

Middle Devonian liverwort herbivory and antiherbivore defence

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Summary

- To test the extent of herbivory in early terrestrial ecosystems, we examined compression–impression specimens of the late Middle Devonian liverwort *Metzgeriothallus sharonae*, from the Catskill Delta deposit of eastern New York state.
- Shale fragments of field-collected specimens were processed by applying liquid nitrocellulose on exposed surfaces. After drying, the film coatings were lifted off and mounted on microscope slides for photography. Unprocessed fragments were photographed under cedarwood oil for enhanced contrast.
- An extensive repertoire of arthropod-mediated herbivory was documented, representing three functional feeding groups and nine subordinate plant–arthropod damage types (DTs). The herbivory is the earliest occurrence of external foliage-feeding and galling in the terrestrial fossil record. Our evidence indicates that thallus oil body cells, similar to the terpenoid-containing oil bodies of modern liverworts, were probably involved in the chemical defence of *M. sharonae* against arthropod herbivores.
- Based on damage patterns of terrestrial plants and an accompanying but sparse body-fossil record, Devonian arthropodan herbivores were significantly smaller compared to those of the later Palaeozoic. These data collectively suggest that a broad spectrum herbivory may have had a more important role in early terrestrial ecosystems than previously thought.

Introduction

Liverworts (Marchantiophyta) are a clade of terrestrial plants that often grow in association with lichens and other nonvascular plants such as mosses and hornworts. The gametophytes of liverworts are structurally diverse. They generally have a dorsal–ventral orientation and can be of the complex-thalloid type, consisting of differentiated tissues and specialized structures such as central cells of the costae, or alternatively a simple-thalloid type which generally lack differentiated tissues, or foliose (leafy) morphologies. The six principal lineages that have been resolved by molecular studies (Forrest *et al.*, 2006) extend back to the Palaeozoic (Heinrichs *et al.*, 2007), with the newly established Haplomitriopsida diverging first, leaving the lineage consisting of complex-thalloid morphology (Marchantiopsida) as sister group to the Jungermannopsida. This last group consists of two paraphyletic simple-thalloid lineages and the two crown-group foliose clades that contain most of the extant 6000–8000 liverwort species. Although lacking in phloem tissue and specialized conducting cells such as the tracheids of xylem tissue, gametophytes of some extant taxa nevertheless possess special elongate cells for conducting water and nutrients (Wang *et al.*, 2010). Assisting this process is direct surface absorption of water and nutrients by the thallus and other specialized structural modifications for external water transport. Simple sporophytes that mature

completely within gametophytic tissue, as well as the absence of stomata support the position of liverworts as extant representatives of one of several earliest diverging clades of land plants (Qiu *et al.*, 1998, 2006), acquiring some distinctive features as a major lineage after land plants were established (Forrest *et al.*, 2006; Wang *et al.*, 2010).

Although lacking a fossil record among the earliest terrestrial ecosystems of the latest Silurian to early Middle Devonian (Kenrick & Crane, 1997), the earliest confirmed and exceptionally preserved liverworts recently were reported from the late Middle Devonian (Givetian Stage) of eastern New York State (VanAller Hernick *et al.*, 2008), equivalent to an age date of *c.* 388 Ma. The modern morphology of these liverworts indicates an earlier, undetected presence in earlier Devonian land biotas. Liverworts are unknown in earlier terrestrial ecosystems, such as the well-documented Early Devonian Rhynie Chert of Scotland and Battery Point Formation of Gaspé, in Quebec (Taylor *et al.*, 2009), and their potential presence may have been a resource for detritivorous organisms. If present in earlier deposits, liverworts would have been susceptible to herbivore attack by small arthropods (Labandeira, 2007), which presumably would have induced some of the earliest antiherbivore responses among land plants.

Evidence for early land-plant herbivory has been documented from several early vascular plant lineages in the Early Devonian that involve three principal arthropod feeding styles, or

functional feeding groups (Labandeira, 2006). The first is consumption of spores, found as coprolites that frequently contain monospecific populations of spores and, often, associated sporangial tissue (Kevan *et al.*, 1975; Edwards *et al.*, 1995; Habgood *et al.*, 2004). Most of these coprolites probably were the result of detritivory, but the presence of associated sporangial tissues and the overwhelmingly greater nutritional value of live spore protoplasts over dead protoplast remnants indicate at least some consumption of live sporangial tissues. Second is piercing-and-sucking of cortical stem tissues, revealed by lesions from repeated stylet probes with accompanying reaction tissue (Kevan *et al.*, 1975; Banks, 1981; Banks & Colthart, 1993). Third are pith borings in the medullary stem tissues of various plants (Kevan *et al.*, 1975), revealing the proliferation of hypertrophic and hyperplastic tissue, and opaque linings of tunnels (Labandeira, 2006). The presence of borings in land plants may be related to the parallel phenomenon of early fungivory (Sherwood-Pike & Gray, 1985; Edwards *et al.*, 2012; Labandeira & Prevec, 2013), and in particular tunnelling within the internal tissues of the giant, columnar, Devonian organism, *Prototaxites* (Hueber, 2001). This may represent an early example of fungivory in the terrestrial fossil record, assuming that identification as a basidiomycete fungus is correct, based on micromorphological (Hueber, 2001) and isotopic (Boyce *et al.*, 2007) data. Alternatively, the possibility remains that *Prototaxites* represents a lichen-like mutualism (Selosse, 2002), an extinct lineage with no modern taxonomic counterpart (Taylor *et al.*, 2009), or more remotely, a liverwort (Graham *et al.*, 2010).

Nevertheless, the presence of these three types of herbivory (sporangivory, piercing-and-sucking and pith boring) during the Early Devonian was limited by the spectrum of plant organs and constituent tissues available for consumption. Early vascular land plants consisted fundamentally of rhizoids, stems and sporangia. Sporangia were resources for sporangivory that included the targeting of spores (Edwards *et al.*, 1995, 2012; Habgood *et al.*, 2004), and stems were substrates for piercing-and-sucking and pith borings (Kevan *et al.*, 1975). Rhizoids appear not to be herbivorized until considerably later, associated with the origin and eventual consumption of true root tissues (Labandeira, 2007). Organs that occurred later, such as leaves and seeds, were not available for consumption during the Early Devonian, becoming nutritionally significant during the Late Devonian. Evidence for folivory and seed predation was delayed until the Carboniferous (Labandeira, 2007), with the earliest documented external foliage feeding occurring during the late Mississippian (Iannuzzi & Labandeira, 2008), and seed predation in the early Pennsylvanian (Labandeira, 2007). Evidence for other Palaeozoic modes of live tissue consumption, such as galling and root herbivory, occur later still, during the middle to late Pennsylvanian (Labandeira, 2007).

