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The origin of herbivory on land: Initial patterns of plant tissue consumption by arthropods

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Abstract The early fossil record of terrestrial arthropod herbivory consists of two pulses. The first pulse was concentrated during the latest Silurian to Early Devonian (417 to 403 Ma), and consists of the earliest evidence for consumption of sporangia and stems (and limited fungivore borings). Herbivorization of most of these tissues was rapid, representing 0 to 20 million-year (m.y.) lags from the earliest occurrences of these organs in the fossil record to their initial consumption (Phase 1). For approximately the next 75 m.y., there was a second, more histologically varied origination and expansion of roots, leaves, wood and seeds, whose earliest evidence for herbivorization occurred from the Middle-Late Mississippian boundary to the Middle Pennsylvanian (327 to 309 Ma). The appearance of this second herbivory pulse during the later Paleozoic (Phase 2) is accompanied by major lags of 98 to 54 m.y. between times of appearance of each of the four organ and tissue types and their subsequent herbivory. Both pulses provide a context for three emerging questions. First is an explanation for the contrast between the near instantaneous consumption of plant tissues during Phase 1, versus the exceptionally long lags between the earliest occurrences of plant tissues and their subsequent herbivorization during Phase 2. Second is the identity of arthropod herbivores for both phases. Third is the cause behind the overwhelming targeting of seed-fern plant hosts during Phase 2. Regardless of the answers to these questions, the trace fossil record of plant-arthropod associations provides primary ecological data that remain unaddressed by the body-fossil record alone.

Key words herbivory, ecological lag, Devonian, Carboniferous, arthropod, plant-insect interactions, wood boring, seed predation, folivory, fecal pellet, response tissue, sporangia, roots, stems
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Introduction

The initial greening of the land along coastlines of Late Silurian to Middle Devonian paleocontinents was a seminal event for the development of terrestrial ecosystems. This event was associated with development of the first terrestrial and freshwater communities harboring macroscopic organisms with differentiated tissues, such as lichens, bryophytic and primitive vascular plants, fungi, and arthropods. Ecosystems containing these organismic groups were trophically organized in simple ways, and consisted of primary producers, saprobes responsible for biotic degradation of tissues, and detritivores that were consuming dead tissues, the latter two of which were trophically recycling primary productivity through a more direct, nutritionally simpler route (Shear & Selden, 2001). Currently, evidence for herbivores, namely animals involved in consumption of live plant tissues (Crawley, 1983; Schowalter, 2000), is modest, although increasingly

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new data indicate that the dominance of detritivorous modes of plant tissue consumption was significantly less than total in these early ecosystems. In this report, I document the earliest occurrences of herbivory in early terrestrial (land-based) communities. Additionally, the timing of herbivory is determined for the earliest appearances of vascular-plant organs and evidence is provided for their near simultaneous colonization by arthropodan herbivores. In addition, evidence is marshaled for a significantly later, second phase of herbivorization of plant organs among more derived lineages of host plants and their arthropod herbivores. Last, inferences are made regarding the structure of these early, mid-Paleozoic, terrestrial communities and the establishment of more herbivore-dominated, trophically complex communities toward the end of the Paleozoic.

Methods

A literature-based search was conducted for the first appearance in the fossil record of the six, most commonly preserved, and obvious plant organs or tissues in the Paleozoic terrestrial fossil record. These organs are sporangia, stems, roots, leaves, seeds, and the tissue type, wood. In addition, the earliest instance of herbivorization of each of these six plant structures in the fossil record was sought. Time lags between the earliest appearance of a plant organ or tissue, and its initial herbivorization were noted. Each occurrence was resolved to the level of the geochronological stage. Absolute dates were estimated as stage midpoints only if stage-level resolution was possible, or with greater accuracy if more temporally circumscribed data was present. Documentation of the relevant plant taxa, geologic ages, localities, and citation sources are detailed in Table 1.

The collection of occurrence data was guided by explicit definitions for each of the six organ or tissue types and varied evidence indicating arthropod consumption (Table 1). *Sporangia* consist of spore masses enclosed by differentiated reproductive tissues that are borne on stems. These structures originated once in land plants, probably among the ancestors of bryophytes (Kendrick & Crane, 1997). The geochronologically earliest instance of sporivory consists of monospecific to heterogeneous assemblages of spores occurring in coprolites (Fig. 1A, B); only during the Pennsylvanian and Permian do insect gut contents provide direct evidence for sporivory (Shear & Kukalová-Peck, 1990). *Stems* consist of shoots or petioles with structural elements (tracheids) for the transportation of water and nutrients, a condition that evidently originated once (Kendrick & Crane, 1991). Mid-Paleozoic examples of stems occasionally display borings (Fig. 1C), lesions (Fig. 1D), and other types of damage to surface and deeper tissues (Trant & Gensel, 1986; Banks & Colthart, 1993). *Roots*, which probably originated twice (Boyce, 2005b), exclude the nonvasculated rhizoids and rootlets of earlier lineages, and comprise typically larger structures that anatomically are an extension of shoot vasculature and possess terminal meristematic tissue (Raven & Edwards, 2001). Root feeding is often indicated by hyperplasic or hypertrophic tissue that surround styletal penetrations (Fig. 1E), endophytic borings (Fig. 1F), or subdermal response to exophytic surface grazing (Labandeira, 2001). *Leaves* include megaphylls only of the euphyllophyte land-plant clade. They are laminate, planated structures whose primary vasculature originates from leaf gaps of the primary axis, and bear complexly branched secondary venation (Gensel, 1984; Kenrick & Crane, 1997). True leaves originated four times, namely in progymnosperms, sphenopsids, ferns and seed plants (Boyce & Knoll, 2002), and thus exclude the lycopsid microphyll that typically is supplied by a single medial vein (Bonamo *et al.*, 1988). The earliest example of folivory is on seed-fern pinnules (Fig. 1G) (Iannuzzi & Labandeira, 2007, unpublished data). *Wood*, or secondary xylem, unlike the previously mentioned plant features, is a tissue type and not a plant organ, and serves as an important substrate for wood-boring Paleozoic arthropods, for which there is limited evidence (Fig. 1H). Within land plants, wood, defined as secondary growth of lignified xylem, originated once within the lycophytes and again in the tracheophytes, and possibly multiple times within tracheophytes, pending a comprehensive cladistic analysis (Kendrick & Crane, 1997). At least some of the developmental and physiological features in modern secondary xylem, such as polar auxin flow that often is important to insect borers, was present in woods such as *Callixylon whiteanum*, representing the trunk of the arborescent progymnosperm, *Archaeopteris*, in deposits as old as the Late Devonian (Late Frasnian) (Rothwell & Lev-Yaudin, 2005). Taxonomically unrelated, lignified mycelial tissues also occur in the massive, lignified, basidiomycete fungus, *Prototaxites*, discussed below. *Seeds*, the latest anatomical feature to evolve during the Devonian, are fertilized ovules of embryophytes, and represent diverse shapes, sizes and internal structures that occur in a variety of positions on the source plant. Apparently, seeds originated only once (Beck & Wight, 1988). The earliest occurrences of seed consumption are indicated by distinctive, circular holes or plugs centrally placed in the early medullosan taxon, *Trigonocarpus* (Fig. 1I, J).

