

Deep-time patterns of tissue consumption by terrestrial arthropod herbivores

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Abstract A survey of the fossil record of land-plant tissues and their damage by arthropods reveals several results that shed light on trophic trends in host-plant resource use by arthropods. All 14 major plant tissues were present by the end of the Devonian, representing the earliest 20 % of the terrestrial biota. During this interval, two types of time lags separate the point between when tissues first originated from their earliest consumption by herbivorous arthropods. For epidermis, parenchyma, collenchyma and xylem, live tissue consumption was rapid, occurring on average 10 m.y. after the earliest tissue records. By contrast, structural tissues (periderm, sclerenchyma), tissues with actively dividing cells (apical, lateral, intercalary meristems), and reproductive tissues (spores, megagametophytes, integuments) experienced approximately a 9-fold (92 m.y.) delay in arthropod herbivory, extending well into the Carboniferous Period. Phloem similarly presents a delay of 85 m.y., but this incongruously long lag-time may be attributed to the lack of preservation of this tissue in early vascular plants. Nevertheless, the presence of phloem can be indicated from planar spaces adjacent well-preserved xylem, or inferred

from a known anatomy of the same plant taxon in better preserved material, especially permineralisations. The trophic partitioning of epidermis, parenchyma, phloem and xylem increases considerably to the present, probably a consequence of dietary specialization or consumption of whole leaves by several herbivore functional feeding groups. Structural tissues, meristematic tissues and reproductive tissues minimally have been consumed throughout the fossil record, consistent with their long lags to herbivory during the earlier Paleozoic. Neither angiosperm dominance in floras nor global environmental perturbations had any discernible effect on herbivore trophic partitioning of plant tissues.

Keywords Angiosperm diversification · Ecological lags · Fossil record · Functional feeding-groups · Land-plant tissues · Trophic partitioning

Introduction

Land plants and their arthropod herbivores overwhelmingly structure modern ecosystems (Futuyma and Agrawal 2009), and there is increasing evidence that the interactions between these two hyperdiverse groups has been continual and increasing since the earliest megascopic biotas were established during the later Silurian, approximately 425 Ma (Kenrick and Crane 1997; Bateman et al. 1998). The deep-time ecological relationships between these arguably two most diverse of terrestrial groups has been studied only recently, using a variety of biological (Herrera and Pellmyr 2002; Futuyma and Agrawal 2009) and paleobiological (Wilf et al. 2006; Currano et al. 2010) approaches. Other studies emphasize a more taxonomic approach, in which clades of co-occurring and interacting plants and insects provide examples of co-speciation, co-radiation or co-evolution (Becerra et al. 2009; Kergoat et al. 2011).

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However, broad patterns that provide the temporal context of trophic dynamics rarely are revealed in recent examinations of deep-time plant–arthropod relationships, indicating a missing link in the inference chain relating plant hosts to their herbivore consumers. Nevertheless, the fossil record of plants, insects and the crucial evidence of inflicted damage and pollination does provide valuable data, trends and sources of inferences (Labandeira 2002) regarding how insects have accessed plants since the mid-Paleozoic.

The diverse paleobotanical and paleoentomological records are only surpassed by the underutilized yet rich record of evidence for their trophic relationships. In particular, these relationships involve the fossil record of arthropod damage (Labandeira et al. 2007) and pollination modes (Labandeira 2010). Although deemed sparse (Futuyma and Agrawal 2009), the fossil record nevertheless is surprisingly robust, particularly for resolving broad patterns in space, time and habitat. The general trophic approach of recorded arthropod-mediated damage on particular plant tissues that I employ here previously has been used to address issues in the fossil history of host-plant use by insects. This rich record has been utilised to determine phenomena such as the regional effects of the end-Cretaceous extinction on plant–insect associations during the succeeding Paleocene (Labandeira et al. 2002; Wappler et al. 2009), the four global phases of plant–arthropod associations (Labandeira 2006a), and evidence for insect herbivore outbreaks at fossil sites (Labandeira 2012).

In this contribution, I examine a finer grained record of plant–arthropod trophic data within the context of a coarse-grained geochronology. In particular, I assess the arthropod herbivore and pollinator use of 14 major types of tissue from the mid Paleozoic to late Cenozoic. This contrasts with an earlier, more generalized examination (Labandeira 2007; Iannuzzi and Labandeira 2008) that documented feeding damage in six types of plant organs for the formative Paleozoic interval representing the beginning of the plant–insect associational record. This study also encompasses and documents specific trophic interactions for the 425 million years from the mid-Paleozoic to the present. It is the first examination in the fossil record of plant–insect interactions wherein plant tissue types consumed by terrestrial arthropod herbivores are tracked through geologic time to assess the availability and partitioning of food resources at the histological level. The intention of the present study is to provide data to address patterns of land-plant tissue use by arthropod herbivores, and to derive general conclusions of trophic evolution from these patterns.

