

*Annual Review of Entomology*Arthropod and Pathogen
Damage on Fossil and Modern
Plants: Exploring the
Origins and Evolution of
Herbivory on LandConrad C. Labandeira^{1,2,3,*} and Torsten Wappler^{4,5}¹Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; email: labandec@si.edu²Department of Entomology, University of Maryland, College Park, Maryland, USA³College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University, Beijing, China⁴Natural History Department, Hessisches Landesmuseum, Darmstadt, Germany; email: torsten.wappler@hlmd.de⁵Paleontology Section, Institute of Geosciences, Rheinische Friedrich-Wilhelms Universität Bonn, Bonn, GermanyANNUAL
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**Keywords**

Cretaceous–Paleogene ecologic crisis, damage types, functional feeding groups, continental scale, Paleocene–Eocene Thermal Maximum, Permian–Triassic ecologic crisis

Abstract

The use of the functional feeding group–damage type system for analyzing arthropod and pathogen interactions with plants has transformed our understanding of herbivory in fossil plant assemblages by providing data, analyses, and interpretation of the local, regional, and global patterns of a 420-Myr history. The early fossil record can be used to answer major questions about the oldest evidence for herbivory, the early emergence of herbivore associations on land plants, and later expansion on seed plants. The subsequent effects of the Permian–Triassic ecological crisis on herbivore diversity, the resulting formation of biologically diverse herbivore communities on gymnosperms, and major shifts in herbivory ensuing from initial angiosperm diversification are additional issues that need to be addressed. Studies of

herbivory resulting from more recent transient spikes and longer-term climate trends provide important data that are applied to current global change and include herbivore community responses to latitude, altitude, and habitat. Ongoing paleoecological themes remaining to be addressed include the antiquity of modern interactions, differential herbivory between ferns and angiosperms, and origins of modern tropical forests. The expansion of databases that include a multitude of specimens; improvements in sampling strategies; development of new analytical methods; and, importantly, the ability to address conceptually stimulating ecological and evolutionary questions have provided new impetus in this rapidly advancing field.

INTRODUCTION

The ecological context for the origins and evolution of arthropod and pathogen herbivory on land plants has been a basic issue that has animated discussions about how diversity is generated in deep time for the terrestrial realm (62). However, the rich fossil record of herbivory historically has not been used in studies to address this issue, offering minimal quantitative input. Nevertheless, during the past two decades, efforts to understand this issue have been invigorated, addressing concerns that we detail below. During the 1980s and 1990s, worldwide studies of plant–arthropod interactions in the fossil record documented a variety of damage in deposits spanning the geologic eras of the Paleozoic (420–252 Ma) (11, 106), Mesozoic (252–66 Ma) (105), and Cenozoic (66 Ma–present) (47, 110). While this effort demonstrated evidence for specific types of arthropod interactions in a variety of ancient ecosystems (62), such assessments were almost always qualitative descriptions of how arthropods used plant resources for diet, shelter, and oviposition. This pattern of discovery was transformed in 1999 when a study quantitatively demonstrated that heightened insect herbivory occurred during a transient, 170,000-year-long interval at 56 Ma in which a dramatic increase in atmospheric temperature and CO₂ levels occurred in an event known as the Paleocene–Eocene Thermal Maximum (PETM) (120). This study initiated the functional feeding group (FFG)–damage type (DT) system of herbivory analysis by demonstrating in detail how insect damage on fossil plants could be used quantitatively to understand ecological, evolutionary, and environmental events in the fossil record (22). Since that time, approximately 165 journal articles have been published that variously use the FFG–DT system (**Figure 1**), often employing newer quantitative techniques, briefly discussed below, to document, analyze, and test hypotheses related to the history of arthropods and pathogens on plants (23, 103) (**Figure 2**).

Historical context is necessary for understanding the importance of arthropod and pathogen damage on fossil plants and for interpreting their response to ecological and evolutionary events. The analyses of preserved interactions are dependent on a fossil record that provides documentation of herbivory and oviposition (2, 80) that, like all plant–insect interactions, require three components: the plant host, the arthropod herbivore, and the interaction (92, 115). There are advantages to focusing specifically on the interaction: Such a focus provides four relevant contexts that clarify the ecological history of the interaction (63). First, fossilized evidence of plant damage occurs in deposits that often lack arthropod body fossils and consequently provides the only data for inferring the culprit of the damage. An exemplary case is two types of damage assigned to two scale insect clades on early angiosperms from the Early Cretaceous (103 Ma) Rose Creek plant assemblage of Nebraska, United States (126). In that study (126), piercing-and-sucking damage was associated with fossil molds of two distinctive damage morphotypes—a wax scale and a soft scale insect (Hemiptera: Coccidae)—in which the plant host and damage were well identified in a deposit that lacked insect body fossils. Second, an interaction–DT involving plant damage almost always