As for wood, two categories of data were included: one for the woody tissues of land plants, and a second category for the unusual,"woody"mycelial tissues from the gigantic,

Table 1 First fossil appearances of six organs and tissues in early land-plant taxa and their earliest consumption by arthropod herbivores[1] ; these data also serve documentation for Figure 2.

First appearances of plant organs and tissues					Earliest occurrences of herbivory on plant organs				
	Taxon	Stage, (Ma)	Locality	Reference		Taxon	Stage, (Ma)	Locality	Reference
				SPORANGIA[2]					
1	*Laevolancis divellomedia* (type 1)	Prídolí (417)	Wales	Wellman *et al*., 1998	**7**	Various spore taxa in coprolites	Prídolí (417)	Wales	Edwards *et al*., 1995
2	*Cooksonia pertonii*	Lochkovian (413)	England	Edwards *et al*., 1986	**8**	Various spore taxa in coprolites	Early Pragian (410)	Scotland	Edwards *et al*., 1995; Habgood *et al*.,2004
3	*Uskiella spargens*	earliest Pragian (411)	Wales	Shute & Edwards, 1989	**9**	*Bensiotheca grievii* coprolites	Late Visean (330)	Scotland	Rothwell & Scott, (1988)
4	*Aglaophyton* (*Rhynia*) *major*	Early Pragian (410)	Scotland	Kidston & Lang, 1921; Kenrick & Crane, 1997	**10**	*Feraxotheca* coprolites	Early-Middle Pennsylvanian (312)	Kentucky, USA	Scott & Taylor,1983
5	*Huvenia kleui*	Pragian (409)	Germany	Hass & Remy, 1991	**11**	Pteridophyte spores as insect gut contents	Late Middle Pennsylvanian (306)	Illinois, USA	Shear & Kukalová-Peck, 1990
6	*Sporogonites exuberans*	Early Emsian (405)	Norway	Halle, 1936; Allen, 1980					
					12	*Florinites* and *Convolutispora*	Late Pennsylvanian (305)	Illinois, USA	Labandeira, 1998a
					13	*Thuringia* coprolites	Latest Pennsylvanian	Germany	Meyen, 1984; Kerp, 1988
				STEMS[3]					
14	*Serricaulis hippocrepiformis*	mid-Lochkovian (414)	Scotland	Kenrick & Crane, 1997	**18**	*Rhynia gwynne-vaughanii* and *Aglaophyton minor*	Early Pragian (410)	Scotland	Kidston & Lang, 1921; Kevan *et al*., 1975
15	*Asteroxylon mackiei*	Early Pragian (410)	Scotland	Kenrick & Crane, 1991	**19**	*Psilophyton coniculum* & *dawsoni* stems	Emsian (403)	Quebec, Canada	Banks, 1981; Trant & Gensel, 1985; Banks & Colthart, 1993
16	*Drepanophycus spinaeformis*	Earliest Emsian (407)	Quebec, Canada	Kenrick & Crane, 1991	**20**	*Acrobulbullites* galls	Early Moscovian (310)	Netherlands, Germany	Thomas, 1969; Amerom, 1973
17	"*Taeniocrada dubia*"	Emsian (403)	Quebec, Canada	Kenrick & Crane, 1997	**21**	*Etapteris* stem	Middle Moscovian (309)	Ohio, USA	Scott *et al*., 1992
					22	*Calamites*, *Myeloxylon*, *Ankyropteris* & lepidodendrid axes	Middle Moscovian (308)	England	Seward, 1906; Stopes, 1907; Holden, 1910, 1930; Wilkinson, 1930; West, 1962

(to be continued)

(continued)