In this study, we document three types of herbivory based on functional feeding groups and distinctive damage types (DTs) on Middle Devonian liverworts. Two of these feeding styles have not been documented previously for the Devonian plant record. Our liverwort material is of the simple-thalloid type that comprises a midrib of elongate cells surrounded by unistratose thallus 'wings,' and was an early host for small, external folivorous

arthropods whose modern ecological equivalents more recently feed on tracheophyte leaves. Also new to the Devonian is galling, a very distinctive association that affects control of a plant's developmental biology through tissue encapsulated by an arthropod or fungal galler. An earlier occurring third mode, piercing-and-sucking, now extends the record from Early Devonian vascular plants to Middle Devonian liverworts. We end on discussing the potential role of liverwort counter-defence in reducing arthropod predation.

Materials and Methods

Geology and palaeobiology

The Catskill Delta of eastern New York State, of late Middle to Late Devonian age, consists of numerous deposits of land plants which historically have provided much of our knowledge of Middle Devonian terrestrial ecosystems (Banks *et al.*, 1985). Some of these deposits, such as the well-preserved biota at Gilboa, have been crucial for reconstructing important components of early terrestrial ecosystems (Stein *et al.*, 2007, 2012). Our focus in this report is on latest Middle Devonian, dark-grey siltstone and shale lenses where preservation of plant compression and impression fossils is excellent. This exceptional preservation is attributable either to rapid deposition in flood plain environments, such as channel fills, or alternatively to deposition in fine-grained dysoxic to anoxic lakes or ponds where likewise there is sealing of entombed plant material from the vagaries of oxidation. Both depositional styles can be found in outcrops bordering the western margin of the Hudson River Valley, southwest of Albany (Fig. 1). These deposits occur at two localities, both within the Plattekill Formation, that are the sources of our liverwort material. The first locality is the Cairo Quarry, a site long known for its rich and diverse macroflora, and a variety of vertebrates and

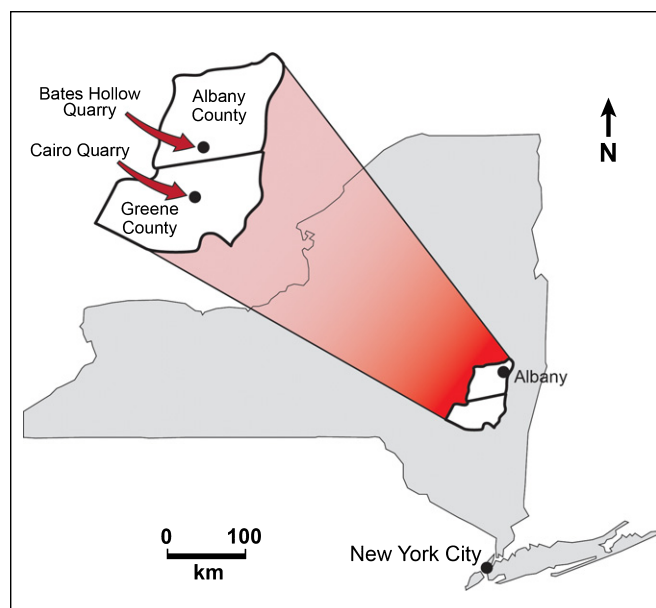


Fig. 1 Locality map showing the two sites in eastern New York state (USA) containing the liverwort material of this report.

invertebrates (Matten, 1973). The second locality, the recently discovered Bates Hollow Quarry, includes a green-grey siltstone that is the second source of our liverwort material, although the preservation is somewhat poorer than that of the Cairo Quarry. Additional background information of the regional and local geological context of these sites, including stratigraphic and sedimentological details, can be found in a recent account about the liverworts retrieved from this deposit (VanAller Hernick *et al.*, 2008).

Specimen preparation techniques

The liverwort material exhibited minimal contrast with the similarly dark-coloured and finely textured matrix, necessitating a special procedure for viewing and microphotographic processing (VanAller Hernick *et al.*, 2008). Because the preservation revealed delicate cellular detail (Figs 2, 3), a procedure was used of applying a film by coating exposed specimens with a liquid solution of nitrocellulose (Walton, 1926; Schaub *et al.*, 1993). Nitrocellulose is a mixture of nitric esters from cellulose that is used in synthetic fibre and plastic materials, including plastic films that are pulled off certain types of fossil specimens (Walton, 1926). Upon drying, the hardened but transparent and flexible coating is pulled from the specimen and mounted with Cytoseal on glass with a cover slip. Microphotography was done using a Canon Eos digital camera mounted on a Meiji compound microscope and processed by an Auto-Montage Pro imaging system. Microphotography of rock surfaces was done by application of water or cedarwood oil on the fossil surface to enhance contrast and clarity (Thomas, 1912). Additional samples were isolated from the matrix by immersing the shale fragments in 48% hydrofluoric acid and after rinsing, were mounted on glass slides using glycerine jelly.

Evaluation of plant damage

Although never applied to examinations of insect herbivore damage from land floras older than the Early Permian (Labandeira & Allen, 2007), we employed an objective system for classification of arthropod-mediated damage based on a compendium of diagnostic damage types (or DTs) from the fossil compression–impression record (Labandeira *et al.*, 2007). This system is based on four criteria that separate arthropod herbivory from detritivory, which is especially critical for Devonian floras (Labandeira, 2006, 2007). These criteria include: (1) most importantly, the presence of reaction tissue such as callus produced by the plant as a response to an induced trauma (Fig. 2, red arrows); (2) the preferential targeting of particular plant taxa or their organs and tissues, indicative of host specialization; (3) a mode of feeding revealed by a recurring, stereotyped pattern of damage, for example, indicated in comparisons of the same, small-sized margin and hole feeding between Middle Devonian (Fig. 2) and modern (Fig. 3j,k) liverworts; and (4) micromorphological features resulting from external folivory such as veinal stringers (Fig. 2, green arrows), tissue flaps (Fig. 2, blue arrows), and, for the surface expression of piercing-and-sucking, cratered depressions (Fig. 3d)

or stylet slits (Fig. 3e), indicated by black arrows. This system categorizes each distinctive DT by diagnostic structural features, providing an explicit description of the damage (Labandeira *et al.*, 2007), and has been used for insect damage in floras ranging from the Early Permian to the recent.

