Palaeogeography, Palaeoclimatology, Palaeoecology 306 (2011) 127–133

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Spatiotemporal extension of the Euramerican *Psaronius* component community to the Late Permian of Cathaysia: In situ coprolites in a *P. housuoensis* stem from Yunnan Province, southwest China

Ashalata D'Rozario [a,*], Conrad Labandeira [b,c], Wen-Yi Guo [d,e], Yi-Feng Yao [d], Cheng-Sen Li [d]

[a] Department of Botany, Narasinha Dutt College, 129, Bellilious Road, Howrah 711 101, India
[b] Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA
[c] Department of Entomology and BEES Program, University of Maryland, College Park, MD 20742 USA
[d] State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Xiangshan, Beijing 100093, PR China
[e] 2 Xiamen Environmental Protection Research Institute, Xiamen 361006, PR China

A R T I C L E I N F O

Article history:
Received 29 November 2010
Received in revised form 7 April 2011
Accepted 13 April 2011
Available online 20 April 2011

Keywords:
Coprolites
Psaronius housuoensis
Plant–arthropod association
Late Permian
South China Block
Insect

A B S T R A C T

We report well-preserved coprolites in the ground tissue of the permineralized stem of *Psaronius housuoensis* D'Rozario et al., from the Upper Permian deposits of Yunnan Province, southwest China. The distinctive coprolites are circular to oval in shape, ranging on average from 944 × 1190 μm to 1065 × 1120 μm, and contain histologically identifiable tracheids, parenchyma, gum sac cells, spores and fungal remains. Several lines of evidence indicate that this association was detritivorous, represented a pith boring, and was made by a diplopod or more likely an insect. This discovery extends the temporal duration of the food web of *Psaronius* plant–arthropod associations from the late Middle Pennsylvanian to now the Late Permian, and extends the biogeographic range from the equatorial wetlands of the Illinois, Northern Appalachian, and German Erzgebirge Basins of Euramerica to now the South China Block of Cathaysia. The *Psaronius*–arthropod–fungi component community is spatiotemporally the most persistent of documented Paleozoic associations in the fossil record.

1. Introduction

Coprolites (fossilized fecal pellets) have an important role for understanding plant–insect associations in terrestrial ecosystems of the deep past. Coprolites, which are attributable to land arthropods have been identified in sedimentary rocks as old as the Upper Silurian by Edwards (1996). Younger coprolites from Upper Carboniferous (Pennsylvanian) compression floras were described by Seward (1935), followed by identifications from both compression (typically shale) and permineralized (mostly coal ball) plant material by Scott (1977), Baxendale (1979), Rothwell and Scott (1983), Scott and Taylor (1983), Taylor and Scott (1983), Rex and Galtier (1986) and Labandeira and Phillips (1996a, 1996b, 2002). Earlier identifications of coprolites in Carboniferous woods reported by Brongniart (1877) and Williamson (1880) probably are misattributions and require re-evaluation. By contrast, Scott (1977) and Rothwell and Scott (1983) have described a variety of larger sized and more varied shapes of coprolites than previously described for the Euramerican Paleozoic; as well, smaller, tiny coprolites in coal balls were observed by Mamay and Yochelson (1953, 1962). In the more recent part of the fossil record, Harris (1946, 1956, 1964) and Hill (1976) reported Middle Jurassic coprolites from the Yorkshire Flora containing caytonialean microsporophylls and *Ptilophyllum* leaf cuticles, respectively, both attributed to small terrestrial tetrapods. Stoval and Strain (1936) described Paleogene fecal structures, referred to a mammalian origin. This brief survey of coprolites from the late Palaeozoic to more recent occurrences clearly indicates that plant–animal associations have an ancient history, and were relatively abundant in late Paleozoic deposits, both as generalized detritivory but also as more specialized and highly varied types of herbivory (Kevan et al., 1975; Scott, 1977; 1980; Scott and Taylor, 1983; Labandeira, 2002; Labandeira and Allen, 2007).

To date, the *Psaronius* assemblage of arthropod associations probably provides the best evidence of a co-associated plant–arthropod system that the Paleozoic has to offer, comparable to modern-day source–plant communities (Southwood, 1973; Lawton, 1976; Hamilton; 1978; Swain, 1978; Gilbert, 1979; Thompson, 1994). Detritivore and herbivore records of coprolites occurring in permineralized *Psaronius* contexts are either recorded sporadically in coal-ball floras within plant tissues and dispersed into the ambient peat; or alternatively, have sparser occurrences within tissues of isolated trunks, rachises, and foliage in compression–impression deposits. Evidence for *Psaronius* associations commences with pith borings inside the carbonate-permineralized stems of the "layered cells morphotype" during the latest Middle

* Corresponding author.
E-mail address: ashalatandc@gmail.com (A. D'Rozario).

0031-0182/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.palaeo.2011.04.009

Pennsylvanian, from the late Moscovian Herrin Coal of the Illinois Basin, in the United States (Lesnikowska, 1989; Labandeira et al., 1997; Labandeira and Phillips, 2002). *Psaronius* associations especially expand during the Late Pennsylvanian, particularly involving several herbivore associations on carbonate-permineralized *Psaronius chasei* Morgan vegetation from the Calhoun Coal of the Illinois Basin, including distinctive but primitive galls that indicate the existence of insect holometaboly (Lesnikowska, 1990; Labandeira and Phillips, 1996b; 2002; Labandeira, 2011). The pith borings in the *Psaronius* "layered cells morphotype" and *chasei* stems, consisting of spheroidal to ellipsoidal coprolites with distinctive contents and ground-tissue fragments, and are nearly identical to coprolites in *P. magnificus* (Herzer) Rothwell and Blickle stems from the Redstone Coal of the northern Appalachian Basin in Ohio (Rothwell and Scott, 1983). By contrast, the Permian reveals fewer instances of detritivorous or herbivorous associations of *Psaronius* organs. Rößler (2000) reported small-sized coprolites in tunnels representing oribatid mites in silicified adventitious roots of *Psaronius* sp. from the Lower Permian (Asselian) of Chemnitz, in the Erzgebirge Basin of Germany; however, he did not find larger, insect-like coprolites in the cortical parenchyma, as in Pennsylvanian-age specimens from the United States. By contrast, Permian compression–impression record from north-central Texas had fewer instances of detritivorous and herbivorous associations, and consumption of *Psaronius*-affiliated *Pecopteris* foliage either was virtually absent in the case of the Lower Permian (late Sakmarian) Coprolite Bone Bed Flora (Labandeira and Allen, 2007), or occurs at (very) low levels in other, similarly aged Texan floras that have been preliminarily studied (Beck and Labandeira, 1998). Notably, it is the seed plants, particularly medullosan and gigantopterid pteridosperms, that overwhelmingly display the highest herbivory levels in these compression floras (Labandeira, 2006a).