First appearances of plant organs and tissues					Earliest occurrences of herbivory on plant organs				
	Taxon	Stage, (Ma)	Locality	Reference		Taxon	Stage, (Ma)	Locality	Reference
					23	*Psaronius* sp. stems	Late Moscovian (306)	Ohio, Illinois, USA	Scott & Taylor, 1983; Labandeira & Phillips, 1996
					24	*Psaronius chasei* petioles	Early Kasimovian (305)	Illinois, USA	Labandeira & Phillips, 2002 Lesnikowska, 1990
ROOTS[4]									
25	*Asteroxylon* sp.	Early Pragian (410)	Scotland	Raven & Edwards, 2001	**32**	Stigmarian root	Moscovian (309)	England	Weiss, 1904
26	*Drepanophycus qujingensis*	Late Pragian (408)	Yunnan, China	Algeo *et al*., 2001; Driese & Mora, 2001; Gensel, Kotyk, & Basinger, 2001	**33**	*Psaronius* roots	Early Kasimovian (305)	Illinois, USA	Labandeira, 2001
27	Large root traces	Mid Emsian (403)	Quebec, Canada	Elick, Driese & Mora, 1998					
28	*Cyclostigma* sp., stigmarian roots	Early Eifelian (396)	Germany	Schweitzer, 1969; Algeo *et al*., 2001					
29	*Lorophyton goense*	Lower Givetian (390)	Belgium	Fairon-Demaret & Li, 1993					
30	*Archaeopteris* sp.	Earliest Frasnian/ latest Givetian	Pennsylvania, New York,USA	Algeo *et al*., 2001					
31	*Rhacophyton* sp.	Fammenian (367)	West Virginia, USA	Cornet *et al*., 1976; Algeo *et al*., 2001					
LEAVES[5]									
34	*Euphyllophyton bellum*	Pragian (409)	Yunnan, China	Hao & Beck, 1993; Hao *et al*., 2003	**39**	*Triphyllopteris austrina*	Early Serpukhovian (324)	New South Wales, Australia	Iannuzzi & Labandeira, 2007, unpublished data
35	*Pertica* sp., ? *Psilophyton* sp.	Emsian (403)	Quebec, Canada	Boyce & Knoll, 2002	**40**	*Linopteris* sp.	Middle Moscovian (309)	Spain	Castro, 1997
36	Cladoxylalean ferns	Famennian (367)	Germany	Galtier & Scott, 1985	**41**	*Paripteris* sp.	Middle Moscovian (308)	Spain	Amerom & Boersma, 1971
37	*Elkinsia*, *Lyginopteris* & *Heterangium* (seed plants)	Late Famennian (360)	Illinois, West Virginia, USA	Kenrick & Crane, 1997; Boyce & Knoll, 2002	**42**	*Neuropteris* sp.	Late Middle Moscovian (307)	Germany	Müller, 1982

(to be continued)

(continued)

	First appearances of plant organs and tissues					Earliest occurrences of herbivory on plant organs			
	Taxon	Stage, (Ma)	Locality	Reference		Taxon	Stage, (Ma)	Locality	Reference
38	*Sphenophyllum* sp.	Visean (335)	Illinois, USA; France	Taylor, 1969; Boyce & Knoll, 2002	**43**	*Neuropteris scheuchzeri*	Late Moscovian (306)	Illinois, USA	Scott & Taylor, 1983; Labandeira & Beall, 1990; Scott *et al*., 1992; Trout *et al*., 2000
					44	*Alethopteris* sp., *Pecopteris* sp.	Early Kasimovian (305)	Illinois, USA	Labandeira, 1998b
					45	*Sphenopteris* sp.	Late Kasimovian (303)	Spain	Amerom, 1966; Castro, 1997
				WOOD[6]					
46	*Prototaxites* sp.	Wenlockian-Ludlowian (423)	Pennsylvania, USA	Strother, 1988	**53**	*Prototaxites dawsoni*	Emsian (403)	Quebec, Canada	Hotton *et al*., 1996; Hueber, 2001
47	*Rellimia thomsoni*	Givetian (389)	New York, USA	Dannenhoffer & Bonamo, 2003	**54**	*Prototaxites* sp.	Late Famennian (362)	Ontario, Canada	Arnold, 1952; Hotton *et al*., 1996
48	*Pseudosporochnus* sp.	Late Givetian (387)	Belgium	Mustafa, 1978; Stein & Hueber, 1989; Algeo *et al*., 2001	**55**	*Trivenia arkansana*	Early Serpukhovian (326)	Arkansas, USA	Dunn *et al*., 2003
49	*Eospermatopteris* sp.	Late Givetian (386)	New York, USA	Algeo *et al*., 2001	**56**	?Calamite wood	Early Kasimovian (305)	Illinois, USA	Labandeira, 2007, unpublished data
50	*Aneurophyton germanicum*	Givetian/Frasnian (384)	Germany	Serlin & Banks, 1978; Schweitzer & Matten, 1982					
51	*Callixylon* sp.	Middle Frasnian (380)	Pennsylvania, New York, USA	Scheckler, 1975; Meyer-Berthaud *et al*., 1999; Algeo *et al*., 2001					
52	*Prototaxites* sp.	Late Famennian (362)	Ontario, Canada	Arnold, 1952; Hueber, 2001					

(to be continued)

(continued)

	First appearances of plant organs and tissues					Earliest occurrences of herbivory on plant organs			
	Taxon	Stage, (Ma)	Locality	Reference		Taxon	Stage, (Ma)	Locality	Reference
				SEEDS[7]					
57	*Moresnetia zalesskyi*; *Elkinsia polymorpha*	Middle to late Famennian (368)	Belgium; West Virginia, USA	Rothwell & Serbet, 1992; Algeo *et al*., 2001	**61**	*Trigonocarpus parkinsoni*	Bashkirian (314)	Illinois, USA	Jennings, 1974
58	*Spermolithus devonicus*	Early late Famennian (366)	Ireland	Chaloner *et al*., 1977	**62**	*Setoisporites praetextus* megaspore	Early Moscovian (310)	England	Scott & Taylor, 1983
59	*Archaeosperma arnoldii*; *Aglosperma quadripartita*	Early late Famennian (365)	Pennsylvania, USA; Wales	Gillespie *et al*., 1981; Algeo *et al*., 2001	**63**	*Trigonocarpus* sp.	Middle Moscovian (308)	England	Scott & Taylor, 1983
60	*Xenotheca devonica* sp.	Late Famennian (359)	England	Algeo *et al*., 2001	**64**	"*Samaropsis*" sp.	Late Gzhelian Russia	Siberia,	Sharov, 1973

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[1] Although this is not an exhaustive list of the earliest known appearances of organs in the fossil record, every attempt was made to list several of the earliest known taxa bearing the organ or tissue type in question. The earliest known occurrences of herbivory for each of the examined organ or tissue types also are listed; see Labandeira (2006) for additional documentation. Time assignments are from Gradstein *et al*. (2004).

[2] **Sporangia**: Includes both intact sporangia with constituent spores and other tissues attached to plants as well as dispersed spores occurring singly or as clumps in sediment matrix.

[3] **Stems**: Consists of shoots with structural elements (tracheids) for the transportation of water and nutrients. Also included are petioles that give rise to pinnule-bearing fronds.

[4] **Roots**: Comprises only anatomically true roots, bearing an extension of shoot vasculature, possessing terminal meristematic tissue, and typically consisting of structures significantly larger than rhizoids and rootlets.

