further the detection of insect outbreaks in the fossil record and determine if insect behavioral or physiological correlates of outbreak phenomena can be assessed directly in the fossil insect or plant–insect associational record.

13.2 A broad operational definition of insect outbreaks in the fossil record

I shall not today attempt further to define the kinds of material I understand to be embraced ... but I know it when I see it.

Supreme Court Justice Potter Stewart's
concurrence in the *Jacobellis v. Ohio*
obscenity case: 378 US 184 (1964)

One of the challenges in examining the variety and levels of insect herbivory in the fossil record is recognizing intuitively that there are instances of plants being targeted and consumed apparently by a single insect herbivore. However, often it is uncertain as to what metric to use for measuring the aftermath. This assuredness in intuitively recognizing outbreak levels of herbivory, but indecision in using the most appropriate measure for documentation, is reminiscent of Justice Stewart's celebrated statement in attempting to define obscenity in an issue facing the US Supreme Court in 1964. Similarly, presented below are several issues that indicate the presence of insect outbreaks in the fossil record, ranging from the late Paleozoic to the Holocene.

The first issue is the relevant unit of measurement. Holocene material typically is collected as peat cores to depths from 1 to 8 m that contain several types of microfossil information. Most important are pollen, charcoal, and fungal sporangia and spores that are used principally for plant community and habitat reconstruction. Seeds, leaf fragments, and wood fragments often provide ancillary data. For the Holocene insect outbreak record, accumulations of fecal pellets, related fungal material, insect head capsules, other disarticulated arthropod sclerites, and coprolites are used as proxy data to infer intervals of elevated herbivore intensity. These subfossil constituents are individually displayed as frequency abundance profiles, with time as the vertical axis, and data expressed as counts of the units of interest, such as pollen and spores itemized at the genus or form-genus level of resolution. For example, in each analyzed stratum or level, coprolites (fossilized fecal pellets) or head capsule abundance frequencies are used to infer insect herbivore intensity, often standardized to an equal volumetric measure to record the density of occurrence. (For additional details, see Chapter 7, this volume.)

When compared to Holocene deposits, the older, pre-Holocene fossil record employs different measures to indicate herbivore activity. This deep-time (pre-Holocene) approach instead focuses on items of consumption – typically foliage and seeds – whereas the shallow-time (Holocene) tack is to emphasize rather the bodily effects of the insects themselves, such as coprolites, head capsules, and other frass used to assess herbivory. Given this shift in focus, there are three commonly used metrics in the deep-time record that document the variety and intensity of insect herbivore feeding. The first metric is feeding diversity, or tallying the number of different, diagnosable damage types (DTs) that occur on a particular plant host (Labandeira *et al.* 2007). The second metric is the frequency of attack, or the proportion of leaves that are herbivorized, revealed by one or more DTs. The third metric is a measure the amount of herbivorized leaf surface area, typically as cm^2 , as a proportion of total foliar surface area. These three metrics can be used to evaluate herbivory levels at the organ level for a plant species in a flora, such as external feeding on foliage (Prevec *et al.* 2009), or as comparisons of species both within (Wilf *et al.* 2006, Wappler *et al.* 2009) or among (Wilf *et al.* 2001, 2005; Labandeira *et al.* 2002b) floras, or spatiotemporally among species within plant lineages (Labandeira *et al.* 2007, Currano *et al.* 2010). Such approaches have been used in floras ranging in age from the Early Permian (Beck and Labandeira 1998, Labandeira and Allen 2007) to those at the Oligocene–Miocene boundary (Wappler 2010), and represent worldwide plant taxa from many localities and habitats.

Second, what is the herbivory level that must exceed a particular background level to warrant designation as an insect outbreak? The measures mentioned above represent several methods that could be used to indicate a significant increase of herbivory on a particular plant taxon relative to other taxa within a bulk flora, or to a bulk flora compared with other such bulk floras. In general, at least a twofold or threefold (preferably higher) increase in some measure of herbivory above the ambient level is desirable. The next section provides examples from the fossil record where significant increases in damage diversity, frequency of attack, or herbivorized surface area relative to total foliage area, appear to reach insect outbreak levels. However, it is difficult to know if such outbreaks occur at very local spatiotemporal scales, are broadly regional phenomena, or represent early attempts at targeted and elevated herbivory. These herbivory levels hopefully establish an operational and more quantitative approach in determining fossil insect outbreaks, and result in an improvement to the “I know it when I see it” approach that was used in the rendering the Supreme Court’s definition of obscenity.

Thirdly, how similar are data from the fossil record to modern methods of data collection? In other words, do separate norms need to be established to demonstrate premodern insect outbreaks? Interestingly, data from the deep-time and shallow-time parts of the fossil record frequently are qualitatively and quantitatively identical to modes of data collection for the present-day record (e.g., Coley and Barone, 1996; Wilf *et al.* 2001; Currano *et al.* 2010). Measures such as herbivorized foliar surface area as a percentage of the total surface area available, or frequency of attack on leaves, either for target host plant species or for bulk floras, have very close parallels with similar studies on modern plant taxa. Less commonly and more difficult to quantify are three-dimensional measures, particularly abundances of distinctive coprolite populations that originate from a single, above-ground insect producer, and accumulate on the surface of plant litter or peat to be incorporated volumetrically in a fossil deposit, such as Late Carboniferous coal ball deposits (Labandeira and Phillips 1996). Yet this category of data also is methodologically equivalent to studies in modern insect outbreaks that record the rate of fecal pellet deposition (Rinker and Lowman 2001), or other measures of frass accumulation on forest floors (Frost and Hunter 2008). With appropriate caveats regarding the differential preservational potential of various types of leaves, coprolite types, and other evidence for insect consumption of plants, the fossil record of insect herbivory should offer an opportunity toward measuring the extent and intensity of insect outbreaks at macroevolutionary time scales.

13.3 The curious case of the discovery, outbreaks, and extinction of the rocky mountain grasshopper

The Rocky Mountain grasshopper, *Melanoplus spretus* Walsh (Acrididae), was the most devastating agricultural pest in the western North America following settlement by Europeans until about 1900, when the last living specimen was found and the species became extinct. The history of this species occurred during the brief 80 years that represented its modern discovery, several major outbreaks, and sudden extinction of probably the most infamous insect of nineteenth-century North America (Table 13.1). The Rocky Mountain grasshopper has been

Table 13.1 Examples of Insect Outbreaks from the Fossil Record of Plant–Insect Associations.

