

Pennsylvanian ‘fossil forests’ in growth position (T⁰ assemblages): origin, taphonomic bias and palaeoecological insights

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Abstract: Fossil forests, buried in growth position in a geological instant (T⁰ assemblages) are far more abundant in Pennsylvanian successions than in any other part of the geological record. In this review paper, we evaluate the fundamental controls on the origin of these phenomena, investigate the taphonomic biases that influence their composition, and summarize their palaeoecological significance. Following earlier workers, we highlight that high rates of burial and accommodation are essential for the formation and preservation of T⁰ assemblages. Contexts especially favourable for their origin include ashfalls proximal to volcanic centres, coastal plains drowned by relative sea-level rise, and fluvial environments such as channel bars, crevasse splays, and distributary lobes. Long-term preservation requires high rates of subsidence. Consequently, the vast majority of Palaeozoic T⁰ assemblages are confined to wetland settings at, or close to, sea level, whereas drylands are poorly represented and uplands rarely sampled, if ever. However, this is not the only major bias in the fossil record; taphonomic processes selectively preserve plants dependent on their anatomy and stature, and on groundwater chemistry. Thus, although T⁰ assemblages offer unrivalled insights into the nature of ancient forests (whole-plant reconstructions, tree density, canopy height, productivity, plant hydraulics, cohort dynamics, spatial heterogeneity, ecological gradients, tree–sediment interactions, and animal–plant interactions, to name but a few), it is naive to believe they provide ‘photographic snapshots’ of palaeoecosystems. None the less, careful taphonomic analysis of T⁰ assemblages offers the potential for a nuanced understanding of these evocative phenomena, and much remains to be learned from these important palaeoecological resources.

Single fossil plants to entire forested landscapes (DiMichele *et al.* 2007) are commonly buried in place in the post-Silurian sedimentary record. For over two centuries, these phenomena have captured the imagination of natural scientists and the general public alike. They are the closest thing in the botanical world to the human landscapes buried at Pompeii and elsewhere (Deem 2005), which preserve a record of human ‘ecology’, and so fascinate us. The famous Carboniferous lycopsid tree stumps enshrined at Victoria Park in Glasgow, Scotland (Fig. 1; MacGregor & Walton 1948; Gastaldo 1986a), for example, have reminded us that there were trees living in the past with which we today have no familiarity and of which we have only limited understanding. Such remains are at the same time familiar and bizarre, the latter ever more so the deeper in time one looks.

Throughout this paper we will use the term ‘tree’ in a relatively colloquial sense, to include large-bodied, upright plants with a main trunk or trunks and most often a crown of some form. Most modern trees are woody, and most definitions of the term ‘tree’ include this as a diagnostic feature. However, trees of the Late Palaeozoic were not so uniformly woody, although many were giants, many metres in height, supported by specialized bark (Boyce *et al.* 2010), mantles of supporting roots (Ehret & Phillips 1977), or even by leaning on one another, while living in tangled thickets (Wnuk & Pfefferkorn 1984). The situation becomes stranger, the further back in time we retreat. The recent discoveries of weird ‘trees’ in Devonian strata, including arborescent fungi (Boyce *et al.* 2007) and cladoxyloids (Stein *et al.* 2007; Meyer-Berthaud *et al.* 2010), well illustrates this point.

For the study of palaeoecology, trees preserved in growth position provide a glimpse of the spatial structure of ancient

ecosystems, something not readily accessible from other kinds of fossil preservation. Nothing gets us closer to the original landscape and its plant cover or reveals so much about plant size, habit, or even ontogeny (e.g. Libertín *et al.* 2009). In this paper, we employ the term ‘T⁰ assemblages’ (after Gastaldo *et al.* 1995, 2004a, 2006; Johnson 2007; DiMichele & Gastaldo 2008) to describe fossil forests preserved in essentially the same spatial conformation as in life. This includes assemblages buried in place; that is, the remains of upright trees rooted in their original soils (autochthonous) and assemblages where all or some of the vegetation has been slightly displaced (e.g. undisturbed leaf litter layers; Burnham *et al.* 1992) but still preserving most of the original vegetational structure (parautochthonous; Gastaldo 1986b; Gastaldo *et al.* 1987; Behrensmeyer *et al.* 2000; Martín-Closas & Gomez 2004). Most parautochthonous assemblages have been transported to some small degree from their original spatial position (Bateman 1991) and, therefore, do not preserve enough original spatial information to permit the drawing of unambiguous inferences about the interrelationships of different plants or groups of plants. Most root-containing palaeosols are also excluded, mainly because plant remains preserved within them may be highly time-averaged, reflecting the intermixing of root systems from different generations of plants (as may be demonstrated from cross-cutting relationships in some coal balls; DiMichele & Phillips 1994).

It is an interesting but little discussed fact that T⁰ assemblages have been reported far more often in Pennsylvanian successions (318–299 Ma) than in any other interval in the geological record. It is unclear whether this is because they are in fact much more abundant or simply more readily observed, a consequence of the



Fig. 1. The famous lycopoid forest at Victoria Park, Glasgow, Scotland, as it appeared in 1887 before construction of an interpretation centre over the site to preserve the fossils (reproduced from Thomas 2005). Trees are buried in tidal deposits (R. A. Gastaldo, pers. comm.).

extent of natural outcrop exposures and coal mining in the heavily studied areas of Europe and eastern North America. There is a long history of interest in such ‘Coal Age’ fossil forests, stretching back to the very earliest years of the nineteenth century (Fig. 2; Proust 1808; Thomson 1816, 1820; Brongniart 1821; Conybeare & Phillips 1822; Anonymous 1827; Hildreth 1827; Wood 1830; Hawkshaw 1840; see Stevenson 1911, for a review of early literature). Careful description of Pennsylvanian T^0 assemblages played a major early role in permitting whole-plant reconstructions (from which our understanding of the biology of many fossil plants derives); for example, allowing stigmarian root systems to be connected to trunks of lycopoid trees such as *Sigillaria* (Logan 1841) or *Lepidodendron* (Brown 1846, 1848). In addition, it was T^0 assemblages that first shed light on the origin of coal; for example, the discovery of abundant horizons with upright fossil trees rooted in coal seams at Joggins, Nova Scotia (Brown & Smith 1829; Gesner 1836) convinced Lyell (1843) that coal was the product of a peaty soil (Calder 2006; Falcon-Lang 2006a). At an even earlier date, Chapman (cited by Thomson 1816) made exactly the same inference based on fossil trees rooted in coal but, compared with the work of Lyell, his findings were relatively poorly documented and failed to have a comparable impact on mainstream thinking.

In this paper, we have three objectives as follows: (1) to review the origin and nature of Pennsylvanian T^0 assemblages; (2) to summarize as much of the literature on the subject as we can find (Table 1; T^0 assemblages are often reported in passing in many palaeobotanical or geological papers, or are reported in limited-circulation journals, so ferreting out all reports or illustrations of these kinds of deposits can be difficult (e.g. Walters 1891; Klusemann & Teichmüller 1954; Dilcher & Pheifer 1975; Wagner & Alvarez-Vázquez 1989, figs. 6 and 7), and we are aware that we have missed many papers, some of which we simply have had difficulty obtaining copies of as this paper goes to press (e.g. Knight 1971; Brzyski *et al.* 1976)); (3) to assess the significance of this kind of preservation for

palaeoecology and, more broadly, ecology. In doing so, we go some way to explaining the extraordinary abundance of T^0 assemblages in Pennsylvanian successions.

What factors control the origin and nature of T^0 assemblages?

T^0 assemblages are not randomly distributed in Pennsylvanian successions but most often are found in association with a narrow subset of sedimentary facies. Before we can begin to decipher the palaeoecological significance of these phenomena, it is essential that we first understand the fundamental controls on their origin and nature.

Rapid rate of burial

The single most important factor in the preservation of a T^0 assemblage is rate of accumulation of sediment around the living or recently dead vegetation. As ‘snapshots’ of ancient vegetation, T^0 assemblages had to be ‘frozen in time’ through rapid burial; the faster a landscape was buried, the greater the fidelity of preservation of vegetation structure (Johnson 2007). The earliest pioneers studying T^0 assemblages understood this principle well. In a report dealing with the Joggins fossil forests, Brown & Smith (1829, p. 431) perceptively wrote that ‘the most reasonable inferences are, that the [fossil] forest was inundated when ... an immense stratum of sand was deposited upon’ it. Similarly, referring to groves of *Calamites* (Brongniart 1821) preserved in sandstone beds in the St. Etienne basin of France, Lyell (1865, p. 481) remarked that ‘the plants seem to have grown on a sandy soil, liable to be flooded from time to time, and raised by new accessions of sediment, as may happen in swamps near the banks of a large river’.

Clearly, to preserve a T^0 assemblage at all, burial must happen more rapidly than destruction of the vegetation by decay or through direct exposure to the elements (Gastaldo & Staub 1999; DiMichele & Gastaldo 2008; Gastaldo & Demko 2010). Such

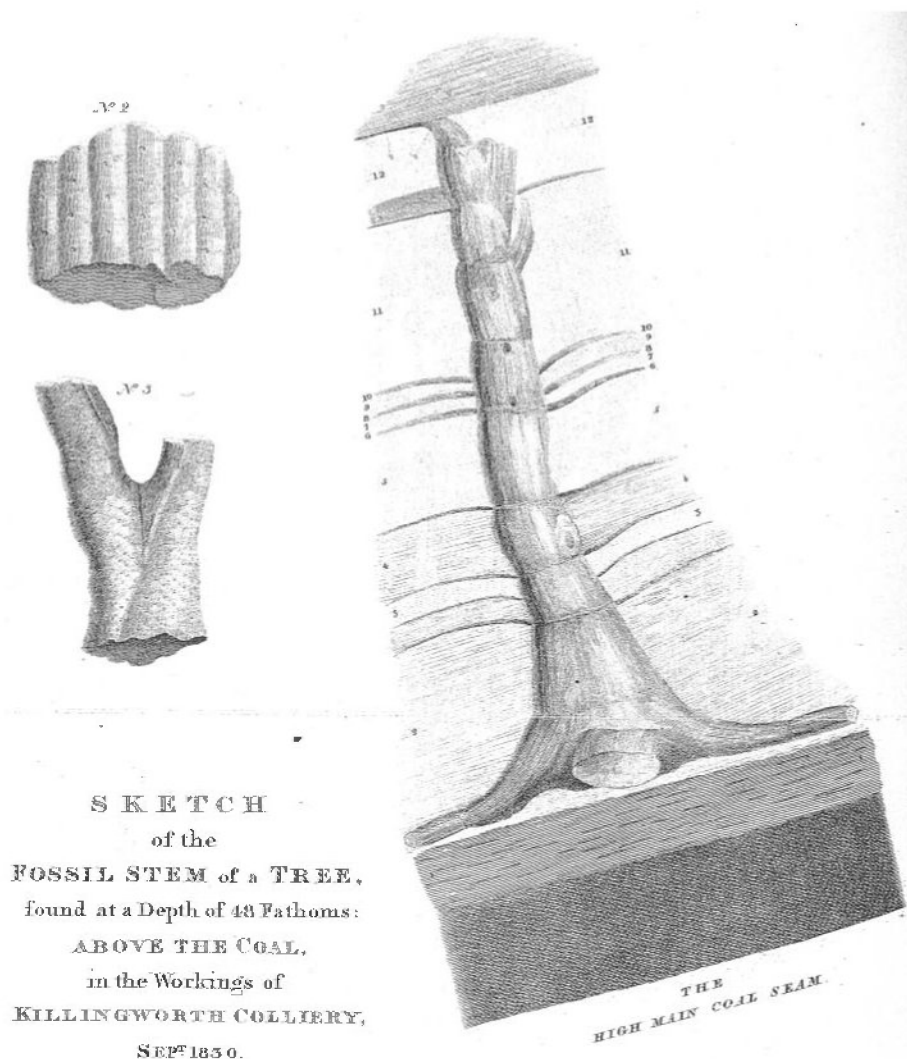


Fig. 2. One of the earliest illustrations of a fossil lycopsid tree in growth position, observed in an underground coal mine, 90 m below the surface at Killingworth Colliery, Northumberland, England (reproduced from Wood 1830). The tree appears to be rooted in the roof shale immediately above the High Main Coal.

