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HERBIVOROUS AND DETRITIVOROUS ARTHROPOD TRACE FOSSILS ASSOCIATED WITH SUBHUMID VEGETATION IN THE MIDDLE PENNSYLVANIAN OF SOUTHERN BRITAIN

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ABSTRACT: **We describe plant–arthropod associations from the Middle Pennsylvanian (late Bolsovian–early Asturian) Pennant Sandstone Formation of southern Britain. Our material comprises calcified cordaitaleans and tree-fern axes, preserved in braided channel deposits, and interpreted as remains of subhumid riparian vegetation distinct from that of coeval coal swamps. The first plant–arthropod association, attributed to herbivorous insects, comprises cambial damage to cordaitalean leafy branches, resulting in traumatic wound response. The second and most widespread association, attributable to detritivorous oribatid mites, includes tunnels and galleries containing widely scattered, clustered, or densely packed microcoprolites within the inner root mantle of marattialean tree ferns and cordaitalean trunks and branches. Diameter data for tunnels and microcoprolites are multimodal, recording four or five instars of oribatid mites that parallel instar-based fecal pellet and body lengths in modern taxa. The third association attributed, possibly, to an arthropleurid, comprises a single, very large (19 × 14 mm) coprolite. Included plant fragments support a previous conjecture that arborescent lycopsids formed part of this iconic arthropod's diet. Mucus-lined burrows within the macrocoprolite imply that fecal material was processed by annelids. The high diversity and frequency of plant–arthropod associations are unusual for Mid-Pennsylvanian time, and may reflect previously undetected interactions in those ecosystems that lay outside "coal forest swamps."**

INTRODUCTION

Mites and insects (arthropods) are the two most diverse groups of organisms that interact with land plants today. Around the time of their Early Devonian origin (Jeram et al. 1990; Norton 1994; Brett et al. 1996; Labandeira 2006), these organisms appear to have been predominantly predatory, but at an early evolutionary stage, they widely adopted detritivory (consumption of dead plant tissues) as an alternative mode of feeding (Labandeira et al. 1997a, 1997b; Norton 1985; Engel and Grimaldi 2004) and occasional herbivory (Kevan et al. 1975; Labandeira 2007). The transition from a predatory to a plant-based diet was undoubtedly aided through association with cellulytic and lignin-feeding fungi (Taylor and Osborn 1996; Renker et al. 2005), although evolution of the latter group may have been delayed until the end of the Carboniferous (Floudas et al. 2012). Herbivory (consumption of living plant tissues) was very limited during the Devonian (Labandeira 2007, 2013), and only significantly expanded several tens of millions of years later, during the Late Mississippian to Early Pennsylvanian, and primarily among insects (Labandeira 2007; Iannuzzi and Labandeira 2008).

In late Paleozoic permineralized plant assemblages (e.g., fossil wood and peat), oribatid and other mites, have left an extensive record of detritivory (Stidd and Phillips 1982; Rex 1986; Chaloner et al. 1991; Goth and Wilde 1992; Zavada and Mentis 1992; Labandeira et al. 1997a; Rößler 2000; Tomescu et al. 2001; Hueber and Galtier 2002; Kellogg and Taylor 2004; Feng et al. 2010; D'Rozario et al. 2011; Slater et al. 2012). At this time, oribatid mites played a major role in recycling dead organic matter (Oconnor 1982; Hansen 1999; Schneider et al. 2005; Maraun et al. 2009), occurring as diverse microvores in soil, plant litter, and other habitats rich in decomposing plant substrates (Hirst 1923; Krivolutsky and Druk 1986; Bernini 1986; Norton et al. 1988; Kethley et al. 1989). The late Paleozoic dominance of oribatid mite detritivory is attributable to their early origin and adaption to dead plant-tissue substrates (Norton 1994; Maraun et al. 2004; Jeyaprakash and Hoy 2009; Dunlop and Selden 2009), and their relatively high, incumbent diversity and abundance (Bernini 1986; Schaefer et al. 2010), based on elevated modern diversities (Schatz 2004; Maraun et al. 2007).

The oldest unequivocal evidence consistent with oribatid mite detritivory is found in Lower and Middle Devonian deposits, in which microcoprolites and traumatic plant tissue damage (Kevan et al. 1975; Labandeira 2006) are locally buttressed by mite body fossils preserving distinctive mouthparts (Hirst 1923; Norton et al. 1988) and surface ornamentation (Norton et al. 1988; Kethley et al. 1989); however, oribatid mite detritivory may have originated even earlier in the Silurian (Hagström and Mehlqvist 2012). More generally, oribatid mite detritivory is recorded in the late Paleozoic fossil record by populations of spheroidal, ovoidal, and short-ellipsoidal microcoprolites found in remains of dead plant tissue (Labandeira et al. 1997a; Kellogg and Taylor 2004; D'Rozario et al. 2011; Slater et al. 2012), their overall shape and dimensions consistent with those of extant oribatid mite microcoprolites (Rusek 1975). The most detailed data for oribatid detritivory exists in the Pennsylvanian peat deposits of tropical Euramerica (coal balls), where the dead material of virtually every known plant group contains such microcoprolites (e.g., Scott 1977; Cichan and Taylor 1982; Scott and Taylor 1983; DiMichele and Phillips 1994).

By contrast, evidence for insect detritivory has a rather spotty fossil record. Although the earliest insect body fossils are from the Early and

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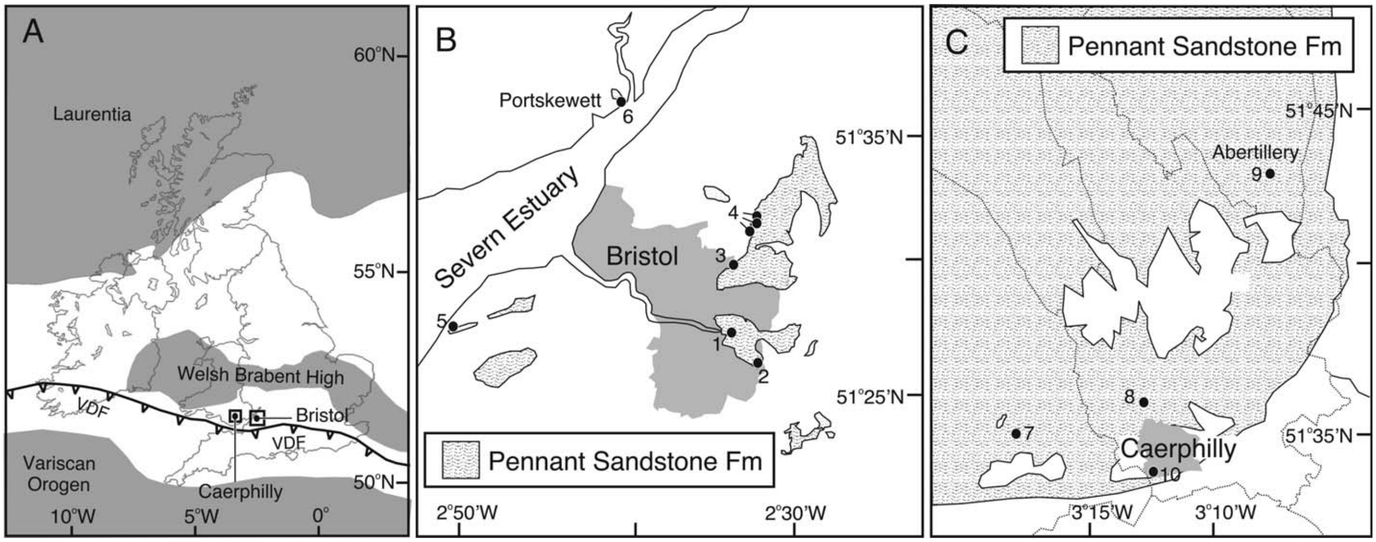


FIG. 1.—Geological context of sample localities, modified from Falcon-Lang et al. (2012). **A**) British Isles showing the location of the two main collecting areas near Bristol and Caerphilly, in the context of late Westphalian paleogeography. Abbreviations and symbols: VDF, Variscan Deformation Front; gray, highlands; white, alluvial lowlands. **B**) Bristol, southern England, showing collection sites as follows: 1 = Conham Quarry; 2 = Hanham Quarry; 3 = Oldbury Court Quarry; 4 = Winterbourne; 5 = Conygar Quarry; and 6 = Portskewett tunnel excavations. **C**) Caerphilly, South Wales, showing collection sites as follows: 7 = Treforest Quarry; 8 = Bute Quarry, Pwllypant; 9 = Abertillery coal mine; and 10 = Caerphilly Common Quarry.

Middle Devonian (Shear et al. 1984; Labandeira and Beall 1990), compelling evidence for insect detritivory is rare. Such evidence, which is mostly of Pennsylvanian and younger age, consists, almost exclusively, of borings of considerably larger diameter than those of oribatid mites, which penetrate cortical and medullary trunk tissues, yet lack the live-tissue response that would indicate herbivory (Rothwell and Scott 1983; Weaver et al. 1997; Labandeira and Phillips 2002, D'Rozario et al. 2011). Judging from this fossil record of borings and related damage of dead plant tissue, insects appear to have invaded different plant tissue types compared to mites. The smaller mites preferred more hardened, sclerenchymatous structural tissues, particularly wood and periderm, whereas the larger insects targeted softer, more nutritious, parenchymatous tissues such as branch piths, cambiums and other meristematic tissues, seeds, and the interiors of leaves, through borings, seed predation, galling, and leaf mining (Labandeira 2006, 2007, 2013).

Varied modes of herbivory first appeared among insects during the Late Mississippian to Middle Pennsylvanian (Labandeira 2007, 2013). This evidence includes external foliage feeding (Iannuzzi and Labandeira, 2008; Labandeira 2013), piercing and sucking (Labandeira and Phillips 1996a), galling (Amerom 1973; Labandeira and Phillips 1996b), seed predation (Jennings 1974), and oviposition (Béthoux et al. 2004). However, the distinction between herbivory and detritivory is not always clear in these mid-Carboniferous assemblages. For example, some typically detritivorous insect borings in Late Pennsylvanian tree ferns (Rothwell and Scott 1983, Labandeira and Phillips 2002) appear to have continued into the upper, live portion of the trunk, where they induced a limited hypertrophic and hyperplasic tissue response typical of herbivory (Labandeira and Phillips 2002).