Reports of coprolites from China are rare and there are no previous instances of their occurrence within the stems of Chinese *Psaronius*. Hilton et al. (2001) recorded plant damage and coprolites from the Yangshuling Mine, from the Pingquan District of Hebei Province, northern China, that were assigned to the Early Permian Taiyuan Formation of northern China. However, the coprolites contained mostly unrecognizable plant fragments dispersed among unaffiliated, permineralized plant fragments (Seyfullah et al., 2009). The only identifiable Taiyuan coprolites were those that occurred within the *Myeloxylon* rachis of a medullosan pteridosperm. The present contribution records for the first time the occurrence of coprolites containing well-preserved plant debris within the permineralized marattialean tree fern stem, *Psaronius housuoensis* (D'Rozario et al., 2011), from the Upper Permian (Lopingian) of China, providing additional—in our case latest Paleozoic—data on this unique assemblage of plant–animal associations.

2. Materials and methods

We collected material for the present investigation from Upper Permian deposits of the Housuo Coal Mine, Fuyuan County, Yunnan Province, southwest China. This deposit is assigned to the Xuanwei Formation, of transitional Wuchiapingian to Changhsingian age (Hilton et al., 2004). Preservation occurs as permineralized fossil trunks in the coal mine. Other taxa in this flora include the calamitalean sphenopsid *Arthropitys yunnanensis* (Wang et al., 2006), and some preserved *Psaronius* stems (Hilton et al., 2004). Most of the Housuo Flora remains undescribed.

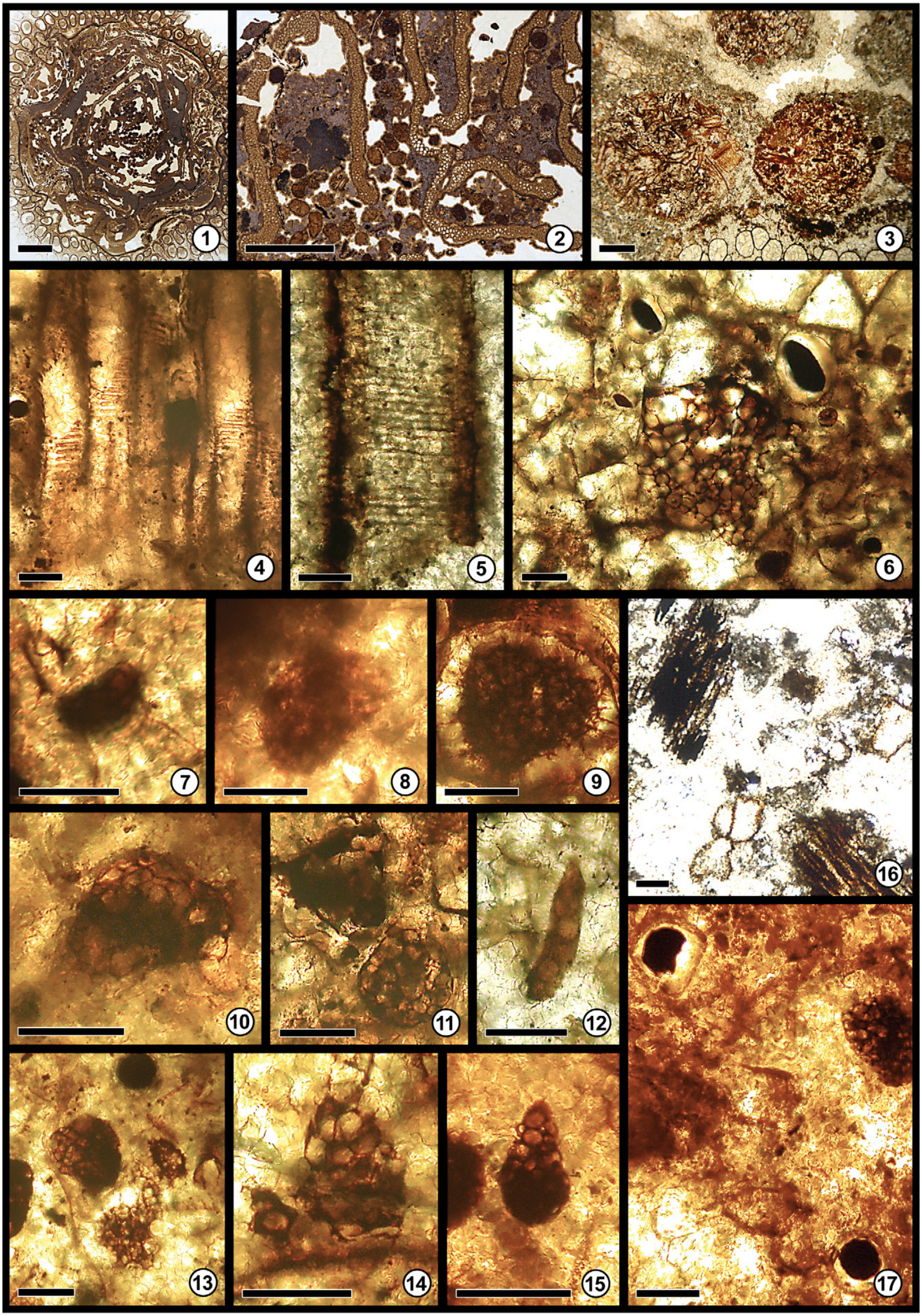
The permineralized specimen of a 23 cm long *Psaronius housuoensis* stem was cut into several, thin, transverse sections with a rock saw (model SPOJ-300). The resulting slabs were ground and polished with 100 to 300 grit carborundum powder, and mounted onto glass microscope slides using epoxy resin and triethanolamine. The slide slabs were further polished with 600 to 1000 grit of carborundum powder on a glass plate to achieve an optical thickness for observation under transmitted and reflected light .The slides were observed and studied by a Leica DMRE microscope, a Leica DM 2500 microscope and an Orient SMI stereo microscope, photographed with Nikon Coolpix 4500, Leica DFC 420 and Cannon EOS 20D digital cameras. Images were adjusted in Adobe Photoshop (V. 7) and plates prepared in Corel Draw (V. 12). All specimens and prepared slides are deposited in the Palaeobotanical Laboratory, Institute of Botany, Chinese Academy of Sciences, Beijing.