Materials and methods

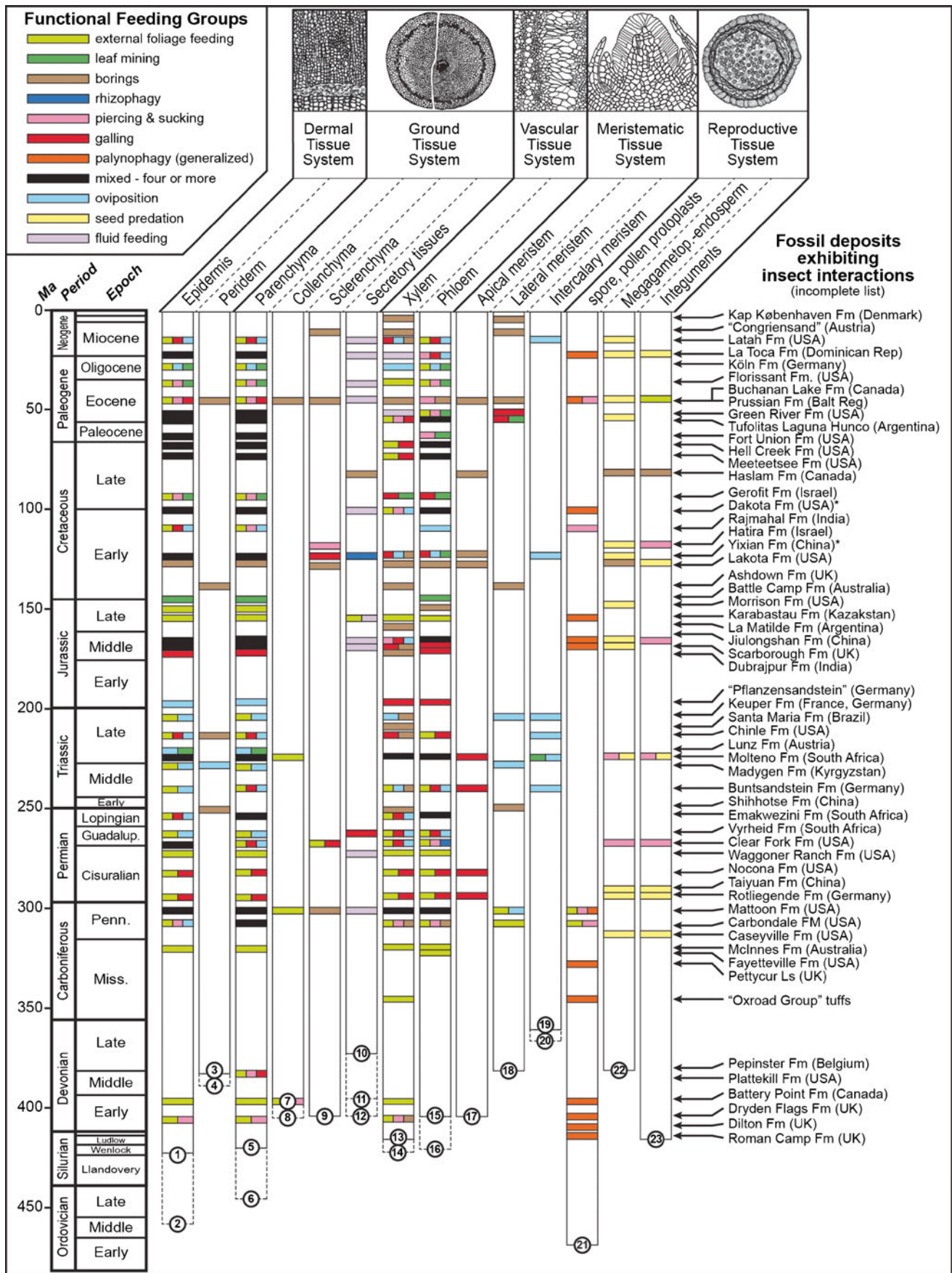
A data set was assembled consisting of 253 instances of plant-host tissues that exhibit damage for one or more functional

