

# Silurian vegetation stature and density inferred from fossil soils and plants in Pennsylvania, USA

Gregory J. Retallack

Department of Geological Sciences, University of Oregon, Eugene, OR 97403-1272, USA

\* Correspondence: [gregr@uoregon.edu](mailto:gregr@uoregon.edu)

**Abstract:** Silurian fossil plants range from small vascular plants (rhyniophytes) to moderately large fungi (nematophytes), but give little idea of the stature, rooting depth and plant density of vegetation on land. Silurian to earliest Devonian palaeosols from the Bloomsburg Formation show unusually deep bioturbation of several distinct kinds. Surface ground-parallel rhizomes of vascular land plants (to 20 cm deep) are penetrated by burrows like those of millipedes (to 80 cm), but the deepest stratum (down to 2 m below the surface) has features interpreted as bioturbation by fungal hyphae and rhizines. Plant-like axes associated with palaeosols are evidence of vegetation with three distinct tiers above ground as inferred from diameters using allometric scaling equations. Nematophytes (*Germanophyton psygmyphylloides*), up to 1.3 m tall, formed a tier above herbaceous vascular land plants (30 cm) and ground cover (<2 cm tall) of thallose organisms and litter. Drab haloed plant bases in the surface of palaeosols demonstrate that nematophytes grew densely (up to 51 m<sup>-2</sup>) with spacing (20 cm) that closed canopy in seasonally dry wetland palaeosols, comparable with modern marsh vegetation. Vascular land plants of well-drained soils in contrast were scattered, with bare earth between. Wetland ground cover was thus more extensive than cover of well-drained soils, and precursor lichens facilitated early evolution of vascular land plants.

**Supplementary Material:** Tables of mineral and grain-size proportions, major-element chemical analyses, and plant spacing and size are available at <http://www.geolsoc.org.uk/SUP18848>.

**Received** 27 February 2015; **revised** 6 May 2015; **accepted** 20 May 2015

Late Silurian greening of the land has been inferred from a rising diversity of fossil plant fragments (Edwards *et al.* 2014) and increased frequency of lateral accretion sets of meandering streams (Davies *et al.* 2011), but direct evidence comes from rooting structures and soil productivity inferred from palaeosols (Driese *et al.* 2000; Hillier *et al.* 2008; Brasier *et al.* 2014). Subterranean ecological tiering is apparent from bioturbation in Silurian palaeosols, including deep burrows comparable with those excavated by millipedes (Retallack 2001), surface disruption with the H and Y branching patterns of tracheophyte rhizomes (Retallack 1992) and diffuse filamentous bioturbation like that attributed by Hillier *et al.* (2008) to nematophytes. Traces of subterranean tiers are preserved directly in palaeosols, but vegetation tiers can also be inferred using allometric growth equations (Niklas 1994) from fossil plant debris largely known as transported fragments (Strother 1988, 1993; Tomescu *et al.* 2009). These combined approaches give a new and detailed view of locally lush late Silurian vegetation during the transition toward Devonian evolution of forest ecosystems (Retallack 1997a; Stein *et al.* 2007; Retallack & Huang 2011).

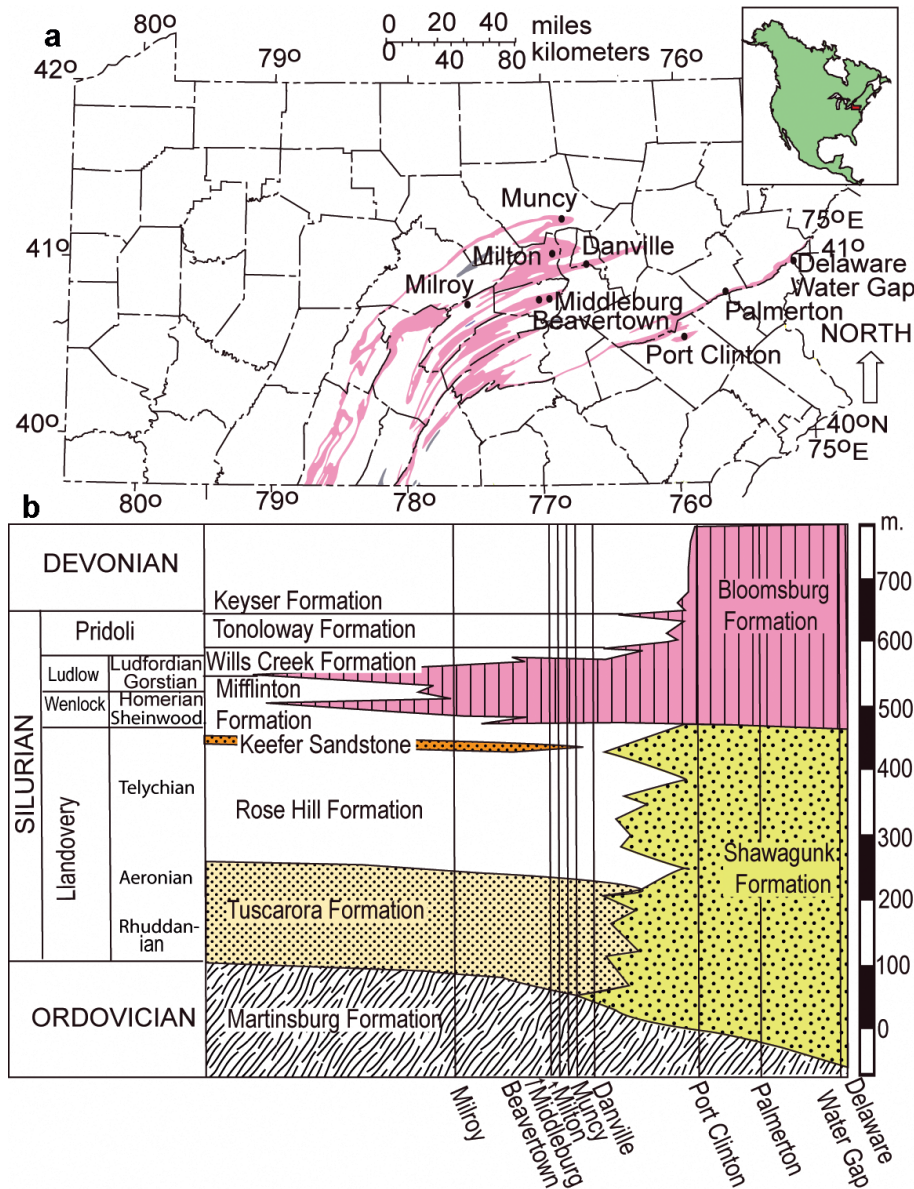
## Materials and methods

Measured sections of Bloomsburg Formation were made at several locations in Pennsylvania (Fig. 1): railroad cut 1 mile north of Milton (41.044748°N, 76.850463°W: Driese *et al.* 1992), road cut east of US highway 61, 1 mile north of the Schuylkill River at Port Clinton (40.588624°N, 76.026876°W: Strother 1988), and Red Hill SE of Palmerton (41.044748°N, 76.850463°W: Epstein *et al.* 1974). This latter outcrop was defoliated by pollution from local zinc smelting by New Jersey Zinc Company from 1898 to 1980 (Roberts *et al.* 2002). Other sites of Gray & Nickelsen (1989) in the Bloomsburg Formation were examined for this research: quarry 0.7 miles NW of Milton (41.024186°N, 76.865888°W), railway cut 1.3 miles north of Milton (41.051189°N, 76.847887°W),

quarry 2 miles north of Milton (41.067229°N, 76.849503°W), road cut north of US highway 11 in Danville (40.966853°N, 76.644826°W), creek banks under a bridge of interstate 180, 1 mile NE of Muncy (41.219314°N, 76.783318°W), quarry south of US highway 522, 2.4 miles east of Middleburg (40.789256°N, 77.014115°W), and old quarry 0.5 miles south of Beavertown (40.740494°N, 77.183070°W).

The principal activity in the field was measurement and sampling of sequences of palaeosols using a cloth tape and level (Figs 2–4). Different kinds of palaeosols (pedotypes) were recognized (Table 1), expanding pedotype nomenclature for Silurian palaeosols of Pennsylvania (Retallack 1985; Driese *et al.* 1992). Pedotype names refer to a particular kind of palaeosol, not necessarily its location. Thus Palmerton and Lehigh Gap pedotypes are found at Port Clinton (Fig. 3b) and elsewhere, as well as near Palmerton and Lehigh Gap (Fig. 4). So many palaeosols were found in the outcrop at Palmerton that well-placed names painted as graffiti were used for some pedotypes.

A variety of palaeoenvironmentally significant measures were taken from the palaeosols (Figs 3 and 4): Munsell hue, nodule size, depth to calcareous nodules, thickness of palaeosol with nodules and depth of rooting (Retallack 1997b, 2005). Samples were collected from a representative profile of each pedotype for laboratory analyses: major and trace element geochemical analysis by X-ray fluorescence (XRF), ferrous iron by potassium dichromate titration (by ALS Chemex of Vancouver, British Columbia) and bulk density determined from the weight suspended in air and then water of a paraffin-coated 25 g sample. Bulk density was determined for the North Milton section, but chemical data for that section are entirely from Driese *et al.* (1992). Petrographic thin sections were cut from the same samples and 500 points were counted using a Swift automated point counter to determine grain-size distribution and mineral composition (Fig. 5).



**Fig. 1.** Silurian rocks of Pennsylvania and studied localities (a) with a schematic east–west cross-section showing stratigraphic relationships (b). Stratigraphic data are from Schuchert (1916), Swartz & Swartz (1931), Hoskins (1961), Epstein & Epstein (1972), Epstein *et al.* (1974) and Laughrey (1999).

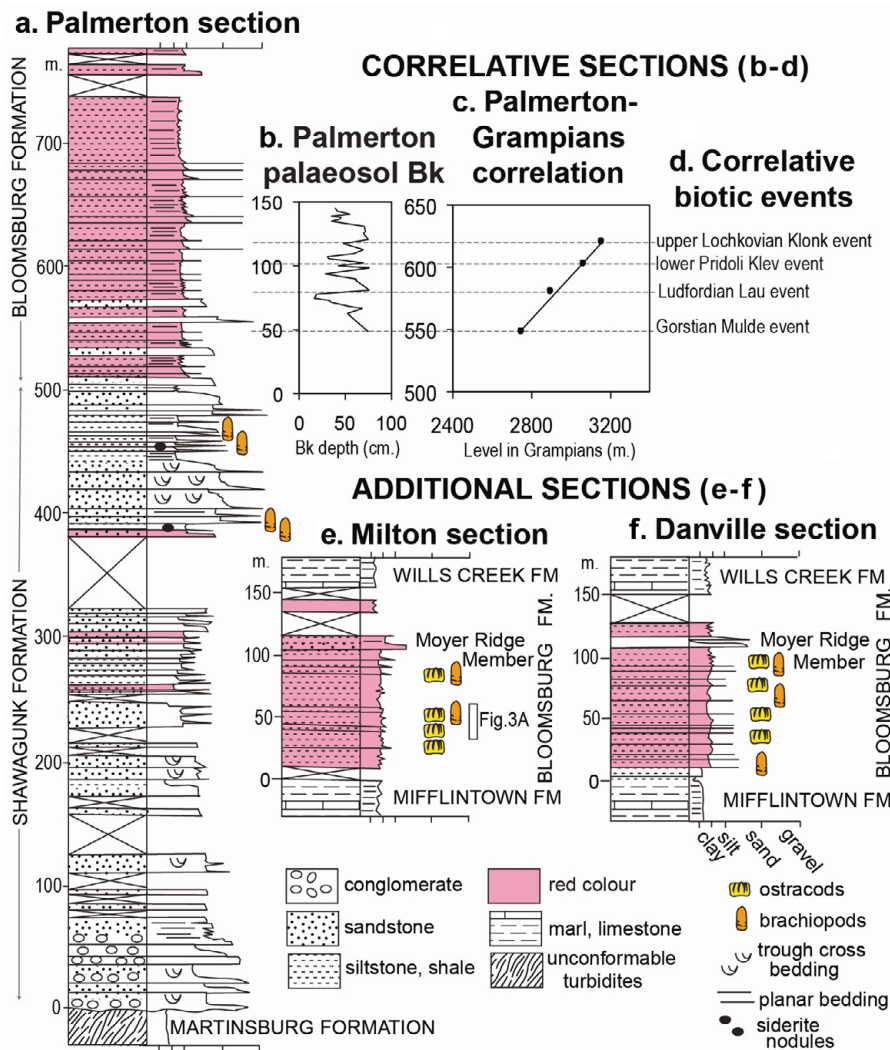
### Geological setting and age

The Bloomsburg Formation is red siltstone widespread in the eastern Valley and Ridge Province of Pennsylvania (Laughrey 1999). To the east the Bloomsburg Formation conformably overlies the Shawagunk Formation, and is unconformably overlain by the Oriskany Sandstone (Schuchert 1916; Swartz & Swartz 1931; Epstein & Epstein 1972). A tongue of Bloomsburg Formation to the west conformably overlies the Mifflinton Formation and is conformably overlain by the Wills Creek Formation (Fig. 1). Each of these units has been folded, thrust and metamorphosed to the quartz–muscovite–albite–chlorite subfacies of greenschist-facies regional metamorphism (Epstein *et al.* 1974). An oxygen-isotope study of fluid inclusions in the Palmerton outcrop of the Bloomsburg Formation (Fig. 4) revealed maximal alteration temperatures of  $171^{\circ}\text{C} \pm 5^{\circ}\text{C}$  (Bradfield & Gray 1999). Alteration of conodonts (CAI 4–4.5) and coalified debris (vitrinite reflectance 3.5%) in Silurian and Devonian rocks of eastern Pennsylvania are evidence of burial temperatures of 190–300°C and burial depths of 6.7–7.9 km (Epstein *et al.* 1977). Burial compaction of 69% of the original volume of the palaeosols in the Bloomsburg Formation can be calculated using a standard compaction formula for calcareous soils (equation (1) for Aridisols of Sheldon & Retallack 2001) to obtain original thickness of soil ( $B_s$  in cm) from thickness of

palaeosol ( $B_p$  in cm) for a known burial depth ( $K$  in km) of 7.9 km, as follows:

$$B_s = B_p / \left[ -0.62 / \left( e^{\frac{0.38}{0.17K}} - 1 \right) \right]. \quad (1)$$

The age of the Bloomsburg Formation is well constrained by correlation with the Willamsport Sandstone of Bluegrass, Virginia, above late Ludlow (middle Ludfordian *Ozarkodina snajdri* zone) conodonts and below latest Ludlow (late Ludfordian *Ozarkodina tillmani* zone) conodonts (Hoskins 1961; Beck & Strother 2008). The age of the thick western part of the Bloomsburg Formation is broadly constrained by its fossil fish (Beerbower & Hait 1959), and is older than the Oriskany Sandstone, with Early Devonian (late Pragian) marine faunas (ver Straeten 2007), and younger than the Shawagunk Formation with a fauna of Early Silurian eurypterids (Epstein & Epstein 1972). Lithological and pedostratigraphic correlations support correlation of the lower part of the Bloomsburg Formation at Palmerton with Bloomsburg Formation within marine shales and limestones of central Pennsylvania, near Milton, Danville and Port Clinton (Figs 1–4). Pedostratigraphic correlation employs climatically sensitive features of palaeosols such as depth to calcareous nodules (Bk horizon), which is a proxy for secondary productivity and greenhouse spikes (Breecker



**Fig. 2.** Measured sections (a, e, f) and correlation of variation of Bk depth in Silurian palaeosols of the Palmerton section (b) with comparable calcareous palaeosols of Grampians National Park, Victoria (c). (d) lists correlative biotic events.