<i>Holocene (11 000 BP to Present)</i>							
<i>Affected region</i>	<i>Deposit, age, and figure herein</i>	<i>Plant community</i>	<i>Dominant plant taxa</i>	<i>Folivorized plant host</i>	<i>Outbreak insect folivore</i>	<i>Outbreak and ambient levels</i>	<i>References</i>
Western Great Plains from 100°W to Rocky Mtn. Crest; from southern Saskatchewan to northeastern-most Mexico	Glaciers, possibly alluvium; early 1800s to 1900 CE from discovery to species extinction (Figure 13.1)	Grassland and savanna; major river floodplains	Poaceae, Asteraceae; riparian associated dicot trees and shrubs	Widely polyphagous; esp Poaceae, Brassicaceae, Apiaceae, Rosaceae, Salicaceae, Juglandaceae, Anacardiaceae, Asteraceae, etc.	Orthoptera: <i>Melanoplus spretus</i> Walsh; (Rocky Mountain Grasshopper; probably margin feeder, DTs 12,13,14,15, 26,143	Very high but quantitatively unrecorded; “they can sweep and clean a field” (Riley 1877, 85; inferred > 95% of all ambient foliage; also fruits and stored products	Riley 1877; Gurney 1953; Lockwood and Debrey 1990; Lockwood 2001; Lockwood <i>et al.</i> 1994;
Mid Holocene Hemlock Forest; Northern United States to Great Lakes Region, north to southern Quebec and Ontario	Unconsolidated peat; 5700–3200 yr BP for mid-Holocene hemlock decline	Northern Eastern Deciduous Forest	Betulaceae, Sapindaceae, Fagaceae, Pinaceae, Rosaceae, Salicaceae	<i>Tsuga canadensis</i> L. (hemlock)	Lepidoptera: Tortricidae: <i>Choristoneura fumiferana</i> (Clemens), spruce budworm; Geometridae: <i>Lambdina fiscallana</i> Gven., East. hemlock looper	Up to eightfold decrease in hemlock pollen; approx. sixfold increase in spruce budworm feces; about 10-fold increase in lepidopteran head capsules	Davis 1981; Bhiry and Filion 1996; Fuller 1998; Foster <i>et al.</i> 2006; Simard <i>et al.</i> 2006

(Continued)

Table 13.1 (Cont'd).

Pre-Holocene (280 Ma to 64.0–64.7 Ma)							
Flora, locality, and repository ¹	Strata and age	Inferred plant community	Dominant plant taxa ²	Folivorized plant host(s) ³	Inferred outbreak insect-feeding type	Outbreak and ambient levels ⁴	References
Taint (USNM49689); Redbed Sequence, NW Baylor Co., National Museum of Natural History	Waggoner Ranch Fm.; Early Permian, Artinskian Stage; c. 280 Ma (Plate 13.1)	Dry Riparian Woodland	Gigantopterids, peltasperms, cycadophyte, indeterminate broadleaf sp. conifers	<i>Zeilleropteris</i> sp., <i>Cathyasiopteris</i> sp. <i>Gigantopteridium</i> sp. (all Gigantopteridaceae)	Orthoptera; external foliage feeder (several margin, hole and surface feeding DTs)	Gigantopterid folivory exceeds the bulk floral value by 2×; gigantopterid DTs much more diverse	Beck and Labandeira 1998; Labandeira <i>et al.</i> 2007
Aasvoëlberg 311 SW Karoo Basin, Western Cape, So. Africa. Bernard Price Institute of Palaeontology, Johannesburg	Molteno Fm.; Late Triassic, early Carnian Stage; c. 228 Ma (Plate 13.2)	Heidiphyllum Thicket	Voltzialean conifer; hamshawvialean ginkgophyte, petriellalean ginkgophyte, equisetalean, crustosperm	<i>Heidiphyllum elongatum</i> (Morris) Retallack (Voltziaceae)	Coleoptera, possibly Buprestoidea; leaf miner (DT71)	Herbivory frequency on <i>H. elongatum</i> is 7.2% (10 358 total leaves versus 741 mined) compared to levels <1% elsewhere in other Molteno floras	Anderson and Anderson 1989; Scott <i>et al.</i> 2004; Labandeira 2006b; pers. obs.; Labandeira <i>et al.</i> 2007

Somebodys Garden (DMNH2203); Williston Basin, Slope Co., North Dakota, Denver Museum of Nature and Science a	Hell Creek Fm.; Late Cretaceous, latest Maastrichtian Stage; 54.0 m below K–Pg boundary; circa 66.0 Ma (Plate 13.3)	Herbaceous Meadow	Urticaceae sp. 1, Cercidiphyllaceae, Rosidae, Urticaceae sp. 2 Cercidiphyllaceae, ?Rosidae, dicot indet.	Undescribed leaf morphotype HC81 (Urticaceae)	Coleoptera: Chrysomelidae, Curculionidae; hole feeder (DT57, DT50)	Comprises 50% of flora but 61.8% of folivory; elevation of about 1.62 × that of bulk floral value	Johnson 2002; Labandeira <i>et al.</i> 2002a, 2002b, 2007
Mexican Hat (USNM 42090, DMNH1251) Powder River Basin, Custer Co., MT. National Museum of Natural History	Fort Union Fm., Lebo Mbr.; early Paleogene, early Danian Stage, age 64.0–64.7 Ma (Plate 13.4)	Mesic Riparian Woodland	Platanaceae, Juglandaceae, dicot indet. 1, Lauraceae, ?Salicaceae, dicot indet. 2, dicot indet. 3	<i>Platanus raynoldsi</i> Newberry (Platanaceae)	Diptera: <i>Phytomyzites</i> <i>biliapchaensis</i> Winkler, Laban- deira and Wilf; leaf miner (DT104)	Attack frequency of mined interval (68.0%) is approx 2 × that of entire deposit for this host plant (37.9%), which already is high	Lang 1996; Wilf <i>et al.</i> 2006; Labandeira <i>et al.</i> 2007; Winkler <i>et al.</i> 2010

¹USA Museum repository abbreviations: USNM, National Museum of Natural History, Washington, DC; and DMNH, Denver Museum of Nature and Science, Denver, CO.

²In rank order of the seven most abundant taxa in the flora.

³In order of folivorized abundance for multiple species in the same taxonomic clade.

⁴Various indices to measure folivory are used to assess outbreak versus ambient levels.

the subject of considerable popular interest (Lockwood 2004), including studies of the causes of migratory outbreak cycles and factors responsible for its extinction (Lockwood and Debrey 1990, Lockwood *et al.* 1994), paralleling interest in the passenger pigeon, *Ectopistes migratorius* L., which became extinct in the wild at about the same time. The earliest records of the Rocky Mountain grasshopper are recounted by Riley (1877), who mentions early “breakouts” of the grasshopper in the Great Plains during the 1830s–1860s, describing the outbreaks as a series of “locust plagues.” The Rocky Mountain grasshopper consumed vast amounts of forage, typically grasses and associated forbs in Short Grass Prairie that constituted much of the habitat extending from southern Canada of Saskatchewan and Alberta, through the United States between the 100th meridian and the crest of the Rocky Mountains, and southward to extreme northeastern Mexico. This widely polyphagous insect additionally consumed riparian trees, fruits, stems, other insects, and exhibited cannibalistic tendencies (Riley 1877). Although consumption levels of the Rocky Mountain grasshopper were not precisely quantified (Lockwood 2004), anecdotal historical references indicate that practically all photosynthetic tissue and even structural tissue such as bark and seed tests were consumed. This suggests foliar frequency of attack levels near 100% and herbivorized leaf-area removal rates approaching 100%. Such comprehensive herbivory would mimic vertebrate herbivore feeding, presumably as such near-complete levels of foliage removal would not provide items to enter the fossil record, except for the occasional leaf fragments with resistant veinal stringers typical of intense free feeding (Coulson and Witter 1984). In addition, historical records suggest that these regional feeding events were regulated by a periodical control mechanism, similar to that during the twentieth century occurring along the northern African to south Eurasian belt and extending eastward to the savanna and grasslands of India. Even if foliar items could enter the fossil record, detection of periodic outbreaks from decadal to century cycles of recurrence would be below stratigraphic resolution of the fossil record, except under such exceptional circumstances of uninterrupted accumulation as fine-grained strata in basins such as shallow lakes. In the rare case of preservation of an outbreak event attributable to a widely polyphagous insect, such as a migratory locust, one would expect the same recurring assemblage of externally feeding DTs across all plant taxa, representing a unique, highly stereotyped, but not specialized feeding pattern that would be conspicuous in the fossil record. Such a pattern would not be expected with typical monophagous insects whose feeding patterns would be reflected by single DT feeding marks on a single or group of closely related host plants.