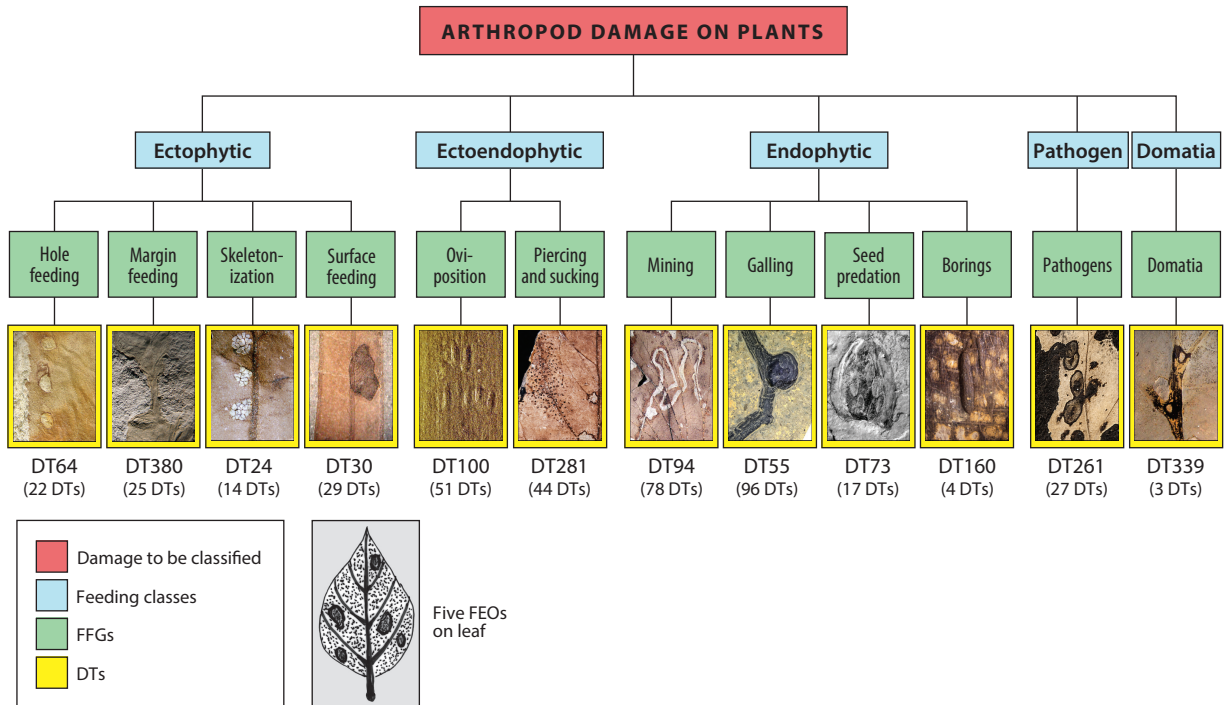
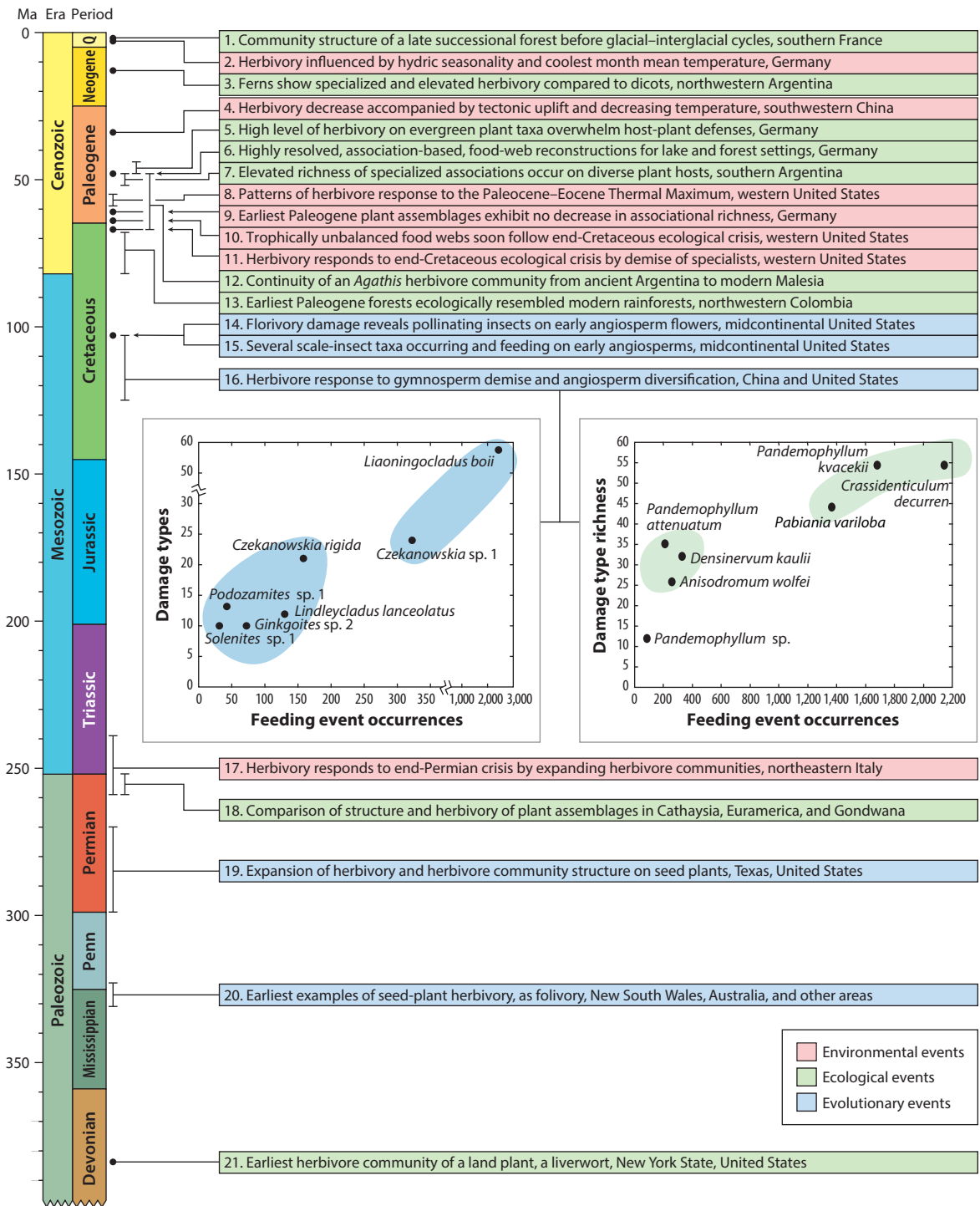


Figure 1

The FFG-DT system (75) for documenting and analyzing herbivory in the fossil record. Abbreviations: DT, damage type; FEO, feeding event occurrence; FFG, functional feeding group.