Fig. 1 The fossil history of terrestrial arthropod herbivore feeding on plant tissues. With the exception of early herbivore occurrences for each tissue type from the earlier Paleozoic, the documentation for this inventory is not exhaustive because of space limitations. Sources for evidence of arthropod consumption of plant tissues are Labandeira (2002, 2006a, 2006b, 2007, 2012). Sources referencing the earliest occurrences of major land-plant tissue types for the mid Paleozoic, in circles at the bottom, are: (1) earliest megafossils (Kenrick and Crane 1997); (2) epidermal cuticles (Edwards 2003); (3) lignophyte bark (Stein et al. 2012); (4) earlier lignophyte occurrences (Scheckler et al. 2006); (5) earliest liverwort megafossils (Edwards 1990); (6) possible liverworts (Kenrick and Crane 1997); (7) feeding damage on collenchyma (Banks and Colthart 1993); (8) earlier occurring, probably collenchyma-bearing trimerophytes (Taylor et al. 2009); (9) earliest sclerenchyma (Powell et al. 2000); (10) secretory tissue flaps (Taylor et al. 2009); (11) possible secretory cells in the zosterophyll *Oricilla* (Taylor et al. 2009); (12) “possible secretory structures” (Taylor et al. 2009); (13) earliest vascular plants (Kenrick and Crane 1991); (14) tracheid-like tubes (Kenrick and Crane 1997); (15) phloem tissue (Satterthwait and Schopf 1972); (16) possible phloem tissue in a cooksonioid plant (Kenrick and Crane 1997); (17) terminal shoot meristem (Eggert 1974); (18) bifacial vascular cambium (Stein et al. 2012); (19) earliest sphenophyte with nodal meristem (Wang et al. 2006); (20) older sphenophyte with possible nodal meristem (Mamay 1962); (21) earliest definitive land-plant spores (Gray 1993); (22) earliest functional ovule (Gerienne et al. 2004); (23) sporangial tissue envelope (Remy et al. 1993). The *asterisk* after the Yixian Formation indicates that coeval deposits from the Aptian Black Hawk locality of South Dakota, USA, were included. Similarly, the *asterisk* after the Dakota Formation signifies that the Frontier Formation, of similar age, was included

feeding groups (FFGs) of herbivorous arthropods (Fig. 1). These records of tissue damage originated from 59 fossil floras that represent two-dimensional compression–adpression and three-dimensionally permineralized states of preservation (Taylor et al. 2009). The data are pegged to a standard global geochronology (Gradstein et al. 2012). Figure 1 presents these data in matrix form, and represents an updated, reorganized, and more finely resolved version of data used in earlier compilations and analyses (Labandeira 2002, 2006a, b, 2007). Data sources can be found in Appendix 1 of the electronic supplementary material which includes unpublished personal observations.

Characterization of plant tissues

Land-plant tissues are categorized into tissue systems, each of which contains multiple tissue types. Tissue types, in turn, consist of cell types (Evert 2006). For example, the ground tissue system consists of parenchyma, collenchyma, sclerenchyma and secretory tissues. Sclerenchyma, in turn, consists of two cell types, fibers and sclereids. Occasionally, there is disagreement among plant anatomists about the extent of inclusion and what constitutes an identifiable tissue system or type. Figure 1 follows the standard fourfold categorization of tissue systems: dermal, ground, vascular and meristematic. However, a fifth category has been added that, although not considered a true tissue system, consists



of reproductively associated tissues that typically occur as fossils in the same contexts as those preserving leaves, stems and roots.

Characterization of insect herbivory

FFGs are the fundamental ways that terrestrial herbivorous arthropods (insects, mites and millipedes) consume plant tissues (Table 2). Important for the fossil record, FFGs are recognized in the fossil record by distinctive, often stereotypical, damage patterns that are left on well-preserved plant tissues (Labandeira 2002; Labandeira et al. 2007). The ten FFGs used in Fig. 1 are distributed on tissue-type occurrences throughout the data matrix by a coordinate color scheme. Three FFGs are exophytic, in which the feeding herbivore is positioned outside the consumed tissues: external foliage feeding, palynophagy (the consumption of spores or pollen), and fluid feeding, defined by the imbibing of secretory products such as nectar or glandular exudates. By contrast, endophytic feeding modes, characterized by feeding arthropods entombed within their plant host's consumable tissues, consists of leaf mining on planar foliar and stem tissues, galling that causes control of the developmental machinery of its host to produce tumor-like swellings, seed predation that results in feeding access to nutritive embryonic tissues, and borings that typically penetrate three-dimensional, often hardened trunk tissues. A third, intermediate, category is recognized where the arthropod herbivore is located externally but feeds on internal tissues; this includes piercing-and-sucking, oviposition and root feeding. Oviposition, while not a true feeding strategy because of the use of a female ovipositor to lay eggs instead of employing mouthparts to feed on tissues, nevertheless has been considered a FFG, as oviposition has generated a distinctive fossil record of diverse plant tissue damage. Root feeding, or rhizophagy, is rare and can occur either within or external to root tissues. Eleven categories FFGs are provided in Fig. 1, including a mixed category indicated in black of more than three FFGs accessing a single tissue type, in part to track elevated levels of host-tissue partitioning through time.