13.4 Insect outbreaks in shallow time: The holocene spruce budworm and eastern hemlock looper

For some time, palynologists have examined Holocene (circa 11000 yr BP to present) pollen records from subfossil peat and other organically rich sediment cores to document the periodic demise of hemlock, *Tsuga canadensis* L. A principal observation from North American, mid-Holocene core data has been multiple

episodes of decline, beginning at 8200 yr BP, but especially during 5800–4800 yr BP in which there was dramatic range restriction of hemlock. The driver for these pulses of biogeographical contraction and expansion has been attributed to major climatic changes, particularly regional drought and fire, resulting from deglaciation (Lavoie 2001; Foster *et al.* 2006; Zhao *et al.* 2010), perhaps biotically stressing hemlock populations and causing susceptibility to fungal pathogen attack (Davis 1981; Haas and McAndrews 2000). Alternatively, some have suggested that repeated rounds of hemlock decline were caused by insect outbreaks involving the spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) (Bhiry and Filion, 1996; Filion *et al.* 2006); the eastern hemlock looper, *Lambdina fiscellaria* (Guenée) (Lepidoptera: Geometridae) (Simard *et al.* 2002); and possibly the hemlock wooly adelgid, *Aldeges tsugae* Annand (Heard and Valente 2009). Both contending hypotheses – climatic change and insect outbreaks – postulate major regional events of degradation in hemlock decline, the apparent common denominator of which was introduction of a pathogen responsible for the severe reduction of the species (Allison *et al.* 1986). The possibility remains that both attributed causes are linked at some level, a phenomenon long appreciated by studies of North American wood-boring beetles and their conifer hosts (e.g., Bonello *et al.* 2003).

Several types of data from soil cores have been used to buttress hypotheses of climate change, insect outbreaks, or indirectly pathogens as explanations accounting for hemlock decline (Simard *et al.* 2002). These data include frequency–abundance profiles of distinctive coprolite types to distinguish background levels of herbivory from the peak levels during insect outbreaks. Informative contents from coprolites provide an opportunity to diagnose source plant species, a technique used by foresters to assess tree vigor in modern forests (Weiss 2005). Not only coprolite abundance levels of spruce budworm and hemlock looper are checked against the hemlock decline intervals in postglacial northern North America, but so also are the corresponding head capsule abundance profiles of these species (Simard *et al.* 2006). Coprolite, head capsule, and charcoal frequency profiles often are used separately as internal checks for validation of data, to indicate that drought and fire exhibit a strong correspondence to degradation of forests.

13.5 Insect outbreaks in deep time: focused folivory from four fossil floras

Four fossil deposits have been identified that contain particular plant taxa with exceptionally elevated levels of herbivory (Table 13.1). These case studies document collections of bulk floras from quarries measuring up to a few square meters in surface extent and traversing 0.4–2.0 m of stratal section. In these four deposits, all recognizable foliar material greater than a minimum established size of circa 1.0 cm² in surface area was collected, evaluated, and analyzed, regardless of preservational state, plant taxonomic status, or the presence or absence of insect damage. This approach provides an unbiased sample of all available plant fossils retrieved from the preserved, original plant community. In addition, this collection strategy includes evaluation of all multiple foliar or other plant organs

occurring on each shale or siltstone slab, often of considerable surface extent, indicating an accurate capture of dispersed plant taxa at the time when they were originally incorporated in a stratum of sediment.

The four deposits collectively represent a variety sedimentologic facies within the fluvial depositional environment. These deposits overwhelmingly or exclusively contained plant material, as nonplant fossils such as insects were frequently absent, and vertebrates were more rarely preserved. The material is housed in museum repositories, and, with the exception of Aasvoëlberg 311, has been published using a variety of methods to indicate herbivory, especially the frequency and diversity analyses derived from the presence or absence of data of damage types (DTs) recorded from each fossil flora or plant host morphotype (Labandeira *et al.* 2007). In each of the four floras discussed in this section, seven of the most abundant plant taxa are listed, including the most highly herbivorized plant taxon. Interestingly, the most abundant plant taxon in each of the four floras, as measured by the frequency of specimens, is the presumed outbreak taxon. The proposed insect outbreak taxa in two of the floras are exophytically feeding mandibulate insects, and the other two floras are attacked by endophytically feeding leaf miners. Other examples of different DTs with conspicuously high levels of herbivory occur on other plant hosts from similar basinal deposits within the same regional megaflora. For example, some localities sample the Paleocene–Eocene Thermal Maximum, a brief 2×10^5 yr long interval when global temperatures were significantly elevated, consisting of an interval of time when North American temperate floras became subtropical, accompanied by considerably elevated herbivory levels (Curran *et al.* 2008, 2010). These patterns suggest that insect outbreaks may be a common phenomenon in the fossil history of insect herbivory.

13.5.1 Gigantopterids at Taint: Early Permian of the redbed sequence, northern Texas

The informal designation “Taint” was given to a site in Baylor County, in north-central Texas (USNM loc. 40689), United States, of Early Permian (Artinskian) strata corresponding to circa 280 Ma. This site was retrieved from the long-studied redbed sequence that historically has produced various synapsid reptiles, especially pelycosaurs. The Taint locality sampled 15 m of horizontal outcrop that consisted of five adjacent trenches from 0.4 to 1.0 m in depth and approximately 0.5 m in width for which all plant material was collected, identified to the genus level, analyzed, and published (Beck and Labandeira 1998). The results of this study indicated that 2.55% of the all foliar surface area in this deposit was removed by insect herbivory, a seemingly high mean value for a Paleozoic flora (Labandeira and Allen 2007). More importantly, there was considerable variation in the level of herbivory with some taxa lacking or having a trace amount of damage (*Asterophyllites* sphenopsids, *Brachyphyllum* conifers, and *Taeniopteris* cycadophytes), whereas most ferns and seed ferns (*Callipteris*, *Comia*, *Sphenophyllum*, and *Wattia*) displayed low to intermediate levels of herbivory. However, it was the gigantopterid seed ferns (*Gigantopteridium*, *Cathaysiopteris*, and *Zeilleropteris*) that received about twice the amount of damage compared to the mean for the bulk flora (Table 13.1, Figure 13.1), having a much greater



Figure 13.1 A gallery of gigantopterid seed fern leaves showing elevated levels of herbivory from the Early Permian (Artinskian Stage, about 280 Ma) redbed Taint locality (USNM loc. 40689), of the Waggoner Ranch Formation in north-central Texas, United States. The most prominent examples of insect feeding on the Gigantopteridaceae are medium to large sized, polylobate hole feeding in (A–C), (E), and (H–J). Less pronounced margin feeding occurs in (E) and (F). Significant herbivory also is present as surface abrasion, shown in (D) and (G). Based on these distinctive feeding patterns, the same or perhaps several orthopteroid insect taxa probably were responsible for this spectrum of plant damage. This material is housed in the Department of Paleontology, National Museum of Natural History, in Washington, DC. Further details are provided in Beck and Labandeira (1998).

variety of damage than any other plant taxa. Insect folivory of gigantopterids included overwhelmingly hole-feeding damage types (DTs 3, 4, 5, 77, and 113), as well as margin feeding (DT 12) and surface abrasion (DT 30 and 31) (Labandeira *et al.* 2007). This is different from the highly stereotyped damage in the more recent sites, of which the outbreak host plant is represented by a single DT. Taint damage consists of a distinctive spectrum of external foliage-feeding DTs (Figure 13.1), and is significant, particularly for a compression–impression flora occurring early in the launching of late Paleozoic, Euamerican herbivory on land. This elevated level of herbivory may not constitute an outbreak given current definitions, but it does represent the first documented instance in a fossil compression flora of the extensive targeting of a group of closely related plants by a recognizable syndrome of external foliage feeding.