antedates the body-fossil record of the arthropod or pathogen responsible for the damage. This time gap is largely due to general deficiencies in the insect fossil record versus the considerably better-preserved plant fossil record, which includes insect damage to plants (63). For every preserved insect body fossil, there are many more occurrences of damage produced by that insect on often very abundant foliage (63), although there are rare exceptions (51). One exception is the rare, distinctive seed predation on a coconut fruit in a Paleogene (58–60 Ma) deposit from Colombia by pachymerine beetles (Coleoptera: Chrysomelidae), a seed-predator lineage with a much more recent fossil record (45). Nevertheless, in that study (45), distinctive seed-predation damage on a fossil specimen of a coconut fruit was determined to occur 24 Myr before the first occurrence of a culprit body fossil. Third, damage on plants provides essential data for understanding insect behaviors that otherwise would be difficult or impossible to infer by relying solely on body fossils (**Supplemental Figure S1**). A case in point is the stereotypical death grip damage on foliage typical of a behavior by an ant (Hymenoptera: Formicidae) that has been zombified by a parasitoid fungus (Ascomycota: Ophiocordycipitaceae) found at the Messel locality (48 Ma) of Germany (53). Leaves with distinctive death grip damage can be used, in lieu of matching body fossils, to indicate that these unusual behaviors among an ant, its parasitoid, and a plant were present. Fourth, insect damage in plant assemblages documents trends in herbivory immediately before and after a major ecological and evolutionary crisis, such as the Cretaceous–Paleogene (K–Pg) event that extinguished major lineages such as ammonite cephalopods and dinosaurs (75) (see the sidebar titled Abbreviations and Terms Used in This Review). Studies of plant–arthropod interactions during this globally catastrophic interval indicate a major negative impact on plant–host specialists and

Supplemental Material >



(Caption appears on following page)

Figure 2 (Figure appears on preceding page)

Important studies of plant–insect interactions from plant assemblages of the fossil record. The data are taken from References (1) 4; (2) 4 and 1; (3) 97; (4) 30; (5) 119; (6) 36; (7) 122; (8) 26, 29, and 120; (9) 116; (10) 123; (11) 34, 69, and 70; (12) 33; (13) 15, 46, and 125; (14) 127; (15) 126; (16) 128 and 129; (17) 71 and 96; (18) 81; (19) 11, 66, 83, 100, 101, and 131; (20) 54; and (21) 77. The two insets provide an Early Cretaceous example (number 17) of the most herbivorized plant hosts in the shift in herbivory from an earlier gymnosperm-dominated plant assemblage (130) to a later angiosperm-dominated plant assemblage (128, 129). Abbreviation: Q, Quaternary Period.

a minimal effect on plant-host generalists (34, 70), also evidenced by herbivory data suggesting severely unbalanced food webs within 1.7 Myr after the K-Pg crisis (123). These four features of fossilized herbivore damage provide unique opportunities for testing hypotheses that supplement and often replace previous conclusions based solely on insect and pathogen body-fossil data (63).

THE FUNCTIONAL FEEDING GROUP–DAMAGE TYPE SYSTEM

The structure used for quantitatively evaluating herbivory in fossil and modern settings is the functional feeding group–damage type (FFG-DT) system (**Figure 1**) (16, 78, 120). Damage encountered in a plant assemblage initially is categorized into three hierarchical levels: feeding class,

ABBREVIATIONS AND TERMS USED IN THIS REVIEW

- **Calamite:** an arborescent, jointed stemmed horsetail of the Paleozoic that grew up to 18 feet
- **Cathaysia:** a group of geological land masses of the late Paleozoic whose assembly began in the Carboniferous, that formed an integrated supercontinent during the Permian, and that correspond to most of the modern country of China
- **DT:** damage type, in reference to the fundamental unit used in quantitative assessments of herbivory in the fossil record; also a prefix for any of the unique types of herbivory described in Reference 78 and subsequent related publications
- **DT redundancy:** the occurrence of the same damage type on multiple plant host species
- **Euramerica:** a supercontinent that existed from the Devonian Period to the Cretaceous Period; consisted largely of Europe, eastern and central North America, and northern South America; and was integrated into a larger supercontinent, Laurasia, during the Cretaceous
- **FFG:** functional feeding group, a group of DTs united by a common feeding style
- **Glossopterid:** a major group of seed plants of the Permian Period predominant in the Gondwana supercontinent
- **Gondwana:** a supercontinent largely in the southern hemisphere formed in the Carboniferous that began to fragment during the Middle Jurassic
- **K-Pg:** the latest Cretaceous–earliest Paleogene ecological crisis and extinction event
- **Leaf mass per area:** a morphological trait consisting of the leaf volume to area ratio that is relevant for determining foliage palatability to insect herbivores
- **Lignite:** a soft type of coal, intermediate between peat and bituminous coal, that typically preserves plant fossils
- **Ma:** abbreviation for millennium, indicating an absolute date of millions of years ago
- **Myr:** designates a million-year interval of time in the deep past
- **Peltasperm:** a worldwide lineage of seed ferns of Permian to Jurassic age
- **PETM:** Paleocene–Eocene Thermal Maximum, a transient spike 170,000 years long immediately after 55.8 Ma
- **Plant assemblage:** a local deposit of fossil plants representative of a regional flora
- **P-Tr:** the latest Permian–earliest Triassic ecological crisis and extinction event
- **Seed fern:** a group of Paleozoic and Mesozoic plants that bear fern-like foliage and reproduce by seeds
- **WINA:** Western Interior of North America

functional feeding group, and damage type (78, 128) (**Supplemental Table S1**). A feeding class, the most general category of plant damage, is defined by the mode of use of an insect's mouthparts (or ovipositor) relative to its plant host, or alternatively whether it is a pathogen or domatium. A feeding class involving arthropods can be ectophytic, characterized by external feeding, such as the caterpillars of butterflies; endophytic, characterized by internal feeding, typical of leafmining flies; or a combination of the two, the ectoendophytic condition, in which the mouthparts or ovipositor is located within host tissue, but the rest of the arthropod's body is positioned on the host, as in the case of aphids. A fourth feeding class is made up of pathogens consisting of viruses, bacteria, and fungi that consume live host tissue by external enzymatic digestion (6, 74). As in the modern record (128, 129), the fossil record of pathogens can be recognized via signs, which are the actual pathogenic agents such as fungal hyphae or fructifications, or more commonly via symptoms, which are the reactions of a plant host to a pathogen, such as necrotic blotches of tissue or a reaction front (74). Domatia make up a rare fifth class that provide shelter in which, for example, ants excavate live plant tissues and construct entry holes in leaf petiolar bases (16); by contrast, mites prey on other organisms amid tufts of hair or tissue flaps at vein axils to deter herbivores of their host plant (84). An FFG is an intermediate-level category defined by a distinctive group of damage produced by a similar feeding style. A DT is the fundamental category of damage on a plant typified by a stereotyped style of damage defined by size, shape, position, micromorphological features, and plant response tissue and is recognizable across time, space, and habitat. The FFG-DT system currently consists of 5 feeding classes, 12 FFGs, and 416 DTs (78, 128) (**Supplemental Table S2**).