Herbivory is the consumption of live plant tissues, as opposed to detritivory, which is the ingestion of dead plant and other organismic tissues. Separation of herbivory from detritivory in the fossil record follows four explicit criteria, either singly or preferably in combination (Labandeira 2006b). First, for herbivory, it is essential that there is some indication of plant response to a previously induced arthropod trauma. The most common evidence for a plant reaction to herbivory is production of a distinctive tissue, often callus, as a wound response. Second, small structural features at the herbivore-altered plant edge, such as resistant veinal stringers, necrotic tissue flaps, or areas of secondary fungal infection, also indicate herbivory. A third feature is distinctive stereotypy of a feeding pattern on a particular plant tissue, organ or host species. Such specificity would be encountered less frequently for detritivores, which have considerably more eclectic diets than in herbivores. Fourth, important for the more recent part of the record is recognition of a particular feeding syndrome that is present in a closely related and extant descendant lineage with known feeding habits. In practice, the separation of herbivory from detritivory presents few instances of confusion (Labandeira 2002), certain types of skeletonization being the most problematic.

Structure of the study

Table 1 summarizes the important variables depicted in Fig. 1; Appendix 1 of the supplementary material provides data documentation. This study covers the known interval of megascopic terrestrial life for the past 450 m.y. Although recognition of the earliest terrestrial biotas containing discernible plants, arthropods and fungi has been controversial (Gray 1993; Kenrick and Crane 1997), there appears to be an emerging consensus that such an event commenced during the mid- to late Silurian, during Wenlock and Ludlow times (Bateman et al. 1998). The dating of these and more recent events is tied to a recently published time-scale (Gradstein et al. 2012). Plotted within this framework of geologic time and fossil biotas are two fundamental sources of presence/absence data: (1), the 14 land-plant tissue

Table 1 Study structure

Feature	Value
General geochronological duration of the study	425 m.y.
Basic floras examined ^a	59
Arthropod functional feeding groups ^b	10
Land-plant tissue systems	5
Land-plant tissue types	14
Tissue-type occurrences with interactions for all deposits	253
Total functional feeding groups for all tissue-type occurrences ^c	530
Mean number of functional-feeding types for each tissue type occurrence	2.09

^aNot a complete list for Fig. 1; only the major floras are listed.

^bDoes not include (in black) a composite category that represents the presence of four or more functional feeding groups.

^cCorresponds to each colored box in Fig. 1, except for black boxes that range from four to six functional feeding groups

Table 2 Terrestrial arthropod functional feeding groups^a

Feeding system	Functional feeding group	Examples	Tissues consumed	Earliest occurrence ^b
Exophytic	External foliage feeding	Margin feeding, hole feeding, surface feeding, skeletonization	Epidermis, parenchyma, xylem, phloem	Middle Devonian
	Palynophagy	Whole palynomorph consumption, punch-and-sucking of protoplasts	Spores, pollen, megaspores	Middle Silurian
	Surface fluid feeding	Siphonate feeders, spongers, lappers	Secretory tissues, epidermis	Late Pennsylvanian
Intermediate	Piercing-and-sucking	Deep-tissue feeding, mesophyll feeding, punch-and-sucking	Xylem, phloem, epidermis, parenchyma, megagametophyte endosperm tissues, integuments	Early Devonian
	Oviposition	Solitary, rows, multiple clusters	Epidermis, parenchyma, xylem, phloem, periderm	Late Pennsylvanian
	Rhizophagy	[none recognized] ^c	Epidermis, parenchyma, xylem, phloem	Middle Pennsylvanian
Endophytic	Leaf mining	Serpentine mines, blotch mines, cambial mines	Epidermis, parenchyma, xylem, phloem, apical meristem, lateral meristem, intercalary meristem	Middle Triassic
	Galling	Prosoplasmic galls, histioid galls, organoid galls	Epidermis, parenchyma xylem, phloem, collenchyma, sclerenchyma, apical meristem	Middle Devonian
	Seed predation	(None recognized) ^c	Epidermis, megagametophyte endosperm tissues, integuments	Early Pennsylvanian
	Borings	Bark borings, heartwood borings, sapwood borings, pith borings	Periderm, parenchyma, xylem, phloem, collenchyma, sclerenchyma, apical meristem, lateral meristem, intercalary meristem	Early Devonian