As emphasized above, almost all work on Pennsylvanian plant–arthropod interactions has focused on perhumid tropical forest mires, based on coal ball material (DiMichele and Phillips 1994) with little or no explicit documentation of patterns in the subhumid riparian vegetation that it is now inferred to have widely covered the Pennsylvanian tropics (Falcon-Lang 2003; Feldman et al. 2005; DiMichele et al. 2010; Falcon-Lang et al. 2009, 2011a; Bashforth et al. 2014), especially during cooler and drier glacial phases (Falcon-Lang 2004; Falcon-Lang and DiMichele 2010). In this contribution, we document more fully the feeding biology of early Middle Pennsylvanian-age insects, oribatid mites, and other arthropods, and focus on evidence specifically from subhumid riparian ecosystems, through an analysis of their borings and associated coprolites.

GEOLOGICAL CONTEXT

Evidence for plant–arthropod associations reported here occurs within collections of calcic-permineralized fossil plants from the Pennant Sandstone Formation (Warwickshire Group) of southern Britain (Falcon-Lang et al. 2012).

Fossil Localities

Specifically, material comes from twelve localities near Bristol and Caerphilly (Fig. 1A–C). The Bristol localities are Conham Quarry (51°26′50.94″N, 2°32′17.48″W); Hanham Quarry (51°25′42.38″N, 2°30′28.06″W); Oldbury Court quarries (51°29′18.05″N, 2°31′55.28″W); Hambrook (51°30′17.37″N, 2°30′51.14″W); Rock Quarry (51°26′23.11″N, 2°32′45.06″W); Winterbourne Quarry (51°30′49.27″N, 2°30′04.33″W); Conygar Quarry, near Clevedon (51°26′45.74″N, 2°50′04.32″W); and the Severn Tunnel excavations (51°35′22.75″N, 2°43′00.11″W). The Caerphilly localities are Caerphilly Common Quarry (51°36′46.60″N, 3°13′03.47″W); Treforest Quarry, near Pontypridd (51°34′54.93″N, 3°18′43.58″W); Bute Quarry, Pwllypant (51°36′12.48″N, 3°14′04.86″W); and Six Bells Colliery, Abertillery (51°43′50.57″N, 03°07′52.88″W).

Stratigraphy and Facies

Across this study area, the Pennant Sandstone Formation is 700–1350 m thick and dominated by very thickly bedded, coarse-grained, pebbly sandstone units, which show channels many tens to hundreds of meters wide, trough cross-bedded channel-fills that fine upward, and large-scale tabular cross-bedding (Jones and Hartley 1993; Waters et al., 2009; Falcon-Lang et al. 2012). These facies are indicative of the low-sinuosity channels of very large, sandy braided rivers (Jones and Hartley

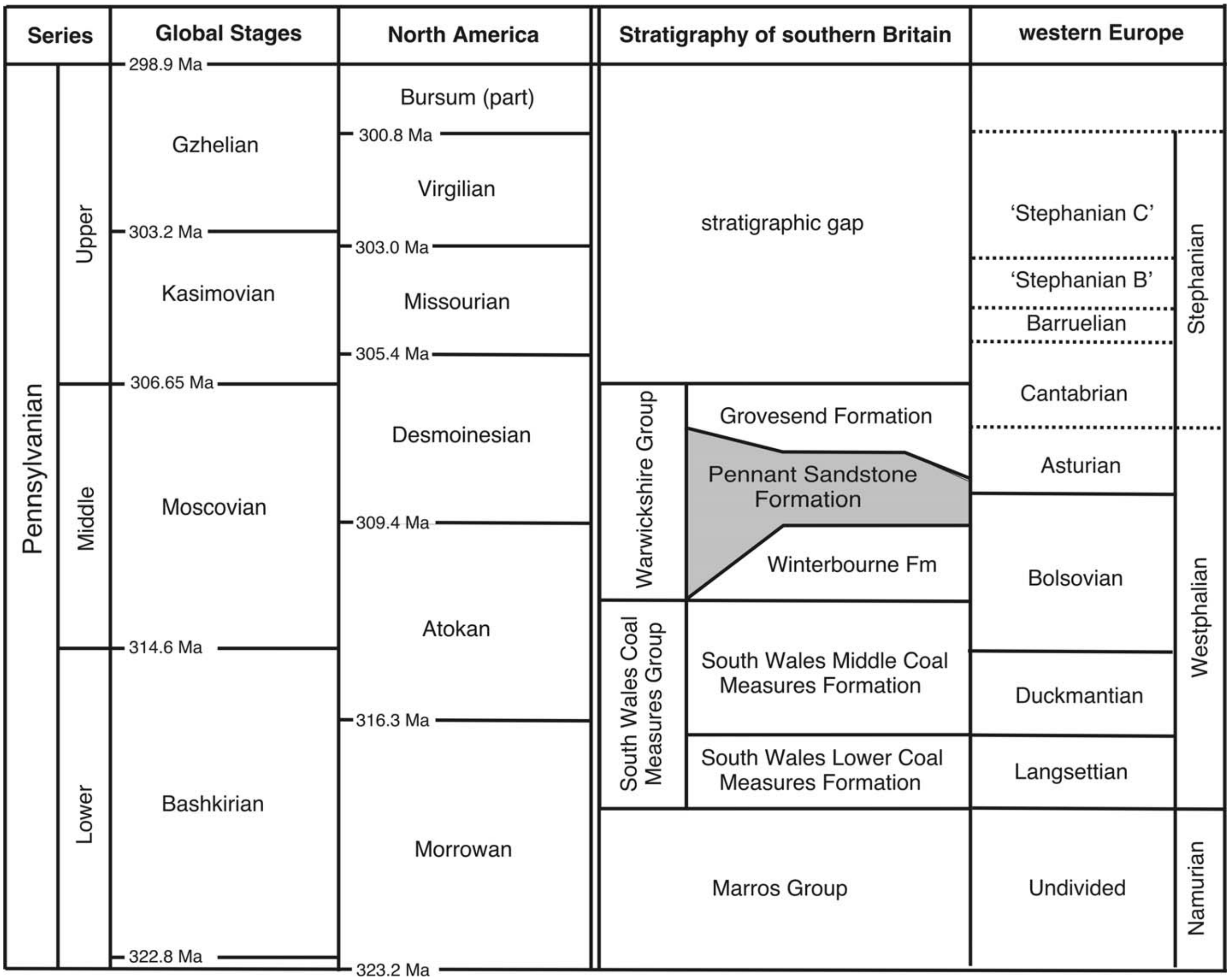


FIG. 2.—Stratigraphic chart showing the position and age of the Pennant Sandstone Formation in relation to global, North American, and European stratigraphic nomenclature (modified from Falcon-Lang et al. 2011a).

1993). Paleocurrent data has a strong north and northeasterly mode, suggesting rivers drained the rising Variscan Orogenic belt to the south (Gayer and Jones 1989). This is supported by sediment petrology and structural studies that show that the edge of the Variscan Deformation Front lay only a few tens of kilometers south of our study areas (Leverridge and Hartley 2006; Fig 1A).

Geologic Correlation and Age

The Cambriense Marine Band (a regional stratigraphic marker bed), which passes through the diachronous base of the Pennant Sandstone Formation (Stubblefield and Trotter 1957), is of mid-Bolsovian age (Waters et al. 2009), whereas the diachronous top of the formation is late Bolsovian near Bristol (Pendleton et al. 2012) rising to mid-Asturian near Caerphilly (Cleal 1997, 2007; Falcon-Lang et al. 2012). Consequently, based on interregional correlations (Heckel 2008; Davydov et al. 2010; Falcon-Lang et al. 2011b; Waters and Condon 2012), the fossils are of early Middle Pennsylvanian (mid-Moscovian) age (Fig. 2).

Taphonomy of Fossil Plant Collections

Although fossil material reported here was mostly collected between 1868 and 1924, the sedimentologic and stratigraphic context of each historic collection site within the Pennant Sandstone Formation is well constrained. Based on field notebook entries made at the time of collection and other archival data (see Crookall 1931; Falcon-Lang et al. 2012), all material originated as allochthonous channel-lag assemblages. This is supported by field visits to several of the localities, where similar material can still be collected from channel-lag deposits today, occurring as water-worn, calcic-permineralized pebbles and cobbles.

MATERIAL AND METHODS

The material comprises 171 petrographic thin sections scattered through various museum collections. Direct observations and museum archival records suggest that these thin sections represent ~ 72 separate fossil specimens (Falcon-Lang et al. 2012). Some specimens are represented by a solitary section only, but for others, sets of multiple, oriented serial sections exist. Unfortunately, hand specimens are not preserved, so additional investigations cannot be made.

Museum Collections

The thin sections studied here are in the collections of the Bristol City Museum and Art Gallery (BCMAG: Cc. 5194–5209); the National Museum and Galleries of Wales, Cardiff (NMGW: 28.3.G17, G19, G21, G23–G27, G31, G33–G40; G47–G48, G52, G55–G56, G260; 2011.19.G1–4); the British Geological Survey, Keyworth (BGS: MPK 14123–14159; PF 7394, 7400, 7402, 7413–7414, 7416, 7424–7427; PB 309 – 318, 604; RC 1–6, 17–18, 41, 47); and the British Museum of Natural History, London (BMNH: J.P. 405–406, 827; V. 537, V. 673abc, V. 674ab, V.5237E1–2; V. 5237(19, 20, F, G), V. 5875abc, V. 8906–8930, V. 9911–9912, V. 51430, V. 51543); all in the UK.

Plant Biology and Ecology

Of the ~ 72 separate plant specimens represented, 62 (87%) are cordaitaleans (44 *Dadoxylon*, 11 *Mesoxylon*, 7 *Amyelon*), five (7%) are marattialean tree ferns (*Psaronius* trunks), two are lycopsids (2.5%), two are sphenopsids (2.5%), and one is a pteridosperm (1%) (see Falcon-Lang et al. 2012 for a full systematic description of this assemblage). One additional specimen (not described in Falcon-Lang et al. 2012) is not a plant fragment but comprises a large, solitary coprolite.