Sampling is a critical issue involving how collected plant samples can be representative of the larger, original plant assemblage (101, 102). Various indicators are used to detect sampling robustness, including number of samples collected; absence of bias; specimen to plant species or morphotype ratio; density of plant samples per rock slab; and, importantly, rarefaction analyses based on sample or surface area coverage that achieve asymptotic stability (101, 102, 104). Seven guidelines have been established to assess adequacy of sampling (**Supplemental Table S2**).

Six metrics have been used to assess FFG and DT richness and intensity, provided that there is appropriate sample coverage (112). The three richness metrics are DT richness, based on presence-absence data; the structure of an herbivore community, based on the spectrum of DTs present on a host-plant species; and DT host-plant specialization, as determined by the degree to which a particular DT occurs on one or more host-plant species in a plant assemblage (103, 112). The DT host-plant specialization metric assumes a functional approach that is defined by a DT having a broader (generalized) or narrower (specialized) occurrence on plant species within a plant assemblage (128, 129). DT host-plant specialization differs from taxonomically based metrics used in modern studies of an herbivore's dietary breadth, which are defined by the number and distribution of plant species consumed (43).

The three major intensity metrics are DT frequency, based on count data; herbivore-damaged surface area as a fraction of total surface area; and feeding event occurrence, which is the frequency of DT feeding events on individual plant organs (**Figure 1**). These three intensity metrics can be evaluated at the level of a host-plant species; at the level of a plant group or clade, such as evergreen dicots or Lauraceae; or for the entire plant assemblage. The FFG-DT system, initially developed for fossil data, recently has been extended to modern plant assemblages (16). In contrast, metrics used in modern studies that employ taxonomic data are not applicable to fossil data. This lack of equivalence is based on the contrasting procedures by which modern data are collected, dissimilar definitions of analogous terms such as specialization, and different methods used for calculation of metrics such as herbivorized surface area. Most important of all is that we do not know the taxonomic identities of the arthropod and pathogen species responsible for damage in

fossil plant assemblages. A relevant example (109) cited the lack of equivalence between fossil and modern plant assemblages; however, it did not invalidate the use of functional–ecological units of the FFG-DT system for the study of herbivory in modern plant assemblages (16).

APPROACHES TO STUDYING FOSSIL PLANT-ARTHROPOD AND PLANT-PATHOGEN ASSOCIATIONS

Numerous studies have quantitatively examined fossil (and modern) arthropod and pathogen interactions with plants (74, 109, 116, 128). These studies have raised questions about the ecological and evolutionary responses of such associations to the Earth's profound biotic and abiotic changes. Below, we emphasize studies that have used the FFG-DT system to examine herbivory during specific time intervals of the geologic past (**Figure 2**).

How Did Herbivory Get Launched on Land?

The earliest evidence for arthropod herbivory is provided by sporadic occurrences of coprolites (fossilized fecal pellets) associated with land plants from late Silurian to Early Devonian deposits of the United Kingdom (18, 105). Two principal occurrences throughout the relevant 104-Myr interval from the late Silurian Period to the end of the Mississippian Period are notable. The first is the plant community surrounding the Early Devonian Rhynie Chert hot-spring deposit in Scotland, which includes evidence for spore consumption, plant stem borings, piercing and sucking of sporangia and stems, and pathogens entering stomata of permineralized vascular and nonvascular land plants (18, 93, 94, 105). Later, during the Middle Devonian, a liverwort species from a different environment was preserved as compression fossils, revealing nine DTs of hole, margin, and surface feeding; piercing and sucking; and galling representing a seemingly diverse herbivore community on a liverwort (79). This early, sparse record of herbivory continues into the Mississippian with rare coprolite occurrences attributable to herbivores (105); later in the period, the first evidence of folivory by margin feeding occurs on seed-fern pinnules from eastern Australia (54). It is striking that during this interval, fossils are missing of relevant, land-dwelling herbivores that could have created the damage. Is this sparse record attributable to geologists and paleobotanists being primarily interested in the stratigraphic, sedimentologic, and floristic context of the fossil deposit, rather than plant fossils with arthropod damage? Alternatively, is the absence of evidence of herbivory during this interval due to an intrinsically poor record that should be read literally and that thus represents a major delay by several tens of millions of years of substantive herbivory in terrestrial ecosystems (54)? Only two disparate occurrences are known that provide the overwhelming body of evidence—environments surrounding hot springs and ground-based liverworts. The two limited instances of earlier Devonian herbivory were initiated during the fledgling diversification of land plants, after which plant stature increased, the seed habit appeared, and the first forests arose by the end of the period. Was DT richness limited until the rapid expansion of herbivory during the Pennsylvanian Period?

How Did the Initial Expansion of Land Plants Affect Herbivory Patterns?

During the Pennsylvanian Period, there was substantial expansion of herbivory, as represented by the FFGs of margin feeding (106), oviposition (12, 61), piercing and sucking (73), galling (20, 65), seed predation (18), and pathogens (74). Overall, the incidence of DTs from these six FFGs was uncommon to rare across regional landscapes; the most prominent associations were margin feeding and pathogens on the extinct seed plant *Macroneuropteris scheuchzeri* (63, 106) and oviposition on calamites and other horsetail stems (12, 61). Patterns of herbivory were sporadic in geographic occurrence that were present within narrow time intervals, indicating a highly

idiosyncratic presence on host plants in time and space (20). The data are overwhelmingly from equatorial, wetland communities of Euramerica.

Evaluations of the richness and intensity of herbivory are needed using evidence from additional deposits of the Pennsylvanian Period from highly documented, speciose, and well-preserved Euramerican plant assemblages. Such plant assemblages should be sufficiently robust in sample size (101) and similar in scope to those from other Pennsylvanian and lowermost Permian deposits (32, 131). These additional data could determine the nature of this transition between the early, sparse record characterized by two margin-feeding DTs on a Late Mississippian seed fern from Gondwana (58) and the broad spectrum of herbivory represented by 47 DTs of nine FFGs from equatorial wetland communities at the end of the period (131). These proposed studies would provide evidence for how the most dramatic expansion of Paleozoic herbivory occurred. Specifically, was an increase in herbivory level accomplished by species with increased FFG and DT richness that were opportunistically targeted in particular communities, or was the increase in herbivory indiscriminate and random among plant species in assemblages across regional floras?