Results

We identified three major functional feeding groups of arthropod and fungal herbivory from the examined liverwort material on our host plant, *Metzgeriothallus sharonae* VanAller Hernick *et al.* (2008), shown as relatively intact specimens in Fig. 2(a). The identified arthropod functional feeding groups consist of external foliage feeding, piercing-and-sucking and galling, encompassing nine damage types (DTs). This system of damage categorization is based on diagnostic arthropod herbivory patterns (Labandeira *et al.*, 2007), mentioned in the previous section, strongly indicating that the damage on *M. sharonae* is attributable to herbivory and not abiotic modification. These criteria have been used in at least 25 previous studies. Although we examined herbivory on only one host plant, sampling was inadequate in terms of the numbers of specimens examined and, especially, the total surface area exposed. We did not tabulate the frequency of DT occurrence on *M. sharonae*, and consequently comparisons could not be made with other more recent plant–host taxa in the same general type of deposit or to potentially coeval floras. Nevertheless, a preliminary analysis of available thallus fragments ($N=128$) indicated that 17.8% of specimens in one sample and 27.1% in the second showed one or more type of arthropod damage. We did not assign fungal damage to any DT, as the current system (Labandeira *et al.*, 2007) does not allow for fungal DT subcategories.

External foliage feeding

Three of the four subtypes of external foliage feeding were represented on *M. sharonae*: margin feeding, hole feeding and surface feeding. Only skeletonization, wherein all foliar tissue is consumed except for the vascular tissue meshwork, was absent. This is a type of feeding extremely rare for the Palaeozoic, and anatomically impossible for liverworts, as these plants lack a vasculature that would be more impervious to externally feeding herbivores than surrounding fleshier tissue. At least some of this damage is very similar to that of modern liverwort external foliage feeding (DT01, DT12), illustrated in Fig. 3(j,k).

Margin feeding (DT12, DT13). Margin feeding consists of whole-tissue consumption of the margin of a leaf or equivalent flat photosynthetic organ by an arthropod with mandibulate mouthparts. Our two examples of margin feeding include consumption as a U-shaped excision along the lateral margin of the thallus (DT12), in one example involving much of the thallus but not reaching the costa (Fig. 2c). Another type is consumption of the thallus distal tissue, including the central costa and tissue of the wing on both sides (DT13), creating a terminal C- or U-shaped notch (Fig. 2b). In all cases of margin feeding there is