rapid rates of burial, capable of preserving T^0 assemblages, are normally restricted to one of three sedimentary contexts. Typical entombing facies include (1) volcanic ash-falls or surges and/or associated lava flows, (2) coastal flooding brought about by rapid eustatic sea-level rise, regional subsidence, or more often a combination of the two, and (3) fluvial processes including within-channel sedimentation, riparian crevasse splays, progradation of distributary lobes, and general sediment aggradation in low-lying areas of floodplains. Each of these sedimentary environments results in T^0 assemblages with distinctive time-averaging characteristics, and the processes operating therein also strongly control the spatial scale of preservation, as discussed below.

Volcanic ash-falls or surges and lavas have the capacity to bury vegetation almost instantaneously (snapshot = minutes to days). Several excellent examples of such phenomena have been observed across the volcanically active Variscan Orogen (Fig. 3; Wagner 1989, 1997; Opluštil *et al.* 2009a,b). Sudden, catastrophic burial of vegetation in ash-falls can preserve even the most subtle ecological details; for example, an arachnid has been observed perched on a leaf of *Cordaites borassifolius* in an example of a Pennsylvanian fossil forest buried in a tuff in the Czech Republic (Selden & Penney 2010). However, fossil assemblages in ash-fall tuffs can also have complex character-

istics such as temporal and spatial separation of litter and ground cover from tree crown foliage, which require careful interpretation (Burnham & Spicer 1986). Furthermore, where ash-falls comprise relatively minor and repeated events, plants may continue to grow through the tuffaceous layers, resulting in a time-averaged succession containing an intermixture of pre-, syn-, and post-eruption vegetation (Wünsch 1865; Walton 1935; Scott 1990; Falcon-Lang & Cantrill 2002). Needless to say, ashfalls may preserve vegetation *in situ* over a vast area around a volcano, and some Pennsylvanian examples have been traced over many tens of kilometres (Libertín *et al.* 2009; Pfefferkorn & Wang 2009).

In contrast, entombment of forests by pyroclastic surge deposits or lava flows is usually on a more restricted spatial scale. In both cases, preservation is limited to the position on a landscape of charred trees; for example, the so-called 'lava trees' of Hawaii (Lockwood & Williams 1978), or charred stumps rooted below pyroclastic surge deposits in Monserrat (Scott & Glasspool 2005). Lava trees have been noted in the Tertiary basalts of Mull, Scotland (Bell & Williamson 2002), but no Pennsylvanian examples have yet been conclusively reported, although one possible example occurs in the Pennsylvanian of Norway (Larsen *et al.* 2008), where what appears to be a 'tree stump' is entombed in the base of a rhomb-porphyr lava flow

Table 1. Selected examples of Carboniferous (primarily Pennsylvanian) and earliest Permian T⁰ assemblages from the literature or personal observations of the authors

Age	Growth environment	Burial environment	Mode of preservation	Upright trees	Associated adpressions	Paper
Asselian	Peat swamp	Ashfall	Cast, adpression	L, P	×	Pfefferkorn & Wang (2009)
Asselian	Channel bar	Sandstone bar	Cast	C		Wagner & Mayoral (2007)
Asselian	Wet floodplain	Ashfall or surge	Cast, petrification	L	×	Wagner & Mayoral (2007)
Asselian	Floodplain swamp	Ashfall or surge	Petrification, cast	L, C, T, P, Co	×	Röbber & Noll (2006)
Stephanian C	Floodplain swamp	Clastic deposition in flood	Cast	L		Schmidler <i>et al.</i> (2004)
Stephanian C	Channel margins	Sand bars	Cast, adpression	C	×	Martin-Closas & Martínez-Roig (2007)
Stephanian C	Channel bars?	Sand bars	Cast	L		Walters (1891)
Stephanian B	Channel margin	Sand bars	Hollows	Co	×	Bashforth <i>et al.</i> (2011)
Stephanian B	Lake margin	Flooding from lake	Cast	C	×	Bashforth <i>et al.</i> (2011)
Stephanian B	Channel bars	Sand bars	Cast, adpression	C	×	Bashforth <i>et al.</i> (2011)
Stephanian B	Floodplain hummock	Drowned-lake sediments	Cast, adpression	P	×	Bashforth <i>et al.</i> (2011)
Stephanian B	Peat swamp	Clastic deposition in flood	Cast, adpression	T	×	Bashforth <i>et al.</i> (2011)
Stephanian B	Peat swamp	Drowned swamp; mud	Cast, Adpression	L, T	×	Martin-Closas & Galtier (2005)
Stephanian B	Channel margin	Sand bars	Cast, adpression	C, T	×	Martin-Closas & Galtier (2005)
Stephanian	Clastic swamp	Sandstone	Petrification	T	×	Stout (1945)
Stephanian	Peat swamp	Ashfall	Cast	L		Wagner (1989)
Stephanian	Clastic swamp	Clastic deposition in flood	Cast	L		Wagner & Alvarez-Vázquez (1989)
Stephanian	Semi-arid coastline	Sabkha	Petrification	Co/Cn		Jud <i>et al.</i> (2009)
Cantabrian	Channel bars	Clastic deposition in flood	Cast	L, C, T, P		Falcon-Lang (2006a, 2009)
Cantabrian	Peat swamp	Clastic deposition in flood	Cast	L, T		Falcon-Lang (2006a)
Cantabrian	Coastal wetland	Clastic deposition in flood	Cast	L, T		Falcon-Lang (2006a)
Cantabrian	Fluvial wetland	Crevasse splay	Cast	C		Pfefferkorn <i>et al.</i> (2001)
Asturian	Channel belt	Sand bars	Cast	L, C	×	Fielding <i>et al.</i> (2009)
Asturian	Clastic swamps	Flooding; lake development	Cast, adpression	L, C, P	×	Wnuk & Pfefferkorn (1987)
Asturian	Clastic swamps	Drowned swamp; mud	Cast, adpression	L	×	Dilcher & Pfeifer (1975)
Asturian	Peat swamp	Drowned swamp; mud	Cast	L	×	DiMichele <i>et al.</i> (1996)
Asturian	Peat swamp	Tidal rhythmites	Cast	L	×	DiMichele & DeMaris (1987)
Asturian	Peat swamp	Tidal rhythmites	Cast, adpression	L	×	DiMichele & Nelson (1989)
Asturian	Peat swamp	Tidal rhythmites	Cast, adpression	L, C, T, P, Co	×	DiMichele <i>et al.</i> (2007)
Asturian	Peat swamp	Tidal rhythmites	Cast, adpression	L, C, T, P, Co	×	DiMichele <i>et al.</i> (2006b)
Asturian	Peat swamp	Clastic deposition in flood	Cast	L, C	×	DiMichele <i>et al.</i> (2009)
Asturian	Clastic swamp	Clastic deposition in flood	Cast	L		Zodrow <i>et al.</i> (2010)
Asturian	Clastic swamp	Clastic deposition in flood	Cast	L		Sneider <i>et al.</i> (2005)
Asturian	Clastic swamp	Clastic deposition in flood	Cast	L, C	×	Calder <i>et al.</i> (1996)
Asturian	Peat swamp	Clastic deposition in flood	Cast	L	×	Calder <i>et al.</i> (1996)
Asturian	Channel bar	Sand bars	Cast, Adpression	L, C		Gibling & Rust (1990)
Bolsvian	Peat swamp	Tidal rhythmites	Cast, Adpression	L, C	×	Archer <i>et al.</i> (1994)
Bolsvian	Dryland floodplain	Ashfall	Petrification	Cn		Galtier <i>et al.</i> (1992)
Bolsvian	Clastic swamp	Clastic deposition in flood	Cast	L	×	Greb <i>et al.</i> (2001)
Bolsvian	Clastic swamp	Clastic deposition in flood	Cast	L, C	×	Legun & Rust (1982)
Bolsvian	Peat swamp	Ashfall	Cast, adpression	L, C, P, Co	×	Libertin <i>et al.</i> (2009)
Bolsvian	Peat swamp	Ashfall	Cast, adpression	L, C	×	Oplustil <i>et al.</i> (2007)
Westphalian	Peat swamp	Ashfall	Cast	L, C, T	×	Libertin <i>et al.</i> (2009)
Duckmantian	Clastic swamp	Clastic deposition in flood	Cast	L	×	Calder (1994)
Duckmantian	Abandoned channel	Drowned swamp; mud	Cast	L		Scott (1984)
Duckmantian	Clastic swamp	Clastic deposition in flood	Cast	L		Scott (1978)
Duckmantian	Clastic swamp	Drowned swamp; mud	Cast	L, C	×	Falcon-Lang & Jones (2005)
Duckmantian	Clastic swamp	Clastic deposition in flood	Cast	L		Wood (1830)
Duckmantian	Clastic swamp	Drowned swamp; mud	Cast	L, C	×	Gradzinski & Doktor (1995)
Duckmantian	Clastic swamp	Drowned swamp; mud	Cast	L, C		Pfefferkorn <i>et al.</i> (2001)
Duckmantian	Fluvial wetland	Clastic deposition in flood	Cast	C		