13.5.2 *Heidiphyllum elongatum* at Aasvoëlberg 311: Late Triassic of the Karoo Basin, South Africa

In the stratigraphically lowest sequence of the Molteno Formation, in the Northern Cape Province of South Africa, seven Aasvoëlberg sites represent lake deposits that contain diverse assemblages of foliar material, seeds and other reproductively associated structures, stems, and roots (Anderson and Anderson 1989; Scott *et al.* 2004; Labandeira 2006b). These sites are of Upper Triassic age and are assignable to the lower Carnian Stage, corresponding to circa 228 Ma. One of these sites at Aasvoëlberg, Aas 311, consists of 11 677 specimens representing 15 taxa of plants, and is dominated by the voltzialean conifer leaf *Heidiphyllum elongatum* (Plate 13.1). This broad, parallel-veined leaf, similar to modern *Agathis* (Araucariaceae), consists of 88.7% of all specimens, and 91.9% of the material assigned to this whole-plant taxon when *Dordrechtites elongatus*, its dispersed seed, is added. The remaining seven most abundant and identifiable taxa, in decreasing rank order, are the ginkgophyte *Spenobaiera schenckii* (1.1%), three species of the ginkgophyte *Kannaskoppifolia* (0.5%) considered together, the sphenopsid *Equisetites kanensis* (0.5%), the corystosperm *Dicroidium crassinervis* (0.5%), the moss *Muscites guescelini* (0.3%), the liverwort *Marchantites* (0.3%), and the voltzialean conifer *Rissikia media* (<0.1%), all of which total to 95.1% of the flora. The remaining flora consists of very rare ferns, lycopods, unaffiliated seeds, and unidentifiable foliage. Notably, at Aas 311, 7.2% of the 10 357 *H. elongatum* specimens are leaf mined (DT71), indicating an exceptionally high level of herbivory, particularly as this plant is one of the earliest known leaf mined hosts in the fossil record (Table 13.1, Plate 13.1). Other Molteno sites with leaf-mined *H. elongatum*, other seed plants, ferns, and sphenopsids are at least an order of magnitude less abundant, suggesting by comparison that the leaf-miner at Aas 311 was an outbreak species.

13.5.3 HC81 at Somebody's Garden: Latest Cretaceous of the Williston Basin, North Dakota

Eighty localities from outcrops across the Williston Basin in southwestern North Dakota, United States, represent the best published example worldwide of plants and their insect associations above and below the Cretaceous–Paleogene (K–Pg)

boundary (Lang 1996, Johnson 2002, Labandeira *et al.* 2002a, 2002b). The K–Pg boundary consists of the Hell Creek Formation below and Fort Union Formation above, and defines a major extinction event that affected major clades of terrestrial animals, including dinosaurs, as well as a considerable plethora of marine life, such as mosasaurs, rudistid clams, and ammonites. Also affected were terrestrial plants and their associations with herbivorous insects (Labandeira *et al.* 2002a, 2002b), although the effect may have been considerably dampened in Eurasia (Wappler *et al.* 2009). One locality, “Somebody’s Garden” (DMNH loc. 2203), positioned 54.2 m below the boundary, consists of almost entirely herbaceous species, dominated by dicot angiosperms, and occupying an extensive sand bar or similar ephemeral habitat associated with a stream. From this locality was collected 412 plant specimens, of which almost half (207) are of the intensely attacked herbaceous dicot plant, morphotype HC81, an unnamed nettle (Urticaceae) (Table 13.1, Plate 13.2). The other half of the flora consists of 20 plant taxa, of which the seven most abundant and identifiable taxa are, in decreasing rank order, are HC229 (Cercidiphyllaceae indet.), HC224 (Rosidae indet.), HC228 (Urticaceae, sp. 2), HC212 (*Cercidiphyllum ellipticum*), HC90 (?Rosidae indet.), HC92 (“*Cinnamomum*” *lineafolia*, fam. indet.), and HC226 (Ranunculaceae indet.). The most important aspect of this flora, other than its overwhelming herbaceousness, is the distinctive herbivorized pattern on HC81, a palmately veined mesic leaf consisting of extensive hole feeding at primary vein angles (DT57) and associated circular to ovoidal feeding DTs 1, 2, and 3 elsewhere on the leaf blade (Labandeira *et al.* 2002a; Plate 13.2). Approximately half (51.2%) of the HC81 specimens exhibit one or more examples of this syndrome of plant damage, frequently with several instances of damage per leaf. When considered from a bulk floral perspective based on presence or absence data, 61.8% of all damage in the flora is on HC81, representing a 1.62 increase in damage level above the ambient level of attacked plant hosts other than HC81. Of the four candidate sites for insect outbreaks, though visually arresting, the weakest case perhaps lies with HC81 folivory at Somebody’s Garden.

13.5.4 *Platanus raynoldsi* at Mexican Hat: Early Paleocene of the Powder River Basin, Montana

Mexican Hat (USNM loc. 42090, DMNH loc. 1251) is an early Paleocene site from the Lebo Member of the Fort Union Formation, dated between 64.0 and 64.7 Ma (Belt *et al.* 2004), in the Powder River Basin of eastern Montana, United States. This site historically has been known for the presence of pollen and small vertebrates occurring approximately within a million years after the K–Pg event, and provides a distinct contrast with the pre-event, more subtropical Cretaceous Somebody’s Garden site mentioned in Section 13.5.3 (Wilf *et al.* 2006). Characterized by 15 dicot taxa totaling to 2218 leaves, Mexican Hat is dominated by the sycamore *Platanus raynoldsi* (Platanaceae), which consists of 52.9% of all leaves recorded from the deposit (Plate 13.3). The next seven most abundant leaves, in decreasing rank order, are *Juglandiphyllites glabra* (Juglandaceae), *Zizyphus flabella* (affiliation unknown), MH–Lauraceae sp. 2, “*Populus*” *nebrascensis* (?Salicaceae), *Dicotylophyllum anomalum* (affiliation unknown), “*Ficus*” *artocarpoides* (Lauraceae), and *Ternstroemites aureavallis*

(Theaceae). When *P. raynoldsi* is considered throughout the entire deposit, 37.9% of the leaves are attacked, exhibiting one or more occurrences of a broad spectrum of 28 DTs. This value is at the upper end of herbivory values for taxa in the flora, ranging from 18.8% for *J. glabra* to 43.6% for *Z. flabella* for all leaves with a rank of 7 or above ($N \geq 84$). However, when only the *P. raynoldsi* leaf-mined interval is analyzed, which is defined as the relatively thin stratum between the first and last appearances of leaf mine DT104 on *P. raynoldsi* (Winkler *et al.* 2010), the herbivory incidence rate almost doubles to 68.0% of all leaves. In this confined stratigraphic layer there are 32 leaf mines, and each *P. raynoldsi* leaf hosts a mean of 2.15 mines per leaf, some harboring up to 6 mines that obliterate much of the foliar mesophyll and other parenchymatic tissue (Table 13.1, Plate 13.3). While *P. raynoldsi* is clearly the dominant leaf and most heavily attacked at Mexican Hat, it is the stratally confined leaf-mined interval that exhibits qualities of an insect outbreak, particularly when damage frequencies and the extensive removal of inner leaf tissue are taken into account.