& Retallack 2014). Spikes of unusually deep Bk horizons in the section at Palmerton (Fig. 4) correlate proportionally with spikes of unusually deep Bk horizons in Silurian palaeosols of Grampians National Park (Victoria, Australia: Retallack 2009). This correlation (Fig. 2c) has an  $R^2$  of 0.99 and F-test ANOVA probability of 0.00007. Thus the deep calcic palaeosol at 120.3 m in the measured section at Palmerton may have been Lochkovian, and supports correlation by Epstein & Epstein (1972) and Laughrey (1999) of the upper Bloomsburg Formation at Palmerton and Delaware Water Gap with the Early Devonian marine Keyser Formation.

## Palaeosol recognition and interpretation

### Recognition

The Bloomsburg Formation of Pennsylvania includes a few grey beds of sandstone with primary sedimentary structures, and some fossiliferous horizons (Beerbower & Hait 1959; Hoskins 1961; Strother 1988, 1993). Most of the Bloomsburg Formation is red siltstone with surprisingly abundant burrows (Fig. 6a and d) and other bioturbation (Fig. 6b and e) for Silurian rocks with many other features of palaeosols: gradational horizons beneath sharp tops (soil horizons: Fig. 6c and f), bowl-shaped slickensides (vertic deformation: Fig. 6d) and calcareous nodular horizons (caliche: Fig. 6e). Previous documentation of such soil features (Retallack 1985; Gray & Nickelsen 1989; Driese *et al.* 1992; Mora & Driese 1999) is here organized into different kinds of

palaeosols as recognized in the field (pedotypes), for the purpose of attempting to reconstruct Silurian local soil-forming regimes and their vegetation.

### Pedotypes

The Lehigh Gap pedotype of Retallack (1985) and the North Milton pedotype of Driese *et al.* (1992) are here augmented with eight additional pedotypes (Tables 1 and 2) to document the variety of palaeosols seen throughout the formation. Pedotypes are defined on differences such as the degree of destruction by bioturbation of primary sedimentary structures and the depth within profiles of burrows and calcareous nodules. Each pedotype is based on a type profile, sampled in detail for petrographic and geochemical study (Fig. 5). These additional data allow identification of pedotypes as if they were modern soils (Table 1). Petrographic analysis has confirmed that these Silurian palaeosols all lack argillite horizons (illuvial clay-rich horizons of Soil Survey Staff 2010), despite their bioturbation and thickness, which are comparable with those of Argillisols (Mack *et al.* 1993), Podzols (Stace *et al.* 1968), Chromosols (Isbell 1998), Luvisols (Food and Agriculture Organization 1974) and Alfisols (Soil Survey Staff 2010).

The degree of chemical weathering of Silurian palaeosols can also be evaluated by tau analysis and comparison with Miocene calcareous red palaeosols from Pakistan, which formed on similar silty and clayey outwash of a sedimentary fold-mountain range (Retallack 1991). As recommended by Brimhall *et al.* (1992), the



**Table 1.** *Pedotypes of the Bloomsburg Formation*

Pedotype	Diagnosis	Type example	Palaeosol classification (Mack <i>et al.</i> 1993)	US taxonomy (Soil Survey Staff 2010)	FAO map (Food and Agriculture Organization 1974)	Old Australian (Stace <i>et al.</i> 1968)	New Australian (Isbell 1998)
Alice	Silty red surface (A) with deep (>65 cm) calcareous nodules (Bk), over drab Mn-rimmed mottles (Bg)	Palmerton 48.2 m	Calcisol	Aquic Calciargid	Calcaric Gleysol	Wiesenboden	Supracalcic Calcarosol
Barry	Silty red surface (A) with shallow (<65 cm) calcareous nodules (Bk), over drab Mn-rimmed mottles (Bg)	Palmerton 70.5 m	Calcisol	Aquicambid	Calcaric Gleysol	Wiesenboden	Supracalcic Calcarosol
Brenda	Red–green mottled clayey surface (A) over deeply mottled subsurface (Bg and AC)	Palmerton 18.5 m	Protosol	Haplaquept	Humic Cambisol	Humic Gley	Redoxic Hydrosol
Debbie	Red silty surface with weakly gleyed subvertical red pedotubules (A) over bedded siltstone (C)	Palmerton 60.5 m	Protosol	Fluvent	Fluvisol	Alluvial soil	Stratic Rudosol
Lehigh Gap	Red silty surface (A) over deep (>65 cm) calcareous nodules (Bk)	Palmerton 125 m	Calcisol	Ustropept	Calcic Cambisol	Calcareous red earth	Hypocalcic Calcarosol
Lisette	Silty red with shallow drab mottled (A) over bedded grey shale and siltstone (C)	Palmerton 30 m	Protosol	Aquent	Fluvisol	Alluvial soil	Stratic Rudosol
Milton	Grey–green silty surface (A) over thick slickensided claystone (Bw)	North Milton 23.3 m	Vertisol	Chromustert	Chromic Vertisol	Grey clay	Brown Vertosol
Muddy	Silty red with shallow drab mottled (A) over bedded red shale and siltstone (C)	North Milton 20.3 m	Protosol	Fluvent	Fluvisol	Alluvial soil	Stratic Rudosol
Palmerton	Red silty surface (A) over shallow (<65 cm) calcareous nodules (Bk)	Palmerton 71.6 m	Calcisol	Calcid	Xerosol	Calcareous red earth	Hypocalcic Calcarosol
Turbot	Silty red and drab mottled surface (A) over red mottled siltstone (Bw)	North Milton 19.5 m	Vertisol	Vertic Ustropept	Vertic Cambisol	Brown earth	Brown-Orthic Tenosol

mass transfer of elements in a soil at a given horizon ( $\tau_{w,j}$  in moles) can be calculated from the bulk density of the soil ( $\rho_w$  in  $\text{g cm}^{-3}$ ) and parent material ( $\rho_p$  in  $\text{g cm}^{-3}$ ) and from the chemical concentration of the element in soils ( $C_{j,w}$  in wt%) and parent material ( $C_{j,p}$  in wt%). Changes in volume of soil during weathering were called strain by Brimhall *et al.* (1992) and are estimated from an immobile element in soil (such as Ti used here) compared with parent material ( $\epsilon_{i,w}$  as a fraction). The relevant equations (2) and (3) (below) are the basis for calculating divergence from parent material composition (origin in various panels of Fig. 7):

$$\tau_{j,w} = \left( \frac{\rho_w C_{j,w}}{\rho_p C_{j,p}} \right) (\epsilon_{i,w} + 1) - 1 \quad (2)$$

$$\epsilon_{i,w} = \left( \frac{\rho_p C_{j,p}}{\rho_w C_{j,w}} \right) - 1. \quad (3)$$

The degree of chemical mass transfer and strain in Miocene and Silurian palaeosols are very similar for all but the Silurian

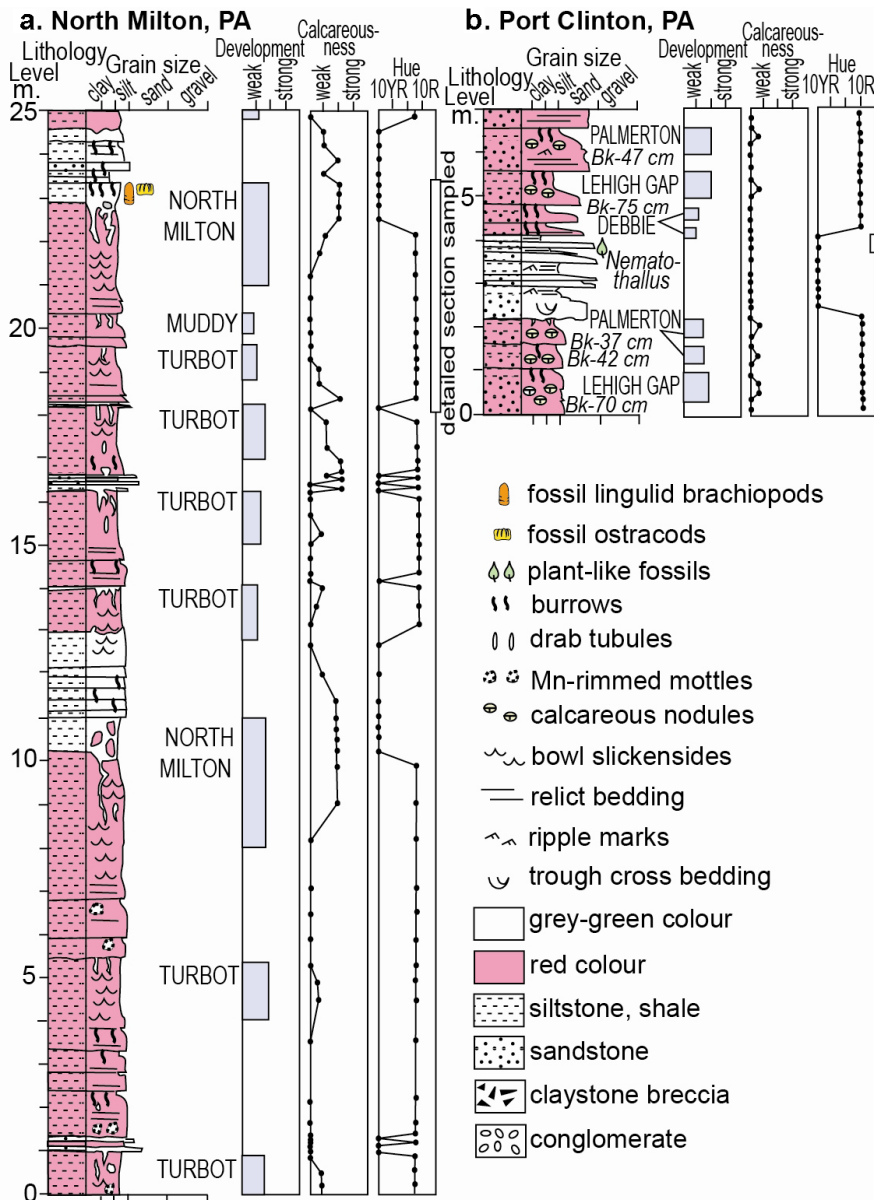
North Milton palaeosol, which gained volume and also mass, perhaps owing to its unique history of marine hydromorphism (Driese *et al.* 1992). Chemical and physical weathering of Silurian and Miocene palaeosols were comparable, and modern climofunctions are applicable to palaeosols of the Bloomsburg Formation other than the marginal marine North Milton pedotype.

### Parent material

Tau analysis quantifies alteration of palaeosol profiles from the initial sediment on which they formed (at origin in Fig. 7), which for the Bloomsburg Formation was quartzofeldspathic silt and sand derived from erosion of pre-existing sedimentary rocks during Acadian uplift of the Appalachians (Epstein *et al.* 1974). The most common components of the parent material of the palaeosols revealed by point counting are quartz, feldspar and clay, with lesser amounts of opaque minerals, mica and rock fragments (Fig. 5). Chemically and mineralogically, sedimentary parent material of soils that became Bloomsburg Formation palaeosols



## Silurian vegetation



**Fig. 3.** Detailed measured section of palaeosols in the Bloomsburg Formation near North Milton (a) and Port Clinton (b). Development of the palaeosols is based on degrees of destruction of primary bedding by roots and cracks, calcareousness is a scale of reaction with dilute (0.1M) HCl, and hue is from a Munsell Chart (as outlined by Retallack 1997b).

was probably very similar to that of the Siwalik Group of Pakistan (Retallack 1991), so that palaeosols in both formations overlap substantially in composition (Fig. 7).