3. Observations

Transverse sections of the entire length of the petrified stem of *Psaronius housuoensis* exhibits a well preserved, polycyclic dictyostele embedded within poorer preserved parenchymatous ground tissue (Plate I, 1). Tracheary elements of the xylem are undisturbed and most of the parenchymatous ground tissue is either degraded to amorphous masses (Plate I, 1–2), or is completely replaced by well-packed

Plate I.

1. Cross section of the examined stem of *Psaronius housuoensis* D'Rozario et al. showing separate meristeles of the polycyclic dictyostele and ground tissue replaced by coprolites occurring among highly decomposed, structureless tissue. The stem consists of an inner region with looping sheets of tracheid-bearing vascular tissue, vague interstelar parenchyma, and is bounded outward by a thin zone of sclerenchyma; a distinctive root mantle occurs beyond the outer periphery of the stem. Slide HS-27-10; scale bar = 10 mm.
2. A part of the stem, enlarged from (1) at left, showing compactly disposed coprolites occurring among highly degraded, structureless parenchymatic tissue. Note larger celled and thicker walled xylem (tracheids with white centers) toward the center of the meristeles, surrounded on the periphery by thinner walled and much smaller celled phloem (with occluded, brown centers). Slide HS-27-02; scale bar = 10 mm.
3. Portion of the stem enlarged from (2) at left, exhibiting coprolites containing identifiable *Psaronius* plant tissues, principally tracheids as linear features, gum-sac cells with opaque centers, stem parenchyma, and xylem-rich vascular tissue. Note unconsumed vascular tissue strand at bottom margin. Slide HS-27-15; scale bar = 100 μm.
4. Eight xylary tracheids linearly arranged within a coprolite, each showing scalariform thickenings. Slide HS-27-01; scale bar = 100 μm.
5. Enlargement of a tracheid similar to one at left in (4), showing scalariform thickenings. Slide HS-27-01; scale bar = 50 μm.
6. Coprolite containing parenchyma and embedded gum-sac cells (with opaque contents). Slide HS-27-08; scale bar = 100 μm.
7. A kidney shaped sclerotium, occurring within a coprolite. Slide HS-27-12; scale bar = 50 μm.
8. A second kidney-shaped sclerotium, occurring within a coprolite. Slide HS-27-14; scale bar = 50 μm.
9. A distinctive, triangular-shaped, spinose spore, occurring within a coprolite, characterized by linear spines along its periphery. Slide HS-27-12; scale bar = 50 μm.
10. An ovoidal fungal sclerotium, with spores, occurring within a coprolite. Slide HS-27-03; scale bar = 50 μm.
11. Two spheroidal fungal sclerotia, with spores, in a coprolite. Slide HS-27-06; scale bar = 50 μm.
12. A cylindrical fungal sclerotium, with spores, in a coprolite. Slide HS-27-13; scale bar = 50 μm.
13. Six fungal, spore-bearing sclerotia of various shapes, including a polylobate form, in a coprolite. Slide HS-27-07; scale bar = 50 μm.
14. An ellipsoidal, spore-bearing fungal sclerotium at center, within a coprolite. Slide HS-27-14; scale bar = 50 μm.
15. An ovoidal fungal sclerotium, with spores, in a coprolite. Slide HS-27-16; scale bar = 50 μm.
16. Stem contents containing scattered, angular fragments of probable sclerenchyma, degraded parenchyma cells, and cross-section of tracheids in xylary vascular tissue, among empty space. Slide HS-27-09; bar = 100 μm.
17. Plant tissues within a coprolite containing *Psaronius*-degraded parenchyma and conspicuous gum-sac cells containing opaque centers; occasional spheroidal fungal structures also are present. Slide HS-27-12; scale bar = 50 μm.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17

fecal pellets that occur among the amorphous material (Plate I, 2). The coprolites are subcircular to ovoidal in shape, and rather uniform, ranging in size from 944 × 1190 μm to 1065 × 1120 μm. and vary from dark to light brown in external color (Plate I, 3). They are composed of plant remains containing mostly fragments of indurated tissue particles represented by tracheids (Plate I, 4–5), parenchyma and contained gum sac cells (Plate I, 6, 17), spore-bearing fungal sclerotia (Plate I, 7–8, 10–15, 17), triangular-shaped, spinose spores (Plate I, 9), and other non-identifiable plant matter (Plate I, 16–17). The fragmentary tracheids within the coprolites have scalariform thickenings (Plate I, 4–5). The fungal sclerotia are all spore-bearing and occur in a variety of shapes, including reniform (Plate I, 7–8), ovoidal (Plate I, 10, 15), spheroidal (Plate I, 11), cylindrical (Plate I, 12), polylobate (Plate I, 13), and ellipsoidal (Plate I, 14, 17), and other shapes (Plate I, 13). Lastly, embedded within the amorphous parenchymatous matter surrounding the coprolites and other stem tissue are occasional occurrences of scattered, angular fragments of parenchyma, xylary tissue, and possible sclerenchyma, as well as enigmatic ovule-like structures, surrounded by empty space (Plate I, 2, 16). The stem is surrounded by a mantle of adventitious roots (Plate I, 1).