Plant–arthropod associations are observed only in the cordaitalean and tree-fern axes. Cordaitaleans were woody gymnosperms with varied growth forms (Rothwell 1988), but the type found in the Pennant Sandstone Formation is inferred to have been a large tree with a substantial trunk of pycnoxylic, *Dadoxylon*-type wood (Falcon-Lang and Bashforth 2004, 2005), deeply penetrative roots of *Amyelon* type, and juvenile axes (mostly branches) of *Mesoxylon* type bearing evergreen leaves (Falcon-Lang et al. 2011a, 2012). The marattialean tree fern, *Psaronius*, was characterized by a buttressing skirt of subaerial adventitious roots, composed of a compact inner root mantle and an outer root mantle of larger-diameter, aerenchymatous free rootlets (Morgan 1959; Ehret and Phillips 1977; DiMichele and Phillips 1994).

The cordaitalean dominance of this allocthonous permineralized assemblage differs markedly from pteridophyte-dominated megaflora and palynoflora assemblages, obtained from coals and gray roof shales (coal swamps) that intermittently occur between the channel sandstone bodies of the Pennant Sandstone Formation (Pendleton et al. 2012). Based on the widespread development of weakly developed growth interruptions in the cordaitalean woods (cf. Falcon-Lang et al. 2011b), preservation as calcareous permineralizations (Matysová et al. 2010), and taphonomic and sequence stratigraphic considerations (Falcon-Lang et al. 2012), this distinctive allochthonous channel-lag assemblage is interpreted as remains of a better-drained ecosystem that grew in riparian environments, probably under somewhat drier (subhumid) climatic conditions (Falcon-Lang et al. 2011a, 2012) than those prevalent in the coeval coal swamps.

Methods

In our study of plant–arthropod associations, material was examined and imaged using an Olympus binocular BH-5 microscope with a Nikon digital camera system and software. Qualitative descriptions of associations in transverse (TS), radial longitudinal (RLS), and tangential longitudinal (TLS) sections were supplemented, in some cases, with quantitative analysis of microcoprolite and tunnel diameter data. The short and long axis of microcoprolites was measured as a proxy for arthropod instar size. Diameter data were obtained, to the nearest micron, using the measurement tool in the Nikon software. A population of up to 400 microcoprolites (the first 400 encountered in the slide, as measured from a random point), and all available tunnels, were measured for each specimen.

INSECT HERBIVORE ASSOCIATION

Wound Response in a Mesoxylon *Branch (Type 1)*

Description.—This plant–arthropod association is only seen in two of eleven (18%) cordaitalean axes of *Mesoxylon* type (BGS PB 312–318; BCMAG Cc. 5194–5196). The following description is based solely on the BGS sections, which comprise multiple sections through the same axis, and most clearly illustrate the association.

Viewed in seven serial TS sections, cut over a longitudinal distance of 14 mm, the BGS axis is slightly flattened, comprising a pith area, 3.5 × 6 mm diameter, surrounded by a radius of secondary xylem, 3.1–4.6 mm wide (Fig. 3A). Four growth interruptions (1–4) are seen in the secondary xylem (Fig. 3B). Leaf traces, originating from protoxylem bundles adjacent to the pith, persist to the outer preserved edge of the axis (Fig. 3A–C). No extraxylary tissue is preserved.

A prominent feature seen in all seven serial sections is a wound, encompassing up to 30% of the circumference of the axis. The wound involves the excavation of the cambium, secondary xylem, and presumably extraxylary tissue (although this is nowhere preserved), as well as the entire contents of the pith assuming that parenchyma was present earlier (Fig. 3A, B). Only the outermost pith cells adjacent to the primary vasculature have survived (Fig. 3B).

Later-formed traumatic secondary xylem (postdating the wound) wraps round the truncated surface, infilling the excavation and most of the innermost pith space (Fig. 3C). It preserves some relicts of the cambial zone and periderm where it spills into the former pith area (Fig. 3B). Wound reaction tissue consists of bulbous tuftlike regions, composed of hyperplasic, and occasionally hypertrophic, files of secondary xylem tissue (Fig. 3C). Based on the radius of the zone between the secondary xylem formed before and after the wound, damage was incurred when the secondary xylem was 0.3 mm thick, coinciding with the growth interruption 1 in the wood (Fig. 3B, C). The outer surface was entirely healed when the secondary xylem layer was 1.2 mm thick, coincident with growth interruption 4 (Fig. 3B).

Running the entire observed length (14 mm) of the former pith area, there is an open chamber, 0.98–1.64 mm diameter (Fig. 3A, B). This contains a few spheroidal macrocoprolites (310–708 μm diameter, mean: 616 μm, n = 6) composed mostly of equant thin-walled parenchyma (probably pith cells), equant thick-walled sclerenchyma (possibly pith or periderm cells), and a few elongate tracheids derived from the xylem (Fig. 3D).

Interpretation.—The association consists of damage to cordaitalean branches resulting from the near-complete consumption of a narrow radial segment of cambial tissue and nearby xylem and pith. The thickness of the secondary xylem predating the trauma (0.3 mm) shows that the wound was made to a young leafy shoot, probably less than 1 year old, and reaction tissue further demonstrates that the shoot was alive. Hence, the tracemaker is inferred to have been herbivorous. If growth interruptions were caused by tropical rainfall fluctuations, the leafy branch may have been stripped during the dry season; however, conversely, the interruptions could have been directly induced as wound response. The contents of macrocoprolites suggest that pith parenchyma cells were the primary target of feeding, with a few tracheids probably ingested incidentally. Based on the relatively large diameter of the macrocoprolites (~ 0.3–0.7 mm), and the clear evidence for herbivory, the tracemaker was, probably, an insect (Labandeira and Phillips 2002).

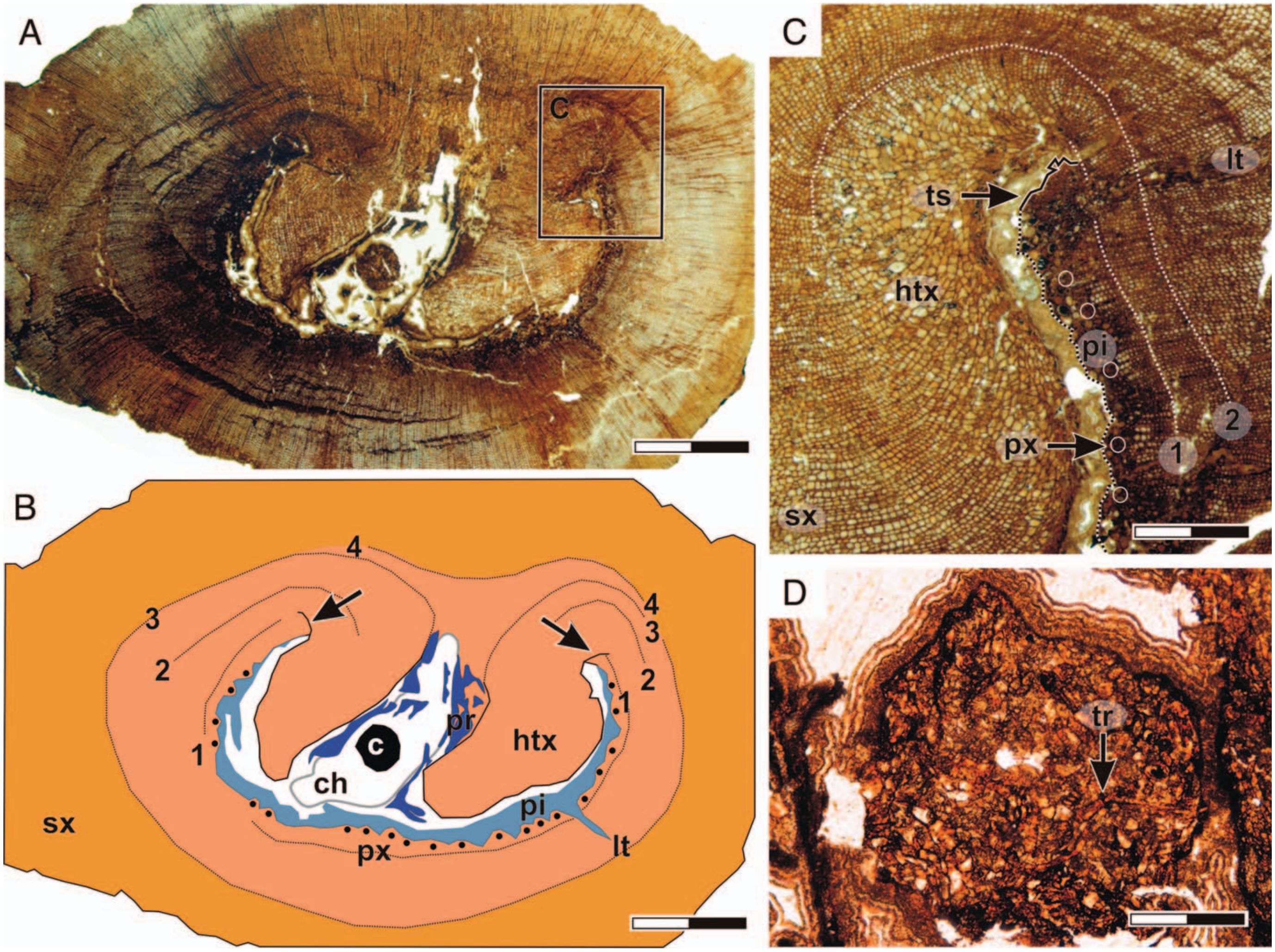


FIG. 3.—Type 1 association: Herbivore cambial wound response and macrocoprolites in cordaitalean (*Mesoxylon* cf. *sutcliffii*) branches. **A**) Branch showing wound, where cambial tissue, xylem, and pith have been consumed, prior to subsequent healing by traumatic xylem; TS, BGS PB 312, scale bar = 2 mm. **B**) Interpreted sketch of branch in view A showing that wound (demarked by the two arrows) was incurred shortly after growth interruption 1 and had not fully healed until growth interruption 4; TS, based on BGS PB 312, scale bar = 2 mm. **C**) Enlargement of boxed area in view A (but in adjacent serial section) showing damaged edge of secondary xylem (solid line, ts) and pith (dotted line), which occurred at the time of growth interruption 1. Prior to growth interruption 2, growth of traumatic secondary xylem had partly healed the wound; TS, BGS PB 313, scale bar = 600 μm. **D**) Enlargement of macrocoprolite from central chamber, but seen in a different serial section than that in view A. Contents mostly include parenchyma, sclerenchyma with some partially digested tracheids; TS, BGS PB 315, scale bar = 200 μm. Abbreviations: c = macrocoprolite; ch = chamber; htx = xylem with hyperplasic and hypertrophic tracheids; lt = leaf trace; pi = pith parenchyma (pale blue in B); pr = periderm (purple in B); px = primary xylem poles (circles); sx = normal secondary xylem (orange in B); tr = tracheids; ts = truncation surface along wound; tx = traumatic secondary xylem (pink in B); 1–4 = successive growth interruptions.