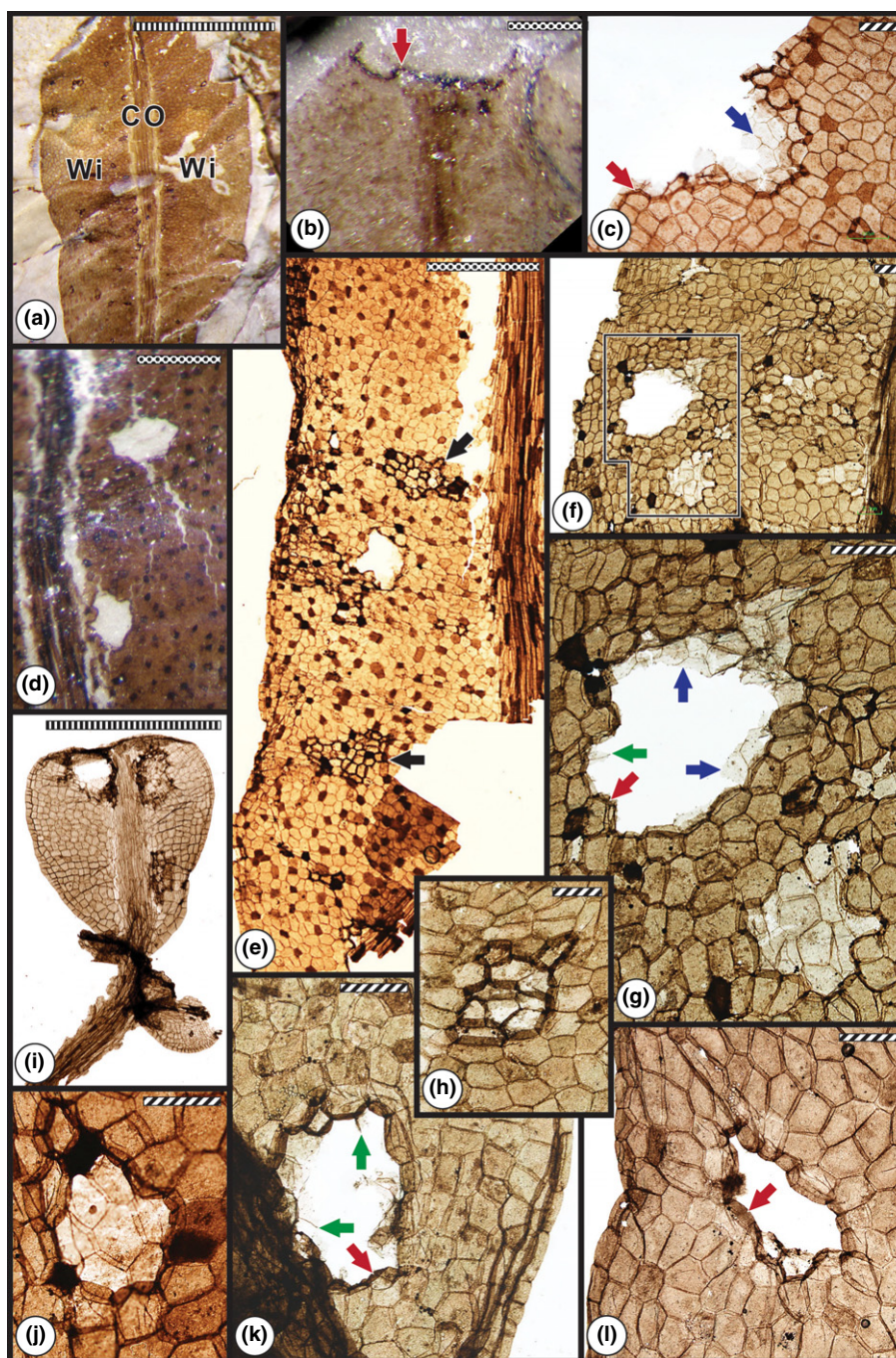


Fig. 2 External foliage feeding damage on *Metzgeriothallus sharonae*. Arrows indicate structural features resulting from herbivory: red arrows show reaction tissue; blue arrows designate tissue flaps; and green arrows point to veinal stringers. (a) Well-preserved, unherbivorized, gametophyte thallus showing left and right wings (wi) and a median costa (co) (NYSM18060). (b) Terminus of thallus, exhibiting margin feeding (DT13), with reaction tissue indicated (NYSM 18061). (c) Margin feeding along a thallus edge (DT12), with reaction tissue and a tissue flap (UCMP 250151.06). (d) Hole feeding (DT01), illustrating polylobate edges and reaction rims (NYSM 18063). (e) Hole feeding (DT01) at centre and surface feeding (DT30) above and below at black arrows (UCMP 250156.23). (f) Hole feeding (DT01) at centre-left and surface feeding (DT30) below at centre-bottom, enlarged at (g) below from the template (UCMP 250150.21). (g) Enlarged area outlined in (f) above, showing tissue flaps, veinal stringers and reaction rims of hole feeding (DT01) at centre; also note surface abrasion (DT29) with sinusoidal, polylobate reaction rims. (h) Another example of surface abrasion (DT29) with a polylobate, sinusoidal reaction rim (UCMP 250150.20). (i) A branch bearing two thalli, with upper thallus exhibiting DT01 at left, and DT30 at right top and right bottom (UCMP 250155.30). (j) Structure of DT29 damage showing removed surface tissue, remaining underlying cell walls, and enveloping reaction rim (UCMP 250155.07). (k) Informative example of hole feeding (DT01) displaying a reaction rim and veinal stringers interspersed among exposed tissue flaps (not marked) (UCMP 250150.20). (l) An example of hole feeding (DT01) adjacent to a thallus margin, with reaction rim indicated by an arrow (UCMP 250150.19). Convention for arrows: red, reaction rims; green, veinal stringers; blue, tissue flaps; black, surface feeding of DT30. Bars: ■■■■, 5 mm; ■■■■, 1 mm; ■■■■, 0.1 mm.