4. Discussion

The single petrified stem shows anatomically well-preserved tracheids and poorly preserved ground tissue, which has been replaced mostly by fecal pellets and sediments. The coprolites, in turn, contain tracheids and other vascular tissue, parenchyma, fungal remains and non-identifiable plant matter that occupy an irregular tubular volume that is approximately 3.5 cm in diameter (Plate I, 1). This indicates that the food source of the coprolite-producing organism was *Psaronius* stem parenchyma, and the identity of the culprit was a pith-boring myriapod or insect. The suspect myriapod or insect that invaded the partly rotted stem of *Psaronius housuoensis*, eventually consumed its way through partially decomposed parenchymatic tissue and empty spaces formed by the ongoing decomposition process. In the process, the culprit avoided the structurally more resistant vascular tissue, peripheral sclerenchyma and root mantle, while simultaneously depositing fecal pellets (e.g., Wallwork, 1976; Ausmus, 1977). The comparatively intact and pristine vascular tissue, outer sclerenchyma band and root mantle indicate that in the ambient decomposing environment, the parenchymatous ground tissue decayed earlier than more lignified elements, also seen in stem tissues in older Euramerican *Psaronius* plants (Rothwell and Scott, 1983; Labandeira, 2001). The insect or possibly myriapod occupied the partly rotted stem and deposited fecal pellets while advancing through the decaying parenchyma cells, causing further decomposition, such that only partial and amorphous ground tissue remain.

Based on coprolite contents and tunneling preferences in the stem, the myriapod or insect depositing the fecal pellets did not feed on more indurated tissues of the *P. housuoensis* plant. This is evident from the near pristine microanatomical condition of the xylem from both the stem and root of this plant, albeit some xylary tissue was consumed, as evidenced by tracheids in the coprolites. As there is no abundant occurrence of extraneous plant debris among the coprolites, except possibly a few scattered plant fragments and ovule-like structures, the likelihood that coprolites were washed into the stem from the surrounding environment is minimal. Moreover, the juxtaposition of the coprolites indicates that they were extruded as a string of fecal pellets from an endophytic insect, rather than being washed in as particles from the ambient environment. These myriapods or insects therefore must have fed on the constituent ground parenchyma of the stem pith, as evidenced from coprolite contents of collapsed parenchyma cells and especially distinctive gum-sac cells with opaque centers of a resinous substance. This further indicates that the coprolites were deposited and preserved *in situ*, within the stem. This condition is similar to that reported by Rößler (2000) for *Psaronius* sp, by Rothwell and Scott (1983) for *P. magnificus*, and by Labandeira and Phillips (2002) for *P. chasei*, in which the ground tissue was consumed, evident by the presence of fecal pellets that contain tissue fragments and cell types representing *Psaronius* parenchyma. The presence of fungal sclerotia in the coprolites indicates secondary colonization by saprobes soon after fecal-pellet deposition.

4.1. Who was the myriapod or insect culprit?

The myriapod or insect involved in this association with *P. housuoensis* evidently was a litter-dwelling, pith-boring arthropod occurring within hardened tissues that exhibit early signs of decay. This conclusion is based on the known microhabitat, pattern of tunneling, absence of any evidence for herbivory on stem tissues, and coprolite contents. The presence of fungi in the coprolites indicates that colonization of the coprolites occurred soon after the stem became necrotic and possibly after the death of the causative arthropod. These fungal sclerotia within the coprolites may represent multiple genera, based on shape and spore size, and evidently were secondary colonizers of coprolites and plant tissues, a recurring pattern seen in late Paleozoic coal balls such as the Calhoun Coal (Agashe and Tilak, 1970; Baxter, 1975; Wu et al., 2007).

General evidence indicates that the principal herbivores of the Pennsylvanian and Permian were arthropods, in particular smaller sized mites and larger sized myriapods or insects (Hughes and Smart, 1967; Scott, 1977, 1980; Labandeira et al., 1997; Labandeira, 2001, 2006b). In addition to oribatid mites, which represent the small-borer detritivore guild (Labandeira et al., 1997), there are a variety of myriapods and insects that bore into various indurated and softer plant tissues that typically fabricate order-of-magnitude larger tunnel diameters, consistent with the dimensions of the *P. housuoensis* pith boring. A possible candidate is a myriapod, such as a diplopod or immature arthropleurid (Rolfe, 1969), which fed primarily on decaying plant matter, especially rotting stems and foliage (Rolfe and Ingham, 1967; Rolfe, 1969, 1983). Dawson (1860, 1878), for example, reported the occurrence of the fossil diplopod *Xylobius sigillariae* in a *Sigillaria* stem. Members of the extinct class Arthropleurida inhabiting Carboniferous coal measures have been reported by Rolfe and Ingham (1967) to be phytophagous and the gut contents of the myriapod *Arthropleura armata* contained remains of carbonized tracheids with scalariform thickenings and epidermal fragments of lycopod affinity (Rolfe, 1969). However, the last known arthropleurids are of earliest Permian (Asselian) in age, and probably were long extinct by the end of the Permian.

In addition to diplopods, Late Permian insect culprits responsible for the boring would be those for which some knowledge of endophytic penetration of dead plant tissues is available, such as springtails (Collembola), cockroaches (Blattodea), and orthopterans (Orthoptera) (Chopard, 1938; Chotoko, 1977; Lasebikan, 1977; Rolfe, 1983; Hopkin and Read, 1992: Hopkin, 1997; Nalepa et al., 2001). More likely culprits are the larvae of phylogenetically basal lineages from several holometabolous insect orders (Labandeira and Phillips, 2002; Labandeira, 2011). Many larvae of holometabolous insects, particularly beetles (Coleoptera), are consummate wood borers (Blackman, 1922; Fukuda, 1941; Hamilton, 1978; Crowson, 1981), but there are larvae from other basal lineages, especially sawflies (Hymenoptera), scorpionflies (Mecoptera), and lacewings and relatives (Neuroptera) that also are plausible (Gallard, 1932; Burdick, 1961; Pilgrim, 1972; Togashi, 1989; Byers, 1991). These, basal lineages of holometabolous insects were present during the Late Permian, based on phylogenetic and fossil evidence (Beutel, 2005; Ren et al., 2009; Vilhelmsen, 2009). Curiously, these basal lineages are commonly associated with xylophagy, wood-boring and/or bark-inhabiting habits, such as archostematan beetles, known from the Upper Permian (Geertsema and van der Heever, 1996; Beckemeyer and Engel, 2008), symphytan hymenopterans whose earliest fossil occurrence is the Middle Triassic