Unlike the underlying sandy and conglomeratic Shawagunk Formation, the Bloomsburg Formation is dominantly siltstone, with only thin sandstones and conglomerates (Fig. 2a). Dominance of silt is especially clear in point-count data of palaeosols in the Bloomsburg Formation (Fig. 5). Dominance of silt may also explain the muted expression of vertic structures ('bowl slickensides'; Gray & Nickelsen 1989) in palaeosols of the Bloomsburg Formation, rather than more complex vertic structures of more clayey soils and palaeosols (mukkara structure and lentic ped; Retallack 1997b). Silt dominance is also reflected in muted chemical variation of thick palaeosols, with chemical variation limited to upper horizons enriched in clay (Fig. 5). The Shawagunk and Bloomsburg Formations have been interpreted as fluvial outwash (Epstein & Epstein 1972), but silt-dominance of the Bloomsburg Formation reflects a change in sedimentary regime, to less energetic lacustrine sedimentation or more common aeolian loess deposition. Evidence against swampy, ponded, low-gradient floodplains includes a pervasive red colour, structures interpreted

as deeply reaching burrows and common calcareous nodules (caliche) of the Bloomsburg Formation. Thus some contribution of loess is likely, and bioturbation may not have been entirely responsible for the general lack of bedding. Nevertheless, aeolian sedimentary structures such as inverse grading (climbing translant cross stratification), wind dissected ripples and dunes (Hunter 1977) have not been found in the Bloomsburg Formation. Sources of this loess may have been Late Silurian sabkhas of the evaporitic Michigan Basin of northwestern Pennsylvania and New York (Gill 1977).

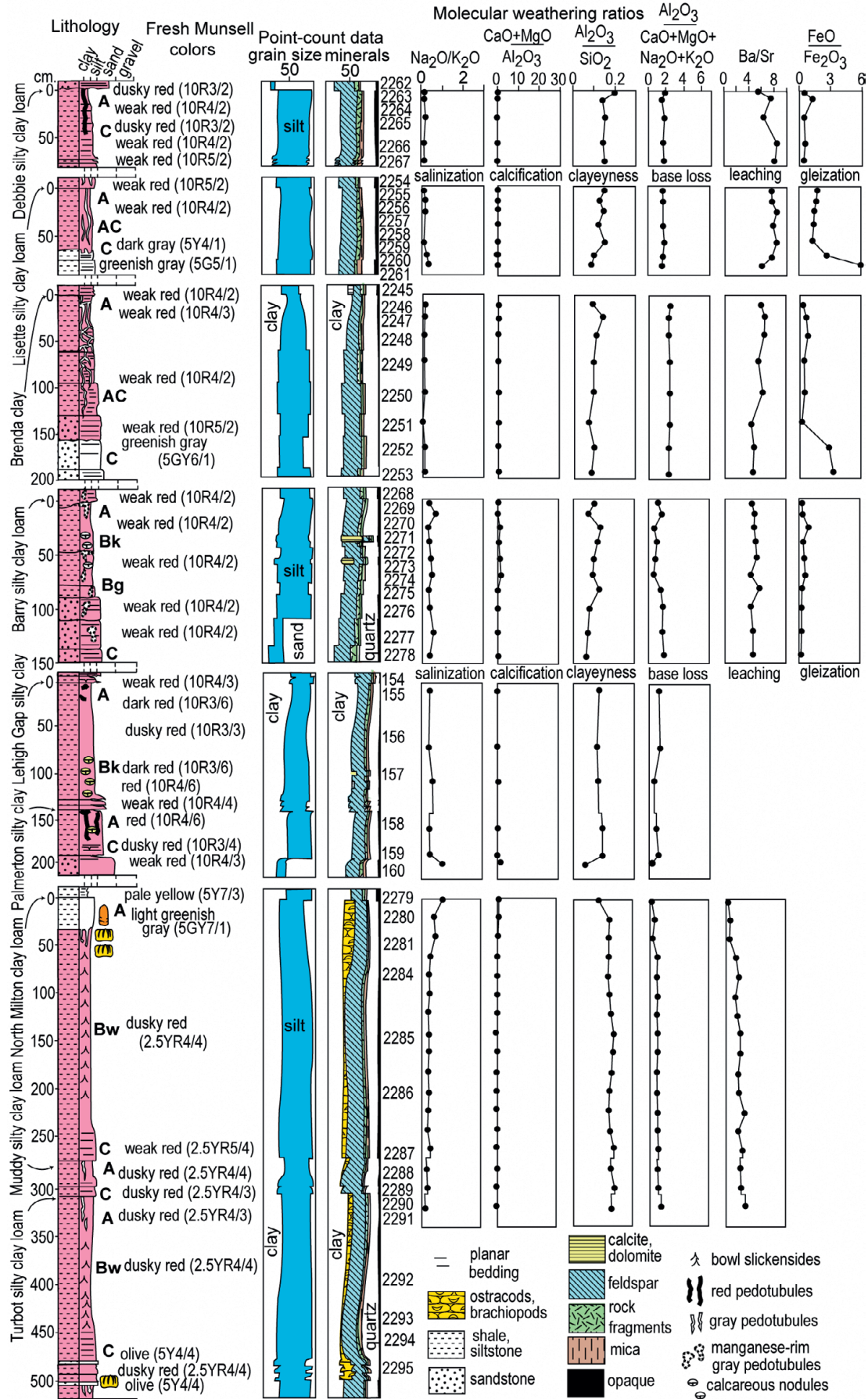
### Palaeotopography

Palaeosols of the Bloomsburg Formation near Palmerton (Fig. 4) and Port Clinton (Fig. 3b) cap fining-upwards sequences that include grey-green sandy fluvial interbeds, and these sequences have been interpreted as formed on alluvial plains of loosely sinuous streams (Epstein *et al.* 1974). They represent a transitional fluvial style between sheet-braided streams of the Early Silurian Tuscarora Formation and meandering streams of the Devonian Catskill Formation of Pennsylvania (Cotter 1978),



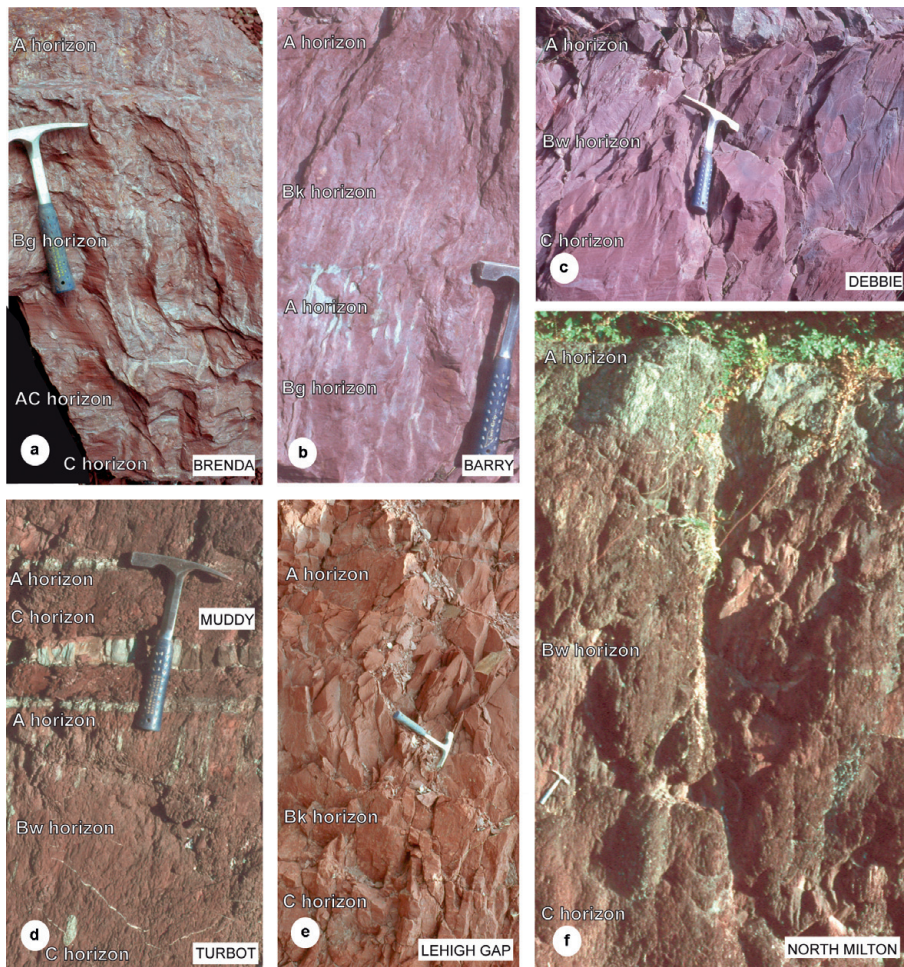


Silurian vegetation



**Fig. 5.** Petrographic and chemical data on distinct kinds of palaeosols (pedotypes) in the Bloomsburg Formation of Pennsylvania. Grain-size and mineral composition data are from point-counting petrographic thin sections cut vertical to bedding at the numbered locations. Molar weathering ratios are calculated to approximate common weathering reactions (Retallack 1997b) from XRF from whole-rock analysis and dichromate titration (for Fe<sup>3+</sup>). These analytical and colour data are used to determine former soil horizons.





**Fig. 6.** Field features of Silurian palaeosols of Pennsylvania. (a) Mn-rimmed drab tubular mottles in Brenda pedotype at Palmerton; (b) red pedotubules in upper part and Mn-rimmed drab tubular mottles in lower part of Barry pedotype at Palmerton; (c) destruction of bedding by red pedotubules in surface of Debbie pedotype at Palmerton; (d) drab bands and surface mottles in Muddy and Turbot palaeosols at Milton; (e) red pedotubules and small calcareous nodules and strong schistosity in Lehigh gap pedotype at Palmerton; (f) drab surface and bowl-shaped slickensides in red subsurface of North Milton pedotype, at Milton. Hammers for scale (25 cm long) are in every image. Stratigraphic levels of photographs in Figure 4 are 18.4 m (a), 72.9 m (b), 59.1 m (c) and 125 m (e), and in Figure 3a are 19.6 m (d) and 23.4 m (f).

which is part of a global fluvial transformation owing to spread of land plants (Retallack 1997a; Davies & Gibling 2010; Davies *et al.* 2011).

In contrast, palaeosols of the Bloomsburg Formation near Milton (Fig. 3a) have rare and planar interbeds, and are within that part of the formation interbedded with marine shales and limestones (Fig. 1b). The Milton and Danville sections thus formed on low-gradient coastal plains to the west (Driese *et al.* 1992), whereas Palmerton and Port Clinton palaeosols formed on alluvial plains closer to mountainous eastern source terrains (Epstein & Epstein 1972; Epstein *et al.* 1974). Vertic structures, pedotubules and lack of grey–green colours are evidence that coastal palaeosols were well drained, with water table metres below the surface of the palaeosols (Driese *et al.* 1992).

### Palaeoclimate

Palaeothermometers and palaeohydometers (palaeoprecipitation proxies) based on depth of nodules and chemical composition of modern soils can potentially be used to estimate palaeoclimate from palaeosols of the Bloomsburg Formation. The underlying assumption that Silurian palaeosols have a similar degree of chemical weathering to modern soils is supported by composition overlapping that of Miocene palaeosols (Fig. 7).

The palaeohydometer of Retallack (2005) gives mean annual precipitation (MAP =  $R$  in mm) from depth to carbonate nodules in soils ( $D_0$  in cm) according to equation (4) ( $R^2 = 0.52$ ; standard error (SE)  $\pm 147$  mm). Mean annual range of precipitation (MARP), which is the difference in monthly mean precipitation between the wettest and driest month ( $M$  in mm) is also related in modern soils

to thickness of soil with carbonate, according to equation (5) ( $R^2 = 0.58$ ; SE =  $\pm 22$  mm):

$$R = 137.24 + 6.45D_0 - 0.013D_0^2 \quad (4)$$

$$M = 0.79H_0 + 13.17. \quad (5)$$

For application to palaeosols, measured depths must be corrected for burial compaction using equation (1). Depths in palaeosols could also have been compromised by vertic displacement (Nordt *et al.* 2006; Miller *et al.* 2007), but these are problems only for the North Milton pedotype, which lacks a Bk horizon (Fig. 5).

An additional palaeohydometer of Sheldon *et al.* (2002) comes from chemical index of alteration without potassium ( $A = 100m \text{ Al}_2\text{O}_3 / (m \text{ Al}_2\text{O}_3 + m \text{ CaO} + m \text{ MgO} + m \text{ Na}_2\text{O})$ , in moles), which increases with mean annual precipitation ( $R$  in mm) in modern soils (equation (6) with  $R^2 = 0.72$ ; SE =  $\pm 182$  mm):

$$R = 221e^{0.0197A}. \quad (6)$$

The palaeosol palaeothermometer of Sheldon *et al.* (2002) is based on alkali index ( $N = (\text{K}_2\text{O} + \text{Na}_2\text{O}) / \text{Al}_2\text{O}_3$  as a molar ratio), which is related to mean annual temperature (MAT =  $T$  in  $^\circ\text{C}$ ) in modern soils by equation (7) ( $R^2 = 0.37$ ; SE =  $\pm 4.4^\circ\text{C}$ ):

$$T = -18.5N + 17.3. \quad (7)$$

Results of these calculations are indistinguishable (within error) for Silurian palaeoprecipitation calculated by the two methods of depth to Bk and alkali index (Table 2). These calculations also demonstrate that some pedotypes formed under semiarid precipitation (Barry and Palmerton pedotypes), whereas others were subhumid (Alice and Lehigh Gap pedotypes) and humid (Brenda and