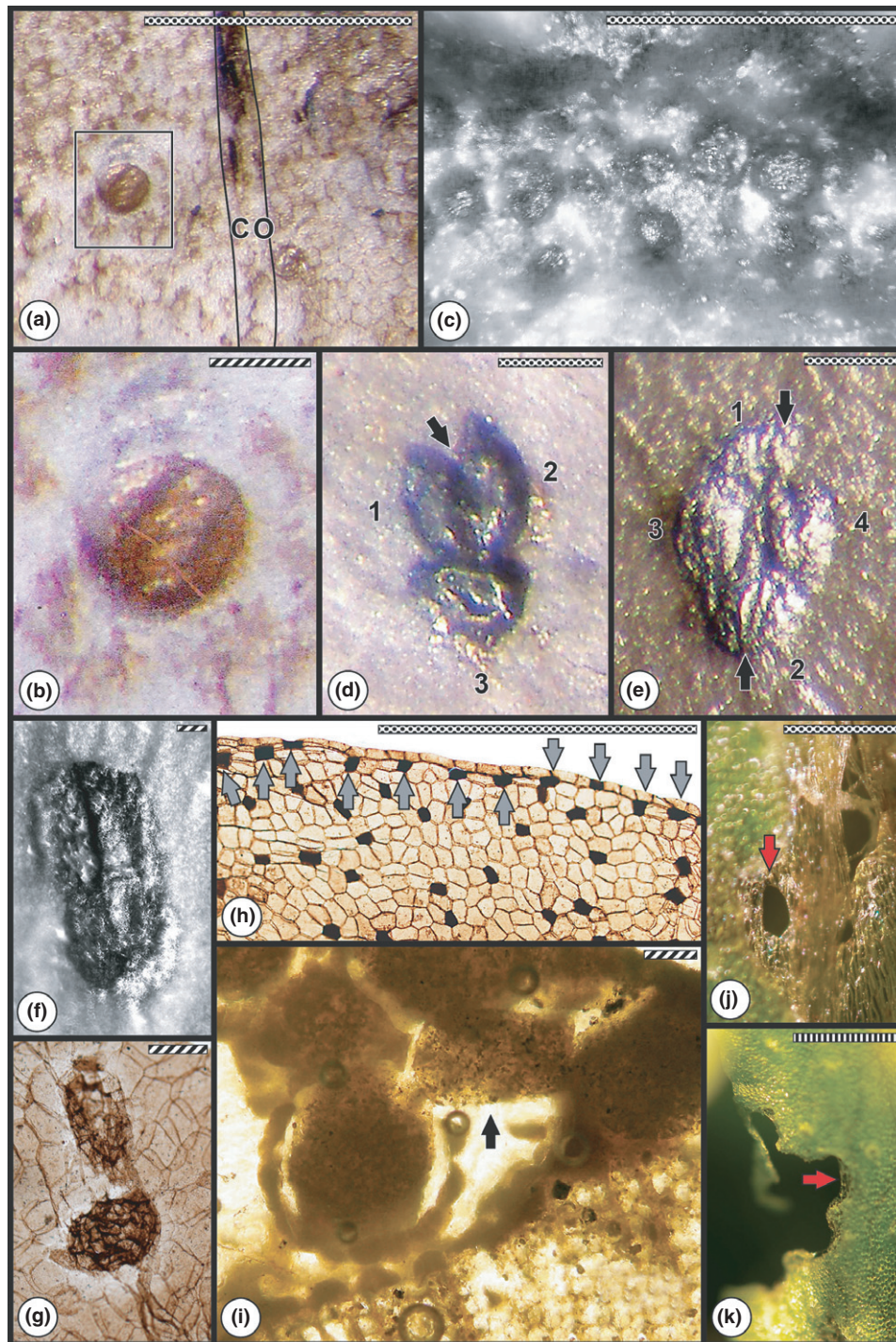


Fig. 3 Piercing-and-sucking (a–e), galling (f, g), and indirect evidence for herbivory (h, i) on *Metzgeriothallus sharonae*, and modern liverwort feeding damage (j–k). (a) Circular piercing-and-sucking (DT46) showing two isolated punctures on wing tissue and avoidance of costal tissue (CO), the left of which (in template) is enlarged in (b) below (NYSM 18071). (b) Detail of isolated puncture scar outlined in (a). (c) An array of three rows of linear puncture scars (DT138); the central row of which has eight punctures (NYSM 18072). Note differences in the diameters of the surface puncture scars. (d) A third type of piercing-and-sucking, showing clustered and overlapping lenticular puncture scars at arrow and cratered depressions (DT273), especially notable in the lower scar (NYSM 18073). This and the next image have numbers designating the sequence of feeding events indicated by stylet damage. (e) Another example of clustered piercing-and-sucking damage (DT273), consisting of four, clustered lenticular punctures, each with stylet insertion marks particularly prominent in the upper and lower punctures at the arrows (NYSM 18074). (f) A large simple gall (DT32) consisting of a single chamber with enveloping hardened tissue (NYSM 18075). (g) Two, adjacent ovoidal galls (DT32), showing internal cellular structure (UCMP 250155.14). (h) An unherbivorized thallus showing the concentration of oil body cells, indicated by grey arrows, along the thallus edge (UCMP 250149.02). (i) Short ellipsoidal coprolites containing small, undigested residues (small black splotches) of oil bodies (arrow), associated with *M. sharonae* (NYSM 18078). Microarthropod external foliage feeding on a modern liverwort, displaying hole feeding (DT01) in (j) and margin feeding (DT12) in (k) (unaccessioned specimens). Bars: ■■■■, 5 mm; ■■■■, 1 mm; ■■■■, 0.1 mm.

the presence of reaction tissue, indicated by red arrows along the excised margins in Fig. 2(b,c).

Hole feeding (DT01). Hole feeding is the whole-tissue consumption of the interior of a leaf or equivalent flat photosynthetic organ by an arthropod with mandibulate mouthparts. Our example of hole feeding consists of small regions of polylobate (Fig. 2d–g, i, k–l) or more circular (not illustrated) holes surrounded by thin reaction rims. These excisions were assigned to DT01 because the maximum size dimension did not exceed 1 mm (Labandeira *et al.*, 2007), and displayed distinct rims of response tissue.

Surface feeding (DT29, DT30). Surface feeding is the consumption of one or more outer tissue layers of a leaf or equivalent flat photosynthetic organ where at least one tissue layer remains present, typically made by an arthropod with scraping mandibulate mouthparts. Two examples of surface feeding are present. The first (DT29) evidently consists of removal of an uppermost tissue layer, revealing a subsurface layer of polygonal cells and a thin rim of response tissue (Fig. 2g, lower right); near this circular damaged area are two similar but much smaller damaged areas. The second, more common, example of surface feeding are specimens with a distinctive and robust reaction rim (DT30), shown by the black arrows in Fig. 2(e), and exhibiting a distinctly thick outer margin of response tissue and subsurface intercellular thickenings. Two excellent examples also occur toward the right of the medial costa in Fig. 2(i), consisting of a more elongate and irregularly margined, altered surface (enlarged damage is shown in Fig. 2(h,j)).

Piercing-and-sucking

Punctures occurring singly (DT46), in rows (DT138) or as clusters (DT273). Piercing-and-sucking refers to the consumption of fluids from internal plant tissues where access is external to the plant and mediated by punctures from the stylet mouthparts of an arthropod. Three categories of punctures are present, although the most common is DT46, consisting of small, circular punctures on the thallus blade, typically occurring in isolation (Fig. 3a,b). The second type of piercing-and-sucking is DT138, based on 13 punctures of subequal size and shape aligned in three linear arrays along the thallus long axis (Fig. 3c). The centre row of this field of punctures is the most extensive, consisting of eight successive punctures that are accompanied to the left by a parallel row of three punctures and to the right by a third parallel row of two to four indistinct punctures. The third distinctive type of piercing-and-sucking (DT273) consists of clusters of three to four or possibly more elongate, lenticular punctures that overlap (black arrow) in a detectible sequence numbered in Fig. 3(d,e). These clusters are exposed on the foliage surface, one of which exhibits a cratered centre defined by a white ovoidal border (Fig. 3d and Supporting Information Fig. S1a). The specimen in Fig. 3(e) is a cluster of four stylet scars, the bottom and top punctures exhibiting elongate stylet incision scars (black arrows), and indicated by an inferred sequence of emplacement (see Notes S1 for a description of this DT).

Galling

Simple galls (DT32). Galling is the encapsulation within plant tissue of usually a bacterium, fungus or often a subadult arthropod, whereby adjacent host tissue production is under the developmental control of the galler. Galls result in a protective and nutritive benefit to the galler, and thus represent an interaction detrimental to the plant host. Galls are found in the fossil record as simple structures, typically consisting of one chamber, or more rarely as compound structures in various degrees of proximity. A simple, ellipsoidal, single-chambered gall (DT32) was found on *M. sharonae*, oriented along the long axis of subsurface cells and exhibiting enlargement of tissue and thickening along intercellular walls in Fig. 3(f). Two galls of DT32 occur in Fig. 3(g). Each spheroidal gall bears a hardened and resistant outer wall that encloses a (presumed) single inner chamber.

Metzgeriothallus sharonae galls are differentiated from two potential structures that may be confused with galls. First, *M. sharonae* galls could be mistaken for piercing-and-sucking damage which likewise have a rounded external form and are characterized by interdigitating convolutions similar to a gall surface. However, piercing-and-sucking damage is characterized by circular or lenticular puncture marks that overlap and often display stylet insertion features such as central crater or stylet insertion slits. Second, some co-occurring spore-like structures could be misidentified as galls. However, such spores have a more constant size and shape, bear a distinctive, unadorned cell-wall surface, and frequently form biserially arranged, compound structures in arrays ranging from four to *c.* 14 spores.

Discussion

Modern liverwort herbivory

Historically liverworts have been consumed by a variety of herbivores, given the extent that invertebrates, especially arthropods, consume or otherwise alter modern liverwort tissues (Gerson, 1982; Glime, 2006; Haines & Renwick, 2009). Generalized herbivory, usually in the form of external foliage feeding, has been recognized on epiphyllous liverworts from several tropical sites (Olarinmoye, 1974; Lawrey, 1987; Monge-Najera, 1989; Coley *et al.*, 1993). More recently, specialized associations have been described, such as consumption of tissues within the lobules of two species of the epiphytic liverwort *Frullania*, one by a bdelloid rotifer in the eastern United States (Puterbaugh *et al.*, 2004), and the other by an oribatid mite in northern Queensland, Australia (Colloff & Cairns, 2011). Other liverwort–animal associations involve insects, particularly the Lepidoptera, in which a subclade of the basal-most Micropterygidae has radiated extensively during the late Cainozoic on the Japanese liverwort *Conocephalum* (Imada *et al.*, 2011), as an obligate association (Hashimoto, 2006). Associations between other micropterygid moths and liverworts have been noted in the earlier literature (Jolivet, 1998), suggesting that this general dependency may be ancient and extends to the earlier Mesozoic. Another basal but dietarily generalized clade, the Mnesarchaeidae, is known to

consume significant amounts of live liverworts (Gibbs, 1979). A more derived clade of moths, the Lithiniinae of the Geometridae, has radiated on ferns throughout the world, although a nonspecific subclade in Indonesia feeds on liverworts secondarily (Weintraub *et al.*, 1995). Another holometabolous insect, the larva of the crane fly *Geranomyia recondita*, feeds on liverworts in Costa Rica (Arroyo-Rodriguez *et al.*, 2007). Lastly, there have been multiple colonization events of liverwort hosts within the plant-feeding mite families Tetranychidae and Tenuipalpidae, some of which form gall associations (Tuttle & Baker, 1976).