Duckmantian	Peat swamp	Tidal rhythmites	Cast	L		Kvale <i>et al.</i> (1989)
Langsetian	Channel bar	Sand bar	Cast with anatomy	T	×	Chesnut <i>et al.</i> (1992)
Langsetian	Microtidal coastline	Clastic deposition in flood	Cast, adpression	Co	×	Falcon-Lang (2005)
Langsetian	Peat swamp	Tidal rhythmites	Cast, adpression	L, C, P, T	×	Gastaldo <i>et al.</i> (2004a)
Langsetian	Clastic swamp	Clastic deposition in flood	Cast	C		Gastaldo (1992)
Langsetian	Peat swamp	Tidal rhythmites	Cast, adpression	L, C, P, T	×	Gastaldo <i>et al.</i> (2004b)
Langsetian	Peat swamp	Tidal rhythmites	Cast, adpression	L, C	×	Demko & Gastaldo (1996)
Langsetian	Clastic swamp	Clastic deposition in flood	Cast	L, C		Demko & Gastaldo (1996)
Langsetian	Peat swamp	Tidal rhythmites	Cast	L	×	Gastaldo (1986b)
Langsetian	Peat swamp	Tidal rhythmites	Cast	L, C		Klusemann & Teichmüller (1954)
Langsetian	Dryland floodplain	Clastic deposition in flood	Petrifaction	Co	×	Falcon-Lang (2003a,b)
Langsetian	Dryland floodplain	Clastic deposition in flood	Petrifaction	Co	×	Falcon-Lang (2006b)
Langsetian	Channel margin	Sand bars	Cast	L, C		Falcon-Lang (2006b)
Langsetian	Clastic swamp	Clastic deposition in flood	Cast	L, C	×	Calder <i>et al.</i> (2006)
Viséan	Clastic swamp	Ashfall reworked	Petrifaction	L		Walton (1935)
Viséan	Clastic swamp	Tidal rhythmites	Cast	L		MacGregor & Walton (1948)
Viséan	Back-barrier marsh	Coastal sediments	Cast	L		Gastaldo <i>et al.</i> (2006)

Tree types: L, lycosid; C, calamitalean; T, marattialean tree fern; P, pteridosperm; Co, cordaitalean; Cn, conifer. This list is incomplete. The authors welcome additional examples, particularly from the past 110 years, that can be added to the database.

(H. J. Falcon-Lang, unpublished observations). However, preservation of trees by hot pyroclastic surges has been suggested for instances where many trees are knocked over, charred, and even moved slightly, such as the Pennsylvanian conifer-like trees reported from the West Midlands of England (Galtier *et al.* 1992) or in the spectacular Early Permian forests from Chemnitz in Germany (Rößler 2006).

Coastal flooding also can result in rapid burial of vegetation. Such processes generally operate at a slower rate than volcanic ash-falls, however, such that T⁰ assemblages have a higher degree of time-averaging (snapshot = hours to years). Furthermore, given that relative sea-level rise preceding final burial may alter the make-up of vegetation on a coastline over a period of decades, vegetation entombed by coastal flooding may be preserved in a state of ecological flux (DiMichele *et al.* 2007). None the less, where forests are buried in tidal rhythmites (Fig. 4), the amount of time taken to entomb the trees may be determined precisely (with an error of a few days to weeks; Kvale *et al.* 1989; Gastaldo 1990; Archer *et al.* 1994). Coastal environments in which forests are entombed are generally diverse and complex, including estuaries, tidal flats and sabkhas among others (Francis 1984; Jud *et al.* 2009), their nature determined by tidal amplitude (microtidal to macrotidal) and climate (humid to arid). As with volcanic eruptions, this sedimentary context has the potential to entomb forested landsurfaces over huge areas, if triggered by earthquakes, compaction-induced subsidence, eustatic sea-level rise or commonly a combination of two or more of these processes. Effects of such relative sea-level rise would have been particularly dramatic for Pennsylvanian tropical landscapes, where coastal plains had minimal gradients over a vast area (DeMaris 2000; Falcon-Lang 2003c; Falcon-Lang & Miller 2007; Falcon-Lang & DiMichele 2010), on a scale with few modern analogues (e.g. the Gulf of Carpentaria; Chivas *et al.* 2001). Preservation of forests may have been especially common on macrotidal coasts (Gastaldo *et al.* 2004a,b) although they also are known from microtidal settings (Falcon-Lang 2005). The largest Pennsylvanian example of a fossil forest preserved in this context spans *c.* 1000 ha (DiMichele *et al.* 2007). Late Quaternary 'drowned forests' are, of course, extremely abundant in intertidal and subtidal zones today worldwide (e.g. Dawson 1855; Lyon & Goldthwait 1934; Heyworth 1978; Fedje & Josenhans 2000), reflecting abrupt eustatic changes in sea level of *c.* 50 mm a⁻¹ during deglaciation-driven meltwater pulses (Blanchon & Shaw 1995; McCulloch & Esat 2000; Clark *et al.* 2004). However, the commonness of this kind of preservation in the Pennsylvanian record (another glacial interval) has only recently begun to be recognized.

Fluvial settings in which T⁰ assemblages are preserved are perhaps the most diverse, encompassing a wide range of sedimentary settings and time intervals of plant burial (snapshot = hours to decades, although still geologically instantaneous). In addition, they may be variable in the nature of the information they preserve, including plants rapidly buried in place (Gastaldo *et al.* 2004a,b; DiMichele *et al.* 2007) or buried over some extended time after death, permitting degradation of some floral elements (Calder *et al.* 1996, 2006; DiMichele *et al.* 2009). They also may capture complex interactions between vegetation and sediment, such as instances of tree-ferns growing up and regenerating through alluvium (Fig. 5; Falcon-Lang *et al.* 2006) or *Calamites* stems that lived through and recovered from repeated burial (Brongniart 1821; Dawson 1851; Gastaldo 1992; Gradzinski & Doktor 1995). Assemblages preserved in fluvial deposits (the product of autocyclic processes) are usually much more limited in spatial scale, ranging from a few tens of square

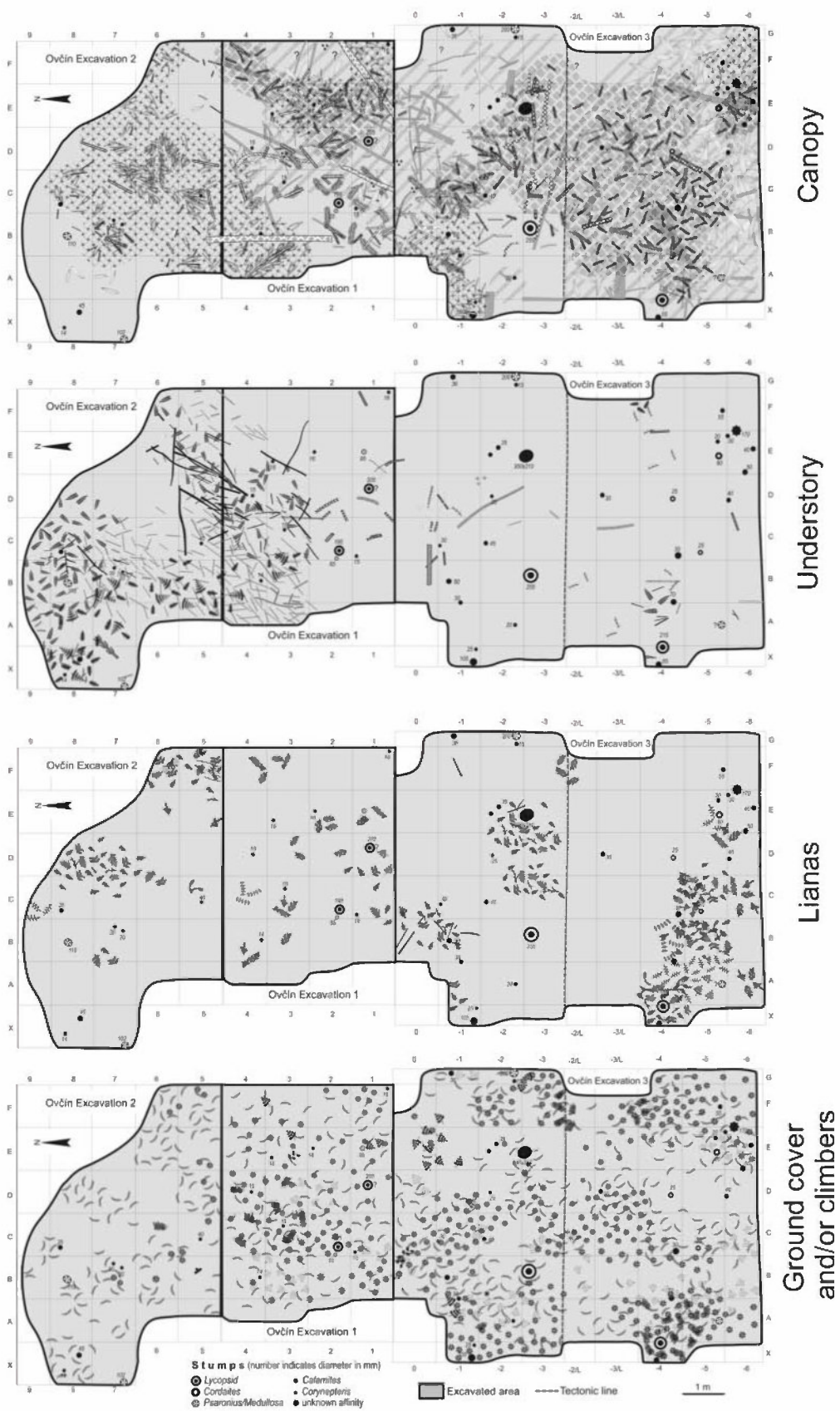


Fig. 3. Remains of a lepidodendrid–*Cordaites* forest buried in ash-fall tuff and uncovered over a 93.5 m² area at Ovčín, Czech Republic (Opluštil *et al.* 2009b, fig. 12; reprinted courtesy of the Society for Sedimentary Geology, SEPM).