[5] **Leaves**: Includes megaphylls only, defined as planated, laminate structures whose primary vasculature originates from axis leaf gaps, and with evident secondary venation. Microphylls, characterized by a single vascular strand, such as those occurring in lycopods, are excluded.

[6] **Wood**: In addition to vascular plant secondary xylem, we have also included "woody", lignified *Prototaxites* stipes; two Devonian examples of this fungus evidently were bored by arthropods similar to true wood.

[7] **Seeds**: In addition to the fertilized ovules of embryophytes, we have included under this term the analogous megaspore structures from more basal plants.

columnar basidiomycete fungus, *Prototaxites* (Hueber, 2001). Interestingly, *Prototaxites* includes an earliest first occurrence in the Late Silurian (Strother, 1988), and its earliest documented consumption is an Early Devonian specimen with arthropod borings in indurated, chitinous cortical tissue (Hotton *et al*., 1996). Intriguingly, one of the last, Late Devonian, occurrences of *Prototaxites* (Arnold, 1952) also bears borings, though apparently of a different type. The indurated mycelial tissue of *Prototaxites* is a structural analog to the wood of vascular plants, and the presence of borings may indicate the origin of this feeding guild initially on massive fungi (Wu & Labandeira, 2007, unpublished data), which may have been subsequently transferred to land plants. Both lignified fungal and land plant hosts provide a rich source for the origin of wood boring as a major functional feeding group.

Care was taken to distinguish detritivory from herbivory. Four explicit criteria were used, either singly or in combination, to establish the presence of herbivory over detritivory, which typically is assumed to be a default trophic strategy (Labandeira, 1998a, 2002). First, and most important, was the presence of histological response, including thickened callus, hypertrophic or hyperplasic files or tufts of cells (Fig. 1C, E, F), punctures with stylet trajectories (Fig. 1D), necrotic areas surrounding plant damage, or other manifestations of induced tissue alteration. Second is a class of evidence involving herbivore modification of plant tissue, typically expressed as distinctive micromorphological features, such as tissue plugs or highly circular cross sections in wood borings or seeds (Fig. 1H–J), or veinal stringers or tissue flaps on the cuspate, chewed edges of leaf margins (Fig. 1G) (Coulson & Witter, 1984). Alternatively, coprolite (preserved fecal pellet) constituents can indicate the consumption of live tissue, such as intact but partly ruptured spores (Fig. 1B), or can be dominated by vegetative tissues (Fig. 1A). Occasionally pristine foliar tissue, with associated distinctive trichomes and cuticular sheets of identifiable plants, are major coprolite constituents (Labandeira, 2001). A third line of evidence is damage stereotypy that likely would be attributable to herbivores rather than the less specialized and more erratic feeding patterns of detritivores (Brues, 1924; Swift *et al*., 1989; Tallamy, 1994), often rendered more palatable by epiphyllous or other litter fungi (Valiela & Rietsma, 1984). Abiotic damage also results in considerably different patterns of damage than that expected from herbivory (Wilson, 1980; Vincent, 1990; Katterman, 1990). Lastly, detritivore damage is more evenly distributed on plant taxa and tissues when compared to the more stereotyped and often host- and tissue-specific herbivore damage (Labandeira *et al*., 2002). Taxonomic uniformitarian approaches were not used because of the ancient nature of the lineages and the lack of any extant analogous taxa. However, commonly recognized damage by modern arthropod herbivores, when available, were examined to assess the likelihood of herbivory or detritivory.

Results

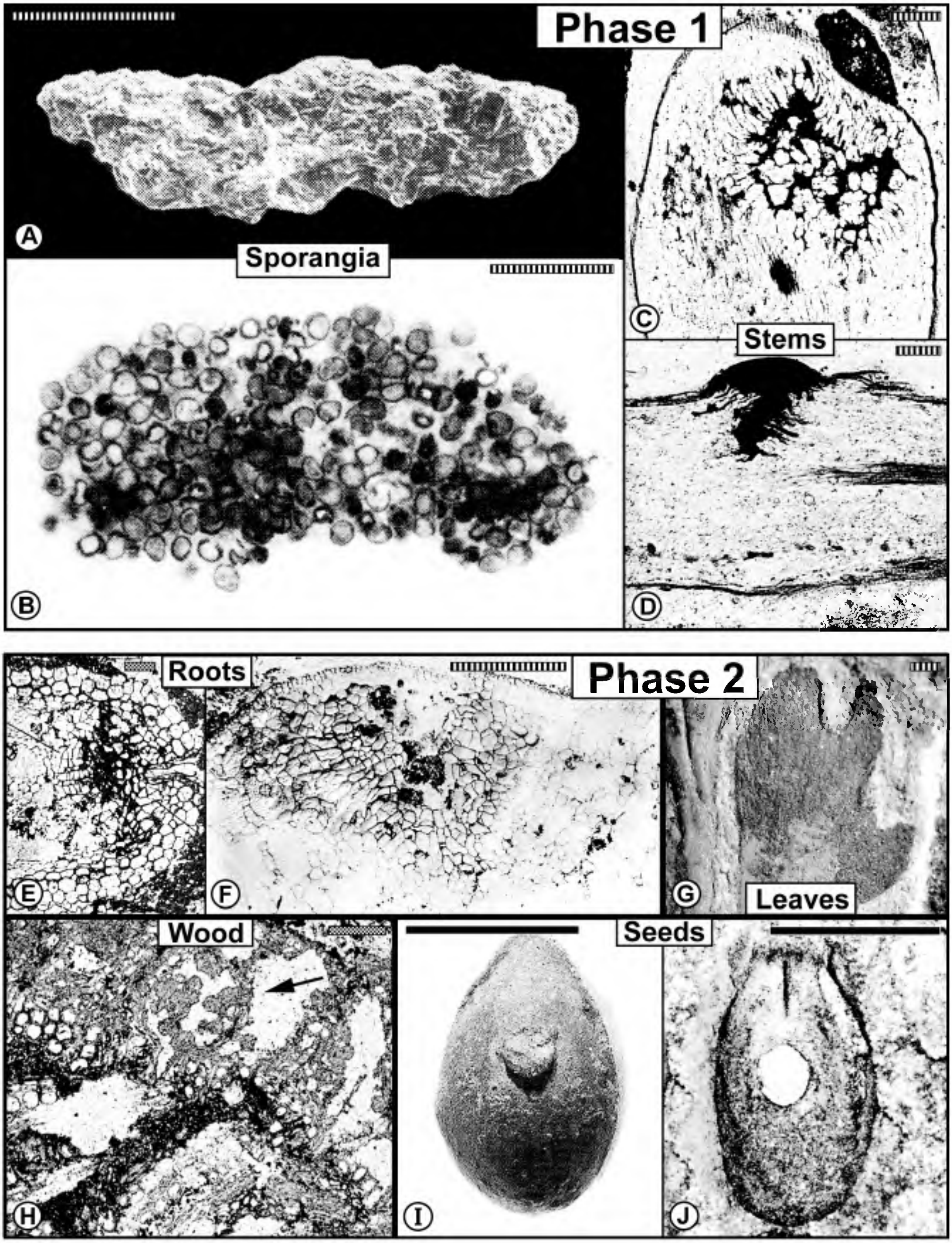
The data are presented in Table 1, and are distilled in Figure 2. Two major origins of herbivory are apparent. An earlier, Late Silurian to Early Devonian event, consisted of the first appearances of sporangia and stems, as well as lignified fungal tissues. Their near immediate (sporangia), rapid (stems), or more prolonged (fungal thalli) colonization occurred within a 20 m.y. interval by arthropod herbivores. A second, considerably later, colonization event targeted roots, leaves, wood and seeds of land plants. This second event occurred after a major interruption, during which novel herbivore patterns were absent, spanning an average lag of approximately 75 m.y. from the earliest appearance of true roots to the earliest herbivorization of leaves, and representing a hiatus from the later Early Devonian to Middle Mississippian. Depending on the organ or tissue, these plant structures had appeared from 54 to 98 m.y. earlier, prior to their initial herbivorization. The mid-Visean to Late Moscovian event constitutes a distinct, second phase of herbivory on a considerably wider variety of plant tissues and taxa than the earlier phase.