Food resource partitioning by arthropod herbivores during the Devonian

Liverwort gametophytes are considerably smaller, and particularly in the case of the simple-thalloid lineages, histologically much simpler than vascular plant sporophytes. Crandall-Stotler *et al.* (2005) reconstructed the ancestral liverwort gametophyte as a simple-thalloid type. Although the two simple-thalloid lineages had most likely not diverged from the main Jungermanniopsida lineage by the Middle Devonian, both Devonian taxa described so far do have the diagnostic features of simple-thalloid liverworts and have been taxonomically placed in those lineages, supporting the simple-thalloid model of liverwort ancestry. Despite this morphological divide, the diversity of herbivory documented herein for Middle Devonian liverworts can be regarded as an early experiment in small arthropod herbivory. This experiment targeted exophytic use of tissues by external foliage feeders and piercer-and-suckers and endophytic use of tissues by gallers. Regardless of whether there was continuity of these associations to the modern record (Gerson, 1982; Glime, 2006), apparently there was a separate colonization of vascular plants and consumption of their more diverse tissue types during the later Carboniferous to Permian (Labandeira, 2006), with crown clades emerging during the later Permian and providing a subsequent, parallel pathway of plant resource use by herbivorous arthropods.

As in the examples documented from the later Palaeozoic, there are indications of opportunistic plant-host use of *M. sharonae* by herbivores, attributable to a broad functional repertoire of feeding types. External foliage feeding included three of the four major subtypes – margin feeding, hole feeding and surface feeding – are found in late Carboniferous and later biotas; only skeletonisation is absent, wherein all nonvascular tissues of foliage are consumed. In any event, skeletonisation appears later in the Permian and is rare until the appearance of angiosperm-dominated floras (Labandeira & Allen, 2007). External foliage feeders fed on all portions of the *M. sharonae* thallus, including the costa and adjacent wing tissues; these latter included dark cells (Fig. 2f) which strongly resemble the specialized oil body cells found in extant representatives of some early-diverging lineages of liverworts (Schuster, 1966–1992). As host plants were consumed, a response was elicited to external foliage feeding by formation of a thickened edge of callus or similar reaction tissue. External foliage feeding herbivores probably represented multiple species of microarthropods, based on the variety and small size of the documented damage patterns.

It is conceivable that the surface abrasion damage could have been caused by terrestrial pulmonate gastropods, in particular slugs. Pulmonate gastropods have a distinct mouthpart ensemble, the radula, consisting of many rows of spinules that abrade foliage surface tissues. Foliar damage by radulae leave a distinctive damage pattern of arcs of striae interrupted by perpendicularly oriented denticle marks that overlap, typically associated with the delamination of one to a few surface tissue layers (Frank, 1998; Cranshaw, 2004). However, the surface abrasion damage pattern occurring on *M. sharonae* is inconsistent with a pulmonate gastropod. In addition, the ecological and evolutionary radiation of pulmonate gastropods likely commenced during the early Mesozoic (Wade *et al.*, 2001), and the oldest evidence for land snails occurred in the late Carboniferous (Solem & Yochelson, 1979), *c.* 80 Myr after the occurrence of *M. sharonae*.

The physical removal of surface tissues in modern liverworts may resemble the surface abrasion of DT29 and DT30, producing reaction tissue similar to that of surface-abrading herbivores (S. L. Tremblay, pers. obs.). Such damage, consisting of removal of one to a few cellular layers of thallus tissue, is likely attributable to abiotic processes such as nutrient deficiency, thermal shock, moisture stress or lack of ambient oxygen (Katterman, 1990; Labandeira & Prevec, 2013). Superficially, such damage is similar to surface abrading mandibulate insects, mites or pulmonate gastropods, but there is the absence of distinctive, subsurface marks and patterns made by arthropod mouthparts or gastropod radulae, as well as the general avoidance of indurated micromorphological features such as cell walls and miniscule veinules (Alford, 1991).

For gallers, it is unclear whether they similarly were avoiding the dark cells we interpret as specialized oil body cells. The galler evidently directed the developmental response of the liverwort in the immediate area of the encapsulated gall, such that anomalous protective and nutritive tissues were produced, probably through hypertrophy and hyperplasy. The most likely gall culprit is a mite, some interactions of which have been recorded on modern liverworts (Tuttle & Baker, 1976). Tydeid mites are known from the Early Devonian (Hirst, 1923), and modern representatives feed on plant tissues, fungi and insect eggs, although many are predatory (Flaherty & Hoy, 1971). Alicorhagiid mites occur in the Middle Devonian (Kethley *et al.*, 1989), but extant descendants are almost entirely predatory, particularly on nematodes (Shear & Selden, 2001). Other mite lineages, including overwhelmingly detritivorous oribatid mites (Labandeira *et al.*, 1997), and varied phytophagous forms probably were present during the Middle Devonian (Walter & Proctor, 1999). Modern mite gallers of vascular plants, such as the Tetranychidae and Tenuipalpidae, are not known to occur in the Devonian; fossil evidence suggests a probable earliest occurrence during the Permian (Schmidt *et al.*, 2012). We do not know of any insect lineage present during the Middle Devonian that would have been a galler. A fungal or bacterial culprit also is possible as the inducer of this gall.