## Silurian vegetation

**Table 2.** *Palaeoenvironmental interpretation of the Bloomsburg Formation*

Pedotype	Palaeoclimate	Vegetation	Animals	Palaeotopography	Parent material	Time of formation (kyr)
Alice	Subhumid (MAP 686–691 ± 147 mm), seasonally wet (MARF 63–77 ± 22 mm)	Nematophyte woodland	Unknown	Low-lying floodplain	Quartzofeldspathic silt	0.1–1
Barry	Temperate (MAT 9.9 ± 4.4°C), semiarid (MAP 280–551 ± 147 mm, or 507 ± 182 mm), seasonally wet (MARF 35–82 ± 22 mm)	Zosterophyll brakeland	Unknown	Low-lying floodplain	Quartzofeldspathic silt	0.1–1
Brenda	Temperate (MAT 11.9 ± 4.4°C), humid (MAP 1214 ± 182 mm), seasonally wet	Nematophyte woodland	Unknown	Low-lying floodplain	Quartzofeldspathic silt	0.1–1
Debbie	Not diagnostic of climate owing to insufficient development	Zosterophyll brakeland	<i>Scoyenia beerboweri</i> (millipede burrows)	Well-drained floodplain	Quartzofeldspathic silt	0.01–0.1
Lehigh Gap	Temperate (MAT 10.1 ± 4.4°C), subhumid (MAP 658–691 ± 147 mm, or 855 ± 182 mm), seasonally wet (MARF 57–91 ± 22 mm)	Zosterophyll brakeland	<i>Scoyenia beerboweri</i> (millipede burrows)	Well-drained floodplain	Quartzofeldspathic silt	4.4 ± 0.6
Lisette	Not diagnostic of climate owing to insufficient development	Nematophyte shrubland	<i>Scoyenia beerboweri</i> (millipede burrows)	River bank	Quartzofeldspathic silt	0.01–0.1
North Milton	Not diagnostic of climate owing to marine hydromorphism	Rhyniophyte salt marsh	<i>Chondrites</i> , <i>Palaeophycus</i> (worm burrows), <i>Lingula</i> sp. (brachiopod), <i>Kloedenia normalis</i> , <i>Kloedenella berdanae</i> , <i>Dizygopleura punctella</i> , <i>Herrmanina</i> sp. (ostracods)	Well-drained coastal terrace	Calcareous clay	1–7
Muddy	Not diagnostic of climate owing to insufficient development	Rhyniophyte early successional	<i>Palaeophycus</i> (worm burrows)	Supratidal flat	Calcareous clay	0.05–0.5
Palmerton	Temperate (MAT 11.4 ± 4.4°C), semiarid (MAP 393–613 ± 147 mm), seasonally wet (MARF 44–99 ± 22 mm)	Zosterophyll brakeland	<i>Scoyenia beerboweri</i> (millipede burrows)	Well-drained floodplain	Quartzofeldspathic silt	3.3 ± 0.6
Turbot	Temperate (MAT 10.2 ± 4.4°C), humid (MAP 910 ± 182 mm), seasonally dry	Nematophyte coastal shrubland	<i>Palaeophycus</i> (worm burrows)	Estuary bank	Calcareous clay	1–2

Turbot). Other pedotypes are not diagnostic of palaeoclimate owing to insufficient soil development (Muddy, Lisette and Debbie pedotypes) or marine hydromorphism (North Milton pedotype of Driese *et al.* 1992). Nevertheless, a pattern of precipitation variation through time is indicated, as indicated graphically by the proxy of depth to Bk (Fig. 2b).

Seasonality of precipitation during the Late Silurian and Early Devonian was also revealed by spread of carbonate nodules within single calcareous palaeosols (Table 2), as suspected from the development of vertic structures in North Milton and Turbot palaeosols (Gray & Nickelsen 1989; Driese *et al.* 1992). However, the difference between monthly means of precipitation would not have qualified as monsoonal (more than 100 mm difference: Retallack 2005). Siluro-Devonian palaeosols also have limited intergrowth of carbonate and haematite (Fig. 8d), unlike monsoonal Miocene palaeosols and modern soils (Retallack 1991).

The palaeosol palaeothermometer of Sheldon *et al.* (2002) indicates temperate climates for palaeosols of the Bloomsburg Formation (Table 2), a result that could have been compromised by introduction of bases during lower greenschist-facies metamorphism (Epstein *et al.* 1974). However, comparable palaeoclimatic results can be derived from application of these same climofunctions to geochemically comparable unmetamorphosed Miocene palaeosols from Pakistan (Fig. 7): mean annual temperatures of 11.9–13.3°C and mean annual precipitations of 642–1110 mm

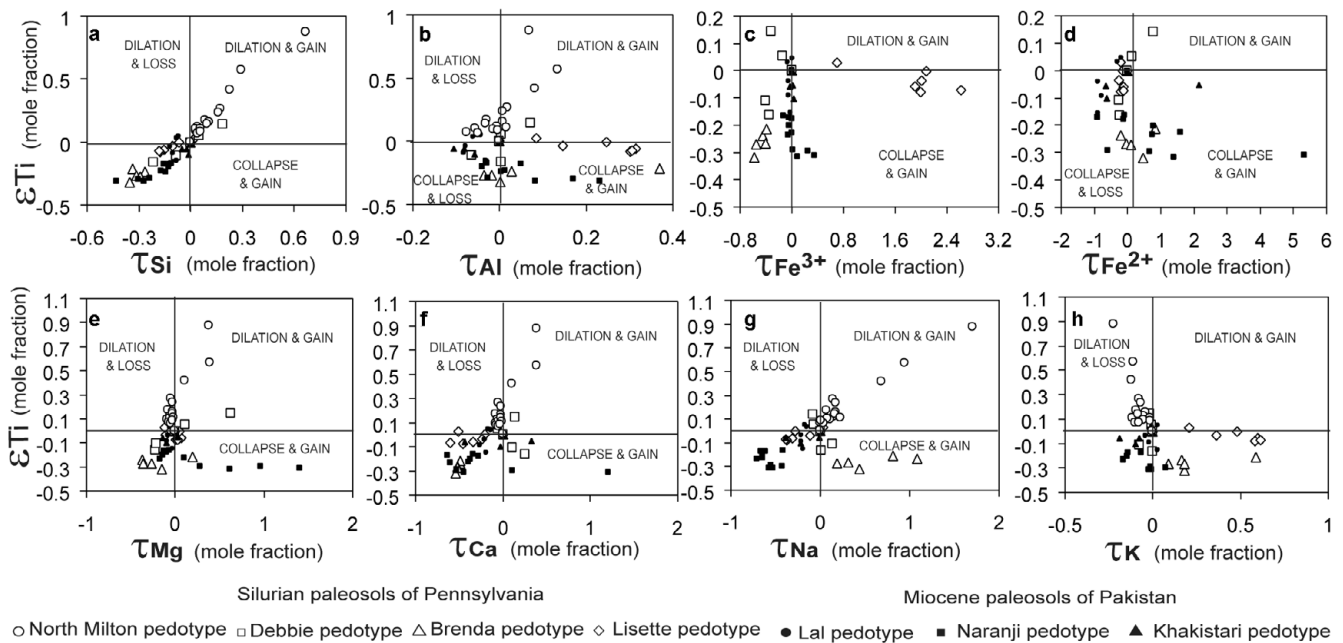
(Retallack 1991). A broadly temperate palaeolatitude of 32°S for central Pennsylvania during the Late Silurian can be calculated from plate reconstructions incorporating palaeomagnetic studies of the Bloomsburg Formation (Scotese 1997).

### Soil animals

Many palaeosols (Debbie, Lisette, Lehigh Gap and Palmerton pedotypes) in the Bloomsburg Formation have abundant burrows (*Scoyenia beerboweri*), comparable with those attributed to polyzoniid millipedes from Late Ordovician (Katian) palaeosols of Pennsylvania (Retallack 2001). The idea of Ordovician millipedes was challenged by Wilson (2006) and Davies *et al.* (2010), who considered millipedes no older than Late Silurian and noted differences between *Scoyenia* and burrows of advanced julliid millipedes (Hembree 2009). These objections do not rule out millipedes in the Late Silurian Bloomsburg Formation, and overlook Late Ordovician (Sandbian) polyxenid or polyzoniid millipede trackways (Johnson *et al.* 1994), Cambrian millipede-like fossils (Hou & Bergström 1998; Budd *et al.* 2001; Retallack *et al.* 2011), and phylogenomic (Rota-Stabelli *et al.* 2013; Misof *et al.* 2014) and biogeographical (Shelley & Golovatch 2011) evidence for Cambrian origin of millipedes.

*Scoyenia* burrows run subparallel to the ancient land surface, and also vertical to the surface. Vertical burrow densities in a line





**Fig. 7.** Strain relative to Ti (mole fraction) and mass transfer (mole fraction) of Silurian palaeosols of Pennsylvania (herein) was comparable with that of Miocene palaeosols from Pakistan (data from Retallack 1991).

transect parallel to the land surface of Lehigh Gap palaeosol were  $29\text{ m}^{-1}$  (equivalent to  $868\text{ m}^{-2}$ ), and in two Barry palaeosols were  $33.3 \pm 1\text{ m}^{-1}$  ( $1110 \pm 69\text{ m}^{-2}$ ). *Scoyenia beerboweri* has backfill structures (Fig. 9j and k), and is encrusted and filled with caliche nodules (Fig. 9l), which are evidence that the burrows formed at the same time as the palaeosols (Retallack 2001). A difference between Silurian and Ordovician burrows of *Scoyenia beerboweri* is the encrustation of Silurian burrows by structures comparable with roots and hyphae. Root traces and hyphae in soils and palaeosols exploit burrow fills because they are less compact than surrounding matrix (Retallack 1991).

Another distinct trace fossil found in a thin section of the surface of the type Brenda clay palaeosol is flask-shaped hollows, 2–3 mm diameter, lined with ferruginized clay and filled with sand from above (Fig. 10a). There is no useful ichnogenus for such remains, morphologically similar to thicker walled and larger *Coprinisphaera*, which are attributed to dung beetles (Genise *et al.* 2004). Most similar to these unnamed trace fossils of the Bloomsburg Formation are modern millipede moult and egg chambers (Romell 1935; Toye 1967), and trapdoor spider burrows (Bond & Opell 2002). Late Silurian millipedes and spider-like trigonotarbids are known, but not beetles (Ward *et al.* 2006).

Other pedotypes (North Milton, Muddy, Turbot, Brenda) have subhorizontal burrows (*Palaeophycus*), 4–5 mm wide (Fig. 8c) and downward branching burrows (*Chondrites*) 1–2 mm wide (Driese *et al.* 1992). Muddy and Turbot pedotypes also contain ostracods and lingulid brachiopods in their subsurface, whereas in the nearby North Milton pedotype these fossils are common in surface horizons. Driese *et al.* (1992) interpreted the drab and partly pyritic surface of the North Milton palaeosol with *Chondrites* as produced by marine inundation of a vertic palaeosol by anoxic marine-lagoonal waters. Muddy, Turbot and Brenda palaeosols lack surficial marine fossils, pyrite or drab surfaces, so that *Palaeophycus* within them is unlikely to represent a marine or aquatic organism, and may have been a worm-like soil organism.

### Vegetation

A variety of mottles and root-like features are notable for their density and extensive destruction of primary bedding in palaeosols of the Bloomsburg Formation. Despite their superficial resemblance

to drab-haloes root traces of palaeosols (Retallack 1983, 1997b), grey-green tubular structures of the Bloomsburg Formation lack central tubular features replaced by calcite or clay after stout tracheophyte roots. Instead, these pedotubules are penetrated by abundant ramifying and anastomosing carbonaceous filaments (Figs 8b, g and 10b, c). These can be distinguished from local schistosity by variation in orientation (Fig. 8g), branching (Fig. 8b) and soft sediment up-arching of primary lamination (Fig. 10c). Where associated sand-filled tubes are found, they end bluntly (Fig. 8c), and therefore are interpreted as animal burrows. Some of these features stand out as grey-green pedotubules in red siltstone (Fig. 6a and d), like most drab-haloes root traces (Retallack 1997b), but others have thin, dark grey, Fe–Mn rims (Figs 6b and 9h), like pedotubules of Ogi palaeosols of Retallack (1983).