13.6 The macroevolutionary significance of insect outbreaks

There are important implications in any attempt to document insect outbreaks in deep time. A basic issue is whether insect outbreaks can be documented at all in the fossil record. Once an insect outbreak is known to occur, identification of culprits may be possible only if the evidence surrounding the damage is compelling. If the damage is distinctive and sufficiently abundant, and given an appropriate plant host or geochronological context, it may provide primary data to address major insect phylogenetic events. Most important, though, the fossil record of insect outbreaks can provide insight into the paleobiology of how insects have had a major effect on their plant resource environment and when they acquired the behaviors and physiologies that would allow outbreaks, at least as the term currently is understood.

13.6.1 How limited are fossil data on past insect outbreaks?

It is difficult to distinguish in the fossil record the difference between an insect outbreak of broad regional scope versus a more localized area containing a plant host or group of hosts that has been intensively herbivorized. This issue is related to the areal dimensions and nature of the examined, surviving outcrop. For example, fluvial sedimentary rocks representing certain restricted habitats, such as exposed sandy point bars or finer grained overbank deposits that form particular floodplain deposits, may be annually colonized by particular herbaceous or shrubby plants and subsequently attacked by host-specialist herbivores. But such ephemeral, restricted habitats do not necessarily represent regional insect outbreaks. Although fluvial deposits are abundant in the terrestrial sedimentological record and may provide equivocal evidence for fossil insect outbreaks, more regional outbreaks would more likely be preserved in extensive lacustrine deposits, particularly if exact stratigraphic correlations can be made across distant outcrops.

Another, related issue is the portion of the original insect outbreak region that is recoverable from the fossil record. Fossiliferous deposits in the terrestrial record are sporadic in time; but more important for insect outbreak phenomena, in space as well. Consequently, a deposit with plants providing evidence for an insect outbreak invariably preserves only a small area of what would have been an originally extensive region of a plant host (or hosts) with anomalously high levels of herbivory. This is attributable to two processes. Firstly, plant organs from regional plant host species or entire floras may have been deposited minimally in the first place, and thus preserved outcrops would provide a limited snapshot of what was once present. Most areas of the world, today as in the past, occur in landscapes of net erosion and are uncommonly deposited in basins of sediment accumulation. Secondly, many basinal deposits are uplifted, tectonically ravaged, eroded, or otherwise taphonomically altered such that they either preserve an even smaller fraction of the original outbreak record, or otherwise disappear entirely from the fossil record. Consequently, it is difficult to determine the extent of the original, two-dimensional regional surface that once contained an outbreak, even assuming that stratigraphic correlation among outcrops is not an issue.

13.6.2 Can culprits ever be assigned to fossil insect outbreaks?

For the deep-time part of the fossil record, generalized insect DTs, particularly those made by exophytic consumers such as external foliage feeders, are rarely assignable to specific insect lineages. By contrast, stereotyped DTs that are produced by endophytic, host-specialist consumers, such as leaf miners and gallers, frequently produce plant damage that allows taxonomic assignment to well-identified culprits. In addition, those DTs occurring in the more recent part of the fossil record, where a descendent association still may persist, typically are more amenable to reliable assignment than those from the more distant past. As a result, identification of insect culprits responsible for insect outbreaks in the more remote part of the fossil record is variable: rather poor for exophytic feeders and occasionally good for endophytic feeders. This is in distinct contrast with Holocene occurrences, where relevant data – fecal pellets, larval head capsules, and DT distinctiveness – frequently are present on the same hosts living in the same region, thus providing high certainty for an identification. In addition, the biology of many important Holocene associations in forests often is documented in the economic entomological literature, revealing much about their current biology.

13.6.3 What is the effect of phylogenetic constraints on herbivory patterns?

The recognition of specific features of insect herbivore behavior is detectable in fossil floral material, such as ovipositional probing by leaf miner flies (Winkler *et al.* 2010). One prominent telltale damage pattern involves stereotyped foliar galls on particular organs and tissues that are found on particular plant lineages, such as tenthrinid sawflies attacking the Salicaceae (willows and poplars) (Price 2003). The role of plant secondary chemistry in determining gall placement is

crucial, in part because of considerable control that gall-forming insects have on the tissue localization of host plant secondary compounds such as phenolics (Nyman and Tiiitto 2000), which frequently lead to galling intensities that reach outbreak status (Price 2003). Such patterns, including gall outbreaks and host switching, should be detectable in the better documented Paleogene and Neogene fossil record where well-preserved and identifiable galls and their host plants are often linked to extant lineages.

Similarly, more deep-time, coarser grained opportunities for recognition of the effect of phylogenetic events on herbivory patterns, including outbreaks, should be detectable in the fossil record. One example, broached earlier, would be the extensiveness of outbreak patterns in dominantly gymnosperm-dominated floras predating the Jurassic Parasitoid Revolution, and conversely in angiosperm-dominated floras subsequent to this event (Labandeira 2002). The Parasitoid Revolution, with major trophic implications for herbivores, was launched during the Early Jurassic with the appearance of aculeate and other parasitoid clades in the Hymenoptera and Diptera (Whitfield 1998, Eggleton and Belshaw 1992). Most major parasitoid lineages were established by the Early Cretaceous (Labandeira 2002). An important test for the influence of the Parasitoid Revolution on herbivory would be the contrast of herbivory intensity levels, plant concealment patterns, and other examples of herbivore defense (e.g., Krassilov *et al.* 2008), whether outbreak or otherwise, between ecologically analogous pre-Jurassic and post-Jurassic floras. Such an investigation could reveal whether earlier bottom→up regulation of herbivory driven by primary producers was dominant, versus later top→down regulation by parasitoids.

13.6.4 Do snapshots of insect outbreaks inform us about biotic communities from the deep past?

Insect herbivore specialization on particular plant hosts undoubtedly occurred early in terrestrial ecosystem evolution (Labandeira 2006a), recognizing that the trace-fossil record of insect-damaged plants typically occurs earlier in time than the corresponding body-fossil record of the insect culprits themselves (Labandeira 2007). Thus, fossil documentation of insect-caused plant damage is the only record of the expansion of herbivory across landscapes during the late Paleozoic, in lieu of insect body fossils. Particular Euramerican plant hosts were preferentially targeted, such as virtually all tissues of marattialean tree ferns in Late Pennsylvanian coal swamp forests (Labandeira 2001, Labandeira and Phillips, 1996), and subsequently leaves of giantopterid seed ferns in Early Permian open woodland communities dominated by seed plants (Beck and Labandeira 1998; Glasspool *et al.* 2003). In Gondwana, certain species of glossopterid seed ferns were preferentially subjected to high levels of oviposition and margin feeding (Prevec *et al.* 2009). A crucial question is at what point in this strengthening of plant–insect associational nexus of relationships did outbreak behavior in insects originate? Giantopterids may be a reasonable early candidate, as they are an early seed fern lineage that had angiosperm-like features (Hilton and Bateman 2006) and were extensively herbivorized. An answer to this question involves

identification of those insect lineages responsible for the recorded high levels of damage. In the case of the earliest, late Paleozoic example, it appears that insects responsible for gigantopterid damage at Taint, in northern Texas, probably were external foliage-feeding orthopteroids. The Early Permian age of this deposit suggests the absence of other mandibulate herbivore lineages that would create the suite of DTs occurring on Taint gigantopterids, such as phytophagous adult beetles or herbivorous larvae from several early holometabolous clades. During this time, when particular plant resources soon became available as food and while most enemy-free space was bereft of top-down regulation by parasitoids (Labandeira 2002), insect outbreaks would be expected.