^a See Labandeira (2002, 2006a, 2006b) and Labandeira et al. (2007) for further elaboration of the functional feeding groups (FFGs). ^b From Fig. 1. ^c No widely recognized subtypes of rhizophagy or seed predation have been established or are commonly used

types and (2), the ten FFGs that are plotted from 59 fossil arthropod-damaged plant tissues recorded from these biotas, which are allocated to 530 occurrences of FFGs, yielding an

Table 3 Lag times separating the first definitive appearance of tissue types from the first reliable occurrence of the corresponding insect herbivory

Herbivore delay type	Tissue type	Geochronologic interval (Ma) ^a	Delay (in m.y.) ^b	Mean for herbivore lag time (in m.y.) ^b
Short term	Epidermis	426–410	16	10 (for short-term)
	Parenchyma	424–410	14	
	Collenchyma	403–403	0 ³	
	Xylem	420–410	10	
Long term	Periderm	386–253	123	92 (for long term)
	Sclerenchyma	410–303	97	
	Secretory tissues	378–303	75	
	Phloem	410–325	85	
	Apical meristem	410–296	114	
	Lateral meristem	386–311	75	
	Intercalary meristem	365–243	122	
	Palynomorph protoplasts	475–421	54	
	Megagametophytic and endosperm tissues	386–318	68	
Integuments	421–318	103		

^a Absolute years. ^b Millions of years. ^c The earliest occurrence coincides with the earliest herbivory of this tissue

average of 2.09 FFGs per tissue-type occurrence. Each tissue type occurrence harbors from one to six FFGs; four or more FFGs are indicated by a black bar. Within a deposit or flora, an isolated, single, tissue with a single FFG indicates that there was specialized consumption of a single target, such as xylem feeding for a piercer-and-sucker. By contrast, multiple adjacent tissues with multiple FFGs frequently suggest that an entire organ, such as a leaf, was consumed by a single feeding event.