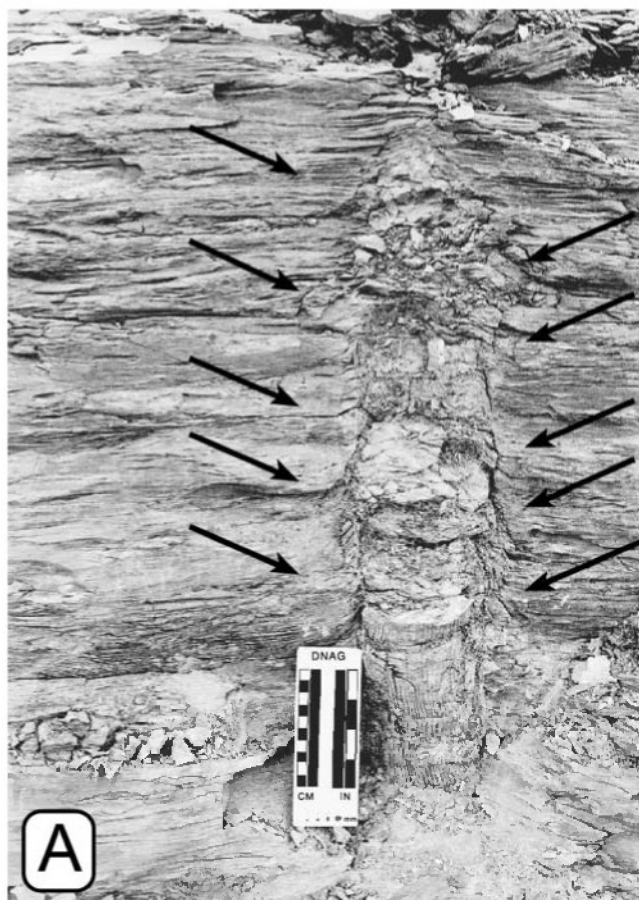


Fig. 4. A *Calamites* tree buried in tidalites in Alabama, USA (reproduced from Gastaldo *et al.* 2004a, fig. 5A, courtesy of R. Gastaldo, Colby College). Arrows indicate tidal rhythmites. The whole succession was deposited in only a few months.

metres adjacent to a small splay (Schindler *et al.* 2004) or within a channel (Bashforth *et al.* 2010), to a few hectares adjacent to a distributary lobe (Calder *et al.* 2006). Larger tracts of interfluvial forest may be preserved rarely following levee breaches adjacent to very large (Amazon-scale) fluvial systems, provided that drainages carry sufficient sediment load (Pfefferkorn *et al.* 1988).

High rate of accommodation

To be preserved, not only must T^0 assemblages be buried rapidly, they must also occur in settings subject to high rates of accommodation that permit a longer-term escape from exposure by post-burial erosion. Following burial, their preservation follows a pathway similar to that of any other deposit containing terrestrial organic matter (Behrensmeier *et al.* 2000). First, in the shorter term, the entombed plants must be removed from the effects of aerobic decay in the vadose zone (Gastaldo & Demko 2010); this may occur rapidly following sea-level rise, tectonically driven earth movements, or even compaction, in the case of a substrate such as peat. Second, in the intermediate term of millions to tens of millions of years (or much less were the deposit to have formed at high elevation), the deposit must be buried to a depth sufficient to ensure it will escape erosion; that is, it must reside at, or close to, regional base level and,

ultimately, sea level, if it is to be preserved in the (Pennsylvanian) geological record. Both these factors require high rates of accommodation (Demko & Gastaldo 1992, 1996; Gastaldo *et al.* 2004a,b; Waldron & Rygel 2005). This begs the question of survival of a large volume of Palaeozoic rock in an elevated position for the past several millions of years, exposure of which has made many of these T^0 assemblages accessible to us today; it is partially through the erosion of such rocks that *in situ* forest elements are being exposed and discovered (e.g. the forests continually exposed by erosion at the Joggins cliffs; Calder *et al.* 2006), but these processes in well-lithified rocks are very different mechanically and in their timing from those accompanying early burial and diagenesis.

The fossil record indicates that Pennsylvanian T^0 assemblages were substantially more likely to be preserved in wetlands than in better-drained habitats with lower water tables, even if such drier habitats were in lowland basins at the time of their development (e.g. DiMichele *et al.* 2010). For example, at Joggins, Nova Scotia, 66 fossil forest horizons with lycopsid trees have been exposed in recent years (Davies *et al.* 2005). Of these, 86% occur in wetland deposits even though wetland and dryland successions make up roughly equal stratal thickness in the formation. The predominance of T^0 assemblages in wetland facies relates to the fact that these deposits mostly coincide with times of rising or elevated base level (say, owing to very high levels of regional rainfall) and, simultaneously, with eustatic sea-level rise (Fig. 6; Davies & Gibling 2003; Falcon-Lang *et al.* 2006). These factors tend to reinforce the effects of tectonic subsidence to create very high levels of accommodation on the scale of 10^1 – 10^5 years. Pennsylvanian drylands, on the other hand, tend to coincide with times of stationary or falling eustatic sea level, dampening down the effects of subsidence. This results in moderate to little creation of accommodation space, which allows high rates of destruction of buried organic material. In addition, under very limited rainfall regimes lack of adequate sediment transport will also limit the potential burial of standing vegetation of any kind (Cecil & Dulong 2003; Gastaldo & Demko 2010).

Even when levels of eustatically or isostatically driven accommodation are very high, creation of tectonic accommodation is still necessary for long-term (10^6 – 10^8 years) preservation in the geological record. Fossil forests spectacularly preserved at Joggins, Nova Scotia (Calder *et al.* 2006) and in the Black Warrior basin of Alabama (Gastaldo *et al.* 2004a,b) both occur in regions that experienced exceptionally high rates of subsidence during Pennsylvanian times (Waldron & Rygel 2005; Falcon-Lang *et al.* 2006). For example, recent biostratigraphic revisions for the Joggins section (Utting *et al.* 2010) suggest that the Little River, Joggins, Springhill and Ragged Reef formations, totalling a stratal thickness of *c.* 3100 m (Davies *et al.* 2005), may all fall within the Langsettian substage, which has a duration of <1.5 Ma (Davydov *et al.* 2010). This is equivalent to an accumulation rate of 2 mm a^{-1} and, when sediment compaction is taken into account, a subsidence rate of at least 5 mm a^{-1} .

Whereas many Cenozoic T^0 assemblages formed initially at altitude and remain buried sufficiently to escape erosion temporarily, there are no confirmed Pennsylvanian deposits that originated at elevations of more than a few hundred metres. Although several basins in the Variscan orogenic belt are inferred to have filled at high palaeoaltitude (e.g. Spain, Iwaniw 1985; France, Becq-Giraudon *et al.* 1996; Czech Republic, Opluštil 2005), new findings of brackish deposits in one of these basins indicate that the deposits there formed at, or just above, sea level (Bashforth *et al.* 2010). In those cases where T^0 assemblages

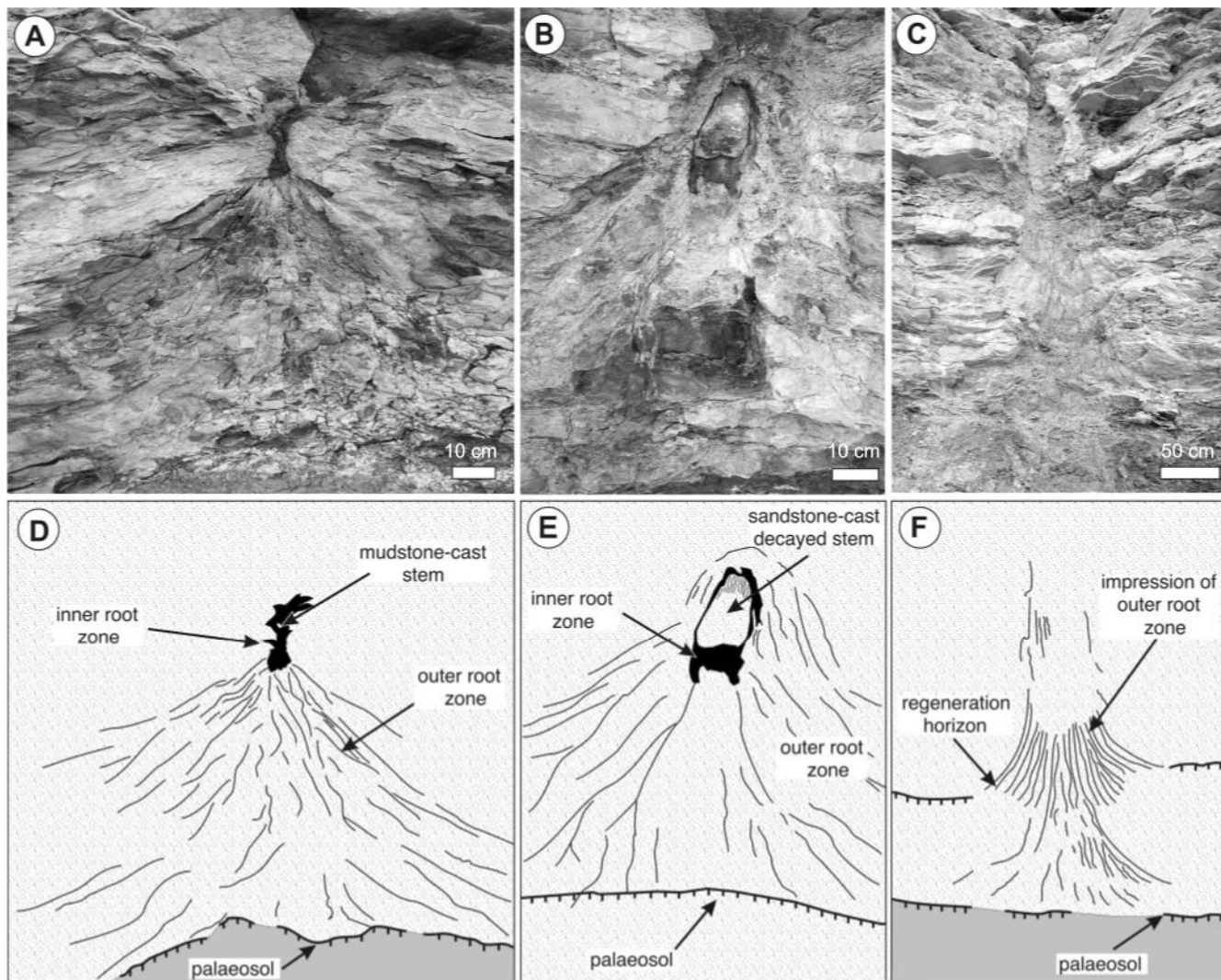


Fig. 5. Tree ferns buried in growth position below the Point Aconi Coal, Sydney Mines Formation at Cranberry Head, Cape Breton, Nova Scotia, Canada (a–c), with interpretative sketches below (d–f). It should be noted that the largest tree (right) appears to show at least one episode of regeneration following partial burial in a sedimentary layer (reproduced from Falcon-Lang 2006b).

occur in basins that may lack such incursions (Opluštil 2005), it is possible to infer that elevation probably exceeded 120 m (the probable maximum amplitude of glacioeustatic fluctuations; Rygel *et al.* 2008), but how much above that level is more difficult to determine. Proposed elevations of 1000 m cannot be ruled out, although documentation of such elevations is highly inferential. Significant compositional changes would be expected at altitudes of 1000 m, using modern tropical vegetation as a guide (Flenley & Bush 2007), but what such changes should look like in the Pennsylvanian, and separating elevational from biogeographical effects, is difficult.

Significance of preserved tree height

Typically the height to which a tree is preserved tells us something about the magnitude of the burial events and the rate of basin accommodation. Pennsylvanian lycopsid trees are commonly preserved with only the lowermost 1–2 m intact. However, Conybeare & Phillips (1822) reported trees up 4.5 m high and Lyell (1845) noted one exceptional tree at Joggins that was 7.6 m high. These extraordinary heights are confirmed by

more recent observations at the Joggins locality, where maximum heights of >6 m have been observed (Calder *et al.* 2006). In addition, Gradzinski & Doktor (1995) observed a 5.5 m high tree in Poland. Even more remarkable is the report of an erect lycopsid tree >8 m high, and possibly as great as 12 m high, found near Wigan, England (Broadhurst & Magraw 1959). All these trees occur in fluvial or coastal strata.