ORBATID MITE DETRIVORE ASSOCIATIONS

Microcoprolite-Filled Galleries in Psaronius *Root Mantle (Type 2a)*

Description.—This association occurs in the inner root mantle of two of five (40%; BCMAG Cc. 5206, 5208) specimens of a *Psaronius* cf. *blicklei* marattialean tree fern. In these specimens, the inner root mantle comprises vertically oriented rootlets, 1–3 mm diameter, embedded in a parenchymatous interstitial tissue. Individual rootlets consist of an exarch stellate actinostele of scalariform-thickened tracheids, 70–200 μm diameter, surrounded by an aerenchymatous cortex containing elongate air chambers (lumina), enclosed within an outer layer of sclerenchyma (Fig. 4A).

The plant–arthropod association comprises spheroidal to slightly ovoidal microcoprolites (length/width ratio 1.16; Table 1), located within long tunnels excavated along cortical lumina (and adjacent tissues) of rootlets, but not in surrounding interstitial tissue (Fig. 4B, C). The tunnels, 120–410 μm in diameter (mean 238 μm, n = 67) are circular in cross section (Fig. 4A), but locally expand into irregular galleries (up to 1.5 mm wide), approximately paralleling the general rootlet axis (Fig. 4B). In several cases, the rootlet actinostele has been displaced to the edge of the rootlet to accommodate the largest galleries (Fig. 4B).

Microcoprolites, 15–97 μm in diameter, are packed in elongate clusters that occupy much of the width of tunnels and galleries, and are separated from adjacent clusters by narrower trails of a few microcoprolites (Fig. 4C). Some microcoprolites are deposited within scalloped hollows excavated into the parenchymatous edge of the cortex (Fig. 4D). In general, the coprolites occur as size-sorted populations, with four or five distinct size classes represented (see data below; three size classes illustrated in Fig. 4E).

Interpretation.—This association of microcoprolites occurring in rootlet lumens and adjacent tissues of *Psaronius* root mantle has been

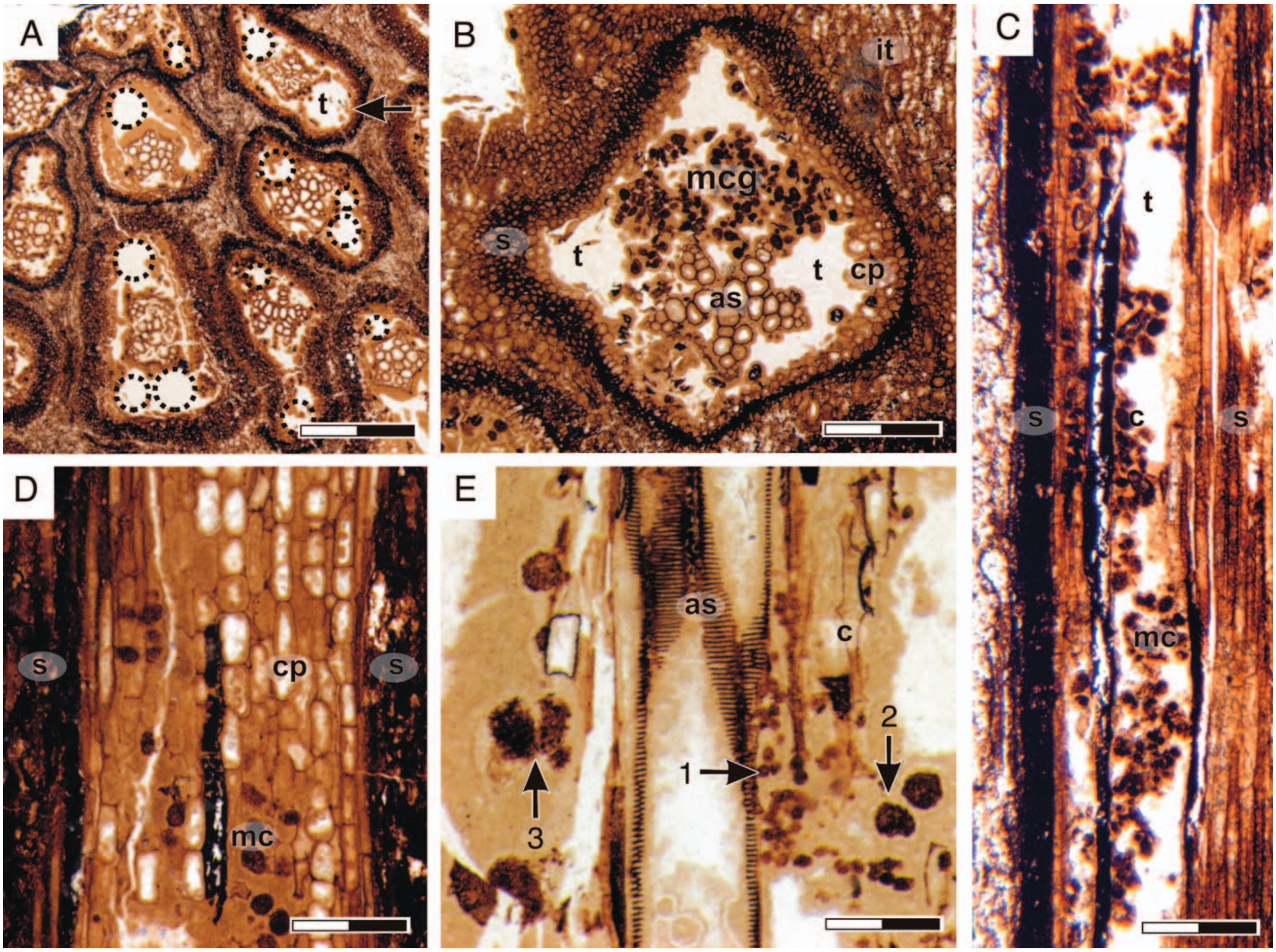
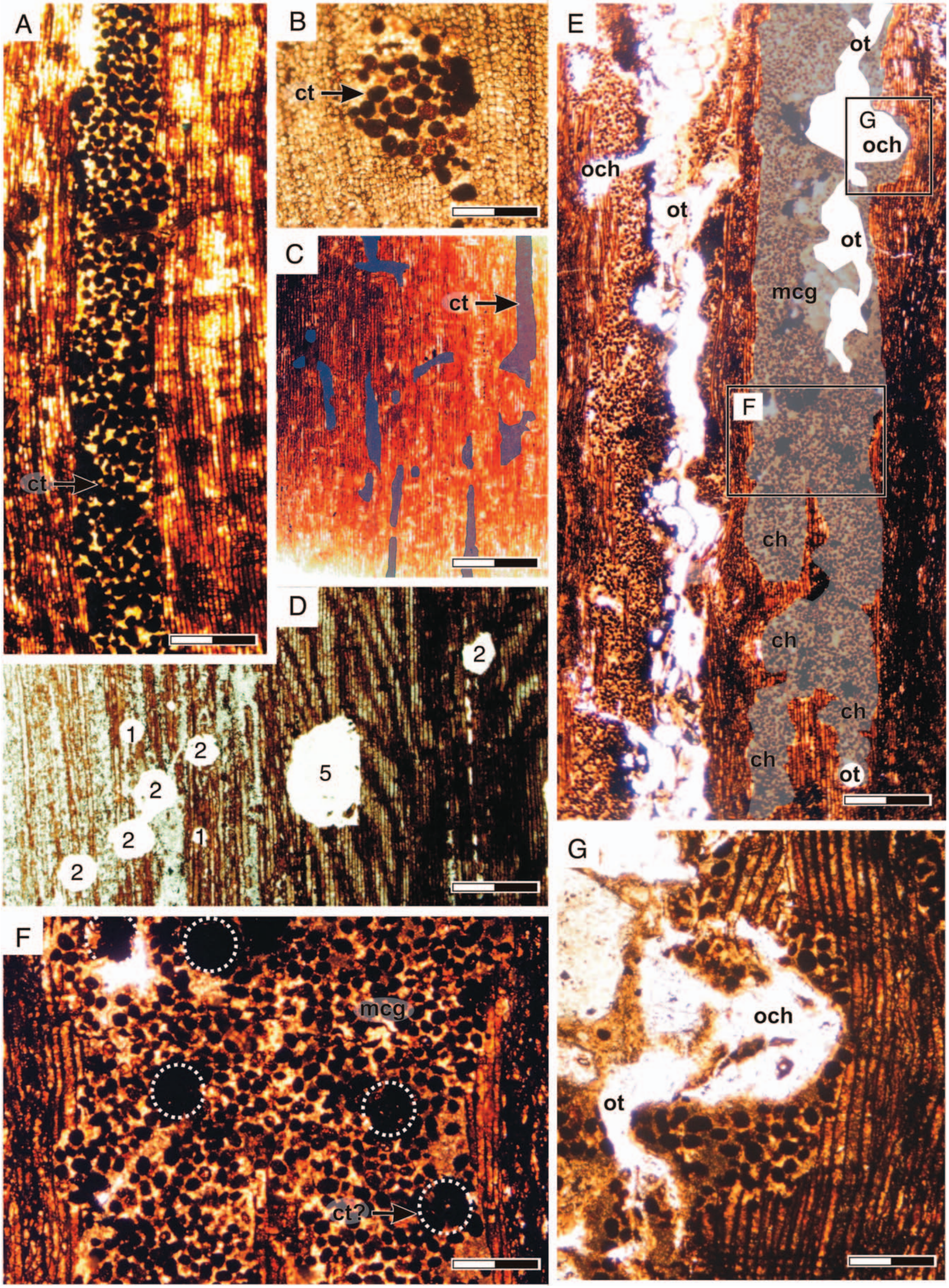