Discussion

Three important issues are broached by the patterns presented in this report. First is the contrast between the origin of plant organs and tissues and their geochrionologically rapid colonization by an earlier herbivory phase, versus a prolonged lag between a similar but subsequent origin of new land-plant organs and tissues and their eventual consumption during a later herbivory phase. The second issue is the identity of herbivores responsible for the consumption of these organs and tissues, particularly during this interval of the terrestrial fossil record in which relevant arthropod taxa are scarce and relevant herbivorous insect clades apparently are absent. The last issue is a discussion of the preferential consumption of seed-plant tissues, particularly in seed-fern (pteridosperm) lineages, within the second phase of herbivory.

Timing of organ origins and their herbivorization

The presence of a rich, 423 m.y. record of plant organs and their tissues in the fossil record should offer a valuable

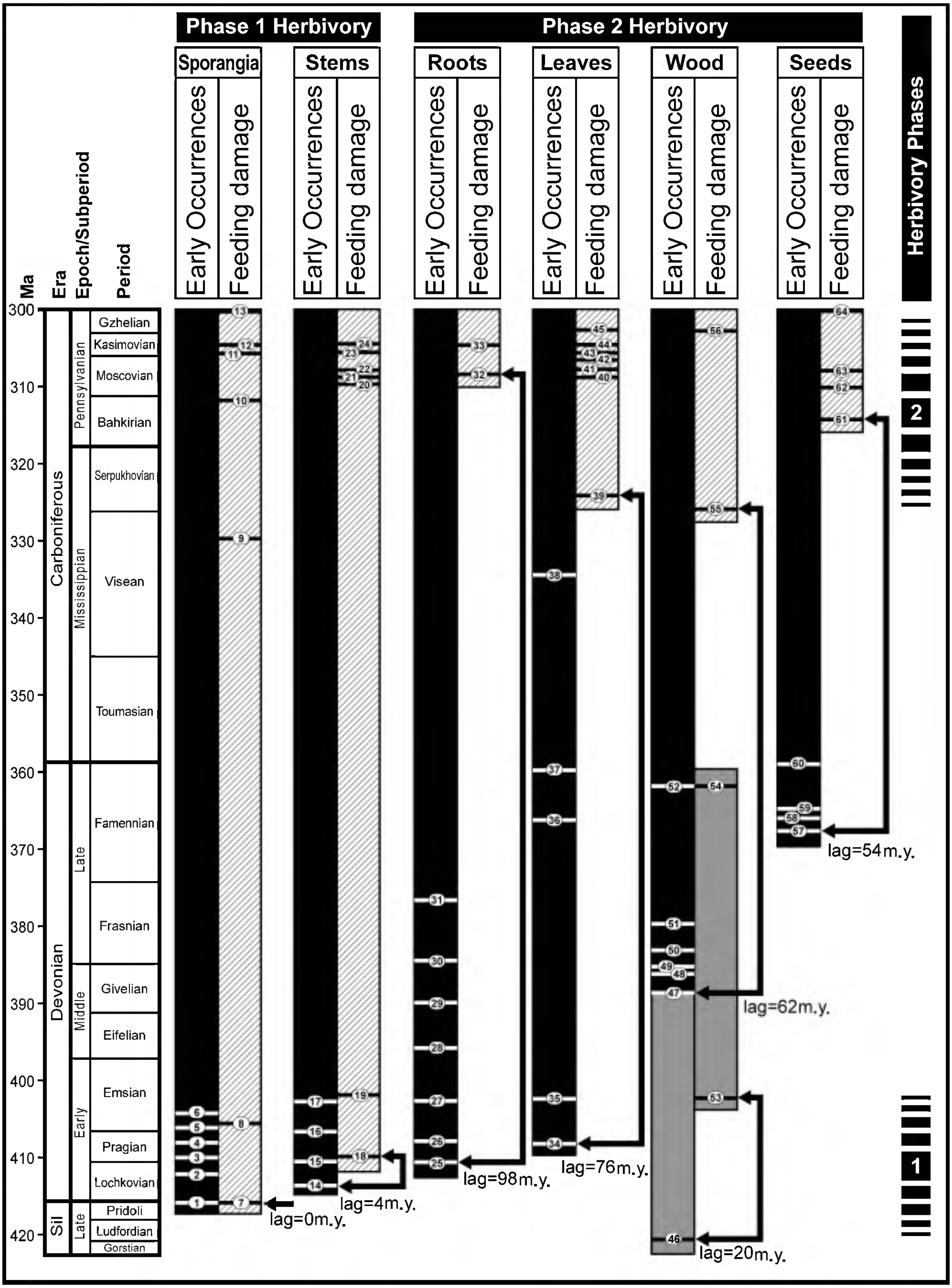

Phase 1
Sporangia
Stems
A
B
C
D
Phase 2
Roots
Leaves
Wood
Seeds
E
F
G
H
I
J

resource for tracking the origin and early ecological history of arthropod herbivory. Apparently, the initial thrust of herbivory during the Late Silurian to Early Devonian was rapid, and involved two of the three principle organs that primitive vascular plants possessed: sporangia and stems as well as "woody" fungal thalli. Currently, evidence for the herbivorization of rhizoids, rootlets or true roots during this interval is lacking. This pattern of geologically quick colonization by herbivores is in contrast to the second pulse of herbivory, which was extensively delayed by several tens of millions of years until the earliest Late Mississippian, and continuing well into the later Pennsylvanian. The question of a delay in consumption of live plant organs and tissues ranging from 54 to 98 m.y. could be attributable to (i) a poor fossil record of plant-arthropod associations, or (ii) the lack of appropriate herbivore lineages that would cause the damage seen during this part of the fossil record. These two explanations can be addressed by contemporaneous biological and environmental phenomena that may provide clues to the absence of noticeable herbivory during the Late Devonian to Middle Mississippian interval.

The suggestion of a major failure of the fossil record for preserving plant-arthropod associational data is poorly supported. For Euramerica, Angara, Cathaysia and Gondwana, preservation either as permineralizations or as compression/impressions of plant tissues is often of high quality (Morris, 1975; Gensel & Andrews, 1984; Meyen, 1987; Taylor & Taylor, 1993; Iannuzzi & Pfefferkorn, 2002), occasionally with anatomical detail that preserve herbivorous associations in the same context as abundant plant fossils (Hueber & Galtier, 2003; Dunn *et al.*, 2003; also see Tomescu *et al.*, 2001). Based on primary documentation of the floras, an alternative cause is more likely than preservational failure.

The Late Devonian, and particularly the Early Mississippian are characterized not only by minimal levels of herbivory (Labandeira, 1998a), but also the absence of significant cladogenesis of arthropod and vertebrate clades under conditions of decreased levels of atmospheric O_2 from a previous later Devonian high (Ward *et al.*, 2006). This pattern of depressed atmospheric O_2 levels has been postulated as mitigating or even suppressing respiratory advances and other terrestrial innovations in arthropods (especially insects) and vertebrates, resulting in a delay of terrestrialization until the mid-Mississippian (Ward *et al.*, 2006). Arthropod terrestrialization resumed during the Mississippian-Pennsylvanian boundary with the radiation of diverse terrestrial arthropodan groups and a modest