Given that these trees would have decayed away rapidly under tropical climates (Gastaldo & Staub 1999), and given that most sedimentary studies suggest burial in the course of a single depositional event, or a small number of such events (Calder *et al.* 2006), the magnitude of the burial event(s) and the rate of accommodation must have been very high to preserve these exceptionally tall trees. In short, preservation of substantial tree heights demonstrates the existence of areas capable of receiving substantial depths of sediment over short time intervals. Thus, they imply the occurrence of very large and sudden accommodation events, possibly triggered by earthquake-induced subsidence (Gastaldo *et al.* 2004a,b) and/or other factors such as rapid eustatic sea-level rise, particularly in areas such as the Midcontinent or Illinois Basin of North America, which were extremely

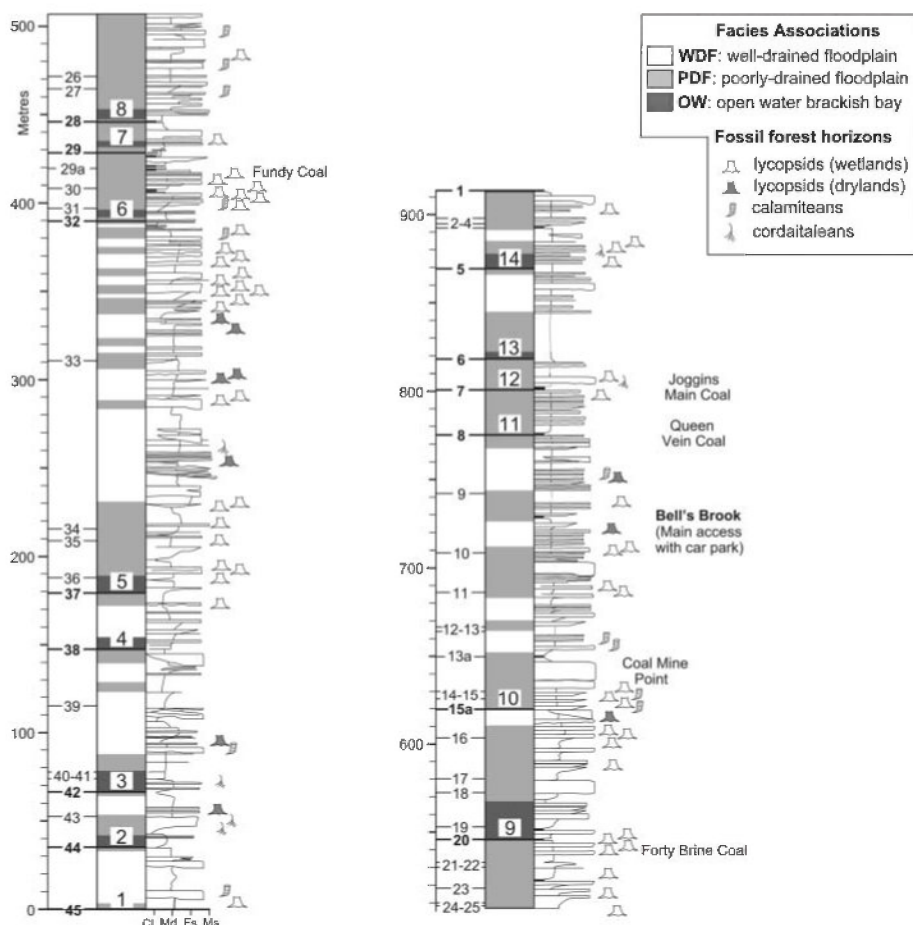


Fig. 6. Summary log of the 915.5 m thick Joggins Formation (Davies *et al.* 2005), showing Logan's coal numbering scheme (left column; Logan 1845), facies associations and cyclothem (middle column; Davies & Gibling 2003), and the position of fossil forests. Rare lycopsid trees rooted in dryland facies associations are highlighted (modified from Falcon-Lang 2006b).

flat (as a parallel, consider that as much as 16 m of sea-level rise may have occurred in as little as 100–500 years during the late Quaternary meltwater pulse 1A; Blanchon & Shaw 1995; McCulloch & Esat 2000; Clark *et al.* 2004). In certain depositional systems, such as areas of upper deltaic plains or alluvial plains, where levees may have formed, a height differential between the levee-tops and floodplain hollows could create such a catchment (Calder *et al.* 2006).

Many buried Carboniferous forests with tall, upright trees occur above coal beds. The commonness of this particular preservational facies, repeated over and over in many stratigraphic successions, calls for a mechanism that is not reliant on temporally asynchronous events, such as the termination of peat formation by an earthquake, particularly when the rock sequences document repeated patterns of climate and sea-level change (e.g. Cecil *et al.* 2003). In such instances, sea-level rise, driven by glacial melting, in combination with a flat cratonic surface, and peat compaction under sediment load, could combine to contribute to the short-term burial of trees to considerable depths (Gradzinski & Doktor 1995; Opluštil *et al.* 2009a), as seen in numerous Late Quaternary 'drowned forests' the world over.

To what extent do T⁰ assemblages contain taphonomic biases?

Whereas rates of burial and accommodation are the fundamental controls on the origin and general nature of T⁰ assemblages, other taphonomic factors may significantly bias what information

is preserved and what is destroyed. Without careful and nuanced consideration of taphonomic factors, palaeoecological analysis of T⁰ assemblages may result in misleading conclusions.

Anatomy of entombed trees

Vegetative anatomy of the entombed trees appears to be a key factor influencing the likelihood of *in situ* preservation of Pennsylvanian plants in growth position. Different kinds of anatomy have different preservational potentials and are most likely to appear in distinct physical environmental settings. Literature review (Gastaldo 1986b; Pfefferkorn *et al.* 2001) demonstrates that the most commonly preserved upright trees in Pennsylvanian strata comprise arborescent lycopsids or *Calamites*, preserved as mud- or sandstone-cast plant stem remains (Table 1). These plants differ from all other contemporaneous groups in having hollow central areas, which formed either during the life of the plant or by decay of parenchymatous tissues shortly after death, surrounded by a resistant rind of woody or sclerenchymatous tissues (Phillips & DiMichele 1992). These hollows apparently provided a natural cavity in which sediment could accumulate, forming casts and facilitating preservation.

In contrast, tree-ferns, cordaitaleans, and pteridosperms do not have this hollow cylindrical form but have stems composed of a more complex mixture of tissue types. The stems of tree-ferns and pteridosperms, in particular, lack a resistant outer layer and are made up of a high percentage of parenchyma arrayed in such a manner that decay is likely to proceed quickly and destroy the stem or lead to its collapse under sediment pressure (Baker &

DiMichele 1997); decay of parenchymatous tissues does not leave a hollow cylinder. Cordaitaleans, if preserved as upright mud casts of hollow stumps forming after decay of the woody trunk (Falcon-Lang 2006c), also might be difficult to recognize definitively because they lack external features that clearly identify them. Consequently, the trees of these three groups are less readily preserved in growth position, or can be difficult to identify if they are preserved, resulting in an inherent bias both in preservation and recognition. This does not mean that these other groups are never preserved as stem casts, they are, and have been reported in upright position (e.g. Falcon-Lang 2005, 2006b, 2009).

This biased preservation and/or recognition of different plant groups is well illustrated by examination of single forest layers and comparison of co-occurring autochthonous and parautochthonous assemblages. In some examples (e.g. in coal 'roof shale' settings buried in fluvial plain or tidal sediments), lycopsid stumps may be the only obvious *in situ* remains on a given horizon, and there is a danger that one may narrowly construe these lycopsid stumps as representing all the trees that grew on that land surface (DiMichele *et al.* 1996). However, abundant co-occurring litter is commonly dominated by fern, pteridosperm and sphenopsid stems and foliage, and may include relatively few lycopsid aerial remains, indicating a more complex and diverse original vegetation matrix. In such instances, casts of upright plants such as lycopsid trees can be found in close association with adpressed tree fern and pteridosperm stems (e.g. Wnuk & Pfefferkorn 1984, 1987; DiMichele *et al.* 2007), some of great size (we have personally observed, in the immediate roof of the Middle Pennsylvanian Springfield (No. 5) coal, 'fallen' fragments of large pteridosperm stems, over 30 cm in diameter and 4 m in length, surrounded by the remains of large, frond-like leaves and foliage of a single species, in this instance *Neuropteris flexuosa*). Such stems are encountered only where transport has been minimal, owing to the nature of their construction. This is particularly the case for marattialean tree ferns, which anatomical studies show were largely composed of tissues filled with small air spaces, particularly in the roots, but also in the stems (Ehret & Phillips 1977; Rothwell & Blicke 1982); where such stems are found in abundance, especially when mixed with large segments of fronds, it can be assumed that transport was minimal.

Woody plants (e.g. cordaitaleans) preserved in growth position can be most precisely identified where they have been permineralized and retain diagnostic cellular anatomy (Grand'Eury 1877; Falcon-Lang 2003a,b, 2005, 2006c). Permineralization of erect trees appears most commonly in dryland settings (Mencl *et al.* 2009) or where volcanic sediments are part of the landscape (Matysová *et al.* 2010), and where abundant carbonate or silica is present in groundwater (Dawson 1877; Walton 1935). In such instances, a wide range of plants may be preserved, such as those entombed in the Early Permian volcanic ash deposits from Chemnitz, Germany (Rößler 2006). Preservation of woody trees as silicifications also may occur in seasonally dry to semi-arid environments, where intense evaporation leads to the development of highly alkaline, saline surface waters capable of dissolving and re-precipitating opaline silica (Matysová *et al.* 2010). Such silicified trees are known from Pennsylvanian and Jurassic sabkha settings (Fig. 7; Francis 1984; Jud *et al.* 2009), as well as in Jurassic desert margin environments (Parrish & Falcon-Lang 2007). If unmineralized, woody trees also may leave trace fossils, particularly in dryland floodplain settings where the organic material decays away leaving 'sediment down-turns', which mark the position of original trees (Fig. 8; Rygel *et al.* 2004).