(Riek, 1955), both taxa undoubtedly existed during the Late Paleozoic based on diverse phylogenetic evidence (Vilhelmsen, 2009). The nannochoristid and related Mecoptera have larval life-habits also consistent with a detritivorous, moist environment, as indicated by Beutel et al. (2009) who describe later instars of the larva of *Nannochorista philpotti* as occurring "… in damp (e.g., bryophyte) vegetation or under bark of decomposing, partially submerged logs" (p. 428).

The existence of detritivore pith borer during the Late Permian on *Psaronius housuoensis* stem from China is an extension of a functional feeding group whose earliest occurrence is on the "layered-cells morphotype" species from the Euramerican Middle Pennsylvanian (Labandeira and Phillips, 2002). Occupants of this feeding niche undoubtedly turned over taxonomically from the late Middle Pennsylvanian through the Late Permian, as lineages of insect pith-borers were extirpated and replaced by other lineages having the same trophic roles. This process was not only long-ranging during a 50 million-year interval, but also widespread biogeographically, shifting from Euramerica to Cathaysia. Given what we know of insect extinction and origination patterns for this interval (Labandeira, 2005), it is highly unlikely that there was any taxonomic carry over in pith-boring arthropods from the late Middle Pennsylvanian (Herrin Coal) of Euramerica to the Late Permian (Housou Coal) of the South China Block. A simple test of this inference can be made by body-fossil identifications of arthropod remains associated with this type of coprolite in other *Psaronius* pith-borings.

4.2. The Psaronius component community in time and space

Currently, the most persistent, Paleozoic community of associations for a single source–plant taxon is in Euramerican *Psaronius* and its detritivores and herbivores. Variable occurrences of these associations are known for at least five deposits ranging in age from late Middle Pennsylvanian (Herrin Coal) to the Late Permian (Housuo Coal), spanning most of the Euramerican equatorial belt and now the paratropical South China Block (Rothwell and Scott, 1983; Lesnikowska 1990; Labandeira and Phillips, 1996a, 1996b, 2002; Labandeira et al., 1997; Rößler 2000; this report). To date, the most diverse nexus of associations at a single locality was documented for *Psaronius chasei* Morgan from the Late Pennsylvanian Calhoun Coal, which features mite, myriapod, and insect detritivory (Labandeira et al., 1997; Labandeira, 2001), including mite coprophagy of insect herbivore coprolites (Labandeira, 2001, unpublished), as well as varied herbivory. The insect herbivore associations involve consumption of various organ form-genera, and include external foliage feeding, as surface abrasion, of *Pecopteris* pinnules (Labandeira, 2001, unpublished); piercing-and-sucking of xylary tissue of *Stipitopteris* rachises (Labandeira and Phillips, 1996a); galling of *Stipitopteris* rachis inner parenchyma (Lesnikowska, 1990; Labandeira and Phillips, 1996b, 2002); stem boring of *Psaronius* trunk ground parenchyma (Labandeira, 2001; Labandeira and Phillips, 2002); palynivory of combined *Scolecopteris* sporangial tissue and their *Punctatisporites* spores (Labandeira, 1998a, 2000, 2001); and root feeding on aerenchymatous tissue (Labandeira, 2001), (a brief summary of the *P. chasei* component community from the Calhoun Flora, is presented in Labandeira (1998b, 2001), which lists several examples of the varied types of herbivore-inflicted damage to a variety of plant tissues). The pervasiveness of these *Psaronius* associations in time and space constitute a component community, as defined by Root (1973), specifically a source host-plant and all consuming herbivores and other trophically dependent detritivores, predators and other nutritionally derivative feeding guilds (also see Lawton, 1976).

The spatiotemporal recurrence of *Psaronius* associations resembles that of a tightly integrated microecosystem, such that both the herbivore associations and the congeneric host-plants co-occur in multiple (currently five), Late Carboniferous to Late Permian deposits in Euramerica, and now Cathaysia (Rothwell and Scott, 1983; Labandeira and Phillips, 1996a, 2002; Rößler 2000, this report). The spatiotemporal co-occurrence of the *Psaronius* host and its associated herbivores and detritivores is evidence for an ecologically enduring association during the Late Paleozoic. However, evidence for recurrence of associations is insufficient (albeit necessary), by itself, for positing true co-evolution (Thompson, 1994). True co-evolution in the fossil record requires, in addition to spatiotemporal co-occurrence, a testable mechanism for explaining a mutualism or other associational type (Thompson, 1994), and, in addition, reciprocal genetic feedback in the case of modern taxa (Janzen, 1980). This former condition—a plausible co-evolutionary mechanism—is not demonstrable in the *Psaronius* case. Nevertheless, as a recurring set of affiliated associations, now variably expressed in five deposits, the *Psaronius* system of detritivores and herbivores is the most pervasive plant–arthropod association in the Paleozoic fossil record.

4.3. Summary

The following four points encapsulate the major findings of our discovery, including description of the specimen, and inferences derived from this and related, late Paleozoic material.

1. A petrified specimen of the marattialean tree fern, *Psaronius housuoensis* (D'Rozario et al., 2011) was found in the Late Permian Housuo Coal from southwest China. Structural details and contents of a longitudinal tunnel through the stem indicate that it was made by a detritivorous, pith boring, terrestrial arthropod that inhabited the litter zone.
2. Attribution of the *P. housuoensis* stem tunneler to a particular diplopod or insect clade is impossible because of the absence of body-fossil evidence. Through consideration of evidence such as the details of the boring, coprolite structure, geochronological window of occurrence, and arthropod phylogeny, suggests that the fabricator most likely is a holometabolous larva, possibly a beetle.
3. This occurrence expands the component community of *Psaronius* detritivores, herbivores and other trophically dependent feeding guilds, first noted in the late Middle Pennsylvanian of Euramerica, and now the Late Permian of the South China Block of Cathaysia.
4. The approximate 50 million-year duration of the *Psaronius* component community, and its occupation of multiple feeding guilds of detritivorous and herbivorous arthropods in equatorial habitats on two paleocontinents, indicates that it is the most persistent terrestrial plant–arthropod association in the Paleozoic fossil record.