Perhaps a better example of an outbreak would be the endophytic leaf miner, probably a polyphagan beetle, at the Aas 311 site from the Late Triassic of South Africa. This elevated level of leaf mining represents even better defended enemy-free space than that of the Early Permian example, as it not only precedes the Jurassic Parasitoid Revolution (Labandeira 2002), but also acquired histological isolation of the larvae by adopting an endophytic feeding habit, probably as protection against active insect predators. As in the Late Permian case, there is high but not exact host plant specificity: the Molteno leaf miner was overwhelmingly on *H. elongatum*, but the same DT71 mine occurs on unrelated seed fern and ginkgophyte taxa. Analogously, the Taint external foliage feeder was consuming four confamilial genera within the Gigantopteridaceae.

During the latest Cretaceous, long after the Jurassic Parasitoid Revolution was established (Labandeira 2002), a different type of insect outbreak emerges at Somebody's Garden, in the latest Cretaceous from the Williston Basin of North Dakota. The intensely herbivorized nettle, HC81 (Urticaceae), was highly defended by dense arrays of resinous glands and integument-penetrating trichomes, indicating use of host secondary chemicals and physical defenses as major feeding deterrents to insect herbivores, which likely were chrysomeloid beetles (Labandeira 2002a). Once the chemical and physical defenses of the nettle host were breached, additional enemy-free space would have been purchased through consumed secondary chemicals occurring in herbivore tissues to ward off parasitoids and predators. Unlike the other deep-time examples, this episode of herbivory targets a herbaceous host within a habitat of few, if any, woody plants which grew in a disturbed, periodically reforming community, suggesting rapid colonization by potential plant hosts and their herbivore host specialists. Under these ephemeral conditions, limited insect outbreaks could be expected and would last as long as the habitat would experience the next flooding event.

After the K-Pg extinction event, the low-diversity Paleocene "dead zone" (Labandeira *et al.* 2002a), was dominated by mire communities, predominant throughout the Western Interior of North America (Johnson 2002). At Mexican Hat, from the early Paleocene in the Powder River Basin of Montana, the presence of a thin stratum of fossil leaves was overwhelmingly dominated by heavily mined *P. raynoldsi* sycamore leaves, strongly suggesting a heavily targeted host by an agromyzid leaf miner. This relationship was probably similar to modern agromyzid leaf miners of *Phytomyza* on the holly *Ilex* (Aquifoliaceae) (Scheffer and Wiegmann 2000), which occasionally achieve outbreak status (Eber *et al.* 2001). Like the analogous Molteno leaf miner, the Paleocene example of an endophytic

habit on woody seed-plant foliage displays host monospecificity and co-evolved features such as leaf surface probes by an ovipositor for evidently assessing host-plant palatability. If this early Paleocene Agromyzidae–Platanaceae system is like other tight leaf miner associations in the fossil record (Lopez-Vaamonde *et al.* 2006), there is reason to infer a significantly earlier origin, presumably during the Late Cretaceous, that would be predicted by the sequential evolution hypothesis (Jermy 1976).

In addition to these examples from the compression–impression fossil record of foliage, a second source of fossil evidence for insect outbreaks is the record of amber. Evidence from Dominican amber, of Early Miocene age (Penney 2010), and considerably older New Jersey amber, of mid-Late Cretaceous age (Grimaldi and Nascimbene 2010), indicates that a relevant fraction of tree resin was produced as a response to beetle infestation, suggested by the presence of associated bark and ambrosia beetle as inclusions, and particularly by elevated δC^{13} values that provide evidence for physiological stress through the production of secondary metabolites (McKellar *et al.* 2011). This relationship has been demonstrated by modern mountain pine beetle, *Dendroctonus ponderosae*, a scolytine curculionid that infests considerable swaths of coniferous forest in western North America, responsible for elevated δC^{13} values (Kurz *et al.* 2009). While amber provides the best type of deep-time evidence for insect outbreaks on coniferous trees, it has serious limitations in addressing folivore-based outbreaks in the fossil record. The amber record does not preserve considerable coverage of foliage surface area, necessary for quantification of herbivory levels, and also amber with culprit wood borer inclusions extends only to the mid–Early Cretaceous, rendering as inaccessible the older two thirds of the deep-time record.

13.7 Summary and conclusions

There are seven major points that can be summarized from these studies. This summary not only provides ways of detecting insect outbreaks in the fossil record, but also indicates the important role of phylogenetic control of insect herbivore macroecology in site-specific increases in herbivory rate. It is anticipated that this contribution will goad paleoecologists to look for insect outbreak evidence in future studies of herbivory in the fossil record.

1. The definition of what constitutes an insect outbreak in the fossil record should remain flexible in terms of the metric used, but always should provide for a distinct, quantitative increase above the ambient herbivory level compared either to most other herbivorized host species within the same source flora, or alternatively to other hosts in spatiotemporally proximal floras.
2. It is unclear if an insect outbreak, such as a “locust plague,” whereby virtually all photosynthetic (and other) tissue is rampantly consumed within one or a few annual seasons, would be preserved in the fossil record. If preserved, special observational and analytic skills would be required for its detection.
3. There are two principal modes of recognizing insect outbreaks from fossils. First is to examine the biological effects of the insect herbivore, such as the

- accumulation of fecal pellets and head capsules in organically rich, three-dimensional deposits in the more recent part of the fossil record. The second is to assess herbivory levels on leaf surfaces from bedding planes of compression–impression deposits using existing methodology that has been applied to the more deep-time part of the record.
4. Exceptional increases in insect herbivory punctuate the fossil record and provide obvious examples of host specialist targeting of particular plant hosts. These exceptional events are spatiotemporally confined and suggest that host plant defenses are occasionally breached by exophytic and endophytic insect herbivores that can result in distinct outbreaks.
 5. Because of the nature of the fossil record, the true extent of an insect outbreak may never be known because of imperfection in the preservation process and the vagaries of erosion that destroy much of what was deposited.
 6. In general, the older the deposit, the more unlikely that the culprit of an insect outbreak is satisfactorily identifiable. This mostly is attributable to more accumulated extinctions, in the deeper time part of the fossil record, or to sufficiently modern plant–insect associational analogs for comparison.
 7. The fossil history of insect outbreak phenomena can provide evolutionary biologists, particularly those who examine plant–insect associations, a better sense of the evolution of insect outbreaks. It is clear that insect outbreaks are a pattern of extensive herbivory that is not confined only to the present day or the Holocene, but extends into deep time, and probably to the late Paleozoic.