Sedimentary processes and facies

T⁰ assemblages occur in a wide range of depositional settings and hence sedimentary facies. However, the depositional environment can have considerable influence on the fidelity with which the fossil deposit reflects the composition and structure of the standing vegetation. The amount of time over which a sedimentary deposit accumulated can control time-averaging, for example, and thus the relationship of the fossil deposit to the original vegetation. Airfall ash deposits may preserve a single generation of plants in its entirety (Libertín *et al.* 2009; Opluštil *et al.* 2009a,b), in which case they have a potential to represent the original vegetation with high fidelity. There may be some distinct asynchronies, however, in the timing of when plant parts detach from the standing vegetation as ash weights them down, resulting in a complex distribution of plant parts within the ash bed relative to the standing stems and floor litter (Burnham & Spicer 1986). Ash flows, as opposed to strictly airfall tuffs, carried in water or as flows of incandescent ash can preserve plants in growth position, but also may displace them to some degree (Rößler 2006). The most variable of all settings where T⁰ assemblages are preserved are fluvio-deltaic environments, which include a broad spectrum of depositional conditions that may vary significantly in rate of sediment deposition and thus in the time it takes to bury standing vegetation.

As noted above, preservation of large, tall stems in upright position indicates that rapid deposition of thick sediment in a standing vegetation environment is possible (e.g. Klusemann & Teichmüller 1954), particularly in environments where tectonics rapidly creates major accommodation space (Gastaldo *et al.* 2004a,b). In other instances, deposition may occur over several years, allowing sufficient time to eradicate certain less resistant elements of the flora, particularly if accumulation is above mean water table (Scheihing & Pfefferkorn 1984; Gastaldo *et al.* 1987; Gastaldo & Demko 2010). This will be less problematic in wetland facies where waterlogging inhibits decay, even if the deposit initially lies above the mean water table. In drylands, however, all but the most recalcitrant material could be removed, meaning that most dryland vegetation preserved *in situ* forms only a limited subset of the original vegetation (Falcon-Lang 2003a,b), or is likely to be from wet parts of the landscape (Falcon-Lang *et al.* 2004; DiMichele *et al.* 2006a).

Tectonics and long-term subsidence rate

Short-term creation of accommodation space is much the same in slowly or rapidly subsiding basinal areas; rise in base level or subsidence creates the initial conditions in which organic remains can be isolated from the aerobic decay process in near-surface environments (Gastaldo & Demko 2010). However, it is the creation of long-term accommodation space that, ultimately, is essential for the preservation of T⁰ assemblages. Cratonic settings, where subsidence is slow or episodic, tend to preserve relatively thin successions with more gaps, especially on low-stand surfaces (e.g. parts of the Illinois Basin, USA; Falcon-Lang *et al.* 2011). In contrast, basins that are more rapidly subsiding, such as southern parts of the Appalachian trough (Gastaldo *et al.* 2004a,b) or Maritime Canada (Gibling *et al.* 2008) offer greater long-term preservational potential with more complete succession. The effects on the distribution of T⁰ assemblages may be marked. For example, in cratonic settings, fossil forests are usually restricted to discrete flooding surfaces associated with the roof shales of coal seams, where subsidence and eustasy reinforce the rate of accommodation. However, in very rapidly



Fig. 7. Late Pennsylvanian silicified conifer-like tree rooted in growth position immediately below a major gypsum layer near Socorro, New Mexico, USA (Photo: W. Di Michele; see Jud *et al.* 2009).

subsiding settings, multiple stacked fossil forests may form. For example, at Joggins, Nova Scotia, where strike-slip tectonics and salt tectonics combined to create some of the highest subsidence rates in Pennsylvanian Euramerica (Waldron & Rygel 2005), many stacked forests occur in coastal and alluvial tracts; for example, 62 lycopsid forest layers are preserved (Davies *et al.* 2005) in a time interval estimated to be only 300 ka in duration (Falcon-Lang *et al.* 2006). At Sydney Mines, Nova Scotia, 13 stacked forests occur in an interval only 25 m thick (Fig. 9). Thus, whereas T^0 assemblages in cratonic settings reflect single points in climatic cycles, fossil forests may represent a wider spectrum of climatic and environmental contexts in rapidly subsiding basins.

What can T^0 assemblages tell us about palaeoecology?

A critical analysis of T^0 assemblages leads to some interesting and unexpected insights. Foremost of these is recognition that finding some, or even many, plants in growth position does not

necessarily indicate that ‘original vegetation’ has been discovered. The interactions of plant structure and growth architecture, sedimentary environment, rate of deposition of entombing sediment, and the effects of decay accompanying short- and long-term burial conditions can lead to considerable and variable divergence between the ‘original vegetation’ and the fossil deposit. Second, there are common and abundant T^0 assemblages that include mixtures of *in situ* plants and adpressions in prostrate positions within the sediment. In many of these cases, the remains preserved on bedding surfaces represent plants from the original assemblage that fell in storms and other disturbances, or were abscised, and that did not have the kinds of anatomies favourable for in place, upright preservation, or the recognition thereof. Conversely, ground-cover plants may be preserved in place and initially confused for typical parautochthonous remains. Pennsylvanian examples of this kind of mixed preservation of T^0 vegetation are numerous (Wnuk & Pfefferkorn 1984, 1987; Gastaldo *et al.* 2004a,b; DiMichele *et al.* 2007).

We wish particularly to stress that analysis of the sedimentary



Fig. 8. A 'sediment downturn' within red bed strata at Joggins, Nova Scotia, Canada (courtesy of M. Gibling, Dalhousie University), marking the former position of a gymnosperm tree, which was oxidized away shortly after sediment accumulation around the trunk (see Rygel *et al.* 2004, for further details).

environment is essential to the interpretation of the taphonomic history of a T^0 assemblage, and it is only from some knowledge of that history that further palaeoecological inferences can be made. Although not providing unmixed and unambiguous access to the past vegetation, T^0 assemblages are a proverbial 'foot in the door' when it comes to reconstructing the past with greater accuracy and authenticity. They are baseline data that can help constrain conceptual and quantitative models of past vegetation structure and dynamics. We review some of the palaeoecological insights that a nuanced analysis of such assemblages may offer.

Forest structure and dynamics

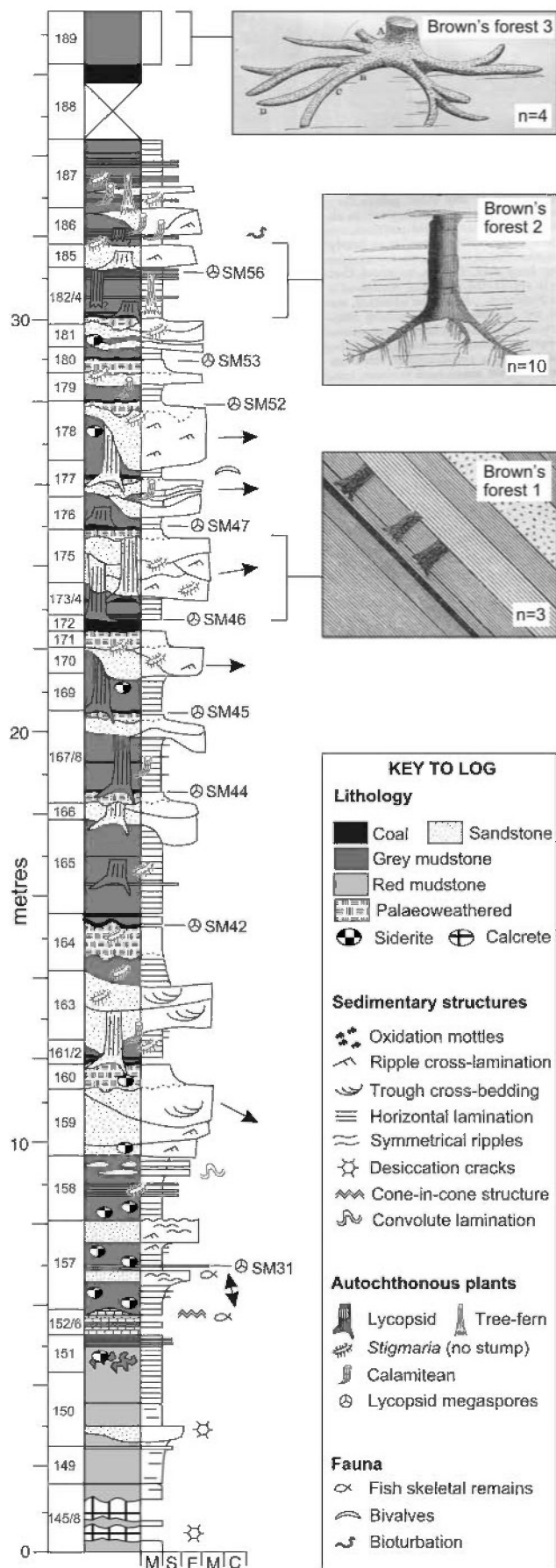
When preserved in place and observable over a sufficiently large area, tree stumps provide a means to gain insights into the structure of ancient arborescent vegetation, including the density and spatial distribution of trees (e.g. Beckett 1845; Sorby 1875; Schmitz 1896; Gastaldo 1986b; DiMichele *et al.* 1996; Falcon-Lang 2006b; Fig. 10). Such preservation also allows estimates of canopy height, via application of biomechanical principles (Niklas 1994; Spatz *et al.* 1998), and forest productivity when data concerning biomass allocation and growth rate are factored into the equation (Creber & Francis 1987; Baker & DiMichele 1997). Where multiple forest horizons with similar composition are preserved, analysis of tree density–diameter relationships allows inferences to be made about cohort dynamics; for example, self-thinning and age profile (DiMichele & DeMaris 1987; Calder *et al.* 1996; Falcon-Lang 2004; Rygel *et al.* 2006). Furthermore, statistical analysis of quantitative plant assemblage data obtained through a consistent and repeatable quadrat approach permits insights into tree or species distribution and heterogeneity (DiMichele & Nelson 1989; Gastaldo *et al.* 2004b), and ecological gradients where assemblages can be compared with independent environmental data from sedimentary facies (Gastaldo 1987; DiMichele *et al.* 2007). Such studies show that heterogeneity in many Pennsylvanian assemblages was scale dependent, appearing stochastic at small spatial scales but

with clear gradients at larger scales (Fig. 11; DiMichele *et al.* 2007).

Plants in growth position also provide direct glimpses of vegetation that might be difficult to infer from parautochthonous assemblages, and certainly from allochthonous accumulations. One such matter of current interest surrounds the use of the term 'rainforest', which implies significant amounts of internally recycled water, as is found in modern angiosperm-dominated tropical rainforests (Johnson 2007). Pennsylvanian T^0 assemblages suggest a wide range of vegetation densities, but many indicate that some of the most common of these forests were very open, lacking closed canopies (e.g. Gastaldo *et al.* 2004b; DiMichele *et al.* 2009), based on the distribution of *in situ* stumps and the architectures of the trees known from prostrate specimens. This means that the potential for extensive recycling of water may have been limited compared with closed canopy angiosperm forests (Boyce & Lee 2010), although recent physiological analyses of the potential of these plants to move water via evapotranspiration is ambiguous, the leaves suggesting limited potential (Boyce 2009), but stem anatomy suggesting the potential for relatively high rates (Cichan 1986; Wilson & Knoll 2010). Alternatively, selective preservation may mask original diversity, with only the most resistant, anatomically suitable plants being preserved in place.