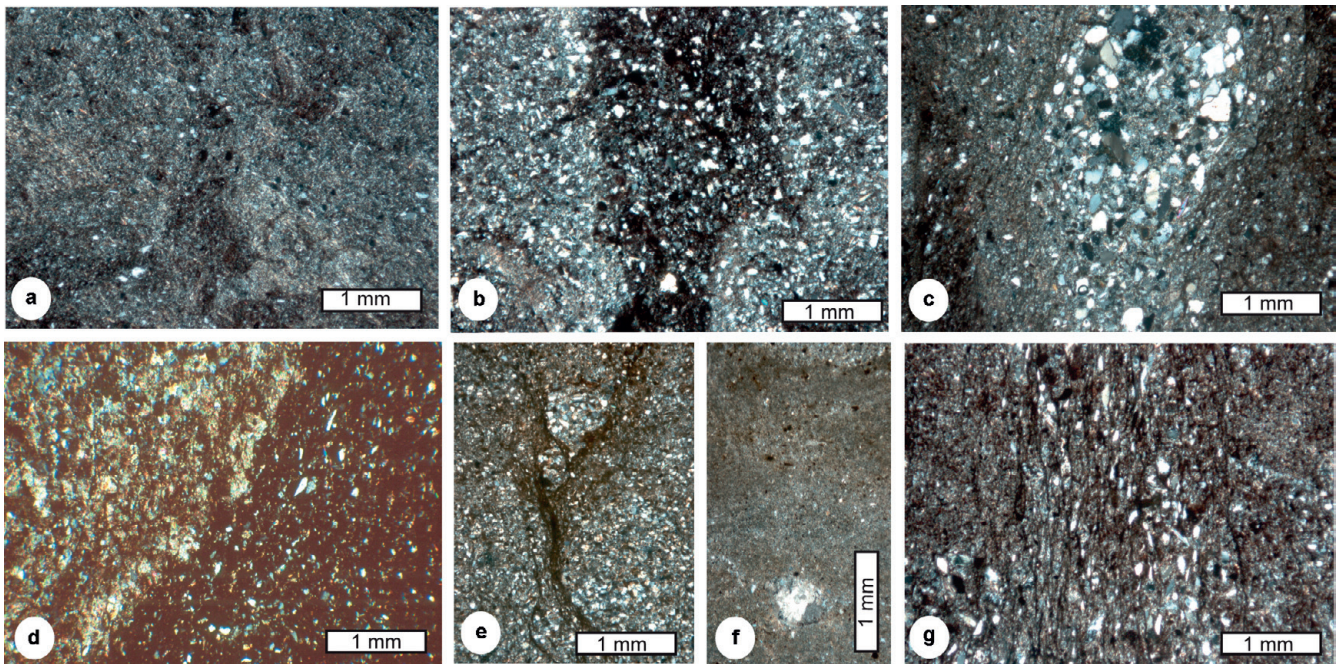
Grey-green pedotubules are extensive in palaeosols of the Bloomsburg Formation: drab tubules reach depths of 130 cm in the Brenda pedotype, whereas Fe–Mn-rimmed grey-green pedotubules in Barry and Alice pedotypes are in a subsurface horizon 50–130 cm below the surface. In all cases these mottled zones are consistent in thickness for the exposed lateral extent of the palaeosol, which is up to 30 m in steeply dipping beds in Red Hill, near Palmerton. Surface grey-green mottles of a Turbot palaeosol (Fig. 6d) have density of  $15.5\text{ m}^{-1}$  in line transect, which assuming comparable density in all directions would be  $239\text{ m}^{-2}$ . The Brenda pedotype, in contrast, has large mottles with density as low as  $3.5\text{ m}^{-1}$  in transect or  $14.8\text{ m}^{-2}$ . Between these extremes are surface drab tubules of two other Brenda pedotypes ( $3.8\text{ m}^{-1}$ , or  $12.8\text{ m}^{-2}$ ;  $7.1\text{ m}^{-1}$ , or  $61.3\text{ m}^{-2}$ ), Lisette ( $5.7\text{ m}^{-1}$ , or  $51\text{ m}^{-2}$ ), Muddy ( $9.7\text{ m}^{-1}$ , or  $93\text{ m}^{-2}$ ), Barry ( $11.0\text{ m}^{-1}$ , or  $120\text{ m}^{-2}$ ) and Lehigh Gap pedotypes ( $15.4\text{ m}^{-1}$ , or  $238\text{ m}^{-2}$ ). Subsurface Fe–Mn-rimmed grey-green pedotubules in two Barry palaeosols showed intermediate density ( $10.4 \pm 0.3\text{ m}^{-1}$ , or  $109 \pm 7\text{ m}^{-2}$ ). These densities are comparable with those of superficially similar features in Cenozoic palaeosols of woody vegetation (Retallack 1983, 1991).

### Fossil plants and their interpretation

#### Plant systematics

Maceration of grey shales of the Bloomsburg Formation has yielded 12 species of tracheophytic early land plant spores and 10 species





**Fig. 8.** Petrographic thin sections of Silurian palaeosols of Pennsylvania viewed under crossed Nicols: (a) soil microfabric (climbimasepic plasmic fabric); (b) root-like pedotubule with lateral branches (drab-haloed orthoisotubule); (c) burrow-like core to root-like pedotubule (drab-haloed metagranotubule); (d) recrystallized caliche nodule with submarginal weathering rind (calciasepic nodule with neomangan); (e) organic fibres and burrow (diffuse organic pedotubule with metagranotubule); (f) calcite-filled tubules (calcitic paraganotubule); (g) tubular fibrous zone with oversized grains (diffuse metagranotubule). Sources of thin sections are: (a, c), A horizon Brenda clay palaeosol (R3347); (b) A horizon Barry silty clay palaeosol (R2269); (d) Bk horizon of Lehigh Gap silty clay palaeosol (R157); (e) C horizon Brenda palaeosol (R2251); (f) above type Milton palaeosol (R2279); (g) Bg horizon type Barry palaeosol (R2275).

of cryptospores, perhaps bryophytes or cryptophytes (Strother & Traverse 1979; Beck & Strother 2008; Edwards *et al.* 2014). The most abundant plant-like remains in the Bloomsburg Formation (Fig. 8a–e) are nematophytes (*Prototaxites* and ‘*Nematothallus*’: of Strother 1988, 1993; Tomescu *et al.* 2009), which have histology unlike either vascular land plants, such as rhyniophytes, or non-vascular plants, such as liverworts (Strother 1988, 1993). These remains are so common as to overlap and form coaly beds in some parts of the Bloomsburg Formation (Strother 1988).

Over the years nematophytes have been identified as conifers, algae and ‘paraphytes’ (Strother 1988), but recent studies suggest affinities with lichenized fungi (Edwards & Axe 2012; Edwards *et al.* 2013). The best known nematophyte, *Prototaxites loganii*, may have been a lichenized glomeromycotan with chlorophyte symbionts (Retallack & Landing 2014). Ascolichens and basidiolichens are also known from the Early Devonian (Honegger *et al.* 2013a,b). Several distinct growth forms of Early Devonian nematophytes are now recognized (Fig. 11). *Prototaxites loganii* had stout wrinkled branches, but *Mosellophyton hefteri* had a crown of slender copiously branched axes (Schweitzer 1983). Tree-sized *Mosellophyton* have been found in fluvial facies (Schweitzer 1983), but stunted or younger examples have been described from low-diversity assemblages on intertidal flats (Schaarschmidt 1974). Comparable remains with characteristic fungal histology and flattened leaf-like branches have been referred to *Germanophyton psymphyloides* (Kräusel & Weyland 1930; Høeg 1942). Some of the laminar fossils in the Bloomsburg Formation have deltoid shape and lineation like *Germanophyton* (Fig. 9a), whereas others are less distinct, like ‘*Nematothallus*’ (Fig. 9b). Also found are axes like *Prototaxites* and *Mosellophyton* of various sizes (Fig. 9c and d), and the largest of these are rounded like abraded driftwood (Fig. 9e). Diffuse filaments of rootlike structures in the Bloomsburg Formation (Figs 8g and 10b, c) and elsewhere (Hillier *et al.* 2008) can be

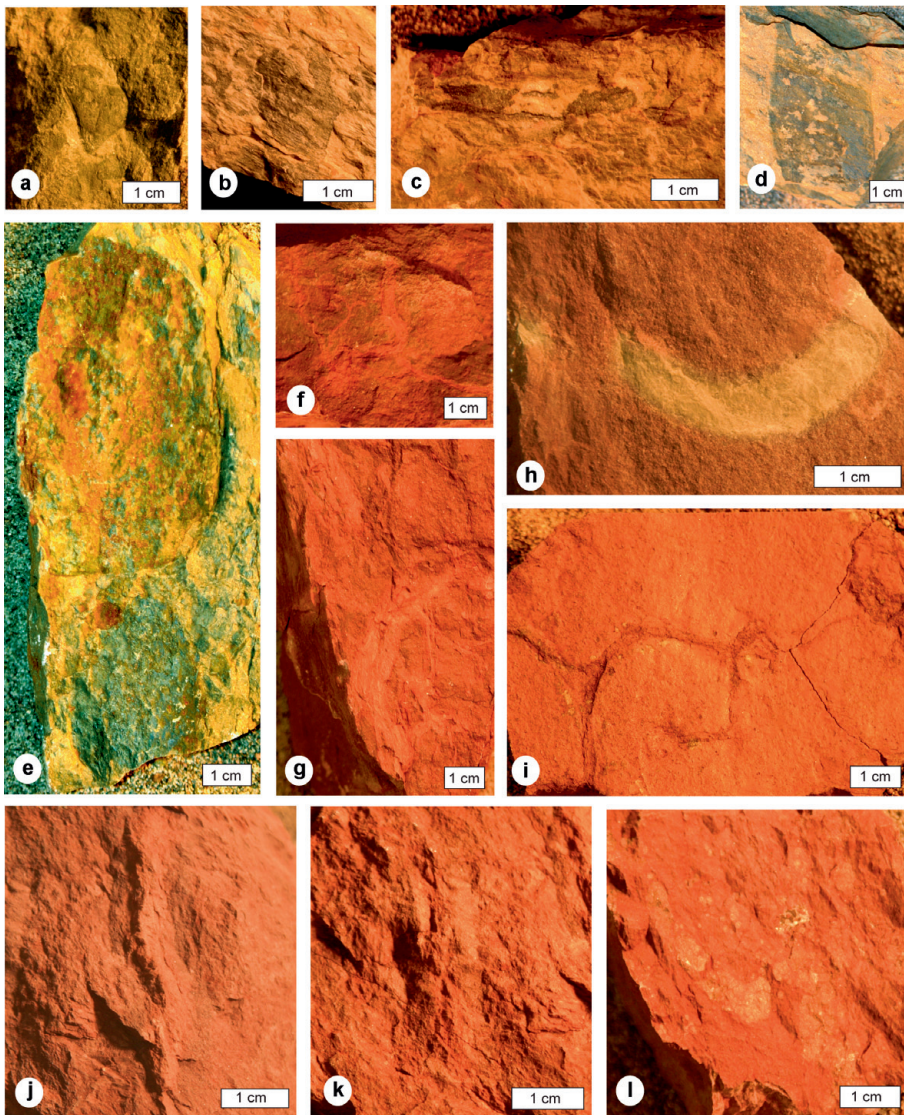
interpreted as lichen or fungal hyphae, which radiated down from the base of nematophyte trunks. These large features do not represent large woody plants, which did not evolve until later in the Early Devonian (late Emsian: Schweitzer 1999; Retallack & Huang 2011). Such deeply reaching systems of filaments are unlikely to have been unicellular rhizoids of herbaceous tracheophytes such as zosterophylls and rhyniophytes (Gensel *et al.* 2001; Boyce 2005). In other locations, filaments at the base of exceptionally preserved nematophyte trunks are organized into substantial tubular structures (Arbey & Koeniguer 1979; Argast 1992), like rhizines of desert lichens (Vogel 1955) and alpine lichens (Poelt & Baumgärtner 1964).

Other fossils in the Bloomsburg Formation have the striated texture of plant fibre arranged in central steles like those of early vascular land plant impressions (Garratt 1978; Gensel *et al.* 2001). Two distinct branching patterns were found in these impressions of herbaceous tracheophytes (Driese *et al.* 1992; Retallack 1992). Lateral branching axes (Fig. 9f and g) like rhizomes of zosterophylls (Lang 1937; Gensel *et al.* 2001) were found in Barry, Debbie, Lehigh Gap and Palmerton pedotypes, whereas dichotomous-branching impressions (Fig. 9i) like rhizomes of zosterophylls and rhyniophytes (Schweitzer 1983) were found in North Milton, Muddy and, rarely, Brenda pedotypes. Most pedotubules in Brenda palaeosols are diffuse filamentous systems of nematophytes, and these also dominate Alice, Lisette and Turbot pedotypes. These observations are evidence of local variation of vegetation in different pedotypes.

#### *Plant sizes and spacing*

Diameter of fossil plants can be measured from their compressed width, because, according to Walton’s compaction law, buried fossil plants cannot spread laterally under lithostatic compaction (Retallack 2007). Interpretations of plant heights presented here





**Fig. 9.** Silurian megafossil plants and trace fossils of Pennsylvania: (a, b) nematophyte thalli *Nematothallus lobata* Strother (1988); (a–e) nematophyte axes *Prototaxites* sp.; (f, g) tracheophyte rhizomes, probably zosterophyll; (h) drab tubular mottle with Fe–Mn halo (cats-eye mottle); (i) tracheophyte rhizomes, probably rhyniophyte; (j, k) burrows of *Scoyenia beerboweri* Retallack (2001); (l), tubular aggregations of small caliche nodules, in burrow. Specimen numbers in Condon Collection, University of Oregon are P16305A (a), P16305C (b), P16302B (c), P63104 (d), P16301 (e), P16316 (f), P16315 (g), P16308B (h), P12809F (i), P16314 (j, k), P16311 (l). Stratigraphic levels in Figure 4 are 51 m (a–e), 143 m (f, g), 65 m (h), 141 m (j, k) and 124 m (l), and in Figure 2f stratigraphic level is 103 m (i).

are based on allometric relationships with diameter at breast height ( $B$  in m) and tree height ( $H$  in m) of 670 species of living plants (Niklas 1994), as follows (SE  $\pm 0.9$  m):

$$H = 21.9B^{0.896} \quad (8)$$

This curve fit to 670 species of tracheophytic plants also applies to extinct nematophytes, as shown by a complete nematophyte tree excavated north of Monroe in New York (Retallack & Landing 2014), measured at 8.83 m long, with six circular branches up to 18 cm diameter in the upper 1.2 m (Fig. 11). At 36 cm diameter its height predicted by equation (8) is  $8.77 \pm 0.9$  m. Similarly, an extinct cladoxyl tree excavated almost entirely by Stein *et al.* (2007) near Manorkill, New York, measured 8 m tall to the base of the crown of branches and had a diameter at breast height (1.5 m) of 45 cm. Equation (8) predicts that the Manorkill tree with canopy was  $10.71 \pm 0.9$  m tall. In both these cases the height diagnostic diameter at breast height (1.5 m) is the same fraction of length (0.16) along the trunk, and this fraction can be used to estimate height from diameter of smaller nematophyte trunks (Retallack & Landing 2014).