Fig. 1 Some of the earliest examples of arthropod herbivory in the terrestrial fossil record, representing earlier Phase 1 (A–D) and later Phase 2 (E–J) associations. **A.** A heterogeneous assemblage of stem tissues, possibly representing herbivory, occurring in a spiral coprolite, from the Early Devonian (Lochkovian) of the Welsh Borderland, U.K. (Reproduced from *Review of Palaeobotany and Palynology*, Vol. 90, Edwards, D., fig. 8, p. 166. copyright 1996, with permission from Elsevier Ltd.). **B.** An elongate coprolite (*Lancifaex simplex*) of mostly trilete-laevigate plant spores, but with occasional fungal spores; from the Lower Devonian (Pragian) Rhynie Chert of Scotland, U.K. (Reproduced from *Transactions of the Royal Society of Edinburgh* (*Earth Sciences*), Vol. 94, Habgood *et al.*, fig. 3A, p. 374, copyright 2004, with permission from the Royal Society of Edinburgh). **C.** An oblique view of a probable bored stem of *Rhynia gwynne-vaughanii*, also from the Rhynie Chert (Kevan *et al.*, 1975, slide V.57833). **D.** A longitudinal view of the effects of a styletal piercing in a stem of *R. gwynne-vaughanii*, also from the Rhynie Chert (slide V.57834. **1C, 1D** were reproduced from *Palaeontology*, Vol. 18, Kevan *et al.*, Interrelationships of early terrestrial arthropods and plants, Plate 54, figs. 1 & 3, p. 399, copyright 1975, with permission from Blackwell Publishing). **E.** Probable styletal penetration, previously interpreted as fungal damage, with some surrounding reaction tissue, in a stigmarian root of a lycopod; from the Middle Pennsylvanian (Moscovian) of England, U.K. (Reproduced from *New Phytologist*, Vol. 3, Weiss, F.E., A probable parasite of stigmarian rootlets, fig. 67, p. 66, copyright 1904, with permission from the New Phytologist Trust). **F.** Boring in the marattialean fern root, *Psaronius chasei*, replete with lumen coprolites and enveloping reaction tissue; from the Late Pennsylvanian (Kasimovian) Calhoun Coal of the Illinois Basin, Illinois, USA (NMNH acetate peel BV51-Abot). **G.** External foliage feeding on the calamopityacean seed fern *Triphyllopteris austrina*, from the Middle-Late Mississippian boundary interval (earliest Serpukhovian) of the Sydney Basin, Australia (Iannuzzi & Labandeira, 2007, unpublished data). **H.** Coprolites in a wood boring, surrounded by secondary phloem, in trunk tissues of the lyginopterid seed fern, *Trivenia arkansana*; from the Late Mississippian (Serpukhovian) Fayetteville Formation of Arkansas (Used from *American Journal of Botany*, Vol. 88, Dunn, M.T. *et al.*, fig. 34, p. 1246, copyright 2003, with permission from the Botanical Society of America). **I.** Plug of matrix infilling a circular feeding hole in the medullosan seed *Trigonocarpus* sp.; from the Middle Pennsylvanian Coal Measures of England, United Kingdom (Reprinted from *Proceedings of the Royal Society of London*, Vol. 335, Scott *et al.*, Interactions and coevolution of plants and arthropods during the Paleozoic and Mesozoic, fig. 17, p. 139, copyright 1992, with permission from the Royal Society of London). **J.** Another example of seed predation showing a mold of a feeding hole, on a *Trigonocarpus parkinsonii* seed; from the Early Pennsylvanian (Bashkirian) Caseyville Formation of the Illinois Basin, Illinois (Reproduced from *Journal of Paleontology*, Vol. 48, Jennings, J.R., Plate 3, fig. 9, p. 467, copyright 1974, with permission from the Paleontological Society). Scale bars: solid, 10 mm; striped, 1 mm; and stippled, 0.1 mm.