Acknowledgements

This research work was supported by the Chinese Academy of Sciences (CAS)–TWAS, the academy of sciences for the developing world Visiting Scholar Fellowship award (2006, 2009) to ADR at the State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing. Thanks are due to Bin Sun and Finnegan Marsh for preparing and formatting the images of the photographic plate. The constructive suggestions and comments by three reviewers are gratefully acknowledged. This is contribution 180 of the Evolution of Terrestrial Ecosystems consortium at the National Museum of Natural History, in Washington, DC.

References

Agashe, S.N., Tilak, S.T., 1970. Occurrence of fungal elements in the bark of arborescent calamite roots from the American Carboniferous. Bulletin of the Torrey Botanical Club 97, 216–218.

Ausmus, B.S., 1977. Regulation of wood decomposition rates by arthropod and annelid populations. In: Lohm, U., Persson, T. (Eds.), Soil Organisms as Components of

Ecosystems. Ecological Bulletin, 25. Swedish National Research Council, Stockholm, pp. 180–192.
Baxendale, R.W., 1979. Plant-bearing coprolites from North American coal balls. Palaeontology 22, 537–548.
Baxter, R.W., 1975. Fossil fungi from American Pennsylvanian coal balls. University of Kansas Paleontological Contributions 77, 1–4.
Beck, A.L., Labandeira, C.C., 1998. Early Permian insect folivory on a gigantopterid-dominated riparian flora from north–central Texas. Palaeogeography, Palaeoclimatology, Palaeoecology 142, 139–173.
Beckemeyer, R.J., Engel, M.S., 2008. A second specimen of *Permocoleus* (Coleoptera) from the Lower Permian Wellington Formation of Noble County, Oklahoma. Journal of the Kansas Entomological Society 81, 4–7.
Beutel, R.G., 2005. Systematic position, basal branching pattern and early evolution. In: Beutel, R.G., Leschen, A.B. (Eds.), Handbuch der Zoologie, Band IV (Arthropoda: Insecta), Teilband 38 (Coleoptera, Beetles). Morphology and Systematics—Archostemata, Adephaga, Myxophaga, Polyphaga partim, volume 1. Walter de Gruyter, Berlin, pp. 1–9.
Beutel, R.G., Kristensen, N.P., Pohl, H., 2009. Resolving insect phylogeny: the significance of the Nannomecoptera in understanding endopterygote relationships. Arthropod Structure & Development 38, 427–460.
Blackman, M.W., 1922. On the succession of insects living in the bark and wood of dying, dead and decaying hickory. Technical Publications of the New York State College of Forestry, Syracuse University 22 (5), 1–229.
Brongniart, C., 1877. Perforations observées dans deux morceaux de bois fossile. Annales de la Societé Entomologique de France 5 (7), 215–220.
Burdick, D.J., 1961. A taxonomic and biological study of the genus *Xyela* Dalman in North America. University of California Publications in Entomology 17, 281–353.
Byers, G.W., 1991. Mecoptera (scorpion-flies, hanging-flies). In: Naumann, I.D., et al. (Ed.), The Insects of Australia (Second Edition), volume 2. Cornell University Press, Ithaca, New York, U.S.A, pp. 696–704.
Chopard, L., 1938. La Biologie des Orthoptères. Paul Lechevalier, Paris. 541 pp.
Chotoko, E.I., 1977. The role of some species of diplopods in leaf litter decomposition. In: Lohm, U., Persson, T. (Eds.), Soil Organisms as Components of Ecosystems. Ecological Bulletin, Swedish National Research Council, Stockholm, 25, pp. 548–550.
Crowson, R.A., 1981. Biology of the Coleoptera. Academic Press, New York. 802 pp.
Dawson, J.W., 1860. On a terrestrial mollusk, a chilognathous myriapod, and some new species of reptiles from the Coal-Formation of Nova Scotia. Quarterly Journal of the Geological Society of London 16, 268–277.
Dawson, J.W., 1878. The Geology of Nova Scotia: New Brunswick and Prince Edward Island, or Acadian Geology. Macmillan, London. 50 pp.
D'Rozario, A., Sun, B., Galtier, J., Wang, S.-J., Guo, W.-Y., Yao, Y.-F., Li, C.-S., 2011. Studies on the Late Permian permineralized tree fern *Psaronius housuoensis* sp. nov. from Yunnan Province, southwest China. Review of Palaeobotany and Palynology 163, 247–263.
Edwards, D., 1996. New insights into early land ecosystems: a glimpse of a Lilliputian world. Review of Palaeobotany and Palynology 90, 159–174.
Fukuda, A., 1941. Some ecological studies on *Cupes clathratus* Solski from Japan (Cupedidae, Coleoptera). Transactions of the Natural Historical Society of Formosa 31, 394–399 [in Japanese with English summary].
Gallard, L., 1932. Notes on the feeding habits of the brown moth–lacewing, *Ithone fusca*. Australian Naturalist 8, 168–170.
Geertsema, H., van der Heever, J.A., 1996. A new beetle, *Afrocupes firmae* gen. et sp. nov. (Permocupedidae) from the late Paleozoic Whitehall Formation of South Africa. South African Journal of Science 92, 497–499.
Gilbert, L.E., 1979. Development of theory in the analysis of insect plant interactions. In: Horn, D.J., Stairs, G.R., Mitchell, R.D. (Eds.), Analysis of Ecological Systems. Ohio State University Press, Columbus, Ohio, pp. 117–154.
Hamilton, W.D., 1978. Evolution and diversity under bark. In: Mound, L.A., Waloff, N. (Eds.), Diversity of Insect Faunas, 9. Symposium of the Royal Entomological Society, London, pp. 154–175.
Harris, T.M., 1946. A coprolite of *Caytonia* pollen. Notes on the Jurassic flora of Yorkshire. Annals and Magazine of Natural History 12, 357–378.
Harris, T.M., 1956. The investigation of a fossil plant. Notes and Proceedings of the Royal Institute of Great Britain 36, 456–468.
Harris, T.M., 1964. The Yorkshire Jurassic Flora. Caytoniales, Cycadales and Pteridosperms. British Museum (Natural History). London, volume II.
Hill, C.R., 1976. Coprolites of *Ptilophyllum* cuticles from the Middle Jurassic of North Yorkshire. Bulletin of the British Museum of Natural History (Geology) 27, 289–294.
Hilton, J., Wang, S.-J., Galtier, J., Glasspool, I., Stevens, L., 2004. An Upper Permian permineralized plant assemblage in volcaniclastic tuff from the Xuanwei Formation, Guizhou Province, southern China, and its palaeofloristic significance. Geological Magazine 141, 661–674.
Hilton, J., Wang, S.-J., Galtier, J., Li, C.-S., 2001. An Early Permian plant assemblage from the Taiyuan Formation of northern China with compression–impression and permineralized preservation. Review of Palaeobotany and Palynology 114, 175–189.
Hopkin, S.P., 1997. Biology of the Springtails (Insecta: Collembola). Oxford University, Press. 330 pp.