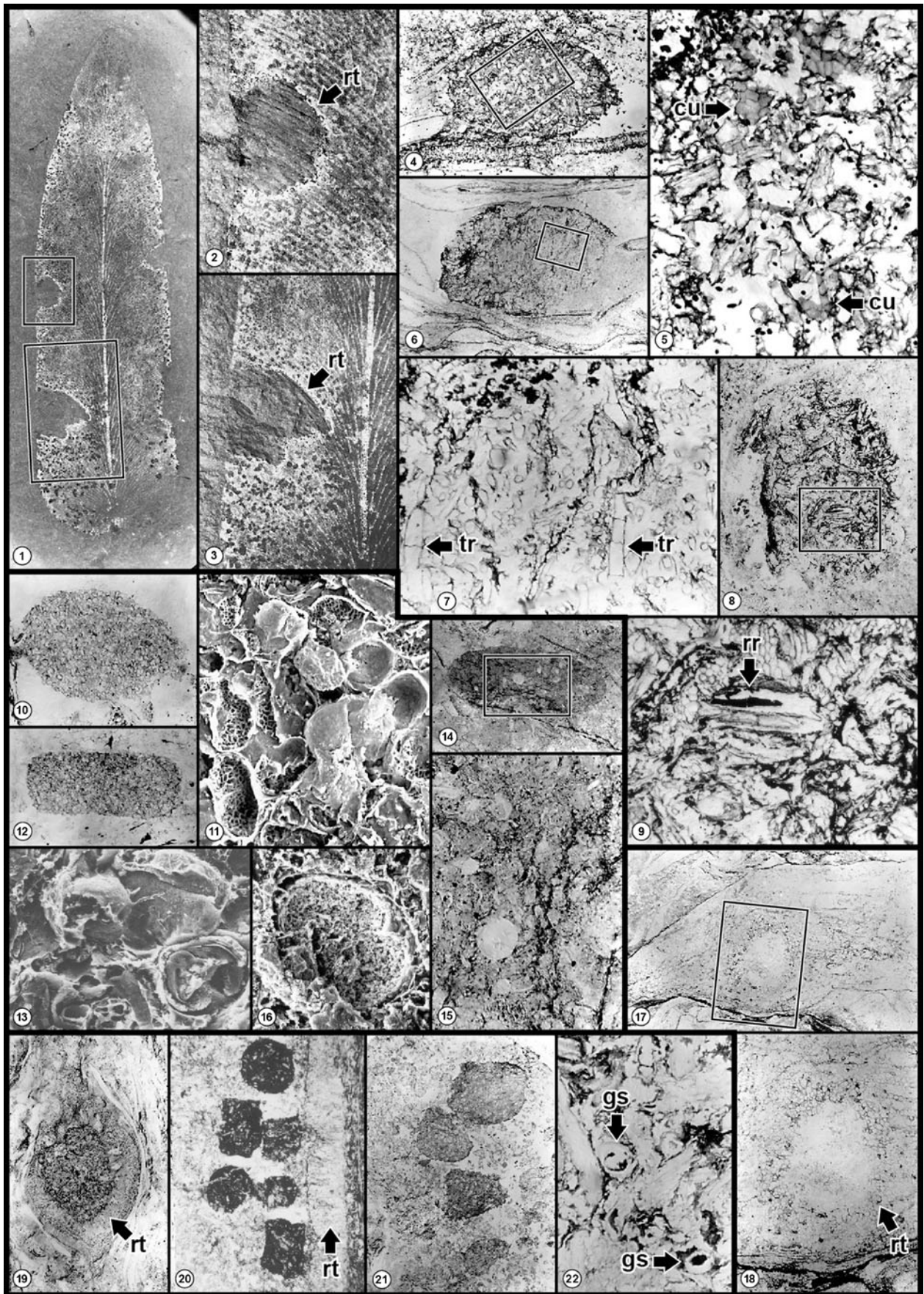
Results

Seven principal results and observations issue from these data and involve the gross nature of the land plant–arthropod associational record throughout their documented ca. 425-m.y. interval of interaction. These results represent a much finer-grained partitioning of the data than other recent findings (Labandeira 2002, 2006a, b, 2007), and offer new insights.

- (1) All of the 14 major tissue types were present by the end of the Devonian (359 Ma), within the first 15 % of the entire documented duration of vascular land plants in terrestrial ecosystems. The one histological exception is endosperm, a feature of angiosperm seeds that probably originated during the earliest Cretaceous (Baroux et al. 2002), but whose nutritional precursor, megagametophytic tissue, was present since the origin of the seed habit during the Middle Devonian.
- (2) Three major time gaps occur in the record of plant tissue and arthropod herbivore associations. They are an extensive, ca. 41 m.y. gap inclusive of the Late Devonian to almost all the Early Mississippian interval, a smaller 5 m.y. gap during the Early Triassic, and a larger ca. 30 m.y. gap in the Early Jurassic.
- (3) There are two major durations of time lags between the first documented appearances of the 14 tissue types and their earliest consumption by insect herbivores (Table 3). These important time lags centre on a set of four tissue types with comparatively rapidly consumed tissues that are characterized by a mean lag time of ca. 10 m.y. A second set of ten tissue types exhibits a 9-fold longer delay of 92 m.y.
- (4) The partitioning of basic tissue types by herbivore FFGs appear to increase through time, as measured primarily by the number of tissue types with four or more FFGs.
- (5) There are six tissues that rarely were significantly used by arthropod herbivores throughout the studied interval. These minimally utilized tissues are the structural tissues of periderm, collenchyma, and sclerenchyma, as well as the three actively dividing tissues of apical, lateral, and intercalary meristem that dictate plant growth and architecture.