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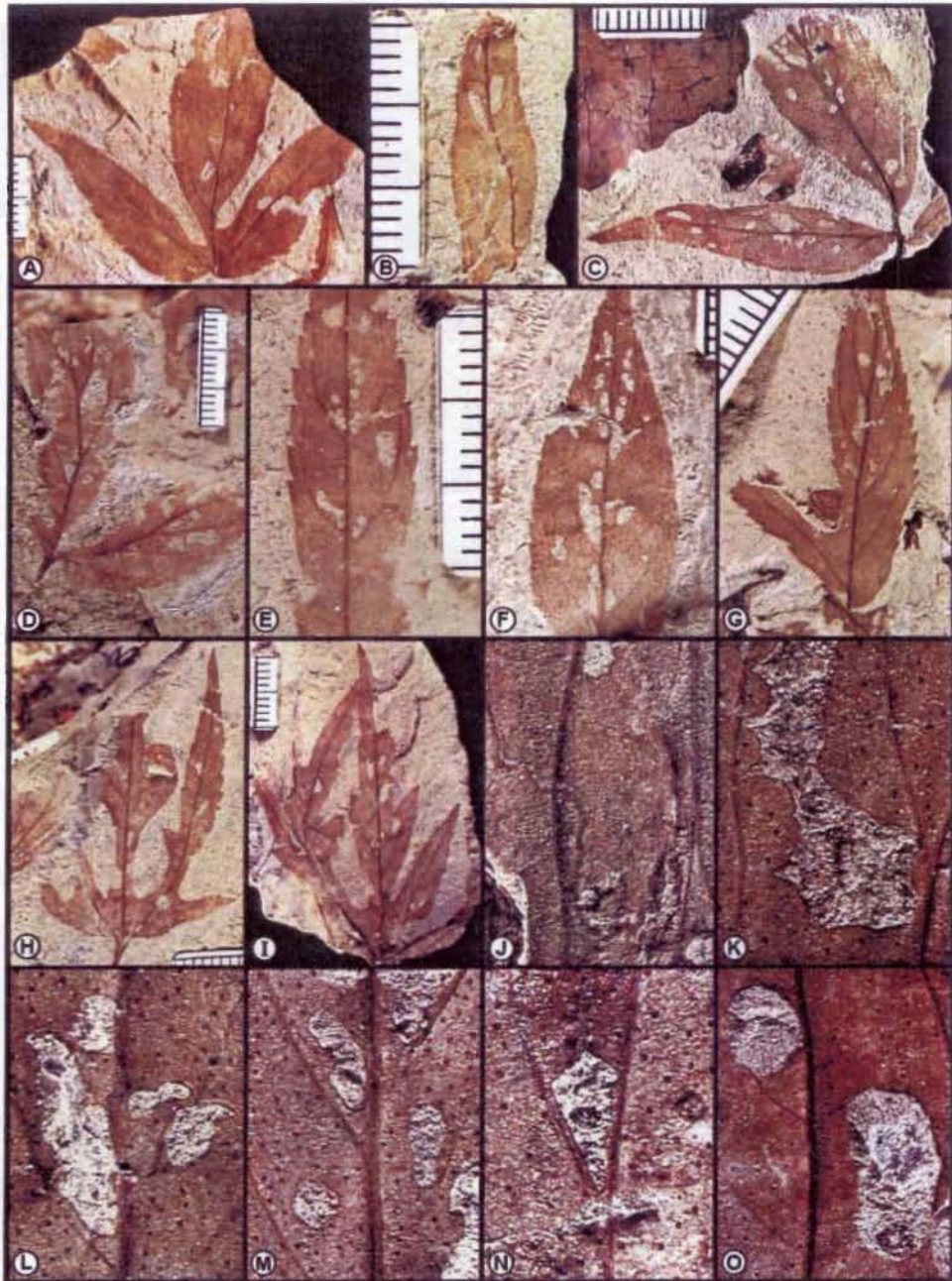


Plate 13.2 A panorama of highly herbivorized leaves of morphotype HC81 (*Urticaceae*) leaves at the Somebody's Garden locality (DMNH loc. 2203) from the latest Cretaceous (Maastrichtian Stage, 65.5 Ma) of the Hell Creek Formation, Williston Basin, southwestern North Dakota, United States. The predominant damage type is DT57, distinctive hole feeding at the axils of primary and secondary veins, seen in (a-i), and enlarged in (l-n). Accompanying DT57 in (a-i) are circular, elliptical, and polylobate holes, magnified in (k), (m), and (o), attributed principally to DT3-DT5. A thin, delicate, leaf mine occurs in (j), attributable to a nepticulid moth. Note in (k-o) the presence of antiherbivore resiniferous or mucilage-laden epidermal glands, appearing as amber dots. This damage was probably produced by a single insect species, most likely a chrysomelid beetle. Scale bars are in millimeter increments. This material is housed at the Denver Museum of Nature and Science, in Denver, CO. Consult Labandeira *et al.* (2002a, 2002b) and Johnson (2002) for additional information.