Hopkin, S.P., Read, H.J., 1992. The Biology of Millipedes. Oxford University Press, Oxford, U.K. 248 pp.
Hughes, N.F., Smart, J., 1967. Plant–insect relationships in Palaeozoic and later time. In: Harland, W.B., Holland, C.H., House, M.R., Hughes, N.F., Reynolds, A.B., Rudwick, M.J.S., Satterthwaite, G.E., Tarlo, L.B.H., Willey, E.C. (Eds.), The Fossil Record. Geological Society of London, pp. 107–117. 827 pp.
Janzen, D.H., 1980. When is it co-evolution? Evolution 34, 611–612.
Kevan, P.G., Chaloner, W.G., Savile, D.B.O., 1975. Interrelationships of early terrestrial arthropods and plants. Palaeontology 18, 391–417.
Labandeira, C.C., 1998a. Early history of arthropod and vascular plant associations. Annual Review of Earth and Planetary Sciences 26, 329–377.
Labandeira, C.C., 1998b. Plant–insect associations from the fossil record. Geotimes 43, 18–24.
Labandeira, C.C., 2000. The paleobiology of pollination and its precursors. In: Gastaldo, R.A., DiMichele, W.A. (Eds.), Phanerozoic Terrestrial Ecosystems, 6. Paleontological Society Papers, pp. 233–269.
Labandeira, C.C., 2001. Rise and diversification of insects. In: Briggs, D.E.G., Crowther, P.R. (Eds.), Paleobiology II. Blackwell Science, Oxford, U.K., London, pp. 82–88.
Labandeira, C.C., 2002. The history of associations between plants and animals. In: Herrera, C. M., Pellmyr, O.M. (Eds.), Plant–Animal Interactions: An Evolutionary Approach, London. Blackwell Science pp. 26–74, 248–261.
Labandeira, C.C., 2005. The fossil record of insect extinction: new approaches and future directions. American Entomologist 51, 14–29.
Labandeira, C.C., 2006a. Silurian to Triassic plant and hexapod clades and their associations: new data, a review, and interpretations. Arthropod Systematics and Phylogeny 64, 53–94.
Labandeira, C.C., 2006b. The four phases of plant–arthropod associations in deep time. Geologica Acta 4, 409–438.
Labandeira, C.C., 2011. Evidence for an earliest Late Carboniferous divergence time and the early larval ecology and diversification of major Holometabola lineages. Entomologica Americana 117, 9–21.
Labandeira, C.C., Allen, E.G., 2007. Minimal insect herbivory for the Lower Permian Coprolite Bone Bed site of north-central Texas, USA, and comparison to other Late Paleozoic floras. Palaeogeography, Palaeoclimatology, Palaeoecology 247, 197–219.
Labandeira, C.C., Phillips, T.L., 1996a. Insect fluid-feeding on Upper Pennsylvanian tree ferns (Palaeodictyoptera, Marattiales) and the early history of the piercing–and–sucking functional feeding group. Annals of the Entomological Society of America 89, 157–183.
Labandeira, C.C., Phillips, T.L., 1996b. A Carboniferous insect gall: insight into early ecologic history of the Holometabola. Proceedings of the National Academy of Sciences, U.S.A., 93, pp. 8470–8474.
Labandeira, C.C., Phillips, T.L., 2002. Stem borings and petiole galls from Pennsylvanian tree ferns of Illinois, USA: implications for the origin of the borer and galler functional–feeding–groups and holometabolous insects. Palaeontographica. Abt. A 264, 1–84 (pls. 1–16).
Labandeira, C.C., Phillips, T.L., Norton, R.A., 1997. Oribatid mites and the decomposition of plant tissues in Paleozoic coal-swamp forests. Palaios 12, 319–353.
Lasebikan, B.A., 1977. The arthropod fauna of a decaying log of an oil palm tree (*Elaeis guineensis* Jacq.) in Nigeria. In: Lohm, U., Persson, T. (Eds.), Soil Organisms as Components of Ecosystems. Ecological Bulletin, 25. Swedish Natural Research Council, Stockholm, pp. 530–533.
Lawton, J.H., 1976. The structure of the arthropod community on bracken. Botanical Journal of the Linnean Society 73, 187–216.
Lesnikowska, A.D., 1989. Anatomically Preserved Marattiales from Coal Swamps of the Desmoinesian and Missourian of the Midcontinent United States: Systematics, Ecology and Evolution. Dissertation, University of Illinois, Urbana-Champaign, U.S.A., 227 p.
Lesnikowska, A.D., 1990. Evidence of herbivory in tree-fern petioles from the Calhoun Coal (Upper Pennsylvanian) of Illinois. Palaios 5, 76–80.
Mamay, S.H., Yochelson, E.L., 1953. Floral–faunal associations in American coal balls. Science 118, 240–241.
Mamay, S.H., Yochelson, E.L., 1962. Occurrence and significance of marine animal remains in American coal balls. U.S. Geological Survey Professional Paper 354–1, 193–224.
Nalepa, C.A., Bignell, D.E., Bandi, C., 2001. Detritivory, coprophagy, and the evolution of digestive mutualisms in the Dictyoptera. Insectes Sociaux 48, 194–201.
Pilgrim, R.L.C., 1972. The aquatic larva and the pupa of *Choristella philpotti* Tillyard, 1917 (Mecoptera: Nannochoristidae). Pacific Insects 14, 151–168.
Ren, D., Labandeira, C.C., Santiago-Blay, J.A., Rasnitsyn, A., Shih, C.-K., Bashkuev, A., Logan, A., Hotton, C., Dilcher, D.L., 2009. A probable pollination mode before angiosperms: Eurasian, long-proboscid scorpionflies. Science 326.
Rex, G.M., Galtier, J., 1986. Sur l'évidence d'interactions animal–végétal dans le Carbonifère inférieur français. Comptes Rendus de l'Académie des Sciences, Paris, Série II 303, 1623–1626.
Riek, E.F., 1955. Fossil insects from the Triassic beds at Mt. Crosby, Queensland. Australian Journal of Zoology 3, 654–691.
Rolfe, W.D.I., 1969. Arthropleurida and Arthropoda incertae sedis. In: Moore, R.C., Kaesler, R.L. (Eds.), Treatise on Invertebrate Paleontology, Part R, Volumes 1 & 2 (Crustacea, exclusive of Ostracoda), Myriapoda & Hexapoda, Geological Society of America and the University of Kansas, Boulder Colorado, and Lawrence, Kansas, pp. 607–625.
Rolfe, W.D.I., 1983. Aspects of the Carboniferous terrestrial arthropod community. Proceedings of the Ninth International Congress of Carboniferous Stratigraphy and Geology, Urbana, Illinois, 1979.
Rolfe, W.D.I., Ingham, J.K., 1967. Limb structure, affinity and diet of the Carboniferous "centipede" *Arthropleura*. Scottish Journal of Geology 3, 118–124.
Root, R.B., 1973. Organization of plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs 43, 95–124.
Rößler, R., 2000. The Late Palaeozoic tree-fern *Psaronius*—an ecosystem unto itself. Review of Palaeobotany and Palynology 108, 55–74.
Rothwell, G.W., Scott, A.C., 1983. Coprolites within marattiaceous fern stems (*Psaronius magnificus*) from the Upper Pennsylvanian of the Appalachian Basin, U.S.A. Palaeogeography, Palaeoclimatology. Palaeoecology 41, 227–232.