FIG. 4.—Type 2a association of detritivore microcoprolites occurring with marattialean (*Psaronius* cf. *blicklei*) root-mantle tissues. **A**) Inner root mantle showing tunnels (= t, and dotted circles and arrow), which are generally circular to subcircular in cross section. TS, BCMAG Cc. 5206, scale bar = 2 mm. **B**) Enlargement of root and associated tissues, showing clustered distribution of microcoprolites within a longitudinal gallery positioned between the inner root actinostele (displaced) and outer wall of sclerenchyma. TS, BCMAG Cc. 5206, scale bar = 750 µm. **C**) Clusters of microcoprolites deployed along a longitudinal tunnel within the root cortex. LS, BCMAG Cc. 5208, scale bar = 500 µm. **D**) Unimodal microcoprolites within scallop hollow excavated into aerenchymatous tissue, along an inner root surface. LS, BCMAG Cc. 5208, scale bar = 300 µm. **E**) Multi-modal size distribution of small (1), medium (2) and large (3) microcoprolites adjacent to a scalariform-thickened tracheid. LS, BCMAG Cc. 5208, scale bar = 200 µm. Abbreviations: as = actinostele; c = cortex; cp = cortical parenchyma; it = interstitial tissue; mc = microcoprolite; mcg = microcoprolite-filled gallery; s = sclerenchyma; t = longitudinal tunnel (also highlighted by dotted circles); 1–3 = microcoprolite size classes from small to large.

well documented, principally, from Late Pennsylvanian coal-ball floras such as the Calhoun Coal of the eastern United States, where it is has been interpreted as the activity of oribatid mites (Labandeira et al. 1997a; Labandeira 2001). The rise of this arthropod association parallels the spectacular emergence and dominance of marattialean tree ferns after the demise of most elements of the coal-swamp flora, including cordaitaleans, near the Middle to Late Pennsylvanian boundary (Phillips et al. 1974). Notably, the association of rootlet detritivores with *Psaronius* is virtually

TABLE 1.—*Oribatid microcoprolite size data. Abbreviations: Sd, Standard deviation; L/S, ratio of the long and short axes.*

Specimen	Taxon	Long (L) axis (µm)		Short (S) axis (µm)		L/S ratio
		Mean ± Sd	Range	Mean ± Sd	Range	
BGS PF 7424	*Dadoxylon*	69.35 ± 20.20	27–122	53.35 ± 15.70	26–92	1.30
BGS MPK 14144	*Mesoxylon*	61.68 ± 20.21	17–128	47.81 ± 18.10	15–93	1.29
BGS PF 7425	*Dadoxylon*	65.33 ± 19.27	25–125	50.78 ± 14.37	20–89	1.29
BGS PF 7427	*Dadoxylon*	74.59 ± 17.11	22–130	58.52 ± 13.37	22–93	1.27
NMGW 28.3.G52	*Dadoxylon*	42.37 ± 9.86	18–75	32.17 ± 6.98	15–52	1.31
BMNH V. 8909	*Dadoxylon*	44.05 ± 12.97	14–79	31.47 ± 8.74	14–57	1.39
BMNH V. 8910	*Dadoxylon*	50.38 ± 16.03	17–106	36.14 ± 11.35	12–73	1.39
BCMAG Cc 5206	*Psaronius*	52.65 ± 18.54	17–97	45.39 ± 17.79	15–92	1.16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nonexistent in earlier, Middle Pennsylvanian floras. For the Calhoun flora, it occurs overwhelmingly on *P. chasei* (Labandeira et al. 1997a; Labandeira 1998), and less so on rarer *P.* cf. *blicklei*, *P. magnificus*, and a fourth, unidentified species. Data indicate that this stereotypical consumption of softer tissues along rootlets of the inner root mantle persisted for approximately eight million years in Euramerica, minimally from the early Moscovian (mid-Westphalian) to the mid-Kasimovian (mid-Stephanian) and into earliest Permian (Rößler 2000); however, this type of oribatid microcoprolite association has not been documented on younger *Psaronius* material from the Late Permian China (D'Rozario et al. 2011). As such the early Middle Pennsylvanian (early Moscovian) association, reported here from the Pennant Sandstone Formation, is one of the earliest known, widespread occurrences of an oribatid mite association with *Psaronius*.

Microcoprolite-Filled Galleries in Dadoxylon *Cordaitalean Wood (Type 2b)*

Description.—This association comprises extensive and widespread tunnels, chambers, and galleries in 16 out of 44 (34%) specimens of *Dadoxylon*-type cordaitalean trunk wood (BMNH V. 5875c, 8910; BGS PB 309, 311, PF 7397–7399, 7400, 7402, 7416, 7424–7425, 7427; NMGW 28.3.G52).

In its simplest form, it comprises predominantly longitudinal to near-longitudinal tunnels (i.e., oriented parallel to the general xylary grain), 58–454 μm diameter (mean: 197 μm, n = 72), which are rarely empty (open) or much more commonly densely packed (closed) with ovoid (length/width ratio: 1.27–1.39) microcoprolites, 14–130 μm diameter (Fig. 5A–C). Tunnels are straight to slightly curvilinear along their length, and may course radially or tangentially for short distances, intersecting with adjacent tunnels to form a weakly anastomosed network in three dimensions (Fig. 5C). One unusual specimen (BGS PB 309) displays 16 tunnels, 52–434 μm diameter, which are circular in cross section, entirely devoid of microcoprolites (empty), deployed into four, or probably, five distinct size categories of tunnel width, oriented tangentially (Fig. 5D; see data below).

Other more complex associations comprise comparatively massive galleries, 1–3 mm wide and >25 mm long, developed parallel to the general xylary grain, and consisting of an apparent amalgamation of smaller tunnels and chambers (Fig. 5E, F), densely packed with microcoprolites (Fig. 5G). Individual microcoprolite-filled tunnels are of similar dimensions (96–411 μm) to those reported in simpler associations, and late-stage tunnels and associated chambers may be empty (open) and truncate earlier microcoprolite-filled excavations (Fig. 5E, G). Within galleries, microcoprolites may be, locally, clustered in areas that are circular in cross section with extremely dense arrangements, possibly representing the position of former tunnels that were subsequently closed (Fig. 5F). Individual galleries are separated by curved, flaplike partitions of apparently more resistant xylary tissue (Fig. 5E). Galleries are often developed along zones of postmortem weakness (cracks), which may also contain silt to very fine sand-grade quartz sediment.

Interpretation.—This association is identical to previously reported material attributed to oribatid mites in cordaitalean wood (Labandeira et al. 1997a). The earliest, abundant occurrence of such an association in cordaitalean secondary xylem (*Dadoxylon protopityoides* Felix) of Euramerica is from the lowermost Pennsylvanian of the Upper Silesian Coal Basin in southern Poland (Brzyski 1969). However, the most extensive documentation of this association has been from coal-ball floras of at least eight overwhelmingly Middle Pennsylvanian deposits in the Illinois and Appalachian Basins of the eastern United States (Cichan and Taylor 1982; Scott and Taylor 1983; Labandeira et al. 1997a). The same style of borings with densely packed microcoprolites also have been found in Middle Pennsylvanian localities from the Midcontinent of the United States, principally in coal-ball deposits in Iowa and Kansas (Baxendale 1979; Raymond et al. 2001), where some cordaitalean taxa arguably had mangrove-like habits (Raymond et al. 2010). Oribatid mite borings in cordaitalean wood are the most pervasive plant–arthropod association of the Middle Pennsylvanian of Euramerica, and represent the extensive, apparently efficient, recycling of decomposing plant material by oribatid mite detritivores, perhaps trophically analogous to modern termites in similar lowland, equatorial ecosystems (Raymond et al. 2001). Both groups also play an essential role in soil aeration and water retention (Bardgett 2005).

The unusual association, reported here, of tangentially oriented tunnels devoid of microcoprolites in BGS PB 309 (Fig. 5D), but of similar dimensions to those containing microcoprolites, is worthy of further comment. These elongate, subparallel tunnels have smooth, confluent borders where individual xylem cells have been snipped with precision, again, presumably by the mouthparts of an oribatid mite. Reasons for the curious absence of microcoprolites in these arthropod borings could include: (1) the original fecal pellets were subsequently washed out of the tunnels during fluvial transport, or (2) clusters of solid, particulate excreta were produced only occasionally within tunnels at intervals that would not be recorded within all sections. A search of the Paleozoic literature revealed only one similar example, a specimen of *Ankyropteris corrugata* root from the Pennsylvanian-age Coal Measures of the UK, showing a coprolite-free region surrounded by a wound response (Holden 1906); however, this specimen indicates herbivory, and differs from the association reported here (Fig. 5D). The reason for the paucity of microcoprolite-free tunnels in the primary literature probably is due to the fact that the presence of microcoprolites is often used as essential evidence for an arthropod fabricator. Although in cross section many forms of fungal decay such as white pocket rot closely resemble the arthropod tunnels described here (Weaver et al. 1997), multimodality in tunnel size makes this alternative interpretation unlikely.

←

Fig. 5.—Type 2b association of detritivore microcoprolite-laden galleries and tunnels in cordaitalean (*Dadoxylon* sp.) trunk wood. **A**) Longitudinal tunnel densely packed with microcoprolites. RLS, BGS PF 7427, scale bar = 300 μm. **B**) Tunnel with circular cross section densely packed with microcoprolites. TS, BMNH V. 8909, scale bar = 250 μm. **C**) General view of longitudinally, radially, and tangentially oriented tunnels (highlighted) suggestive of a weakly anastomosed pattern. RLS, BMNH V, 8909, scale bar = 1 mm. **D**) Open (empty) tunnels occurring as five distinct size classes (only size classes 1, 2, and 5 are illustrated; size classes 3 and 4 are observed elsewhere in the same section). RLS, BGS PB 309, scale bar = 500 μm. **E**) Substantial microcoprolite-filled galleries comprising multiple amalgamated closed chambers (right-hand example is highlighted to show morphology). Networks of open tunnels and chambers truncate earlier galleries. RLS, BGS PF 7427, scale bar = 750 μm. **F**) Enlarged view of microcoprolite-filled gallery shown in view E showing very densely packed clusters of microcoprolites that might mark positions of former tunnels. RLS, BGS PF 7427, scale bar = 200 μm. **G**) Enlarged view of open chamber shown in view E showing truncation (coprophagy) of earlier-deposited microcoprolite-filled gallery. RLS, BGS PF 7427, scale bar = 250 μm. Abbreviations: ch = chamber filled with microcoprolites; ct = closed tunnel filled with microcoprolites; mcg = microcoprolite-filled gallery; och = open chamber; ot = open tunnel.