Whole-plant reconstruction and growth form

In exceptional preservational circumstances, snapshot preservation may permit an unusually high degree of whole-plant reconstruction. Prone trees on a forest floor offer unrivalled opportunity for reconstruction from root systems to tree height, including such things as trunk taper, branching patterns, the distribution of leaves and reproductive structures (e.g. Thomas & Watson 1976; Wnuk & Pfefferkorn 1984), but also require large bedding surface exposures, generally found only in mines, which few palaeobotanists have the opportunity (or the inclination!) to visit in the present day, but more regularly accessed in the past



(e.g. Wood 1830). Recently discovered Pennsylvanian examples include the spectacularly preserved and mapped forests in the Czech Republic (Opluštil *et al.* 2007, 2009a,b; Libertin *et al.* 2009), a storm flattened forest from the Appalachian Bernice Basin, USA (Wnuk & Pfefferkorn 1984, 1987), and fossil forests in underground mine roof shales in the Illinois Basin, USA (DiMichele *et al.* 2006a, 2007; Falcon-Lang *et al.* 2009a).

A broader appreciation of the range of growth forms also is made possible, if preservation is exceptional and includes adpressed parautochthonous as well as upright trunks. Epiphytes, lianas, and other climbers, for example, may be preserved still attached to their host trees (Röbner 2000; Opluštil *et al.* 2007, 2009a), although some of these may in fact represent a collapsed stele wound around the interior of lycopoid trees (Gradzinski & Doktor 1995; e.g. Fig. 12). The ecological importance of this growth form in late Palaeozoic vegetation, although long suspected, only recently has begun to be appreciated (Krings *et al.* 2003; Masselter *et al.* 2006; Cleal 2008; Burnham 2009). However, it remains puzzling that so few climbers have been unequivocally documented attached to the dominant erect lycopoid trees, raising ecological and taphonomic questions that are hard to answer at present (one of the reviewers of this paper suggests that short life span of lycopoid trees and a penchant for wet, periodically to long flooded substrates may have inhibited the germination of vines in the habitats favoured by lycopoid trees and limited vine growth on their trunks). Peculiar growth habits also may emerge, such as sigillarians with sharply tapering conical trunks (Wagner & Mayoral 2007, fig. 11), certain medullosan pteridosperms with lax trunks that appear to have leaned on one around for support (Wnuk & Pfefferkorn 1984; Falcon-Lang 2009; Fig. 13), or sphenopsids with huge woody trunks (Röbner & Noll 2006).

Interactions with sedimentary environments

T⁰ assemblages also may reveal the dynamics of vegetation in 'real time' in some circumstances. Some of the most convincing examples of the ability of the fossil record to deliver a sense of such real time are those documenting plant recovery following burial in flood-borne sediment. This has been described for *Calamites* (Dawson 1851; Lyell 1865; Gastaldo 1992) and tree ferns (Falcon-Lang 2006b). Real-time patterns also have been documented in areas where successional patterns can be found following disturbance (e.g. Bashforth *et al.* 2010, 2011), and where 'nurse logs' have been suggested as essential for the germination and early establishment of juvenile plants (Césari *et al.* 2010). In an interesting twist on such real-time patterns, plant remains can be found in ancient flashy discharge channels showing evidence of being swept by currents, and partially uprooted in floods before being buried by shifting channel bars (Falcon-Lang 2006c, fig. 9K; Fielding *et al.* 2009). Common preservation of centroclinal stratification around erect trees (Leeder *et al.* 1984) and, more broadly, the occurrence of Vegetation-Induced Sedimentary Structures (VISS; Rygel *et al.* 2004) demonstrate that many Pennsylvanian trees existed in

Fig. 9. More than 13 lycopoid forests are stacked in a 25 m thick interval of the Sydney Mines Formation below the Harbour Main Coal at Sydney Mines, Cape Breton, Nova Scotia, Canada (H. J. Falcon-Lang, unpublished data). These fossil forests were first described, in a pioneering series of papers, by Brown (1846, 1848, 1849a,b). Brown's observations were so accurate that it is possible to relate his fossil forests (his beds 145–189) to the present-day succession (left column).

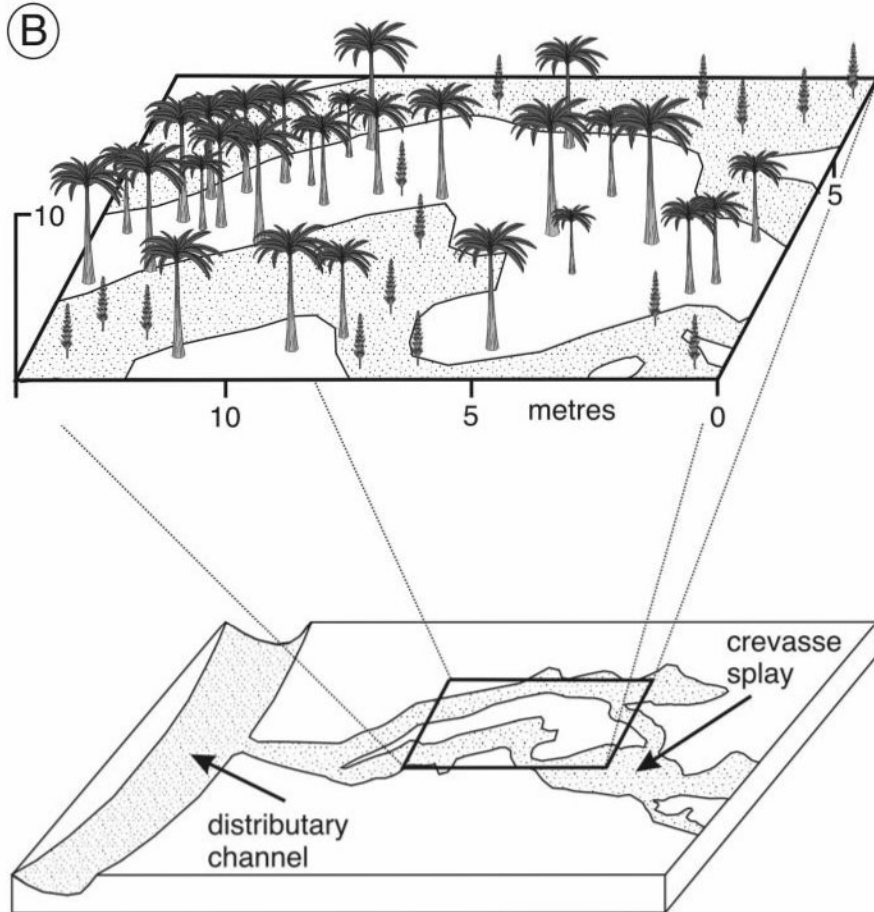
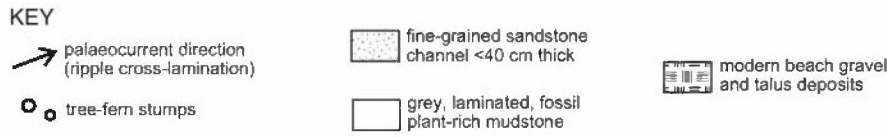
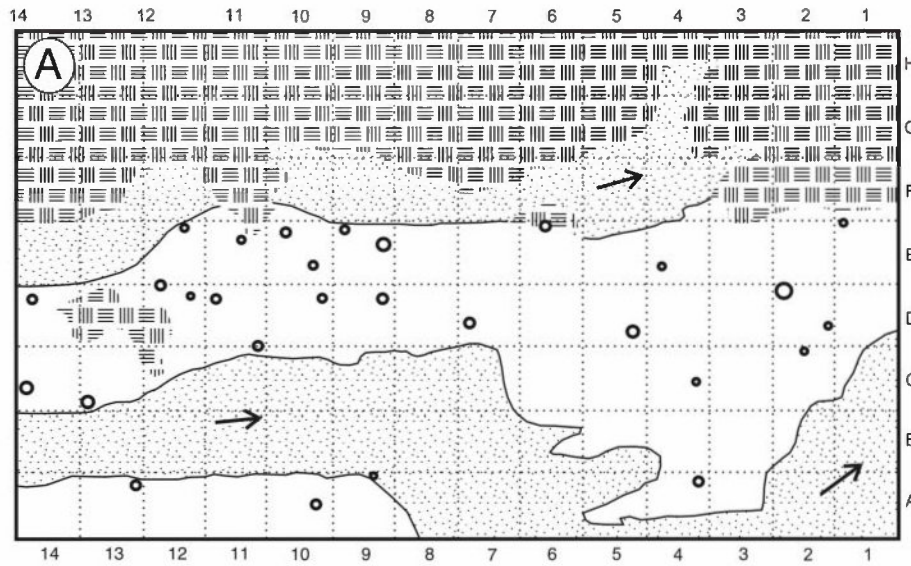


Fig. 10. (a) Bedding surface showing the distribution of tree-fern stump bases dotted between small crevasse feeder channels below the Point Aconi Coal, Sydney Mines Formation at Cranberry Head, Cape Breton, Nova Scotia, Canada; (b), a reconstruction based on these data (reproduced from Falcon-Lang 2006b).

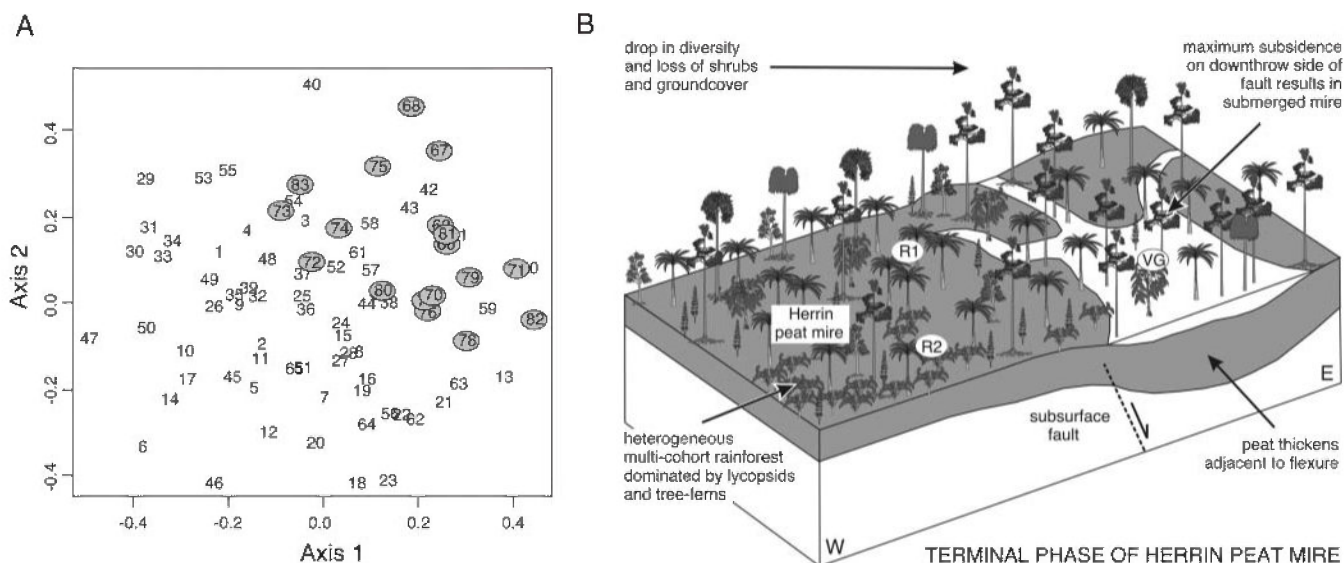


Fig. 11. Quantitative quadrat-based studies of parautochthonous plant assemblages analysed using ordination techniques (a) may be used to reconstruct spatial patterns of vegetation including ecological gradients (b), as in this example from a forest preserved above the Herrin Coal, Illinois, USA (modified from DiMichele *et al.* 2007). R1, R2, VG = separate samples from adjacent Riola and Vermilion coal mines.