By contrast, piercing-and-sucking is a functional feeding group that has a distinct fossil record extending to the Early Devonian. Evidence for piercing and sucking is based on damage to surface

stem tissues of multiple permineralized Early Devonian plant taxa (Kevan *et al.*, 1975; Banks, 1981; Banks & Colthart, 1993), and the presence during this interval of lineages that housed taxa with stylet mouthparts responsible for the observed damage, including collembolans (Hirst & Maulik, 1926; Greenslade, 1986) and mites (Hirst, 1923; Norton *et al.*, 1988; Kethley *et al.*, 1989). Unlike Early Devonian piercing-and-sucking damage on stem tissues, the producers that bore stylet mouthparts during the later Devonian fed on foliose tissues, avoiding the specialized, lengthened conducting cells of liverwort thalli and likely the vascular tissues of tracheophytes.

The generalist damage pattern documented herein and their suggested microarthropodan culprits, indicate a functionally differentiated component community (Root, 1973). This community of herbivores likely is the precursor to food resource partitioning (Fig. S1), based on functional feeding group (how food was consumed), dietary guild (what type of tissue was consumed) and mouthpart type (what type of feeding apparatus was used to consume the food) (Root, 1973; Labandeira, 1997; Labandeira *et al.*, 2007).

Early history of the piercing-and-sucking functional feeding group

Of the major terrestrial functional feeding groups of arthropods that developed during the Devonian, piercing-and-sucking is typified by distinctive, stylet-inflicted insertion scars seen on compression-impression plant surfaces later in the Palaeozoic (Zherikhin, 2002; Prevec *et al.*, 2009). Piercing-and-sucking provides the best potential for revealing the culprits responsible for much of the liverwort damage. In Table S1 and Fig. S2, 15 stylet puncture wounds are illustrated on a variety of foliar, seed and fruit surfaces from the primary literature for comparison to DT273 on *M. sharonae* (Fig. S1a). This gallery consists of piercing-and-sucking marks from insects representing late Carboniferous Paleodictyopteroidea (Fig. S1b,c), and modern Thysanoptera (Fig. S1d,e), Hemiptera–Sternorrhyncha (Fig. S1f–k) and Hemiptera–Heteroptera (Figs. S1l–n), as well as representatives of two mite lineages (Fig. S1o,p). These taxa that have stylet mouthparts and their patterns of surface tissue alteration from single feeding events, provide a broad summary of the types of piercing-and-sucking damage found on a broad spectrum of host plants and organs.

Judging from comparisons of these stylet arthropodan damage patterns on a variety of seed-plant hosts, with that of DT273 on *M. sharonae*, four features can be ascribed to the piercing-and-sucking arthropod culprit. First, the piercer-and-sucker had an overall small piercing mark. Second, the stylet ensemble was laterally compressed, which is significantly different from the circular cross-sections of stylet penetration marks caused by late Carboniferous and Permian paleodictyopteroid insects (Fig. S1b,c), also shown anatomically by stylet cross-sectional profiles in body fossils (Kukalová-Peck, 1985). Third, there was the capability of puncturing into a more limited area of the affected tissue, indicated by a semicircular border of altered tissue within the feeding mark (Fig. S1i,k). Last, a prominent, outer reaction

rim is present, similar to Fig. S1(f,j), suggesting a significant response of callus or other response tissue from the host plant and sealing of the puncture (Shackel *et al.*, 1991). Although these details reveal the effect of the mouthpart apparatus on the liverwort host, they provide insufficient resolution for identifying which later Devonian arthropod was responsible for this damage. Also confounding an affiliation is the near absence of knowledge regarding Late Devonian insects. Although an insect has been described from the Late Devonian (Garrouste *et al.*, 2012), its taxonomic affinities have been questioned, and it may represent a degraded aquatic crustacean (Hörschemeyer *et al.*, 2013). Consequently, there is no solid evidence for positing a particular insect lineage as the culprit for piercing-and-sucking damage, or for that matter, chewing damage on *M. sharonae*. It appears that the stylet marks resemble most closely that of a small hemipteran, although such an attribution would be geochronologically implausible, as the earliest documented, definitive Hemiptera are of Early Permian age (Shcherbakov, 2000). A more definitive attribution would require better understanding of the types of damage that collembolans and mites leave on land-plant tissues, including liverworts (Broadly, 1979; Colloff & Cairns, 2011).

A Devonian microarthropodan herbivore fauna and colonization events

Middle Devonian liverwort herbivory can be compared to earlier biotas of the Early Devonian and those of the subsequent late Mississippian to Permian. For earlier Devonian examples 20–30 Myr older than the liverwort herbivory described here, there is recognition only of piercing-and-sucking, specifically on the peridermal and other tissues of early land plants (Banks, 1981; : Banks & Colthart, 1993). This damage consists of small stylet probes that targeted cells of shallow tissue layers. By contrast, there is no evidence of Devonian external foliage feeding or of galling (Labandeira, 2006, 2007). These absences may be partly attributable to the lack or insufficient abundance of appropriate plant organs, such as leaves or leaf equivalents, for external foliage feeding (Labandeira, 2007). Alternatively, this absence may be due to the lack of adequately preserved early terrestrial biotas such as permineralizations, consisting overwhelmingly of pyrite-, silica- or carbonate-impregnated plants, fungi and arthropods, or otherwise macerated residues from fine-grained sediments which often disallow examination of significant surface areas. In either case, the extensive liverwort surfaces that are revealed by bedding planes have not been widely abundant (or possibly sought for) in the earlier Devonian record, imparting a bias to the plant–insect associational record.

For subsequent associations, the earliest described margin feeding is on an early seed fern from the late Mississippian of Australia (Iannuzzi & Labandeira, 2008), which indicates a significantly larger sized herbivore with a comparatively larger intermandibular gape than any Devonian mandibulate terrestrial arthropod. This occurrence also suggests a delay contingent on the origin of substantively sized leaves during the Devonian (Labandeira, 2007), supported by the evidence on liverworts described here. Subsequently, margin feeding becomes more

noticeable in Pennsylvanian age floras (Scott & Taylor, 1983). Gallings was more delayed than external foliage feeding, with the earliest well-established gall on a sphenopsid of middle Pennsylvanian age, followed by a marattialean fern rachis gall from the late Pennsylvanian, and a conifer gall from the Early Permian (Labandeira, 2006; and references therein). It is notable that the sizes of the largest coprolites from various Devonian terrestrial biotas (Kevan *et al.*, 1975; Edwards *et al.*, 1995; Habgood *et al.*, 2004) are significantly smaller than those of Pennsylvanian age biotas (Scott & Taylor, 1983; Labandeira, 2006).