How Did Arthropod Herbivores React to the Initial Expansion of Seed Plants?

The Permian Period is characterized by expansion of several FFGs compared to the previous Pennsylvanian record. There is increased representation of skeletonization (10, 35, 133), piercing and sucking (131), galling (65, 111), seed predation (9), and borings (39), all of which are present in Euramerican (85, 86), Gondwanan (40), and Cathaysian (40) plant assemblages. The most extensive and continuous record of analyzed Paleozoic herbivory is from six plant assemblages representing a 27-Myr span from the lowermost Permian, immediately above its boundary with the Pennsylvanian, to the earliest middle Permian of north-central Texas (11, 66, 83, 99, 100, 131). These six plant assemblages cover wetland, floodplain, channel, and estuarine environments (88) and collectively represent 71 DTs from nine FFGs (113). Herbivory indices (the percentage of herbivorized leaf area in a plant assemblage) for these six assemblages ranged from 0.86 to 2.58 (mean 1.48), compared to a range of 2.9–9.5 (mean 8.91), or approximately one-sixth, for equivalent modern plant assemblages from North Carolina, United States, and Jalisco, Mexico (6, 50; see also 126). These data indicate that, compared to modern herbivory, DT richness was moderate, whereas DT intensities were low, for each of these six plant assemblages.

In the four best-documented of these six plant assemblages, plant hosts were taxonomically varied and harbored distinctive herbivore communities and DT specialization–generalization levels (113). DT data for plant hosts in the fossil record are different than analogous modern plant host–insect herbivore data due to differing sampling strategies and DT data that do not map necessarily with a one-to-one relationship onto their plant host species (15), resulting in DT redundancies (113). For the latter constraint, in modern, taxonomically based plant host–insect herbivore bipartite webs, each herbivore species is linked directly to one or more plant host species. By contrast, in a fossil functionally based plant host–DT bipartite web, a single DT can be produced by multiple herbivore species that in turn map onto one or more plant host species; alternatively, multiple DTs can be produced by a single herbivore species that maps onto one or more plant host species. In both indirect examples, one-to-one links between a plant host and its insect herbivore are violated, producing the phenomenon of DT redundancy (113). Given these two caveats, a network analysis (113) indicated that it was the local depositional environment of each plant assemblage, rather than the taxonomic identities of the host plants in that locality, that was the most effective predictor of network links between DTs or FFGs and their plant hosts (113). Further tests of this pattern for the initial expansion of herbivory on seed plants from the Texas lower Permian would involve additional plant assemblages from the above four depositional environments represented by streams, but also from lacustrine and coastal settings.

How Did the Permian–Triassic Ecologic Crisis Affect Herbivores?

Very little is known about the response of insect herbivores to the most consequential event in the history of multicellular life, the Permian–Triassic (P-Tr) ecological crisis and extinction event. In continental environments, the P-Tr crisis at 252 Ma represented the demise of most plant, arthropod, and vertebrate lineages and presumably most interactions of plants with arthropods and pathogens. The Late Permian offers several well-preserved plant assemblages in Euramerica (118), Gondwana (96), and Cathaysia (81). However, the only well-preserved, albeit depauperate, occurrences of herbivory soon after the crisis are the Nedubrovo and Vyatkian plant assemblages from European Russia, containing a few surviving Permian plant lineages such as peltasperms and conifers (58). The only other well-preserved Lower Triassic plant assemblage with documented plant–insect interactions is from the Solling plant assemblage in Germany, which dates to the end of the Early Triassic, 4.7 Myr after the P-Tr event, and expresses the FFGs of hole feeding, margin feeding, skeletonization, surface feeding, oviposition, and galling (48, 60). By the Middle Triassic, 8–10 Myr after the P-Tr event, Euramerican plant assemblages from northeastern Italy (67, 71, 118) achieved DT richnesses and intensities equivalent to late Permian plant assemblages.

This long lag time in the recovery of Triassic plant assemblages after the P-Tr crisis raises some questions. First, what ecological and evolutionary processes were responsible for the prolonged establishment of new ecosystems that were repopulated by new plant hosts, new arthropod and pathogen herbivores, and their associations? Second, were subsequent environmental conditions so harsh (59) that establishment of new herbivore associations was inordinately prolonged? Alternatively, was the initial extirpation of lineages during the event so decisive (107) that the subsequent accumulation of new arthropod and pathogen associations among surviving and newly evolved plants was disproportionately slow? Testing these, or other, hypotheses would require analyses of abundant and diverse plant assemblages during the 5-Myr Early Triassic interval to provide insight into the response of arthropod herbivores to a globally calamitous event. One such plant assemblage is the Vyazniki locality of the Volga River Basin in Russia, which includes a rare instance of relatively continuous strata across the P-Tr boundary, revealing that the earliest Triassic fossils, such as a peltasperm seed-plant species, hosted mite galls and the earliest documented leaf mine (58).

What Is Herbivory Like in a Mesozoic Gymnosperm- and Fern-Dominated World?

Mesozoic gymnosperm- and fern-dominated plant assemblages typically are characterized by sporadic arthropod and pathogen associations from collections currently of less than 700 specimens that likely represent an inadequate number of samples. Major assemblages (62) include the Middle Triassic of northeastern Italy (71, 118); the Middle to Upper Triassic of the Paraná Basin of Brazil (17) and Cuyana Basin of Argentina (79); the Upper Triassic of Arizona, United States (65) and Antarctica (13); and the Middle–Late Jurassic boundary of northeastern China (31, 80, 90, 114). While these assemblages represent a limited number of specimens for definitive conclusions based on quantitative data (101, 102), there are two assemblages for which considerable data exist about the composition and structure of arthropod associations of Mesozoic plant communities where gymnosperms are dominant and ferns subdominant—the Late Triassic Aasvoëlberg 411 plant assemblage from the regional Molteno Flora of South Africa (65, 67) and the Early Cretaceous Dawangzhangzi plant assemblage of the regional Jehol Flora of northeastern China (31, 80, 130). These two plant assemblages present the best data for ascertaining the structure of Mesozoic plant communities before initial diversification of angiosperms later during the Early Cretaceous.