Spacing and height of nematophyte vegetation can be estimated from measurements of mottle diameters in the surface of three Brenda palaeosols and one Lisette palaeosol. The Brenda palaeosol at 18.5 m (Fig. 4) had mottles  $37 \pm 22$  mm diameter. This can be converted to a basal trunk diameter ( $21 \pm 7$  mm) using the known

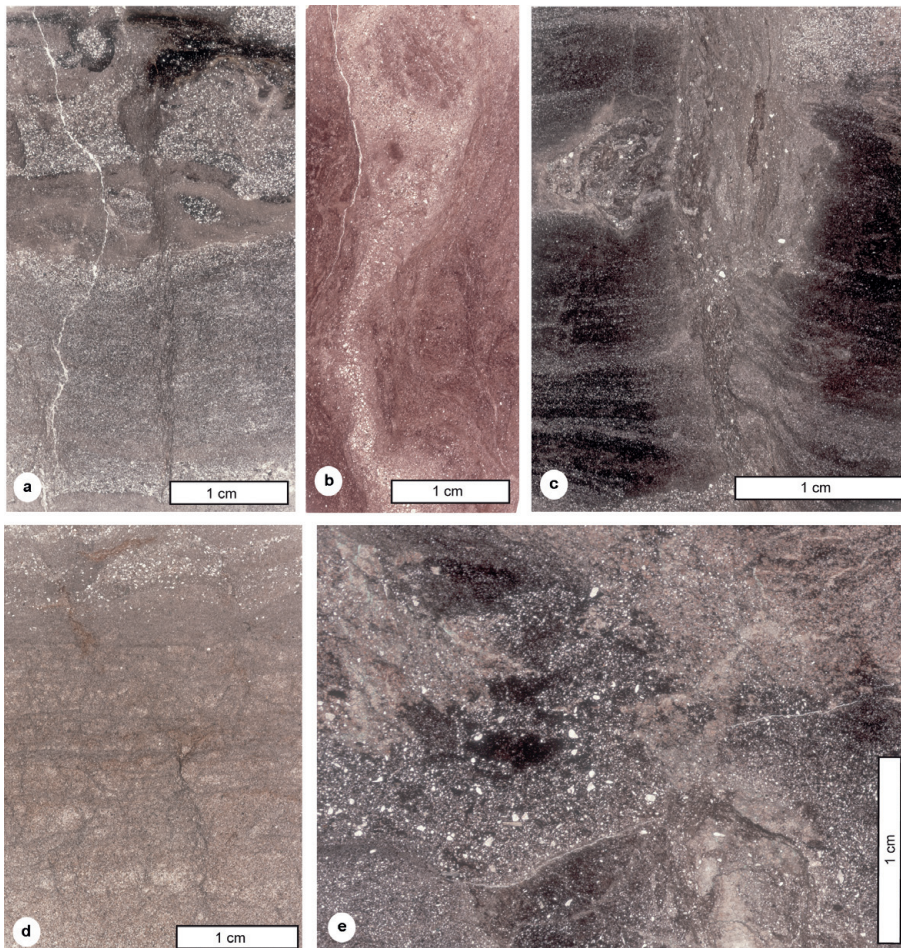
relationship between mottle and root diameter ( $2(D/\pi)^{-2}$ ; Retallack 2008) and to diameter at characteristic height ( $7 \pm 2$  mm) from 0.75 taper factor in the reconstruction of Schaarschmidt (1974). Application of equation (8) gives trunks  $52 \pm 16$  cm tall, spaced at  $17 \pm 6$  cm for a density of  $61 \pm 74 \text{ m}^{-2}$ , with the large variance reflecting clumping. Measurements of two other Brenda palaeosols (10.5 and 8.2 m in Fig. 4) give trunks  $58 \pm 13$  cm tall, spaced at  $31 \pm 11$  cm for a density of  $15 \pm 10 \text{ m}^{-2}$ , and  $61 \pm 10$  cm tall, spaced at  $30 \pm 8$  cm for a density of  $13 \pm 6 \text{ m}^{-2}$ , respectively. Comparable measurements from the Lisette palaeosol (29.8 m in Fig. 4) give trunks  $51 \pm 10$  cm tall, spaced at  $20 \pm 8$  cm for a density of  $51 \pm 70 \text{ m}^{-2}$ . Both Lisette and Brenda pedotypes had high ferrous iron at shallow depths (60 and 110 cm respectively in Fig. 5), and so are interpreted as well-drained soils with a shallow water table, a good combination for luxuriant growth. The known morphology of nematophytes (Fig. 11) and these spacings are indications of wetland marshes with nearly continuous cover. Silurian nematophytes of the Bloomsburg Formation were not scattered poles amid shrubbery as envisaged for Devonian nematophytes (Hueber 2001).

### Silurian ecological tiering and density

Data from Late Silurian to earliest Devonian palaeosols of the Bloomsburg Formation can be used to reconstruct ecological tiering and density of vegetation and animals both below and above ground.



## Silurian vegetation



**Fig. 10.** Petrographic thin sections of bioturbation in Silurian palaeosols of Pennsylvania viewed in plane-polarized light: (a) ferruginized vesicular structures and desiccation crack; (b) burrow within fibrous subterranean organ; (c) bedding disruption by fibrous subterranean organ; (d) organic tubular structures disrupting varved bedding; (e) calcite-filled tubular feature (lower right) central to extensively disrupted bedding. Specimen numbers and sources: (a) A horizon Brenda clay palaeosol (R2247); (b) A horizon Brenda clay palaeosol (R2246); (c) Bg horizon type Barry silty clay loam palaeosol (R2275); (d) C horizon Brenda clay palaeosol (R253); (e) above A horizon type Brenda palaeosol (R2245).

### Deep soil tier (2 m)

Depth of bioturbation is clearest in the type Brenda clay palaeosol (Fig. 5), which caps non-pedogenic strata, rather than other palaeosols. Grey–green pedotubules extend for depths of up to 1.3 m in this profile (Fig. 10b), but fine filamentous extensions of these pedotubules extend to depths of 2 m (Fig. 10d). These filamentous structures were not originally shallow and buried by alluvial aggradation, because filaments down to 1.3 m are grey–green in red siltstone. The formation of drab haloes around root traces in well-drained soils has been demonstrated in several studies to represent burial gleization of remnant organic matter (Retallack 1983, 2008; Arafiev & Naugolnykh 1998). Traces of roots that had died within the well-drained soil are decomposed aerobically and then oxidized to goethite, altered during burial to hematite (Retallack 1997b). Red root traces in palaeosols were thus dead upon burial, but drab-haloed traces represent the last crop of undecayed organic remains before burial.

Structures interpreted as filamentous bioturbation are deepest in the Brenda pedotype, which is non-calcareous and unusually thick. In other pedotypes, similar filamentous bioturbation falls short of the horizon of calcareous nodules, in those pedotypes that have them (Barry, Alice, Palmerton, Lehigh Gap). Depth to Bk is related to soil productivity (Breecker & Retallack 2014) and mean annual precipitation (Retallack 2005), so that the deep tier of bioturbation may have followed local temporal variation in climate, including prominent humid spikes (Fig. 2b). Filamentous bioturbation is also shallower in pedotypes with relict bedding high in the profile (Lisette, Debbie, Muddy, Turbot), which may be evidence of time for soil formation inadequate for full development of the deepest tier (Retallack 1997b).

Only diffuse filamentous bioturbation attributed here to nematophytes was seen in the deep layers of the palaeosols, thus supporting the view of Hueber (2001) of ‘adequate sources of

nutriment for growth of an extensive mycelium’ associated with *Prototaxites*. They are not organized deep in the palaeosols into solid rhizines, but diffusely arrayed throughout the matrix. This organization is compatible with a fungal function as a nutrient and water-gathering system, rather than a mechanical stabilizer of the organism above ground. The loose aggregations of filaments that form large drab mottles higher in palaeosol profiles may have had an anchoring function, as in some modern lichens (Vogel 1955; Poelt & Baumgärtner 1964).

### Intermediate soil tier (0.8 m)

Burrows of *Scoyenia beerboweri* form a tier of intermediate depth in many of the palaeosols, to a depth of 80 cm in the Lehigh Gap pedotype, but only 50 cm in the Alice pedotype, and 40 cm in the Palmerton, Barry and Debbie pedotypes. Animals excavating these burrows were thus responding differently to different soil types, which in turn were forming on different geomorphological surfaces and at different times in the accumulation of the sequence. Bioturbation by threads comparable with fungal rhizines and mycelium is common within this tier as well.

Pedotypes interpreted here (Table 2) to have formed in warm, subhumid palaeoclimate (Lehigh Gap and Alice) had deeper burrows than pedotypes of semi-arid cool palaeoclimates (Palmerton and Barry). Burrows penetrated the Bk horizons of small (2–3 mm) nodules in Palmerton and Lehigh Gap pedotypes (Fig. 9l), but not large (3–4 cm) nodules of Barry and Alice pedotypes. This may have been because the large nodules were mechanical obstacles, but the nodules are not so closely spaced to exclude burrows entirely from this horizon. Barry and Alice palaeosols also have Fe–Mn-rimmed drab tubules (Fig. 9h) scattered among the calcareous nodules, and these indicate seasonal waterlogging, which



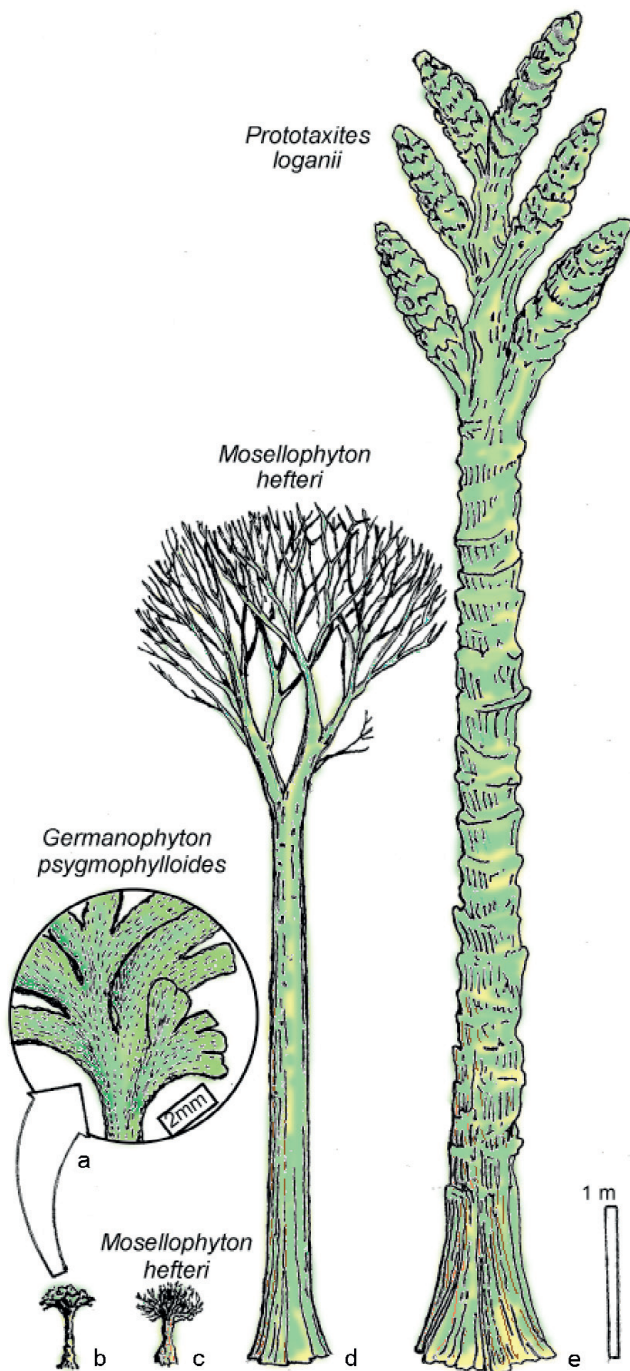


Fig. 11. Reconstructed Siluro-Devonian nematophyte species based on complete remains from Germany (a, b, Kräusel & Weyland 1930; c, Schaarschmidt 1974; d, Schweitzer 1983) and New York (e, Retallack & Landing 2014).

would have excluded air-breathing organisms, as in other comparable palaeosols (Ogi pedotype of Retallack 1983). Debbie palaeosols have relict bedding, and so represent young geomorphological surfaces, perhaps on lower surfaces or nearer streams than other pedotypes with deeper burrows.

#### Shallow soil tier (0.2 m)

The shallowest bioturbation seen in palaeosols of the Bloomsburg Formation consists of unusually wide grey tubules (Figs 6a, d and 10a–c), subhorizontal tubular features with the characteristic striated fabric of plant fibre (Fig. 9f, g and i), and flask-shaped (Fig. 10a) and simple burrows (Fig. 8c). These have been attributed

above to early vascular land plants such as zosterophylls and rhyniophytes, and to spiders, millipedes or worms. Unlike deeper soil tiers, this shallow bioturbation is uniformly within the top 20 cm of the palaeosols, and is relatively independent of soil type.

Land plant rhizomes are the only root-like structures seen in some palaeosol surface tiers (Lehigh Gap, Palmerton, Barry, Debbie, Muddy, North Milton), large nematophyte tubules occur in others (Alice, Lisette, Turbot), and some palaeosols have both, though with only rare vascular land plants (Brenda pedotype). Considering the palaeoenvironmental interpretations offered above and the observed density of these remains, vascular land plants appear to have colonized difficult soils, with saline marine-influenced groundwater (North Milton, Muddy) or in semi-arid inland regions (Lehigh Gap, Palmerton, Barry pedotypes). Nematophytes, in contrast, formed lush stands in humid to subhumid freshwater lowlands and times (represented by Alice and Brenda pedotypes) and on young geomorphological surfaces early in ecological succession (Lisette and Debbie pedotypes).

#### Ground cover tier (0.02 m)

A variety of sheet-like, lobate nematophyte fragments have been described from the Bloomsburg Formation by Strother (1988, 1993) and are illustrated here (Fig. 9a and b). It is uncertain whether these were complete thallose plants forming a ground cover, or were squamules shed from nematophytes. The latter is likely considering their torn appearance and lack of rooting structures or rhizoids. The gametophyte generation of some early tracheophytes may have been a ground-hugging thallus (Schweitzer 1983; Gerienne *et al.* 2006; Boyce 2008), which formed seasonal mats. Finally, the palaeosols include surficial vesicular cavities (Fig. 10a, top left) and threads (Fig. 10a, lower half disrupting lamination), comparable with button lichens and cyanobacterial bundles of biological soil crusts (Belnap *et al.* 2003). The ground cover of Silurian palaeosols is thus envisaged as a litter or mat of laminar, nodular and filamentous forms rising no more than about 2 cm above the soil surface (Tomescu & Rothwell 2006; Tomescu *et al.* 2009).