Phase 1 Herbivory
Phase 2 Herbivory
Sporangia
Stems
Roots
Leaves
Wood
Seeds
Early Occurrences
Feeding damage
Herbivory Phases
Ma
Era
Epoch/Subperiod
Period
300
310
320
330
340
350
360
370
380
390
400
410
420
Carboniferous
Devonian
Sil
Pennsylvanian
Mississippian
Late
Middle
Early
Gzhelian
Kasimovian
Moscovian
Bahkirian
Serpukhovian
Visean
Toumasian
Famennian
Frasnian
Givelian
Eifelian
Emsian
Pragian
Lochkovian
Pridoli
Ludfordian
Gorstian
lag=0m.y.
lag=4m.y.
lag=98m.y.
lag=76m.y.
lag=62m.y.
lag=20m.y.
lag=54m.y.
1
2

increase in major vertebrate clades (Labandeira, 1994; Laurin *et al.*, 2000; Ward *et al.*, 2006). It is probable that the lack of morphological innovation or presence of ecosystem stasis during this interval resulted in simplified trophic webs, allowing for energetically less demanding detritivory to ecologically surpass more metabolically costly herbivory. Arthropod herbivores require atmospheric O_2 levels that must exceed a minimal threshold and the ability to efficiently eliminate CO_2 (Ward *et al.*, 2006), a process that may have opposite effects on plants (Beerling *et al.*, 2001). These conditions are consistent with Scott and colleagues' (1992) observation that, at least with regard to folivory, its "relatively rare" status in Pennsylvanian floras indicates that earlier fossil occurrences may not exist (also see Fig. 1G; Iannuzzi & Labandeira, 2007, unpublished data). Other types of herbivory also may have been delayed because live plant tissues, especially foliage, offer a nutritionally difficult dietary hurdle for terrestrial arthropods to overcome (Southwood, 1973; Mattson, 1980).

A comparison of four major vascular plant innovations during the Devonian—roots, leaves, wood and seeds—is instructive for the timing of herbivory during the second pulse. True leaves (megaphylls), though not necessarily planated, first originated during the Early Devonian (Pragian to Emsian) among some of the earliest euphyllophyte taxa such as *Eophyllophyton bellum* (Hao & Beck, 1993; Hao *et al.*, 2003) and species of *Pertica* (Boyce & Knoll, 2002). These occurrences may represent a non-woody phase of a lineage that subsequently gave rise to progymnosperms (Kenrick & Crane, 1997). Additionally, these taxa represent some of the earliest documented occurrences of true leaves. The innovation of stems bearing lateral branches that support flattened organs of photosynthetic tissue—an advance beyond stem photosynthesis—independently originated in progymnosperms, sphenopsids, ferns and seed plants (Boyce, 2005a). However, the first known incidence of folivory occurs in the earliest Late Mississippian (Serpukhovian) of Australia, on several pinnules of the pteridosperm *Triphyllopteris austrina* (Iannuzzi & Labandeira, 2007, unpublished data), 76 m.y. after the origin of leaves. Likewise, the earliest occurrence of seeds are mid-to Late Fammenian taxa such as *Moresnetia zalesskyi* and *Elkinsia polymorpha* (Algeo *et al.*, 2001), whereas the earliest evidence for seed predation are circular holes on the medullosan *Trigonocarpus*, from the Early and Middle Pennsylvanian of Illinois and England, respectively (Jennings, 1974; Scott & Taylor, 1983), 54 m.y. later. Another major innovation of Devonian seed plants—secondary xylem or wood—exhibits a similar pattern: the earliest accepted occurrences are the lycopsid *Eosperma-topteris*, the fern *Pseudosporochnus*, and the progymnosperms, *Rellimia* and *Svalbardia*, present during the mid- to Late Givetian of the Middle Devonian (Algeo *et al.*, 2001; Dannenhofer & Bonamo, 2003). With the exception of earlier borings in the large, chitin-bearing, "woody" fungus *Prototaxites*, it was 63 m.y. later that the earliest known borings occur on secondary stem tissues of xylem, phloem and cortex of the calamopityacean seed fern *Trivenia*, documented by coprolites and plant response tissue from the mid-Namurian of Arkansas (Dunn *et al.*, 2003). Feeding on true roots was delayed significantly longer, for which good evidence does not occur until the early Late Pennsylvanian (Labandeira, 2001), representing a 98 m.y. delay.