The Aasvoellberg 411 assemblage consists of 53 plant species and morphotypes, 10 FFGs with 44 DTs, and 5.54% of foliage items with herbivore damage. The three most herbivore-damaged species are *Heidiphyllum elongatum* (vltzialean conifer), *Dicroidium crassinervis* (peltaspermalean), and *Sphenobaiera schenckii* (ginkgoalean) (13, 67). The 106-Myr-younger Dawangzhangzi assemblage contains 61 plant species and morphotypes, 10 FFGs with 65 DTs, and 34.4% of foliage items attacked by herbivores, and the three most herbivorized species are *Liaoningocladus boii* (conifer of unknown affinities) and the czekanowskialeans *Czekanowskia* sp. 1 and *Czekanowskia rigida* (130). In both assemblages, ferns are subdominant but minimally damaged by herbivores. These two plant assemblages represent instantaneous snapshots in time and space (67, 130); assessments of multiple plant assemblages within their regional floras would determine variation in herbivory by employing alpha diversity at local and beta diversity at regional scales that would include metrics such as DT richness, turnover, and nestedness (10). For better documentation of beta diversity across time (10), analyses of additional Jurassic plant assemblages, such as the Daohugou assemblages of the regional Yanliao Flora of northeastern China, are needed. Such surveys, using the format of the Dawangzhangzi study (130), would offer better documentation of herbivory in a preangiosperm, Mesozoic world.

How Did the Initial Diversification of Angiosperms Affect Herbivores?

A very consequential biological event that potentially affected the trajectory of arthropod and pathogen herbivory is the geologically rapid diversification of angiosperms during the mid-Cretaceous from 125 to 90 Ma (82). Relevant studies of plant assemblages from this time interval (7, 37, 41, 74) are revealing but less informative than recent analyses (127–130) that used unbiased, abundant, and highly sampled plant specimens in which all available insect and pathogen damage was analyzed. This event, analogous to the expansions of seed plants during the later Paleozoic and grasslands in the later Cenozoic, evidently did not affect insect diversity, based on analyses of insect taxonomic global diversity (19, 76).

The primary data for such an analysis have been assembled from the gymnosperm-dominated Dawangzhangzi plant assemblage of the Lower Cretaceous (126 Ma) (130), mentioned above, and the 23-Myr-younger, angiosperm-dominated Rose Creek plant assemblage of the uppermost Lower Cretaceous (103 Ma), which represents one of several assemblages of the regional Dakota Flora of the Midcontinental United States (128, 129). Exhaustive analyses of herbivory from these two plant assemblages indicate that, for Dawangzhangzi, oviposition and piercing and sucking are the most highly ranked FFGs for their impact on herbivory, whereas for Rose Creek, piercing and sucking and pathogens are the most highly ranked, revealing the importance of these latter two FFGs for the emergence of angiosperm herbivory (128–130). Beta diversity analysis studies of DT richness, turnover, and nestedness (10) are needed to indicate similarities or differences in the broad ecological structures among plant hosts and their arthropod herbivores between the Dawangzhangzi and Rose Creek plant assemblages that were not addressed by diversity studies of insect families through geologic time (19, 76). Other methods, such as a modified bipartite network analysis based on functional units such as feeding event occurrences, also may be important for ascertaining the more detailed structures of herbivore communities in these two plant assemblages (112, 113).

How Did the Cretaceous–Paleogene Ecologic Crisis Affect Herbivores?

Analogous to but milder in intensity than the P-Tr ecological crisis was the global K-Pg ecologic crisis that dramatically affected plants, insects, and their associations. In an analysis of 13,441 overwhelmingly angiosperm specimens from the Williston Basin of North Dakota, representing

a largely unbroken stratigraphic record of 2.2 Myr (earlier latest Cretaceous, 1.4 Myr; later earliest Paleogene, 0.6 Myr), 51 DTs from eight FFGs were recorded from 14 stratal horizons (69, 70). Each of the 51 DTs was categorized into DT host-plant specificities of generalized, intermediate specificity, and specialized and evaluated for their stratigraphic persistence using a technique that allows for fossil preservation potential to inform placement of time-based confidence intervals on each DT (70). The data indicated that functionally specialized (including intermediate specificity) associations of the Late Cretaceous were largely extirpated at the boundary, whereas functionally generalized associations were sustained over the boundary. A major result of this study suggested that the ecologic devastation from an asteroid impact at Yucatan, Mexico, had a dramatic effect, resulting in the survival of generalized and the extirpation of specialized herbivore associations (123).

A follow-up study (34) examined in greater detail mining DTs from the Williston Basin and combined these observations with new leaf-mine DT data from 14 plant assemblages within the 1.7 Myr after the event throughout the Western Interior of North America (WINA) (120, 121, 123). The results of this study indicated that the effect of the K-Pg ecological crisis left no surviving leaf-mine DTs (34). A related study (123) documented highly imbalanced local ecosystems soon after the K-Pg event, with colonization of host plants by new leaf miners likely being due to immigration from outside North America. This post-event pattern, however, was found in Patagonia (33) but not in Europe, indicating that there are varying regional patterns of ecological collapse and recovery that appear to be influenced by distance from the asteroid impact site (116). Future studies of profound global ecological crises should examine the role that habitat, latitude, and distance from the K-Pg impact site had on the survivability of functionally specialized versus generalized associations of arthropods, pathogens, and their host plants.

How Was Herbivory Affected by the Paleocene–Eocene Thermal Maximum?

The most extensively examined interval for herbivory in geological time is the PETM, a brief, transient, 170,000-year episode of temperatures elevated by 5°–8°C and a threefold to fourfold increase in atmospheric CO₂ content beginning at 55.8 Ma, during the early Paleogene Period (29, 124). (From oldest to youngest, the Paleocene, Eocene, and Oligocene are the epochs that constitute the Paleogene Period, and the initiation of the PETM defines boundary between the Paleocene and Eocene epochs at 55.8 Ma.) The seminal study that established the FFG-DT system (22) was used to establish insect herbivory patterns before and after the thermal event in the WINA (120), notably before specific strata were identified by geochemical methods as containing the PETM (124). These patterns of herbivory included damage assessments from bulk census data of dicot leaves. The data included the percentage of leaves with any DTs, the percentage of leaves that displayed a greater amount of external (ectophytic) than of internal (endophytic) feeding DTs, and the percentage of leaves having more than one kind of DT. The analysis showed that these values were significantly greater in the early Eocene than in the late Paleocene (120). For individual plant genera, Eocene taxa displayed significantly greater damage diversity than did Paleocene taxa, a pattern that also is demonstrated when the same host-plant genus occurs in both Paleocene and Eocene localities (120). This trend revealed two distinct herbivory syndromes in which vegetation of the pre-PETM late Paleocene was characterized primarily as deciduous and occurring in humid, warm temperate to subtropical climates, whereas the post-PETM early Eocene consisted of mixed deciduous and thick, evergreen leaves present in a humid, subtropical climate (63, 121).