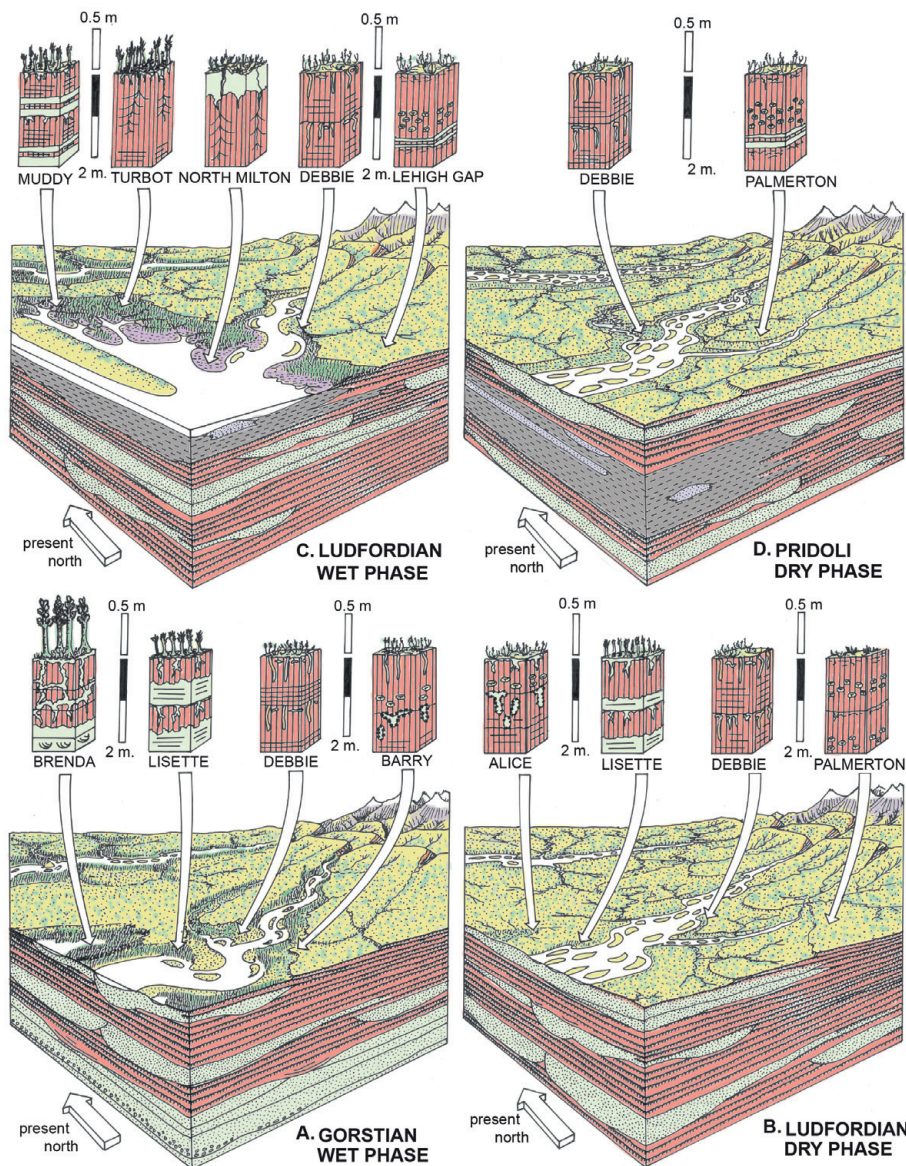
#### Intermediate plant tier (0.3 m)

Rooting structures with either dichotomous or Y-branching (Fig. 9i), or orthogonal lateral or H-branching (Fig. 9g) have been known for some time from the Bloomsburg Formation (Driese *et al.* 1992; Retallack 1992; Driese & Mora 2001). These impressions commonly have within them a compaction-resistant and differently textured core, interpreted as remains of a stele of a zosterophyll land plant (tracheophyte). Comparable branching and histology is widely known from Late Silurian and Early Devonian zosterophylls, rhyniophytes and trimerophytes (Gensel *et al.* 2001; Hotton *et al.* 2001), which grew in clonal clumps from rhizomes that turned upwards into aerial stems with lateral sporangia. With axes up to 8 mm in diameter (Fig. 9f, g and i), the allometric equation (8) (of Niklas 1994) predicts a height of up to 30 cm. Such rhizomes and axes are abundant in the surfaces of the palaeosols, and formed a herbaceous plant formation of well-drained, semi-arid to subhumid soils, which has been called a brakeland (by Retallack 1992), by analogy with fern brakes.

#### Canopy plant tier (1.3 m)

The largest plant axes found in the Bloomsburg Formation have been referred to *Prototaxites* sp. (Strother 1988). With axes 3–4 cm in diameter, the allometric equation (8) (of Niklas 1994) predicts heights up to 1.3 m. This is an isolated and waterworn portion of a trunk (Fig. 9d and e) transported from vegetation not represented by palaeosols. As outlined above, drab haloes in Brenda and

## Silurian vegetation



**Fig. 12.** Reconstructed Silurian soils and their palaeoenvironment in Pennsylvania, through climate cycles from semiarid to subhumid inferred from depth to calcic horizon.

Lisette palaeosols represent seasonally wet marshes of continuous cover some 50 cm high. Tree-sized nematophytes, cladoxyls and progymnosperms did not appear until Devonian times, again in communities of continuous ground cover and canopy height (Fig. 11; Schweitzer 1983; Retallack & Huang 2011; Retallack & Landing 2014).

### Conclusion

A poorly understood element of Silurian and Devonian vegetation has been the enigmatic nematophytes, now considered extinct lichenized Glomeromycota that reached the size of trees (Fig. 11; Edwards & Axe 2012; Edwards *et al.* 2013; Retallack & Landing 2014). This study assembles evidence from palaeosols and their rooting structures for the nature of nematophyte and zosterophyll vegetation through climatic cycles of the Late Silurian. Nematophytes of the Bloomsburg Formation in Pennsylvania may have reached 1.3 m tall, but were mostly 50 cm tall in marsh-like vegetation of seasonally waterlogged lowland soils (Fig. 12). Nematophytes were not isolated poles or rolls envisaged for some Devonian species (Hueber 2001; Graham *et al.* 2010). Early vascular land plants such as rhyniophytes and zosterophylls were smaller, topping out at 30 cm or so tall, and have been reconstructed as clonal patches of lowland marsh vegetation (Gensel *et al.* 2001; Hotton *et al.* 2001; Gerrienne *et al.* 2006). This was

not seen in Bloomsburg Formation red beds, where remains of rhizomes like those of rhyniophytes and zosterophylls form patchy vegetation of well-drained calcareous soils (Fig. 12). Nematophytes were the largest terrestrial organisms during the Late Silurian increase in size and abundance of vascular plant plants (Driese *et al.* 2000; Driese & Mora 2001; Edwards *et al.* 2014). Such fungi were abundant and pervasive both above and below ground (Hueber 2001), and provide additional evidence for the idea of Pirozynski & Malloch (1975) that early vascular land plant evolution was facilitated by fungi (Retallack & Landing 2014).

### Acknowledgements and Funding

R. Beerbower first introduced me to the outcrops near Palmerton and has offered much useful discussion over many years. F. Hueber, S. Scheckler, C. Hotton, K. Boyce, R. Bambach, E. Landing and P. Strother have also been generous with ideas and data.

*Scientific editing by Quentin Crowley*

### References

- Arafiev, M.P. & Naugolnykh, S.V. 1998. Fossil roots from the upper Tatarian deposits in the basin of the Sukhona and Malaya Severnaya Dvina Rivers: Stratigraphy, taxonomy and orientation paleoecology. *Paleontological Journal*, **32**, 82–96.
- Arbey, F. & Koeniguer, J.-C. 1979. Les Nématophytes et les algues de l'Ordovicien et du Dévonien Saharien. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine*, **3**, 409–418.