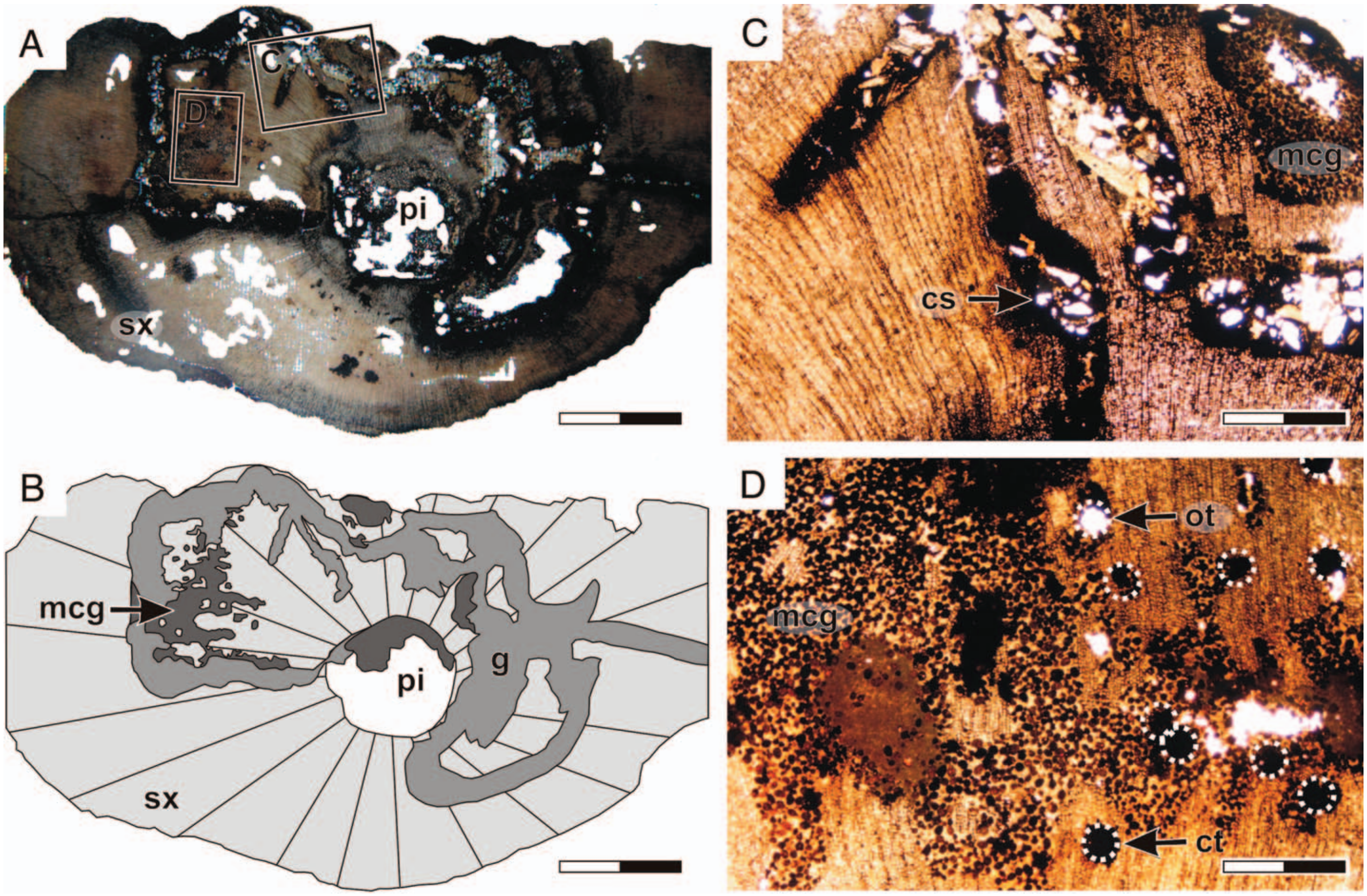

FIG. 6.—Type 2b association of detritivore microcoprolite-laden tunnels and galleries in cordaitalean branch (*Mesoxylon* sp.). All images from BGS MPK 14144. **A**) Cross section of *Mesoxylon* axis showing a network of ~ 0.5–1.5-mm-wide tunnels with internal loops, cul-de-sacs, and an overall curvilinear trajectory filled with dark amorphous matter, quartz-rich sediment, and distinctive microcoprolites; some adjacent areas comprise microcoprolite-laden galleries. TS, scale bar = 3 mm. **B**) Interpreted sketch of structures seen in view A; pale gray = secondary xylem; medium gray = major tunnel system; dark gray = microcoprolite-filled chambers, galleries and tunnels. TS, scale bar = 3 mm. **C**) Enlarged view of part of specimen in view A highlighting looping tunnels filled with clastic quartz sediment, with adjacent microcoprolite-laden galleries. TS, scale bar = 500 µm. **D**) Enlarged view of one microcoprolite-laden gallery, highlighting open (empty) tunnels and closed microcoprolite-filled tunnels. TS, scale bar = 400 µm. Abbreviations: cs = clastic sediment; ct = closed microcoprolite-filled tunnel; g = gallery; mcg = microcoprolite-filled gallery; ot = open tunnel; pi = pith; sx = secondary xylem.

Microcoprolite-Filled Galleries in a Mesoxylon *Cordaitalean Branch (Type 2c)*

Description.—This association is seen in a single *Mesoxylon* axis (BGS MPK 14144) which shows, in transverse section, a network of relatively large, ~ 0.5–1.5 mm wide tunnels with internal loops, cul-de-sacs, branches, and an overall curvilinear trajectory (Fig. 6A, B) filled with dark amorphous matter and quartz-rich sediment (Fig. 6C). While these tunnels also contain, locally, zones of densely packed microcoprolites, 17–128 µm diameter (Fig. 6C), most microcoprolite material is deployed in galleries, chambers, and smaller-scale tunnels developed adjacent to the main conduits (Fig. 6D). The main tunnel system meanders from one or two possible entry points at the outer edge of the axis, through several loops, before entering the pith region, where further microcoprolites are deposited (Fig. 6A, B). As seen in *Dadoxylon* specimens, circular areas of extremely densely arranged microcoprolites probably represent the former position of closed tunnels, while late-stage tunnels remain open (empty) (Fig. 6D).

Interpretation.—This association is very similar to Type 2b reported above and is attributed to oribatid mites (Labandeira et al. 1997a). The unusual meandering geometry of the gallery network, in contrast to the predominantly linear and longitudinal network in *Dadoxylon*, probably reflects the mites tracking concentric and radial lines of weakness in this small-diametered axis rather than any significant difference in behavior.

Oribatid Mite Instars Deduced from Microcoprolite Diameters

Description.—The long and short axis of microcoprolites was measured for large populations (n = 400 per specimen) in *Dadoxylon* and *Mesoxylon* specimens, and quantitatively analyzed to shed further light on oribatid ontogeny. Placed into 1-µm-continuous-size bins (0–1, 1–2, etc.), data were plotted as a frequency histogram, and the noise muted by plotting a 5-point moving average (Fig. 7, overlain black line). This data expression revealed typically four or five microcoprolite size modes for each specimen, with step ratios that steadily decline (Table 2). For example, in MPK14144 (Fig. 7), modes occur at 33, 52, 74, and 100 µm (the subdued peak at 83 µm is probably artifactual), and successive step ratios are 1.58, 1.42, and 1.35. Too few microcoprolites could be measured to perform similar analyses for *Psaronius* specimens; however, qualitative observations suggest four or five modes for this material as well.

Interpretation.—Microcoprolite size multimodality is clearly a significant feature of these fossil populations. We further note that numerous clusters of oribatid mite microcoprolites occur within elongate tunnels in