Fig. 2 Modes of arthropod feeding in forested habitats from Middle (1–3) and Late (4–22) Pennsylvanian-age deposits of the Illinois Basin, USA. The Middle Pennsylvanian material is from the Mazon Creek compression deposit of the Carbondale Formation in north-central Illinois; the Late Pennsylvanian coal-ball permineralized specimens originate from the Berryville locality of the Mattoon Formation in southeastern Illinois. 1–9: At 1–3 is external foliage feeding on *Macroneuropteris scheuchzeri* (Medullosaceae) showing surface abrasion (1, 2), and margin feeding (1, 3) of all foliar tissues. Original axial length of leaf is 8.8 mm; rectangular templates at left are enlarged in (2) and (3); arrows point to herbivore induced reaction tissue (rt). Specimen FMNH PP 26460. 4, A coprolite from feeding on epidermal and perhaps subjacent tissues of *Alethopteris* sp. foliage (Medullosaceae), enlarged in (5), showing indigestible sheets of cuticle (cu, black arrow) and fragmented trichomes. USNM peel BV80nd; slide 553703. 6–7, A coprolite containing *Alethopteris* sp. foliage laden with trichomes, shown in transverse, oblique and longitudinal (tr) sections in (7). USNM peel BV65-Ctop; slide 553704. 8, a coprolite of vascular tissue, magnified in (9) to show elongate amorphous masses that preserve as resin rodlets, one of which (rr) is indicated by an arrow. USNM peel BV39-Gtop; slide 553705. The coprolites at (4), (6) and (8) are 2–3 mm long in greatest axial width. 10–16: Pollen consumption (palynophagy) and related feeding habits from tree-fern, cordaitalean, and probable medullosan host plants. 10, A small ovoidal coprolite consisting entirely of *Punctatisporites* sp. spores from a *Psaronius* tree fern (Psaroniaceae), SEM-enlarged in (11) USNM peel BV30-Cbot; slide 499093. 12, An elongate-cylindrical coprolite containing a monospecific assemblage of *Florinites* sp. cordaite pollen (Cordaiteaceae), enlarged in the SEM in (13) USNM peel BV81-Bbot; slide 499140. 14, Small, ellipsoidal coprolite revealing large pollen grains that are circular in transverse section, attributed to *Monoletes* sp. (Medullosaceae) pollen, enlarged in (15) and further SEM magnified in (16). USNM peel BV40-Ebot; slide 499109. The coprolites at (10), (12) and (14) have long-axis lengths of ca. 1 mm. 17–18: A boring in aerenchymatous tissue of a *Psaronius* sp. aerial root, enlarged in (18) below, exhibiting reaction tissue (rt) at the arrow. USNM peel BV49-Fbot; slide 501007. 19–22: Examples from four specimens of galls of *Stipitopteris* frond rachises of *Psaronius* tree-ferns, showing variously altered tissues and distinctive coprolites with inner parenchymatous tissue contents. At (19) is a transverse section of an entire gall, with reaction (nutritive) tissue (rt) indicated by an arrow. USNM peel BV32-Mtop; slide 553707. An enlargement of the inner chamber in (20) shows reaction tissue (rt) at right, including a cusped chew mark above, enclosing six coprolite fragments and undigested tissues in the central chamber. UIUC peel 30823-Dbot; USNM slide 553708. Another cluster of coprolites is displayed in (21), the two upper ones showing curved coprolite surfaces. USNM peel BV32-Ktop; slide 553709. The highly magnified internal contents of a gall coprolite in (22) shows digestion-resistant gum-sac cells (gs) that occur in normal, unconsumed rachis parenchyma. USNM peel BV32-Mbot; slide 553710. Specimen repository abbreviations: FMNH Field Museum of Natural History paleobotany collections (Chicago, IL); UIUC University of Illinois at Urbana-Champaign coal-ball collections (Urbana, IL); NMNH National Museum of Natural History paleobotany collections (Washington, DC)

- (6) Tissues that have been overwhelmingly accessed by arthropod herbivores during the study interval are the photosynthetic tissues of epidermis and parenchyma, and the water- and nutrient-conducting tissues of xylem and phloem that produce energy-rich products contained in foliage.
- (7) Two patterns are evident in these data that are potentially relevant to major biotic and environmental events. There



is evidence for the end-Permian extinction having a significant effect on Middle Triassic FFG trophic partitioning of plant tissues. By contrast, there is no signal that angiosperm diversification had an effect on increasing the subsequent subdivision of food resources.

Discussion

Three aspects of the above-mentioned patterns especially merit discussion. All three issues involve the patterns of trophic partitioning of host-plant tissues by insect herbivores across major boundaries or significant events in the history of terrestrial life.