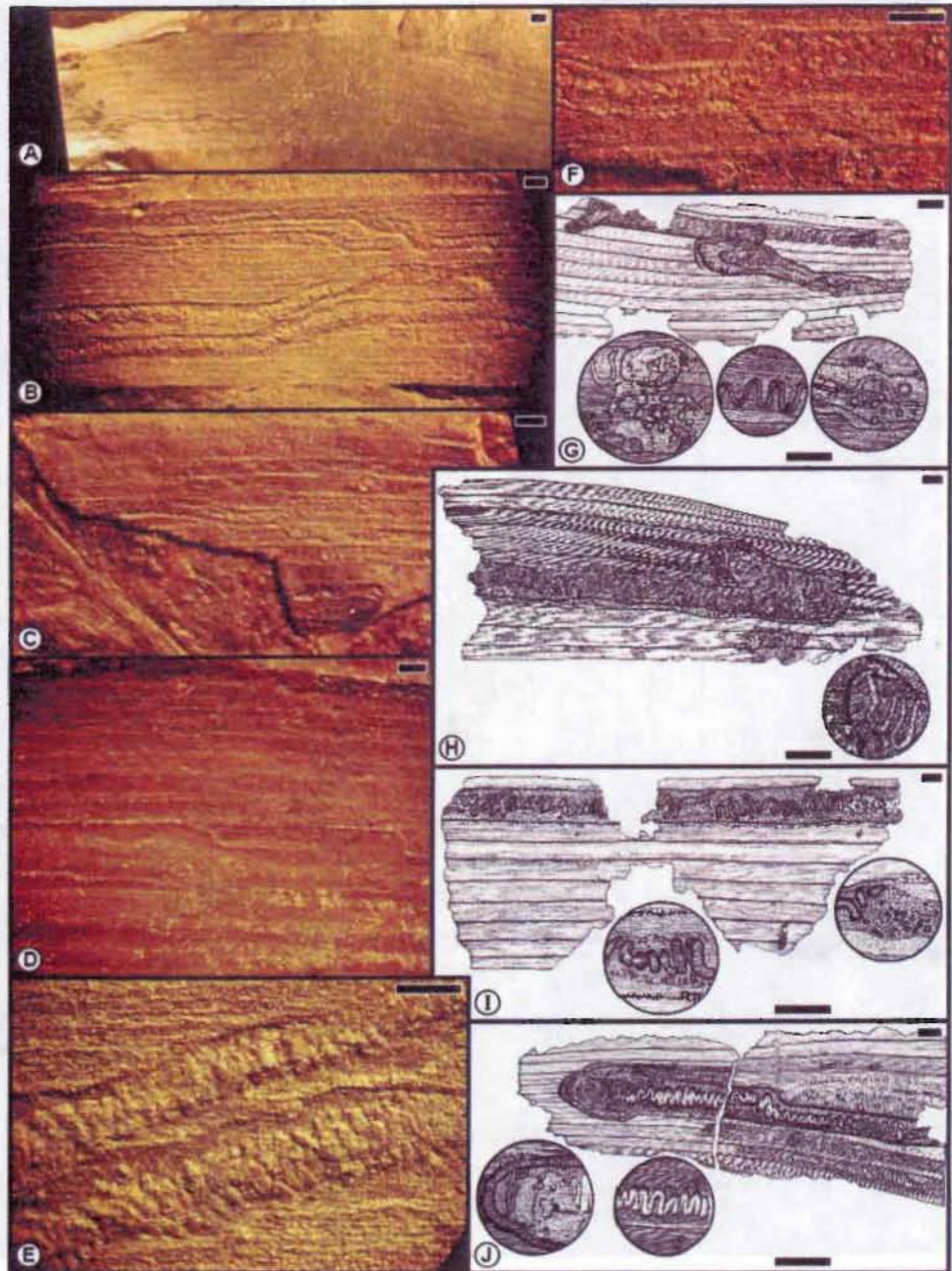


Plate 13.1 Extensive leaf mining of DT71 at the Aasvoëlberg 311 site in the early Late Triassic (Carnian Stage, about 228 Ma) of the Molteno Formation, Karoo Basin, Western Cape Province, South Africa. This is the earliest example of extensive leaf mining in the fossil record, probably produced by an unknown polyphagan beetle, which has extensively targeted the broad-leaved voltzialean conifer, *Heidiphyllum elongatum*. Photo images in (a–f) are of heavily herbivorized leaves, one with a complete mine (a), and others indicating multiple mines (b, c, e) and characteristic enlargements (d, f). In (g–j) are camera lucida drawings of leaf mines showing sinusoidal frass trail variability, the processing of mesophyll and other parenchymatic tissues by a mandibulate insect, and larval mine widths. Scale bars indicate 1 millimeter. This material is housed at the Bernard Price Institute of Palaeontology at the University of the Witwatersrand, Johannesburg, South Africa. See Anderson and Anderson (1989), Scott *et al.* (2004), and Labandeira (2006b) for additional details.

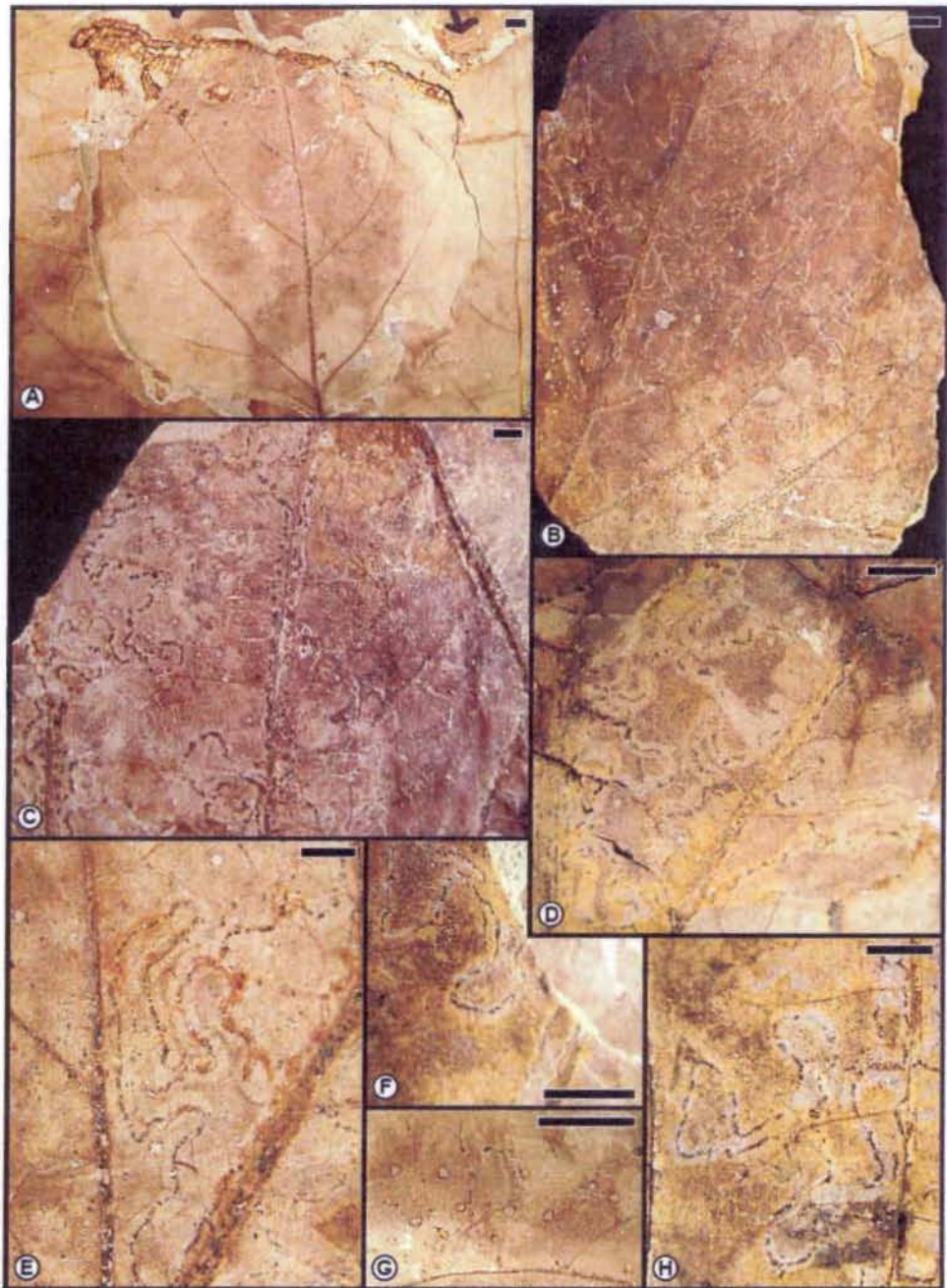


Plate 13.3 Intensively mined *Platanus raynoldsi* (Platanaceae) leaves at the Mexican Hat locality (USNM loc. 42090), from the early Eocene (Danian Stage, about 64.4 Ma), of the Fort Union Formation, Powder River Basin, eastern Montana, United States. The leaf miner is an agromyzid dipteran, the earliest occurrence in the fossil record for this clade. An uncommonly unmined leaf is in (A), but typical are leaves riddled with mines in B–F and H. Leaf mining commonly occurs where primary veins subtend secondary veins (E), at leaf edges (F), or pervasively throughout the entire leaf. Ovipositional probes prior to egg deposition by the leaf miner fly are indicated in (G). Scale bars indicate 1 millimeter. This material is housed at the National Museum of Natural History in Washington, DC. Further details are available from Wilf *et al.* (2006) and Winkler *et al.* (2010).