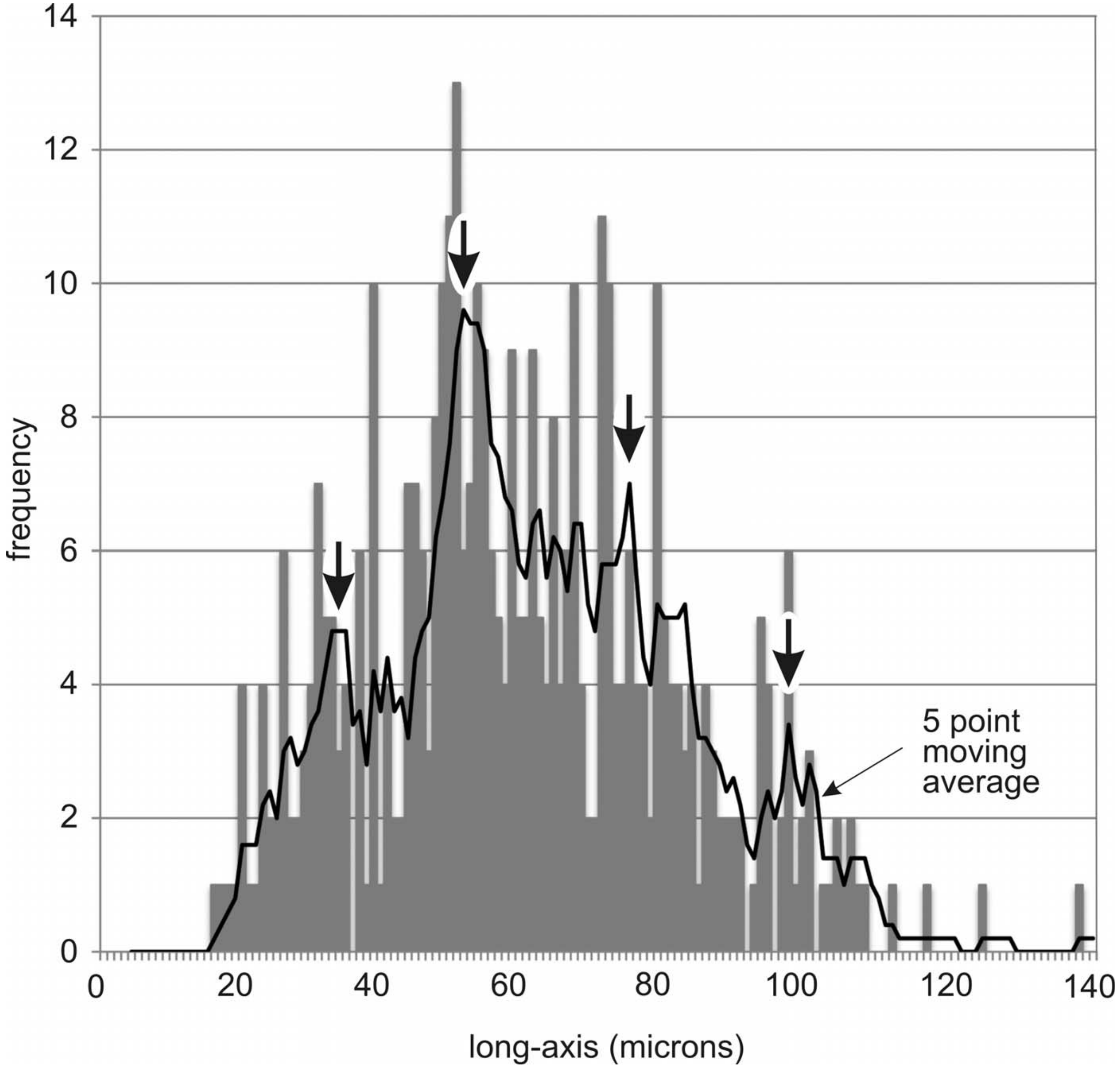

FIG. 7.—Frequency–distribution data of long-axis microcoprolite lengths placed into 5 μm bins (based on 400 measurements from BGS MPK 14144). Data are multimodal with peaks at 33, 52, 74, and 100 μm and mean step ratio of 1.45. The subdued mode at 83 is inferred to be a data artifact.

TABLE 2.—*Analysis of multimodality in oribatid microcoprolite size data. Step-ratios are the ratios of successive modes.*

Specimen	Taxon	Number of modes	Modes (μm)	Step ratios	Mean step ratio
BGS PF 7424	*Dadoxylon*	4	44, 61, 83, 109	1.39, 1.36, 1.31	1.35
BGS MPK 14144	*Mesoxylon*	4	33, 52, 74, 100	1.58, 1.42, 1.35	1.45
BGS PF 7425	*Dadoxylon*	4	36, 50, 68?, 91?	1.38, 1.36, 1.33	1.36
BGS PF 7427	*Dadoxylon*	4	54, 69, 86?, 102	1.27, 1.24, 1.18	1.24
NMGW 28.3.G52	*Dadoxylon*	5	24, 34, 44, 55, 66	1.41, 1.29, 1.25, 1.20	1.29
BMNH V. 8909	*Dadoxylon*	5	26, 33, 42, 53, 64	1.27, 1.27, 1.26, 1.21	1.25
BMNH V. 8910	*Dadoxylon*	5	33, 43, 53, 64, 75	1.30, 1.23, 1.21, 1.17	1.23
BCMAG Cc 5206	*Psaronius*	n/d	n/d	n/d	n/d

the fossil material, and individual clusters of microcoprolites appear, as in modern networks (Drift 1964), with each cluster consisting of microcoprolites of near-identical size. The microcoprolites often are gradationally arrayed along a tunnel from smaller clusters with smaller-sized fecal pellets to larger clusters with larger-sized fecal pellets (Kubiena 1955). The quantitative data collected here therefore provide an opportunity to assess whether size multimodality and size clustering reflect instar-to-instar developmental size increases.

Oribatid mites are members of the morphologically distinct clade, Cryptostigmata (Norton 1994), and almost always exhibit a developmental sequence of five active feeding instars (Norton and Ermilov 2014), separated by a very a brief molt interval. After hatching from the egg, which includes the nonfeeding prelarva, the five active instars are: larva → protonymph → deutonymph → tritonymph → adult. Linear dimensions of body sclerites and fecal pellets scale the same for each posteclosion instar, gleaned from intraspecific populations (Saichuae et al. 1972; Ermilov et al. 2011; Norton and Ermilov 2014), or at the coarser level of congeneric species (Walter and Proctor 1999). Applying this understanding to the fossil material, the expectation would be for five modes, reflecting the five posteclosion instars. While five modes are seen in some specimens, others show only four modes, as in MPK14144 (Fig. 7), where modes occur at 33, 52, 74, and 100 μm. Nevertheless, in modern oribatid mites the first, posthatching, active instar, the larva, typically is miniscule and defecates among the smallest of detectible fecal pellets. Consequently, extending the small detectible mode at 33 μm backward, by inferred step-change values, would imply a mode at about 16 μm, which coincides exactly with the smallest observed microcoprolite size class. Alternatively, the last peak could include pellets from both tritonymph and adult stages, as they are approximately of the same size, and in some oribatid genera the tritonymph is absent. Accepting any one of these explanations, quantitative documentation of microcoprolite multimodality, and indeed, qualitative observations on tunnel multimodality, both of which display four or five modes, is consistent with oribatid mite instar development.

Microcoprolite allometry of fossil material also shows remarkable parallels with that of modern mites. Excluding the largest (1.58) and smallest (1.17) outliers, microcoprolite populations show modal step ratios of 1.20–1.41 (Table 2). Similarly, modern mites exhibit step ratios averaged between all adjacent instar pairs in the range of 1.20–1.41, or slightly more than the square root of 2, which scales with a doubling of mass between consecutive instars (Walter and Proctor 1999; also see Przibram and Megušar 1912). This central tendency of modal values is the same for the much larger hemimetabolous insects (Cole 1980). Another noteworthy aspect of the fossil data is that the second mode (for populations with four modes) or the third mode (five modes) is usually dominant. In modern oribatid mite biology, the dominant feeding phase begins with the protonymph and peaks with the deutonymph (Shereef 1976; Norton and Ermilov 2014). By contrast, the last instar, the adult, also foreshadowed somewhat by the tritonymph, is characterized by a significant diminution of growth rate expressed in the growth ratio. This decrease represents the shift from a feeding to a reproductive phase of the mite life cycle; the fossil data reported here appear to reveal a similar pattern. Remarkably, Middle Pennsylvanian oribatid mites, separated by ca. 311 myr of evolutionary biology, apparently had a similar developmental biology to modern counterparts.

PUTATIVE ARTHROPLEURID ASSOCIATION

Very Large Solitary Coprolite (Type 3)

Description.—This association comprises a solitary, subrounded macrocoprolite (NMGW 28.3.G42) of very considerable size. The macrocoprolite has an incomplete long axis of 19 mm and an incomplete short axis of 14 mm; however, prior to mechanical breakage during transport in the bedload of braided river channels, the original dimensions were, probably, even larger (Fig. 8A). The macrocoprolite is composed of two components, the relative proportions of which were quantified using an eye-piece-mounted graticule. Most abundant are ragged fragments of vascular plant tissue, 0.4–2.1 mm long, and a few spores, which together comprise a loose, somewhat interwoven framework (Fig. 8A); individual fragments showing every stage of decay, from excellent subcellular preservation to near-structureless material (44%; Fig. 8B, C, E). Of the few plant fragments that retain anatomy, most show scalariform-thickened tracheids with localized fimbrils between bars (Fig. 8B), while a few others are thick tracheids showing 5- to 7-seriate alternate pitting, lacking prominent borders (Fig. 8C). The other component comprises subrounded, silt-sized (typically 5–50 μm diameter) fragments of micritic carbonate and quartz (38%), which are randomly distributed through the organic framework (Fig. 8A, D). The remaining cross-sectional area (18%) of the macrocoprolite comprises randomly distributed pore spaces, typically 3–22 μm diameter, which remain permanently black when rotated in cross-polar illumination (Fig. 8A). The macrocoprolite also contains two conspicuous oval burrowlike structures, which are near-identical in size and shape (89 × 53 μm and 87 × 50 μm), and show a distinct 4-μm-thick lining (Fig. 8D). A dark, cryptic segmented feature is also seen (Fig. 8F).

Interpretation.—This is one of the largest, if not the largest, coprolite ever documented from Pennsylvanian strata (at least 19 × 14 mm), significantly larger than the 3.5 mm coprolite described by Labandeira et al. (1997) from the Middle Pennsylvanian (Moscovian) of Illinois, United States. Coprolite size is, very broadly, proportional to the body size of the animal that produced it, so we infer that the producer was in the decimeter to meter size range. We also infer that the coprolite producer was terrestrial because of the macrocoprolite's fluvial context and calcified state, suggesting that it was mineralized in a well-drained soil. There were only two groups of terrestrial Pennsylvanian animal that could have produced a macrocoprolite of this size: tetrapods and giant arthropods. Sahney et al. (2010) synthesized literature on the dentition and postcranial anatomy of Pennsylvanian–Permian tetrapods to infer diet, and suggested that tetrapod herbivory did not evolve until the Kasimovian, ca. eight million years later than our fossil material. Furthermore, the contents of the coprolite; which contains plant material showing a wide range of decay states, mostly derived from trunk wood, coupled with the high sediment content; is more consistent with a detritivorous feeding habit rather than herbivory (Labandeira 1998). These considerations tend to argue against a tetrapod producer, although this unlikely possibility cannot be ruled out. Of the arthropods, the only known group of terrestrial Carboniferous detritivores of sufficiently substantial size to have produced our coprolite were the arthropleurids (Shear and Edgecombe 2010), the larger forms of which have a Mid-Mississippian (early Visean) to earliest Permian (Asselian) range (Martino and Greb 2006). Although arthropleurids originated in the Devonian, body fossils (Wilson and Shear 1999) and possible aestivation burrows (Morrissey and Braddy 2004; Morrissey et al. 2012) are of considerably smaller size than their later Paleozoic descendants.