The appearance of plant tissue types and their delayed consumption by arthropod herbivores

Our results indicate short-term lags of ca. 10 m.y. for consumption of live epidermis, parenchyma, collenchyma and xylary tissues of stems that began earlier, during the mid Paleozoic. They also exhibit a pattern of longer-term lags for more resistant structural tissues (periderm, sclerenchyma), actively dividing tissues involved in growth (apical, lateral and intercalary meristems), and reproductively associated tissues (palynomorphs, megagametophytic/endosperm tissue, and integuments). The occurrence of an 85-m.y. lag before the earliest occurrence of phloem and its consumption by herbivores, however, is odd. This unexpected lag for a relatively undefended tissue whose primary function is transporting the energy-rich products of photosynthesis may be attributable to stereotypically poor preservation of this tissue among the earliest vascularized land plants (Kenrick and Crane 1997) or by the lack of suitable terrestrial depositional environments (Labandeira 2007).

The more finely resolved histological data for the Paleozoic in Fig. 1 support a previous study based on different, coarser-grained organ-level data (Labandeira 2007). An example of more fine-grained histological data, used in this compilation, comes from both coal-swamp and better drained peripheral habitats of late Middle compression–adpression floras and early Late Pennsylvanian permineralized floras from the Illinois Basin, USA (Fig. 2). The finely resolved subtypes of external foliage feeding, such as margin feeding and surface abrasion (Fig. 2, top), represent feeding on all foliar tissues. In addition, palynophagy (the consumption of pollen and spores: Fig. 2, center left), and internal modes of feeding on plant hosts that include borings (Fig. 2, lower right), and galls (Fig. 2, bottom) represent the consumption or major alteration of a variety of tissues, such as epidermis, parenchyma, xylem, phloem and meristems (McLoughlin 2011). These and collateral data (e.g., Labandeira 2006b) indicate that the partitioning

of tissue types was virtually complete by the end of the Pennsylvanian Subperiod.

Collectively, these data provide evidence of an early microarthropodan launch of herbivory on the stems of early vascular plants and spores and their enveloping sporangia (Kevan et al. 1975; Edwards et al. 1995; Labandeira and Curano 2013), compared with a delay in the use of other organs, including leaf or leaf-like organs such as microphylls, rhizoids and true roots. The consumption of spores and sporangia is contemporaneous with stem herbivory, and reflects a much earlier origin during the mid-Silurian. However, confident attribution of spore taxa to vascular land plants earlier than the mid Silurian remains somewhat contentious.

Possible effects of major perturbations in the consumption of plant tissues by insect herbivores

It is possible that the level of the current analysis is too coarse-grained to capture the effects of major environmental episodes, such as the end-Permian and end-Cretaceous ecological crises, documented in other studies of terrestrial ecosystems across major intervals of environmental change (Labandeira et al. 2002; Labandeira 2006b). However, there does appear to be a significant lessening of FFG partitioning of plant tissues during the Middle Triassic, reversed dramatically in the Late Triassic Molteno biota (Scott et al. 2004; Labandeira 2006b). Other widely recognized trends resulting from major abiotic perturbations, such as the end-Cretaceous environmental crisis and the Paleocene–Eocene Thermal Maximum, are not recoverable, at least with the scale presented herein. The addition of significantly more biotas and arthropod-damaged tissue occurrences could result in a substantively more finely resolved dataset. Such data could successfully capture the trophic signals necessary for demonstrating the effects of major environmental crises on tissue use by arthropod herbivores.

Role of angiosperm diversification

The ecological prominence of angiosperms had minimal effect on increased herbivore partitioning of plant tissue types. Based on the data presented, angiosperm diversification evidently had little effect on the FFG partitioning of tissue types. An earlier study (Labandeira 2006a) indicated that the taxonomic diversity of host-plant targets did increase after the establishment of angiosperm-dominated ecosystems (Labandeira 2006a). By contrast, insect mouthpart diversity already had reached modern levels during the pre-angiospermous mid-Jurassic (Labandeira 1997), separately indicating that almost all of the feeding specializations had originated earlier, such as the spectacular long-proboscid pollination mode employed by certain flies, scorpionflies and

lacewings (Ren et al. 2009; Labandeira 2010). When considered together, these three observations — the increase in host-plant taxa diversity following the angiosperm diversification event, the pre-angiospermous establishment of a near-complete repertoire of insect feeding specializations (Hartkopf-Fröder et al. 2011), and the absence of herbivore tissue partitioning — indicate that resource partitioning of plant tissues by insect herbivores was unaffected by angiosperm ecological dominance. Although plant tissues were not consumed differently by insect herbivores before and after angiosperm diversification, there likely was a significant subsequent increase in angiosperm biomass as a food resource. This increase probably was attributable to greater vein densities and consequent increased assimilation rates when compared to those of seed plants (Boyce et al. 2009).

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