Scott, A.C., 1977. Coprolites containing plant material from the Carboniferous of Britain. Palaeontology 20, 59–68.

Scott, A.C., 1980. The ecology of some Upper Palaeozoic floras from northern Britain. In: Panchen, A.L. (Ed.), The terrestrial environment and origin of land vertebrates. Systematics Association Symposium, volume 15. Academic Press, London, pp. 87–115. Special.

Scott, A.C., Taylor, T.N., 1983. Plant–animal interactions during the Upper Carboniferous. Botanical Review 49, 259–307.

Seward, A.C., 1935. Forests of coal age. Abbot Memorial Lecture. University College, Nottingham, United Kingdom. 13 pp.

Seyfullah, L.J., Hilton, J., Wang, S.-J., Galtier, J., 2009. Anatomically preserved pteridosperm stems and rachises from Permian floras of China. International Journal of Plant Science 170, 814–828.

Southwood, T.R.E., 1973. The insect/plant relationship—an evolutionary perspective. In: Van Emden, H.F. (Ed.), Insect/Plant Relationships. Symposium of the Royal Entomological Society of London 6. John Wiley and Sons, New York, pp. 3–30.

Stoval, J.W., Strain, W.S., 1936. A hitherto undescribed coprolite from the White River. Handbook of South Dakota. Journal of Mammalogy 17, 27–28.

Swain, T., 1978. Plant–animal co-evolution: a synoptic view of the Palaeozoic and Mesozoic. In: Harborne, J.B. (Ed.), Biochemical Aspects of Plant and Animal Co-evolution. Annual Proceedings of the Phytochemical Society of Europe, 15. Academic Press, London, pp. 3–19.

Taylor, T.N., Scott, A.C., 1983. Interactions of plants and animals during the Carboniferous. Bioscience 33, 488–493.

Thompson, J.N., 1994. The Coevolutionary Process. University of Chicago Press, Chicago.

Togashi, I., 1989. Japanese sawflies of the family Blasticotomidae (Hymenoptera: Symphyta). Proceedings of the Entomological Society of Washington 91, 406–413.

Vilhelmsen, L., 2009. The phylogeny of lower Hymenoptera (Insecta); with a summary of the early evolutionary history of the order. Journal of Zoological Systematics and Evolutionary Research 35, 49–70.

Wallwork, J.A., 1976. Fauna of decaying wood, rocks and trees. In: Wallwork, J.A. (Ed.), The Distribution and Diversity of Soil Fauna. Academic Press, London, pp. 137–141.

Wang, S.-J., Hilton, J., Galtier, J., Tian, B., 2006. A large anatomically preserved calamitean stem from the Upper Permian of southwest China and its implications for calamitean development and functional anatomy. Plant Systematics and Evolution 261, 229–244.

Williamson, W.C., 1880. On the organization of the fossil plants of the coal measures and including the examination of the supposed radiolarians of the carboniferous rocks. Philosophical Transactions of the Royal Society of London 171, 493–539.

Wu, W.Y., Hotton, C.L., Labandeira, C.C., 2007. Fungal fossils and plant-fungi interactions from a 300 million-year-old coal-ball deposit. The 2007 annual meeting of Mycological Society of America. Baton Rouge, Louisiana, USA, pp. 110–111.