Identifiable plant fragments seen in the macrocoprolite mostly comprise lycopsid wood (Cichan and Taylor 1982; Fig. 8B) and other tissues suggestive of calamiteans or medullosans (DiMichele and Phillips 1994; Fig. 8C). This composition suggests that these plants may have formed a significant component of the arthropleurid diet, consistent with earlier interpretations (Rolfe 1985). Apparently mucous-lined burrows (Fig. 8A, D) within the macrocoprolite imply that possible arthropleurid fecal material was processed by smaller invertebrates, possibly oligochaete annelids. The cryptic segmented feature seen in the macrocoprolite may represent a body fossil of one such annelid (Fig. 8F). Of course,

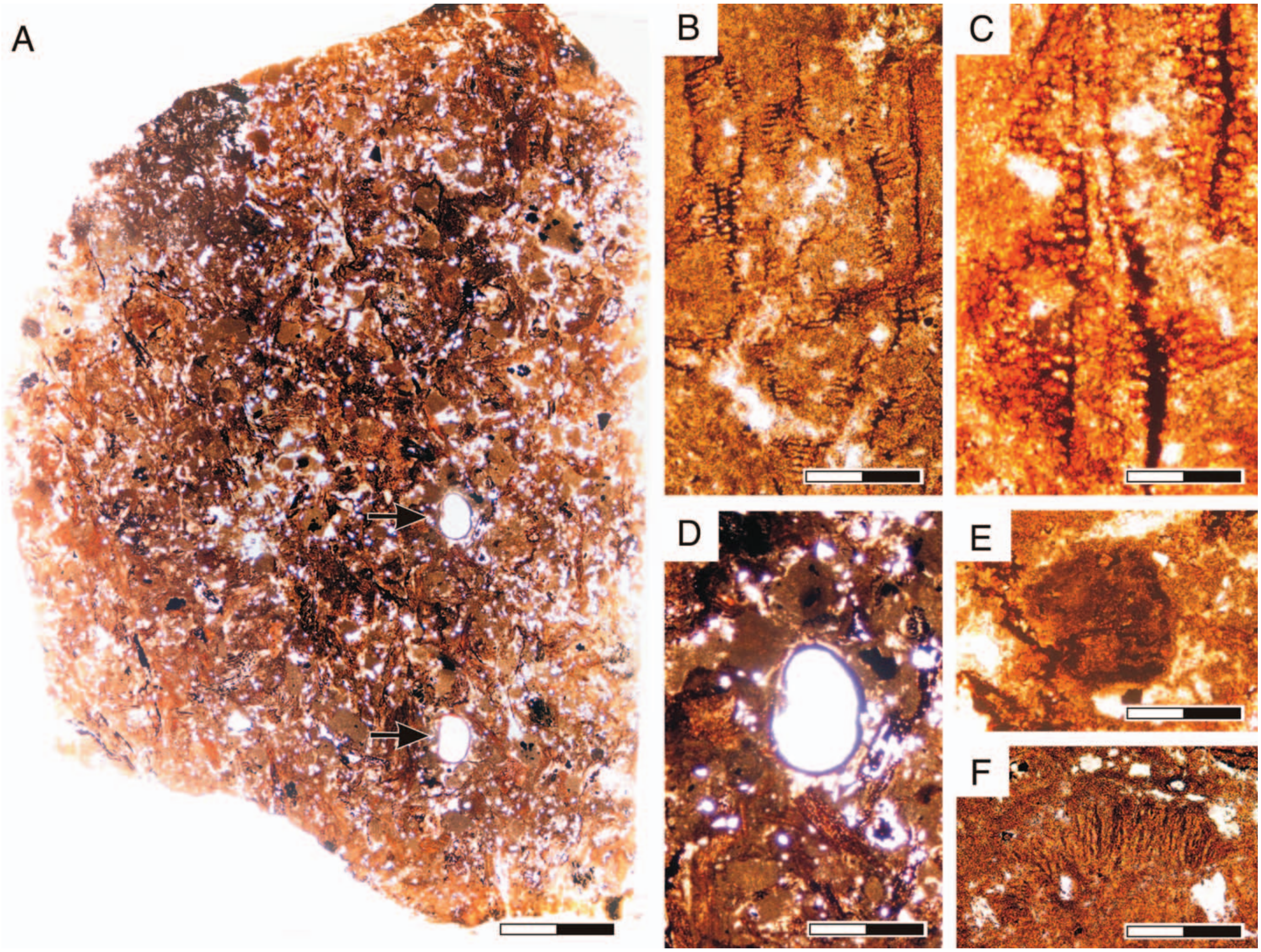

FIG. 8.—Type 3 association of very large (19 × 14 mm) coprolite comprising meshwork of mostly vascular plant fragments, together with spores and clay/silt-grade sediment. All images from NMGW 28.3.G42. **A**) General view of coprolite highlighting two lined tunnels (arrows), scale bar = 2.5 mm. **B**) Tracheids showing scalariform-thickening with microfibrils, scale bar = 100 µm. **C**) Tracheids showing multiseriate, alternate pits, scale bar = 50 µm. **D**) Expanded view of one of the lined tunnels shown in view A, scale bar = 750 µm. **E**) Probable partially digested spore, scale bar = 250 µm. **F**) Detail of cryptic segmented feature, scale bar = 300 µm.

attribution of the macrocoprolite to arthropleurids is not absolutely certain, however, because other large terrestrial detritivores may have existed for which there is currently no fossil record (cf. Fayers et al. 2010).

DISCUSSION

The plant–arthropod associations described here are significantly diverse for their Middle Pennsylvanian age, and are noteworthy in that they represent a rare snapshot of interactions in subhumid tropical environments outside the relatively well-sampled coal swamps (DiMichele and Phillips 1994; DiMichele et al. 2007). It is likely that a taphonomic megabias exists in the fossil record of arthropod associations similar to that recently documented for plant communities (Falcon-Lang et al. 2009, 2011). However, the three associations documented here are also significant in their own right as outlined below:

Insect Herbivory (Type 1)

The intriguing herbivorous association of a large arthropod, most likely an insect, in two cordaitalean stems provides an example of how typical detritivory could be transformed into incipient and subsequent full-fledged herbivory. A close analogue to the cordaitalean example involves *Psaronius* trees, for which greater detail exists regarding pith borings and the distribution of live versus dead tissues within the ontogeny of the plant (Mickle 1984; Rößler, 2000). Standing *P. blicklei* and *P. chasei* trees evidently exhibited trunk necroses caused by fungal heartrot at levels closer to ground level while the same plants simultaneously bore live trunk and photosynthetic frond tissues toward their canopies (Mickle, 1984; Roßler, 2000). Maintenance of tree support would have been assumed by production of structural, buttressing tissues of inner root mantle that anchored the plant basally (Roßler, 2000). For pith borers consuming decaying parenchymatic tissues at the lower trunk regions in *P. blicklei*, *P. chasei*, *P.* “layered cells” morphotype, *P. magnificus*, and *P. housuoensis* (Rothwell and Scott, 1983; Roßler 2000; Labandeira and Phillips 2002; D’Rozario et al. 2011), there was a larval or adult insect progressing vertically upward, eventually encountering live tissues adjacent to the upper trunk reaches near the canopy (Labandeira and Phillips 2002). Feeding encounters on live parenchymatic, especially meristematic tissues, would elicit tissue response, such as production of tufts of hypertrophic and hyperplasic tissue, or callus, similar to that seen in the two cordaitalean specimens described herein. Histological refinements of this interaction between an insect pith borer and *Psaronius* trunk parenchyma could have resulted in a primitive gall association, wherein response tissue is subtly modified into inner nutritive tissue for the gall chamber occupant, and outer structural tissue is designed to provide protection. Transformations of pith borings to stem galls have been demonstrated in anthomiid flies (Gassmann and Shorthouse 1992) and weevils (Shorthouse and Lalonde 1986). Accordingly, primitive galls have been found as host-plant and tissue specialists in *P. chasei* frond petioles from the Late Pennsylvanian Calhoun Coal (Labandeira and Phillips 1996b).

Oribatid Mite Detritivory (Type 2)

Mite associations reported here document a major web of detritivory on cordaitalean and *Psaronius* tissues that now extends biogeographically to eastern Euramerica. Formerly, this mid-Moscovian, few-million-year-long pulse of detritivory, centered on ca. 311 Ma, was documented in three regions of eastern North America—isolated midcontinental basins of principally Iowa and Kansas, the Illinois Basin centered in south-central Illinois, and the Appalachian Region consisting of the Northern, Central, and Southern Appalachian Basins (Baxendale 1979; Cichan and Taylor 1982; Labandeira et al. 1997a; Raymond et al. 2001). It should not be surprising that eastern Euramerica, along the Variscan Deformation Front of the southern United Kingdom, should also exhibit the same nexus of plant hosts and arthropod detritivores and herbivores.

Quantitative aspects of our oribatid microcoprolite analysis extend previous analysis of holometabolous insect larval coprolites (Labandeira and Phillips 1996b, 2002), based on Dyar's Rule and fecal pellet size-increment relationships in modern insect larvae (Dyar 1890; Sardesai 1969; Cole 1980). We reestablished the importance of applying a population concept for understanding the biological importance of coprolites through the use of more robust, discrete statistical data. In the previous study of macrocoprolites made by galler larvae in *Pteridotorichnos stipitopteri* petiolar galls, 102 measurements of macrocoprolite diameters were made, pooled into a single population, which yielded modal frequency classes from which four larval instars were inferred as present within the gall. The data indicated an instar ratio range of 1.23–1.47 (n = 102), averaging to a mean of 1.33 for all four modes. The current study of a mite boring involves a similarly endophytic association, but a near quadrupling of measurements based on macrocoprolite long axis and short axis dimensions, and recording seven separate microcoprolite populations, resulting in four or five modes (depending on the population) encompassing an instar ratio range of 1.23–1.45 (n = 402), and averaging to a grand mean of 1.31. This consistency in replicability of fossil macrocoprolite data from insect galls and mite borings also is comparable with fecal-pellet and body-length measurement data from modern mites (Lebrun 1968; Saichuae et al. 1972; Walter and Norton 1984; Norton and Ermilov 2014).

Putative Arthropleurid Detritivory (Type 3)

Finally, discovery of what is the largest-known terrestrial coprolite of Pennsylvanian age sheds light on arthropleurid behavior, an iconic but poorly understood group of arthropods. Identifiable plant remains within the macrocoprolite support previous conjecture (Rolfe 1985) that arborescent lycopsids formed an important component of the diet of these organisms. Documentation of burrows within the macrocoprolite also provides evidence for two-tiered processing of plant material, perhaps involving annelids.

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