The missing terrestrial arthropod herbivore record

These occurrences provide data for the diets and modes of feeding for a missing terrestrial arthropod herbivore record. Terrestrial arthropod taxa known from the Early and Middle Devonian could have been responsible for the damage on Early to late Middle Devonian stems, such as collembolans (Hirst & Maulik, 1926), mites (Norton *et al.*, 1988; Kethley *et al.*, 1989), or possibly insects (Engel & Grimaldi, 2004). However, it is the hiatus spanning a 65 m.y. interval from the late Middle Devonian to the Mississippian-Pennsylvanian boundary, within the second phase of herbivory, which presents more difficulties. One clue into the nature of these missing hexapod herbivores has been provided by the earliest example of folivory at 326 Ma, at the Middle Mississippian-Late Mississippian boundary, predating the earliest occurrence of likely orthopteroid culprits by 6 m.y. (Iannuzzi & Labandeira, 2007,unpublished data). Possibly a longer lag time of 20 m.y. occurred if a plesiomorphic orthopteran lineage, the Oedischiidae, present during the late Middle Pennsylvanian is the more likely suspect. An alternative

Fig. 2 Occurrence data for the first documented appearance of five selected organs (sporangia, stems, roots, leaves and seeds) and wood tissues from early land plants, and their earliest consumption by arthropod herbivores. These data encompass the latest Silurian to the Pennsylvanian-Permian boundary; early appearance data are presented only for early organ and tissue occurrences, whereas early appearance data are listed for all published examples of herbivory throughout the examined interval. Arrows with lag times in boxes indicate geochronologically rapid colonization of some plant or fungal organs during Phase 1, and a marked delay in the onset of herbivory for other organs during Phase 2. The lignified, massive fungus, *Prototaxites*, is an Early Devonian example of "wood" boring prior to the establishment of associations between arthropod borers and vascular plants that occurred during the later Mississippian. See Table 1 for a register of all occurrence data; geochronology is from Gradstein *et al.* (2004).

hypothesis is that millipedes may have caused the leaf-margin damage, but there is minimal evidence for a folivorous, canopy-associated role for mid-Paleozoic taxa (Kraus & Kraus, 1994; Wilson *et al.*, 2005), and the few modern species that are herbivorous facultatively consume, soft, cryptogamic ground plants such as algae and bryophytes (Hopkin & Read, 1992). In addition, there are sparse occurrences throughout the Mississippian that indicate the presence of herbivores boring into trunk tissues (Hueber & Galtier, 2002; Dunn *et al.*, 2003). Collectively, the folivory, trunk boring, and other data indicate the presence of multiple herbivore strategies that require the presence of unspecified, herbivorous, mandibulate arthropods, probably internally feeding mites and externally feeding (winged) insects, the latter occurring considerably before their first body-fossil appearance at the Mississippian-Pennsylvanian boundary (Brauckmann *et al.*, 1995).

Paleozoic arthropod herbivores that target seed-ferns

An important aspect of the second phase of Paleozoic herbivory is the preferential consumption of seed-plant tissues, particularly various early, seed-fern lineages. Seed-ferns represent a paraphyletic assemblage of extinct, basal seed plants with fern-like foliage that bore radiospermic or platyspermic seeds (Hilton & Bateman, 2006). The earliest seed-fern lineages are the Calamaopityaceae, Callistophytaceae, Lyginopteridaceae and Medullosaceae, which ranged in growth form from vines, to shrubs to monaxial trees (Retallack & Dilcher, 1988; Krings *et al.*, 2002; Dunn *et al.*, 2003). Although the data are sparse, a trend toward herbivore targeting of seed ferns already is detectible during the Middle Mississippian to Early Pennsylvanian, characterized by the first occurrences of folivory, seed predation and wood boring (Table 1, Fig. 1). Root feeding apparently appeared initially on pteridophytes (Rößler, 2000; Lesnikowska, 1990; Labandeira & Phillips, 2002), before seed-fern lineages became targeted during the later Pennsylvanian (Scott & Taylor, 1983; Trout *et al.*, 2000; Labandeira, 2001). During the Middle Pennsylvanian to Early Permian there was an expansion of all four types of herbivory, as well as a renewal of live stem tissue consumption and palynivory worldwide, including Euramerica, (Amerom, 1966; Beck & Labandeira, 1998; Béthoux *et al.*, 2004), Angara (Sharov, 1973; Zherikhin, 2002), Cathaysia (Glasspool *et al.*, 2003) and Gondwana (Plumstead, 1963; Cúneo, 1987; Srivastava, 1987; Holmes, 1995; Adami-Rodrigues *et al.*, 2004). During the Late Pennsylvanian, there is anecdotal evidence for establishment of antiherbivore defense in seed ferns in the form of a resin duct system with unusual chemistry (Bergen *et al.*, 1995) and foliar trichomes (Krings *et al.*, 2002). Although the Mississippian origins of seed-fern herbivory remain obscure, during the Pennsylvanian there was partitioning of tissue types by several insect functional feeding groups, albeit with minimal levels of plant damage (Labandeira, 2006).

Conclusions

Six conclusions are drawn from this study of the earliest fossil records of terrestrial arthropod herbivory. These conclusions have implications regarding the early evolution of herbivory among some of the oldest, well-documented terrestrial ecosystems.

The early history of arthropod, principally insect-mediated, herbivory in terrestrial ecosystems is characterized by two pulses. The first phase, from latest Silurian to Early Devonian, consists of consumption of live sporangial and stem tissues (and limited fungivory), whereas the second phase resulted in the herbivorization of histologically more diverse roots, leaves, wood and seeds during the Late Mississippian to Middle Pennsylvanian.

The absence of significant time lags characterizes the earliest appearance of sporangia and stems and their subsequent but quick herbivorization during Phase 1. By contrast, the considerably more delayed Phase 2 was typified by temporal delays of several tens of millions of years between the origin of roots, leaves, wood and seeds and their initial but prolonged herbivorization during the later Paleozoic.

The likely arthropod culprits of these plant associations are undefined hexapods that lack a body-fossil record, and possibly millipedes with a sparse fossil record.

The considerable time delay in herbivory for Phase 2 may be related to ambient physical variables such as depressed atmospheric O_2 levels and their biological consequences favoring detritivore-dominated food-webs. This interval encompasses Romer's Gap of the Early Mississippian, associated with minimal arthropod cladogenesis, and probably retarded ecosystem development.

The predominant plant–host target during the second phase of herbivory were seed ferns, whose leaves, seeds and woody tissues were consumed by arthropods from different feeding groups.

The plant–insect association record is instrumental in providing evidence for trophic data, such as arthropod feeding types and their plant hosts. Such data typically are unavailable from the insect body-fossil record.

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