- Argast, S. 1992. Enigmatic tubes in Ordovician limestones of the Mohawk Valley, New York. *Palaaios*, **7**, 532–539.
- Beck, J.H. & Strother, P.K. 2008. Miospores and cryptospores from the Silurian section at Allenport, Pennsylvania, USA. *Journal of Paleontology*, **82**, 857–883.
- Beerbower, J.R. & Hait, M.H. 1959. Silurian fish in northeastern Pennsylvania and northern New Jersey. *Pennsylvania Academy of Sciences Proceedings*, **33**, 198–203.
- Belnap, J., Büdel, B. & Lange, O.L. 2003. Biological soil crusts: Characteristics and distribution. In: Belnap, J. & Lange, O.L. (eds) *Biological Soil Crusts: Structure, Function and Management*. Springer, Berlin, 177–191.
- Bond, J.E. & Opell, B.D. 2002. Phylogeny and taxonomy of south-western North America Eucenizinae trapdoor spiders and their relatives (Araneae: Mygalomorphae, Cyrtochaeniidae). *Zoological Journal of the Linnean Society*, **196**, 487–534.
- Boyce, C.K. 2005. The evolutionary history of roots and leaves. In: Holbrook, N.M. & Zwieniecki, M.A. (eds) *Vascular Transport in Plants*. Elsevier, Amsterdam, 479–499.
- Boyce, C.K. 2008. How green was *Cooksonia*? The importance of size in understanding the early evolution of physiology in the vascular plant lineage. *Paleobiology*, **14**, 179–194.
- Bradfield, W.B. & Gray, M.B. 1999. Temperatures of Alleghanian deformation in the Silurian Bloomsburg Formation, Lehigh Gap, Pennsylvania. *Geological Society of America, Programs and Abstracts*, **31**, 5.
- Brasier, A.T., Morris, J.L. & Hillier, R.D. 2014. Carbon isotopic evidence for organic matter oxidation in soils of the Old Red Sandstone (Silurian to Devonian, South Wales, UK). *Journal of the Geological Society, London*, **121**, 621–634.
- Breecker, D.O. & Retallack, G.J. 2014. Refining the pedogenic carbonate atmospheric CO<sub>2</sub> proxy and application to Miocene CO<sub>2</sub>. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **406**, 1–8.
- Brimhall, G.H., Chadwick, O.A. *et al.* 1992. Deformational mass transport and invasive processes in soil evolution. *Science*, **255**, 695–702.
- Budd, G.E., Hogstrom, A.E.S. & Gogin, I. 2001. A myriapod-like arthropod from the Upper Cambrian of East Siberia. *Paläontologische Zeitschrift*, **75**, 37–41.
- Cotter, E. 1978. The evolution of fluvial style, with special reference to the central Appalachian Paleozoic. In: Miall, A.D. (ed.) *Fluvial Sedimentology*. Canadian Society of Petroleum Geologists Memoir, **5**, 361–383.
- Davies, N.S. & Gibling, M.R. 2010. Cambrian to Devonian evolution of alluvial systems: The sedimentological impact of the earliest land plants. *Earth-Science Reviews*, **98**, 171–200.
- Davies, N.S., Rygel, M.C. & Gibling, M.B. 2010. Marine influence in the Upper Ordovician Juniata Formation (Potters Mills, Pennsylvania): Implications for the history of life on land. *Palaaios*, **25**, 527–539.
- Davies, N.S., Gibling, M.R. & Rygel, M.C. 2011. Alluvial facies evolution during the Palaeozoic greening of the continents; case studies, conceptual models and modern analogues. *Sedimentology*, **58**, 220–258.
- Driese, S.G. & Mora, C.I. 2001. Diversification of Siluro-Devonian plant traces in palaeosols and influence on estimates of paleoatmospheric CO<sub>2</sub> levels. In: Gensel, P.G. & Edwards, D. (eds) *Plants Invade the Land: Evolutionary and Environmental Perspectives*. Columbia University Press, New York, 237–253.
- Driese, S.G., Mora, C.I., Cotter, E. & Foreman, J.L. 1992. Paleopedology and stable isotope chemistry of Late Silurian vertic palaeosols, Bloomsburg Formation, central Pennsylvania. *Journal of Sedimentary Petrology*, **62**, 825–841.
- Driese, S.G., Mora, C.I. & Elick, J.M. 2000. The palaeosol record of increasing plant diversity and depth of rooting and changes in atmospheric pCO<sub>2</sub> in the Siluro-Devonian. In: Gastaldo, R.A. & DiMichele, W.A. (eds) *Phanerozoic Terrestrial Ecosystems*. Paleontological Society Papers, **6**, 47–61.
- Edwards, D. & Axe, L. 2012. Evidence for a fungal affinity for *Nematasketum*, a close ally of *Prototaxites*. *Botanical Journal of the Linnean Society*, **168**, 1–18.
- Edwards, D., Axe, L. & Honegger, R. 2013. Contributions to the diversity in cryptogamic covers in the mid-Palaeozoic: *Nematothallus* revisited. *Botanical Journal of the Linnean Society*, **173**, 505–534.
- Edwards, D., Morris, J.L., Richardson, J.B. & Kenrick, P. 2014. Cryptospores and cryptophytes reveal hidden diversity in early land floras. *New Phytologist*, **202**, 50–78.
- Epstein, J.B. & Epstein, A.G. 1972. *The Shawagunk Formation (Upper Ordovician (?) to Middle Silurian) in Eastern Pennsylvania*. US Geological Survey Professional Papers, **744**.
- Epstein, J.B., Sevon, W.D. & Glaeser, J.D. 1974. *Geology and mineral resources of the Leighton and Palmerton Quadrangles, Carbon and Northampton Counties, Pennsylvania*. Geological Survey of Pennsylvania Atlas, **195**.
- Epstein, A.G., Epstein, J.B. & Harris, C.D. 1977. *Conodont Color Alteration—An Index to Organic Metamorphism*. US Geological Survey, Professional Papers, **995**.
- Food and Agriculture Organization. 1974. *Soil Map of the World. Volume I, Legend*. UNESCO, Paris.
- Garratt, M.J. 1978. New evidence for a Silurian (Ludlow) age for the earliest *Baragwanathia* flora. *Alcheringa*, **2**, 217–225.
- Genise, J.F., Belloso, E.S. & Gonzalez, M.G. 2004. An approach to the description and interpretation of ichnofabrics in palaeosols. In: McIlroy, D. (ed.) *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*. Geological Society, London, Special Publications, **228**, 355–382.
- Gensel, P.G., Kotyk, M.E. & Basinger, J.F. 2001. Morphology of above- and below-ground structures in Early Devonian (Pragian–Emsian) plants. In: Gensel, P.G. & Edwards, D. (eds) *Plants Invade the Land: Evolutionary and Environmental Perspectives*. Columbia University Press, New York, 83–102.
- Gerrienne, P., Dilcher, D.L., Bergamaschi, S., Milagres, I., Pereira, E. & Rodrigues, M.A.C. 2006. An exceptional specimen of the early land plant *Cooksonia paransensis*, and a hypothesis on the life cycle of the earliest eutracheophytes. *Review of Palaeobotany and Palynology*, **142**, 123–130.
- Gill, D. 1977. Salina A-1 sabkha cycles and the Late Silurian paleogeography of the Michigan Basin. *Journal of Sedimentary Research*, **47**, 979–1017.
- Graham, L.E., Cook, M.E., Hanson, D.T., Pigg, K.B. & Graham, J.M. 2010. Structural, physiological isotopic evidence that the enigmatic Paleozoic fossil *Prototaxites* formed from rolled liverwort mats. *American Journal of Botany*, **97**, 268–275.
- Gray, M.B. & Nickelsen, R.P. 1989. Pedogenic slickensides, indicators of strain and deformation processes in redbed sequences of the Appalachian foreland. *Geology*, **17**, 72–75.
- Hembree, D.L. 2009. Neochronology of burrowing millipedes: Linking modern burrow morphology, organism behavior and sediment properties to interpret continental ichnofossils. *Palaaios*, **24**, 425–429.
- Hillier, R.D., Edwards, D. & Morrissey, L.B. 2008. Sedimentological evidence for rooting structures in the Early Devonian Anglo-Welsh Basin (UK), with speculation on their producers. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **270**, 366–380.
- Hoeg, O.A. 1942. The Downtonian and Devonian flora of Spitsbergen. *Norges Svalbard Ishavs og Undersøkelser Skrifter*, **83**, 1–228.
- Honegger, R., Axe, L. & Edwards, D. 2013a. Bacterial epibionts and endolithic actinobacteria and fungi in the Lower Devonian lichen *Chlorolichenomyces salopensis*. *Fungal Biology*, **117**, 512–518.
- Honegger, R., Edwards, D. & Axe, L. 2013b. The earliest records of internally stratified cyanobacterial and algal lichens from the Lower Devonian of the Welsh Borderland. *New Phytologist*, **197**, 264–275.
- Hoskins, D.M. 1961. *Stratigraphy and Paleontology of the Bloomsburg Formation of Pennsylvania and Adjacent States*. Geological Survey of Pennsylvania Bulletin, **G36**, 1–125.
- Hotton, C.L., Hueber, F.M., Griffing, D.H. & Bridge, J.S. 2001. Early terrestrial plant environments: An example from the Emsian of Gaspé, Canada. In: Gensel, P.G. & Edwards, D. (eds) *Plants Invade the Land: Evolutionary and Environmental Perspectives*. Columbia University Press, New York, 179–212.
- Hou, X. & Bergström, J. 1998. Three additional arthropods from the early Cambrian Chengjiang fauna, Yunnan, southwest China. *Acta Palaeontologica Sinica*, **37**, 395–401.
- Hueber, F.M. 2001. Rotted wood–alga–fungus: The history and life of *Prototaxites* Dawson 1859. *Review of Palaeobotany and Palynology*, **116**, 123–158.
- Hunter, R.E. 1977. Basic types of stratification in small eolian dunes. *Sedimentology*, **24**, 361–387.
- Isbell, R.F. 1998. *The Australian Soil Classification*. CSIRO, Collingwood, VIC.
- Johnson, E.W., Briggs, D.E.G., Suthren, R.J., Wright, J.L. & Tunnikoff, S.P. 1994. Non-marine arthropod traces from the subaerial Ordovician Borrowdale Volcanic Group, English Lake District. *Geological Magazine*, **131**, 395–406.
- Kräusel, R.M. & Weyland, H. 1930. *Die flora des deutschen Unterdevons*. Abhandlungen der Preussische Geologisches Landesanstalt, **NF131**, 1–92.
- Lang, W.H. 1937. On the plant-remains from the Downtonian of England and Wales. *Royal Society of London Philosophical Transactions*, **227**, 245–291.
- Laughrey, C.D. 1999. Silurian and transition to Devonian. In: Shultz, C.H. (ed.) *The Geology of Pennsylvania*. Geological Survey of Pennsylvania, Harrisburg, 90–107.
- Mack, G.H., James, W.C. & Monger, H.C. 1993. Classification of palaeosols. *Geological Society of America Bulletin*, **105**, 129–136.
- Miller, D.L., Mora, C.I. & Driese, S.G. 2007. Isotopically concentric growth in large carbonate nodules in Vertisols: Implications for climate and ecosystem assessments. *Geoderma*, **142**, 104–111.
- Misof, B., Liu, S. *et al.* 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science*, **346**, 763–767.
- Mora, C.I. & Driese, S.G. 1999. Palaeoenvironment, palaeoclimate and stable carbon isotopes of Palaeozoic red-bed palaeosols, Appalachian Basin, USA and Canada. In: Thiry, M. & Simon-Coignon, R. (eds) *Palaeoweathering, Palaeosurfaces and Related Continental Deposits*. International Association for Sedimentary Geology, Special Publication, **27**, 61–84.
- Niklas, K.J. 1994. *Plant Allometry*. University of Chicago Press, Chicago.
- Nordt, L., Orosz, M., Driese, S. & Tubbs, J. 2006. Vertisol carbonate properties in relation to mean annual precipitation: Implications for paleoprecipitation estimates. *Journal of Geology*, **114**, 501–510.
- Pirozynski, K.A. & Malloch, D.W. 1975. The origin of land plants: A matter of mycotrophism. *Biosystems*, **6**, 153–164.
- Poelt, J. & Baumgärtner, H. 1964. Über Rhizinenstränge bei placodialen Flechten. *Österreich Botanische Zeitschrift*, **111**, 1–18.
- Retallack, G.J. 1983. *Late Eocene and Oligocene Palaeosols from Badlands National Park, South Dakota*. Geological Society of America, Special Papers, **193**.



## Silurian vegetation

- Retallack, G.J. 1985. Fossil soils as grounds for interpreting the advent of large plants and animals on land. *Philosophical Transactions of the Royal Society of London, Series B*, **309**, 105–142.
- Retallack, G.J. 1991. *Miocene Palaeosols and Ape Habitats from Pakistan and Kenya*. Oxford University Press, New York.
- Retallack, G.J. 1992. What to call early plant formations on land. *Palaios*, **7**, 508–520.
- Retallack, G.J. 1997a. Early forest soils and their role in Devonian global change. *Science*, **276**, 583–585.
- Retallack, G.J. 1997b. *A Colour Guide to Palaeosols*. Wiley, Chichester.
- Retallack, G.J. 2001. *Scoyenia* burrows from Ordovician palaeosols of the Juniata Formation in Pennsylvania. *Palaeontology*, **44**, 209–235.
- Retallack, G.J. 2005. Pedogenic carbonate proxies for amount and seasonality of precipitation in palaeosols. *Geology*, **33**, 333–336.
- Retallack, G.J. 2007. Growth, decay and burial compaction of *Dickinsonia*, an iconic Ediacaran fossil. *Alcheringa*, **31**, 215–240.
- Retallack, G.J. 2008. Cambrian palaeosols and landscapes of South Australia. *Australian Journal of Earth Sciences*, **55**, 1083–1106.
- Retallack, G.J. 2009. Early Paleozoic pedostratigraphy and global events in Australia. *Australian Journal of Earth Sciences*, **56**, 569–584.
- Retallack, G.J. & Huang, C.-M. 2011. Ecology and evolution of Devonian trees in New York, USA. *Palaeogeography, Paleoclimatology, Paleocology*, **299**, 110–128.
- Retallack, G.J. & Landing, E. 2014. Affinities and architecture of Devonian trunks of *Prototaxites loganii*. *Mycologia*, **106**, 1143–1158.
- Retallack, G.J., Davies, N.S., Rygel, M.C. & Gibling, M.R. 2011. Marine influence in the Upper Ordovician Juniata Formation (Potters Mills, Pennsylvania): Implications for the history of life on land: Comment and reply. *Palaios*, **26**, 765–769.
- Roberts, D.R., Scheinost, A.C. & Sparks, D.L. 2002. Zinc speciation in a smelter-contaminated soil profile using bulk and microspectroscopic techniques. *Environmental Science and Technology*, **36**, 1742–1750.
- Romell, L.G. 1935. An example of millipedes as mull formers. *Ecology*, **16**, 67–71.
- Rota-Stabelli, O., Daley, A.C. & Pisani, D. 2013. Molecular timetrees reveal a Cambrian colonization of land and a new scenario for ecysozoan evolution. *Current Biology*, **23**, 392–398.
- Schaarschmidt, F. 1974. *Mosellophyton hefteri*, n.g., n.sp., eine sukkulenter Halophyt aus den Unterdevon von Alken an der Mosel. *Paläontologische Zeitschrift*, **48**, 188–204.
- Schuchert, C. 1916. Silurian formations of southeastern New York, New Jersey and Pennsylvania. *Geological Society of America Bulletin*, **27**, 531–554.
- Schweitzer, H.-J. 1983. Die Unterdevonfloren des Rheinlandes. *Palaeontographica*, **B189**, 1–138.
- Schweitzer, H.-J. 1999. Die Devonfloren Spitzbergens. *Palaeontographica*, **B252**, 1–122.
- Scotese, C.R. 1997. *Point Tracker for Windows (computer program)*. Paleomap, Arlington, TX.
- Sheldon, N.D. & Retallack, G.J. 2001. Equation for compaction of palaeosols due to burial. *Geology*, **29**, 247–250.
- Sheldon, N.D., Retallack, G.J. & Tanaka, S. 2002. Geochemical climofunctions from North American soils and application to palaeosols across the Eocene–Oligocene boundary in Oregon. *Journal of Geology*, **110**, 687–696.
- Shelley, R.M. & Golovatch, S.I. 2011. Atlas of myriapod biogeography. I. Indigenous ordinal and supraordinal distributions in the Diplopoda: Perspectives on taxon origins and ages, and an hypothesis on the origin and early evolution of the class. *Insecta Mundi*, **158**, 1–134.
- Soil Survey Staff. 2010. *Keys to Soil Taxonomy*. Pocahontas Press, Blacksburg, VA.
- Stace, H.C.T., Hubble, G.D., Brewer, R., Northcote, K.H., Sleeman, J.R., Mulcahy, M.J. & Hallsworth, E.G. 1968. *A Handbook of Australian Soils*. Rellim, Adelaide, SA.
- Stein, W.E., Mannolini, F., Hernick, L.V., Landing, E. & Berry, C.M. 2007. Giant cladoxypsid trees resolve the enigma of the Earth's earliest forest stumps at Gilboa. *Nature*, **446**, 904–907.
- Strother, P.K. 1988. New species of *Nematothallus* from the Silurian Bloomsburg Formation of Pennsylvania. *Journal of Paleontology*, **62**, 967–981.
- Strother, P.K. 1993. Clarification of the genus *Nematothallus* Lang. *Journal of Paleontology*, **67**, 1090–1094.
- Strother, P.K. & Traverse, A. 1979. Plant microfossils from Llandoveryan and Wenlockian rocks of Pennsylvania. *Palynology*, **3**, 1–21.
- Swartz, C.K. & Swartz, F.M. 1931. Early Silurian formations of southeastern Pennsylvania. *Geological Society of America Bulletin*, **42**, 621–661.
- Tomescu, A.M.F. & Rothwell, G.W. 2006. Wetlands before tracheophytes; thaloid terrestrial communities of the Early Silurian Passage Creek biota (Virginia). In: Greb, S.F. & DiMichele, W.A. (eds) *Wetlands Through Time*. Geological Society of America, Special Papers, **399**, 41–56.
- Tomescu, A.M.F., Pratt, L.M., Rothwell, G.W., Strother, P.K. & Nadon, G.C. 2009. Carbon isotopes support the presence of extensive land floras pre-dating the origin of vascular plants. *Palaeogeography, Paleoclimatology, Paleocology*, **283**, 46–59.
- Toye, S.A. 1967. Observations on the biology of three species of Nigerian millipedes. *Journal of Zoology*, **152**, 67–78.
- van Straeten, C.A. 2007. Basinwide stratigraphic synthesis and sequence stratigraphy, upper Pragian, Emsian and Eifelian stages (Lower to Middle Devonian), Appalachian Basin. In: Becker, R.T. & Kirchgasser, W.T. (eds) *Devonian Events and Correlations*. Geological Society, London, Special Publications, **278**, 39–41.
- Vogel, S. 1955. Niedere 'Fensterpflanzen' in der südafrikanischen Wüste. *Beiträge Biologie Pflanzen*, **31**, 45–135.
- Ward, P., Labandeira, C., Laurin, M. & Berner, R.A. 2006. Confirmation of Romer's Gap as a low oxygen interval constraining the timing of initial arthropod and vertebrate terrestrialization. *Proceedings of the National Academy of Sciences of the USA*, **103**, 16818–16822.
- Wilson, H.M. 2006. Juliform millipedes from the lower Devonian of Euramerica; Implications for the timing of millipede cladogenesis in the Paleozoic. *Journal of Paleontology*, **80**, 638–649.