Once the precise stratigraphic interval defining the PETM was found in the Bighorn Basin of Wyoming (124), new studies targeted specific localities occurring immediately before, during, and immediately after the PETM (21, 26, 27, 29). Correlations between temperature and DTs, and between generalized and specialized damage, for metrics such as total damage diversity, specialized diversity, mining diversity, the proportional distribution of DTs, and the effect of leaf mass

per area associated with leaf palatability were assessed for individual plant genera (26, 29). These metrics show in greater detail the specific physiological responses of individual plant genera and the spectrum of changes in herbivory levels of their arthropod herbivores in response to the dramatic environmental changes during this interval of increased temperature and CO₂ levels. The response of arthropod herbivores to this global change consistently involved an increase in the richness and intensity of herbivory (26, 28, 30). Features such as geographical endemism and temporal succession of certain herbivory styles were determined (25, 28). However, such resolution of data required (a) stratigraphic identification of the PETM interval; (b) excavation of additional localities for regional representation, including other basins; (c) collection of a sufficient number of samples; and (d) new methods of data analysis (8, 23). One persistent question is whether the precise PETM interval is detectible outside of Wyoming.

How Did Herbivores Respond to Later Paleogene and Neogene Environmental Events?

The PETM was followed by other major transient and prolonged environmental events demarcated by changes such as atmospheric temperature and CO₂ levels, aridity, and mountain building. Three studies document relationships among environmental events, plant physiologic accommodation, and arthropod herbivore response and illustrate the types of questions that can be addressed with sufficient sampling across time, space, and habitat. The first study (117) examined long-term Paleogene patterns of herbivory in Spitsbergen, Norway, during an approximate 27-Myr interval. This period was characterized by broadleaved deciduous and conifer forests growing at high-latitude conditions with limited and seasonally absent light levels, reflecting a cooling trend and a shortened growing season. During this time, herbivory declined in richness and intensity. Notably, almost all DTs were attributable to externally feeding herbivores, and rarely to specialized herbivores such as miners, gallers, and many piercers and suckers (117). A second study (30) documented an event at the Paleocene–Eocene boundary interval in a record from the Qinghai–Tibetan Plateau in southeastern China, where there was a shift from subtropical shrubland to alpine forest. This vegetational change was accompanied by a shift in the composition of the regional flora and a precipitous decline in the richness and intensity of insect herbivory attributable to a major decrease in temperature and regional mountain uplift. A third study (89) examined a mid-Paleogene plant assemblage from a lignite mine in central Germany that preserved a lowland riparian forest displaying evergreen dicot foliage characterized by lengthened leaf lifespan, an extended photosynthetic season, and substantial antiherbivore defenses. At this site, there were heightened levels of herbivory and an elevated level of galling but a virtual absence of mining (89), a pattern also documented for evergreen dicot taxa from nearby Paleogene sites (119). Interpretation of the results from the three mid-Paleogene assemblages from central Germany indicate long-term adaptation of arthropod herbivores to short-lived, evergreen leaves (119). Nevertheless, it appears that the adaptation may be site specific and opportunistic, as contemporaneous assemblages from the WINA show an alternative pattern of considerably more herbivory on deciduous, short-lived leaves in areas where they occur more frequently than evergreen, long-lived leaves in the same assemblage (121). Such studies, with large sample sizes of well-preserved foliage and use of appropriate analytical techniques, provide opportunities to discern important patterns of plant hosts and their arthropod and pathogen herbivores. This is especially valid for using these past analog data to understand current patterns in global climate change.

Several studies of the Neogene illustrate additional pathways toward understanding patterns of herbivory in the fossil record. One study analyzed herbivory variation along a latitudinal gradient from three localities in the Czech Republic to Türkiye during the temperate climate of

the early Neogene (3). Results of the study found that DT intensity was associated with abiotic features of temperature and precipitation; by contrast, DT richness was associated with biotic factors such as plant richness and the particular biome occupied. Studies of biome occupancy have shown that historical and biogeographic factors played an important role in determining herbivory richness (5). Another study of the early Neogene examined the Mush Valley of Ethiopia (24). This assemblage includes six stratigraphic levels that were used to analyze variation in DT richness, intensity, and composition among diverse plant taxa for potential correlations to abiotic and biotic features. No correlations were found between the variation in damage metrics and host plant assemblage and any abiotic or biotic variable, with the exception that the presence of Fabaceae (legumes) in one plant assemblage was associated with greater herbivory (24). Symbioses with nitrogen-fixing bacteria render Fabaceae and possibly other plants in the community more nutritious for insect herbivores (24). An additional study (132) from a mid-Neogene plant assemblage in southern China documented high DT richness and intensity that included the same or very similar associations presently occurring on analog plant taxa in the same area. Comparisons of diverse interactions from Neogene deposits of eastern India are identical or nearly so with modern interactions on the same host-plant genera of the same region, indicating that modern herbivore communities extend deep into the Neogene (51, 52, 56). Similarly, evidence shows that the distinctive Malesian insect and pathogen community of kauri (*Agathis*) extends to the earliest Paleogene of Argentina (33), suggesting that past biogeographical patterns of herbivory can be tracked through long stretches of time with detailed association data.

Which Herbivory Patterns Occur on Focal Plant Genera through Time?