There are three principal reasons for suggesting that the arthropods consuming Middle Devonian *Metzgeriothallus sharonae* were of substantively smaller size than their successors on ferns and seed plants of the late Mississippian to Permian. First, none of the external foliage feeding damage on *M. sharonae* exceeds c. 1 mm in maximum dimension (Fig. 2b–l), in contrast to the considerably larger size of analogous, younger late Mississippian and Pennsylvanian damage that ranges from 4 to 10 mm in maximum dimension (Scott & Taylor, 1983; Labandeira, 2006, 2007; Iannuzzi & Labandeira, 2008). The same pattern also exists for the projection of stylet insertion marks on foliage surfaces (Fig. 3a–e) and gall size (Fig. 3f–g) when compared to more recent, analogous Palaeozoic plant damage. Second, the size range of herbivory on *M. sharonae* is similar to earlier feeding damage in Devonian biotas such as piercing-and-sucking damage at Gaspé, in Québec (Banks, 1981; Banks & Colthart, 1993), and at Rhynie, in Scotland (Kevan *et al.*, 1975). Third, the size range of known herbivore arthropod body fossils occurring in Early and Middle Devonian biotas are substantively smaller than those of latest Mississippian and Pennsylvanian (Tillyard, 1928; Shear *et al.*, 1984; Shear & Kukalová-Peck, 1990). Devonian fossils frequently are referred to as ‘microarthropods’ (Shear *et al.*, 1996), and accordingly are commensurate with feeding-damage size inferred from their head capsule and mouthpart element dimensions (Hirst & Maulik, 1926; Tillyard, 1928; Shear *et al.*, 1984; Shear & Kukalová-Peck, 1990). Although hexapod herbivores exhibit a size increase from Devonian (smaller) to latest Mississippian to Pennsylvanian (larger) body fossils, it appears that mites always have been small (Norton *et al.*, 1988; Schaefer *et al.*, 2010), consistent with the assignment of all well-described Pennsylvanian galls to considerably larger insect culprits (Labandeira, 2006).

Based on (1) body-size size distinctions and (2) patterns of temporal lags between the appearance of plant organs and their eventual herbivory (Labandeira, 2007), the herbivore arthropod faunas of the Devonian and subsequent late Mississippian to Permian interval indicate two separate, arthropod herbivore colonization events of land plants. Recognizing that much of the relevant Mississippian fossil record of plant damage is sparse, these arthropod body-size differences and major lags in herbivory suggest an earlier event consisting of small-sized arthropods on liverworts during the Middle Devonian and their precursors found on early vascular plants in the Early and Middle Devonian. Later, a second pulse comprising comparatively much larger arthropods, overwhelmingly insects, was launched on vascular plants during the late Mississippian (possibly earlier) and throughout the

Pennsylvanian (Labandeira, 2007). This suggests a different guild of plant-consuming microarthropods with distinctive mouthpart structures for feeding modes during the Devonian and probably throughout the earlier Mississippian. These microarthropod groups likely were extinguished by the diversification of insects with larger body sizes and more efficient feeding mechanisms during the Mississippian Pennsylvanian boundary c. 318 Ma (Ward *et al.*, 2006).

Antiherbivore chemical defence in ancient terrestrial ecosystems

We spotlight an additional aspect of our study in which we have circumstantial evidence for herbivore deterrence that should receive increased examination in future studies of Palaeozoic liverworts. One reason for suspecting that Devonian liverwort herbivory is of ancient origin is the various antiherbivore metabolic mechanisms of modern liverworts, including mucilage secretion (Duckett *et al.*, 2006), pigment production (Hooijmaijers & Gould, 2007), and particularly the presence of unique organelles, oil bodies, containing concentrated terpenoids and aromatic compounds (Kis & Pócs, 1997). These structures frequently have been interpreted as defensive mechanisms to ward off herbivores (Mueller & Wolf-Mueller, 1991; Hooijmaijers, 2006; Yanoviak *et al.*, 2006), and apparently are shared by modern liverwort clades with an origin deep in the Palaeozoic (Qiu *et al.*, 1998; Heinrichs *et al.*, 2007).

We find fossil evidence for one of these anti-herbivory mechanisms in the presence of scattered, dark cells nearly always observed on *M. sharonae* which have a similar distribution to the specialized oil-body-containing cells that are found in several early-diverging lineages of liverworts (Figs 2e, 3h) and by black, refractory and undigested structures in ellipsoidal coprolites resulting from *M. sharonae* consumption (Fig. 3i). The similarity of the scattered, dark cells of *M. sharonae* and other Palaeozoic liverwort fossils to the terpenoid-containing, specialized oil body cells of modern liverworts (Schuster, 1966 1992; Asakawa, 2004) suggests a major early role for liverwort chemical deterrence of arthropod herbivory (Mueller & Wolf-Mueller, 1991; Hooijmaijers, 2006). We have noted a concentration of the dark cells along the perimeter of the *M. sharonae* thallus (Fig. 3h), suggesting the position-based deterrence of margin-feeding herbivores. Modern liverworts that concentrate terpenoids in oil bodies are known to be toxic to slugs (Frahm, 2004), leafcutter ants and their fungal mutualists (Howard *et al.*, 1988), and other herbivorous arthropods (Crandall-Stotler & Stotler, 2000). Both the data for various forms of herbivory on *M. sharonae*, and the evidence of chemical defence, suggest that not only herbivory, but also plant chemical defences may have played a more significant and ancient role in early terrestrial foodwebs than earlier data had indicated.

The chemical defence mechanism we describe for liverwort oil cells may have been preceded by another similar mechanism postulated for the spines of *Sawdonia ornata*, an Early Devonian vascular plant (Shear & Selden, 2001). *Sawdonia ornata* spine tips frequently are aperturate and contain a dark substance suggestive

of an exudate (Edwards & Selden, 1993). Although *Sawdonia* spines may have been responsible for the elimination of secondary compounds, an equally likely hypothesis is that they were used as a chemical defence against herbivores, a mechanism that may be present in other Devonian vascular plants (Lyon & Edwards, 1991). It may be that the antiherbivore chemical defence that we document in liverworts may have been a development that was paralleled independently in more ancient vascular plants.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 The component community of arthropod herbivores on Middle Devonian *Metzgeriothallus sharonae*.

Fig. S2 A comparison of DT273 on the liverwort *Metzgeriothallus sharonae* from the late Paleozoic of New York state, with published late Paleozoic and modern piercing-and-sucking damage on a variety of land plants.

Table S1 Comparison of various cross-sections of stylet marks indicating piercing-and-sucking damage from late Paleozoic and modern plant hosts

Notes S1 New damage type DT273.

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