Although tracking of arthropod and pathogen herbivore communities on individual plant lineages through time has been established for older Mesozoic lineages such as conifers (31, 33), it is extant representatives of more recent angiosperms that provide the most important data for herbivore community composition on plant-host genera and associated habitat shifts (56). Arthropod damage on southern beech (*Nothofagus*) was tracked for an approximately 48-Myr interval from five time planes, two from the early Paleogene of Antarctica's Palmer Peninsula and three from the late Neogene of southeastern New Zealand (88), and a mid-Neogene locality in southernmost Argentina (44). One study (88) indicated that rich local vegetation surrounding New Zealand's Hindon Maar volcanic lake was supported by local nutrient-rich soils, whereas DT richness was supported by paleoclimate conditions (88). Occasionally, a plant-insect interaction is tracked in multiple plant assemblages in time and space on the same host (52); the best example of this is specialist association DT403 on *Parrotia* (Hamamelidaceae), present for 15 Myr spanning from the mid-Neogene of China, to the late Neogene of Germany, to present-day Iran (1, 2, 5). The *Parrotia*-DT403 interaction is younger than that postulated by Opler (91) for genera of lepidopteran miners on late Neogene *Quercus* (Fagaceae) of the WINA, which indicates that some modern interactions can extend from three to five million years into the distant past.

OTHER FORMATIVE ISSUES THAT REQUIRE FURTHER EXPLORATION

Several ongoing but minimally explored ecological issues have been identified in fossil assemblages and could benefit from new data, novel approaches, and additional analyses (see the sidebar titled Future Issues in the Ecology of Arthropod and Pathogen Herbivory to Be Explored in Fossil Plant Assemblages). At a more focused level, a relevant topic is whether antiherbivore plant defenses (64, 77, 87, 95, 131) or parasitoids (72, 130) are responsible for anomalously low herbivory levels (130) in fossil plant assemblages. Another theme is how studies of herbivore

FUTURE ISSUES IN THE ECOLOGY OF ARTHROPOD AND PATHOGEN HERBIVORY TO BE EXPLORED IN FOSSIL PLANT ASSEMBLAGES

Narrower Issues

- What is the historical role of antiherbivore defenses in plant–insect interactions (64, 77, 87, 95, 131)?
- What is the historical role of parasitoids in affecting plant–insect interactions (72, 130)?
- How long ago did modern plant–insect interactions originate (5, 33, 35, 45, 56, 57, 68, 85)?
- How are insufficient sampling and damage-type redundancy evaluated (108, 112, 113)?
- What are the methodologies appropriate for construction of network structures (113)?

Broader Issues

- What is the biogeography of plant–insect interactions among distant contemporaneous regions of the past (28, 124)?
- Do significant differences exist in plant–insect interactions between ferns and angiosperms in space and time (38, 42, 93)?
- What are the biological causes of the dramatic decline of specialized associations following a major global ecological crisis (15, 34, 39, 69–71, 123)?
- Which plant–insect interaction metrics can be used productively to assess the development of Neotropical forests after the K–Pg ecological crisis (14, 46, 125)?
- Did plant–insect interactions play a role in the emergence of grasslands during the later Cenozoic (49, 55, 65)?

communities (98) can overcome the challenges of insufficient sampling and DT redundancy from data in the fossil record (111, 113). Although herbivore communities have been established for several plant species based on DT data (33, 67, 71, 108, 128–130), considerable insight could be gleaned by methodologically appropriate comparisons, such as network modeling, of functional network structures among herbivore communities in space and time (113). Lastly, how ancient are modern plant–insect associations? Several studies trace distinctive DTs to the early to mid-Neogene (5, 56, 57), although other DTs extend to the earliest Paleogene (33, 45), and highly stereotyped lepidopteran leaf mines extend to the Upper (85) and Lower (35, 68) Cretaceous (**Supplemental Figure S1**). Evaluation of the antiquity of plant–insect interactions provides (a) the establishment of rates of evolution for herbivorous insect clades that leave interpretable damage in the fossil record, (b) assessment of past biogeographical distributions of herbivorous insect lineages, and (c) better calibration of minimal age dates for herbivorous insect clades.

A broader-scale issue is the role that plant–insect interactions play in the emergence, evolution, and distribution of major plant lineages and communities (see the sidebar titled Future Issues in the Ecology of Arthropod and Pathogen Herbivory to Be Explored in Fossil Plant Assemblages). The biogeography of plant–insect interactions can distinguish differences in herbivory richness and intensities between contemporaneous regions, such as Patagonian Argentina and WINA, to test hypotheses on the evolution of regional biodiversity (124). On a local level, hypotheses can be tested regarding the physical or biological barriers between nearly contemporaneous localities within a basin (28). Another question is whether there are significant differences in herbivory between ferns and angiosperms, a contentious issue among ecologists for over 30 years (42). Although herbivory on ferns has been documented in the fossil record (38, 93), limited comparisons have been made only for glossopterids (14) and angiosperms (97). A comprehensive approach is needed to address this issue, including answering the question of whether current fern herbivory is reflective of the past. The decline of specialized herbivore associations has been established for

Supplemental Material >

the global K-Pg crisis in multiple regions (34, 69–71, 123), but considerably less is known about the aftermath following the massive P-Tr ecological crisis (39) or about regional ecological events. Additional issues affecting plant–insect interactions are the roles of DT richness, DT frequency, and other metrics for understanding the origin and early development of modern Neotropical forests soon after the K-Pg ecological crisis (15, 46, 125). However, this approach has not been used to understand the emergence and expansion of grasslands and their presumptive herbivores during the late Paleogene to Neogene. A few studies have traced the early evolution of modern insect herbivores in Miocene savannas and grasslands (49, 55), but virtually nothing is known of herbivore associations on early grasses (65).

CONCLUDING REMARKS

This review provides incomplete answers to important ecological questions in a rapidly advancing field. The challenge is to address the above actionable queries (see the sidebar titled Future Issues in the Ecology of Arthropod and Pathogen Herbivory to Be Explored in Fossil Plant Assemblages) with new data, up-to-date procedures, and conceptually innovative solutions. While the FFG-DT system of herbivory analysis has some challenges, it does represent important proxy data for the arthropods and pathogens that historically have created damage on plants. In many cases, it may be the only data present in the fossil record that relate plant hosts to their interactions with insect herbivores. Arthropod and pathogen damage in the terrestrial fossil record is therefore a valuable resource that can be leveraged to understand patterns of herbivory between plants and their arthropod and pathogen consumers in deep time.

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