Fig. 12. A sigillarian tree in growth position at Joggins, Nova Scotia, Canada. The feature winding around the trunk is not a liana but the collapsed stele of the tree because it occurs within the interior of the cast.

dynamic sedimentary environments subject to highly variable flood episodes.

Plant–animal interactions

In truly exceptional preservational circumstances, animals may be preserved on or within *in situ* vegetation providing unusual indicators of possible behavioural traits. Some of these include evidence of spider hunting strategies from specimens found on the leaves of cordaitaleans preserved in ash-fall tuffs (Selden & Penney 2010), suggestions of arthropleurids winding through *Calamites* thickets (Briggs *et al.* 1984; Schneider & Barthel 1997), or the famous tetrapod dens in hollow stumps at Joggins (Lyell & Dawson 1853; Dawson 1882). In the last case, lycopsid tree-stumps contain a mixture of charcoal, invertebrates and tetrapod skeletons (Falcon-Lang 1999; Falcon-Lang *et al.* 2006), raising the tantalizing possibility that these assemblages originated as land animals sought refuge in rotten stumps from encroaching wildfires (Scott 2001; Calder *et al.* 2005; Falcon-Lang *et al.* 2010), a fire-response behaviour witnessed in many small animals today (Fig. 14).

Discussion

The ancient standing forest is an enduring image, as powerful an attraction for palaeobotanists as for the public at large, promising insights into ancient ecosystems preserved in a sort of suspended animation, a chance to walk through groves long gone and to experience, nearly first hand, a lost world, turned to stone. With specific exceptions, this is a false hope, at least for the Palaeozoic. The vagaries of preservation have robbed most fossil standing forests of some part of their original composition. Certain taxonomic elements are far more likely than others to be preserved standing in place, and different modes of preservation favour different degrees of fidelity between the fossil forest and

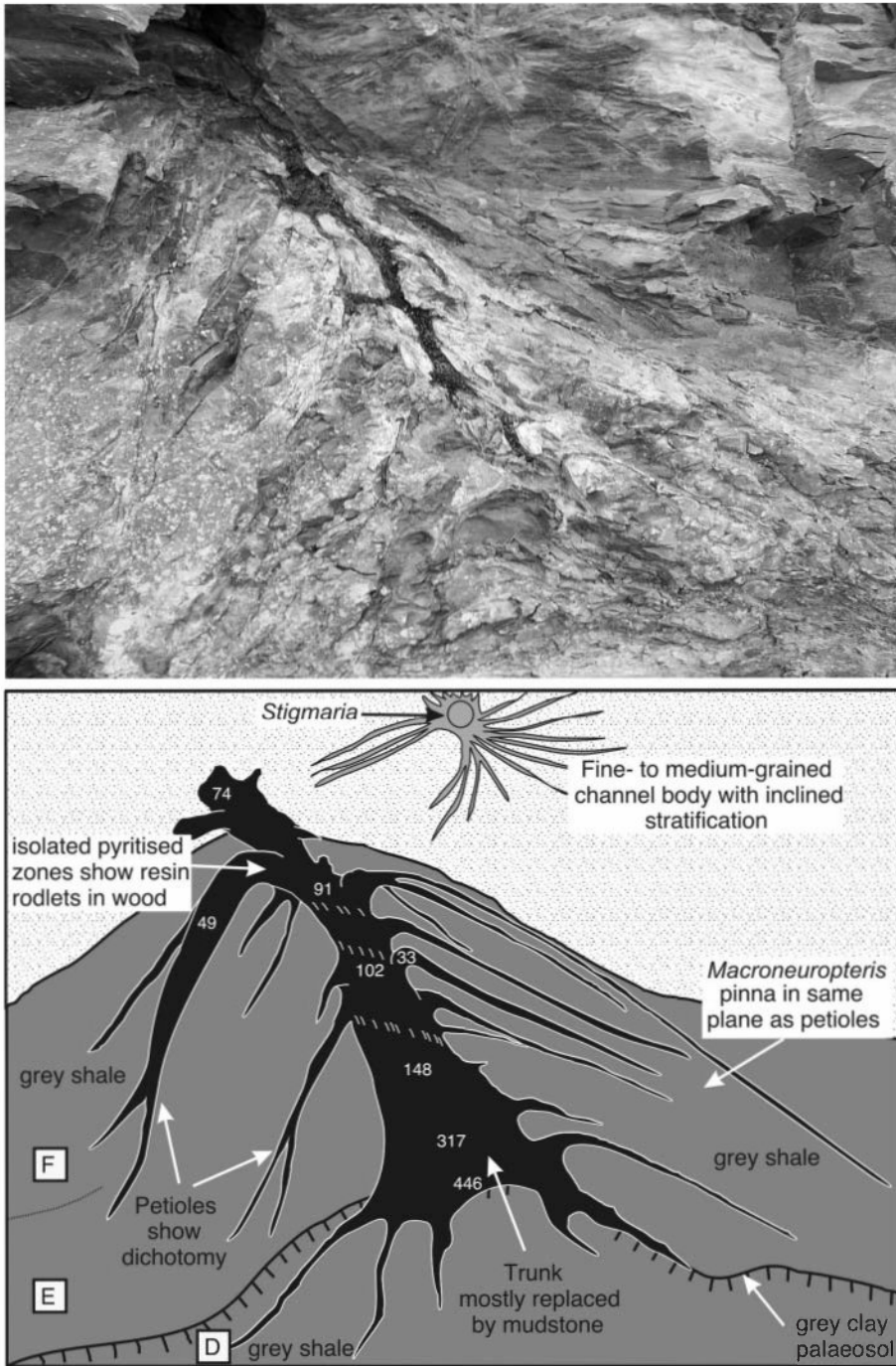


Fig. 13. A *Macroneuropteris* tree preserved above the Point Aconi Coal, Cape Breton, Nova Scotia, Canada (reproduced from Falcon-Lang 2009). The tree apparently shows a lax trunk and may have leaned on adjacent trees for support (reproduced with permission of Atlantic Geoscience Society).

its once-living progenitor. In addition, fossil forests are likely to represent only a portion of the possible ecological spectrum, preserving most often the wetter parts of the landscape, regardless of the prevailing climate, leaving the drylands almost unknown (Falcon-Lang *et al.* 2009b).

Perhaps the most faithful fossilized representations of living forests are those preserved by large and rapidly deposited airfall tuffs. The most recent, and spectacularly documented, of these are the 'coal forests' preserved in the Czech Republic (Libertín *et al.* 2009; Opluštil *et al.* 2009a,b), which preserve the spatial patterns of the standing vegetation, trees and ground cover, as well as the aerial parts of the plants fallen into the entombing

tuff. Such deposits have permitted not only reconstruction of spatial patterns, but also reconstruction of the parent plants in remarkable detail (e.g. Opluštil 2010). The number of forests preserved in tuff is not insubstantial and occurs through much of the record, but, remarkably, there are no examples from North America. This indicates, of course, the need for proximity to sources of volcanic ash, but also serves as a reminder that such ash is needed in sufficient volumes to bury vegetation deeply and effectively remove it from the zone of organic decay. Furthermore, many of the European floras buried in ash are covered with ash flows or mixed airfall and water-borne ash deposits (Wünsch 1865; Walton 1935; Scott 1990). The non-airfall



Fig. 14. Sigillarian stumps at Joggins, Nova Scotia, Canada contain tetrapod skeletons and charcoal, implying that animals used hollow stumps as refuges from fire. In this painting (courtesy of S. Greb, Kentucky Geological Survey), a tetrapod considers its options as the fire front approaches (see Scott 2001, for further details).

deposits have much the same characteristics as floods carrying clastic sediment, except that they may occur independently of particular climatic conditions, and thus can act as a preservational wildcard, in keeping with ash deposits in general.

A common preservational mode, one little commented on in the literature, is the burial of peat-swamp vegetation in tidal sediments. Examples of this appear to represent environments in which tidal rhythmites accumulated rapidly in areas flanking and within the contemporaneous estuaries dissecting, or adjacent to, peat swamps. The thickness, and seemingly rapid accumulation (Kvale *et al.* 1989), of these deposits above coal beds point to syndepositional peat compaction as a likely source of accommodation space, amplifying that created by rising sea level. Thick accumulations of tidal sediments are documented to preserve a mixture of upright stumps, mainly of lycopsids and calamites, but also may preserve less robust trees as prostrate adpressions, apparently close to or at their sites of growth. In addition, some of these deposits preserve the remains of ground cover (Gastaldo *et al.* 2004a,b; DiMichele *et al.* 2007). All of the examples we have found in the literature or in the course of our research are from the Early and Middle Pennsylvanian. The disappearance of

this mode of preservation in the Late Pennsylvanian may reflect a significant change in the size of the Gondwana icecap (Fielding *et al.* 2008) and resultant reduction in the amplitude and rate of sea-level fluctuations. Like airfall ashes, tidalites tend to preserve the forest with high fidelity, based on the diversity of forest strata preserved within the deposits. The change from peat swamp to tidal deposition attests to invasion of the peat swamp by waters with different qualities from those that saturated the peat during its development. Rhythmites herald the rise of sea level and generally presage the transgression of the peat bed by marine waters. Thus, the forests entombed within such deposits tend to represent only the final forest of the peat swamp, one that may reflect the effects of marine encroachment and thus may not be representative of the whole history of the swamp (DiMichele *et al.* 2007).

The least faithful taphonomic modes associated with T^0 preservation appear to be those that involve burial by water-borne sediment, be that sediment diverse clastic material transported in streams and rivers, or water-borne volcanic ash. The time between the death of the standing vegetation and its burial may be highly variable and could, in light of modern actualistic analogues (such as vegetational remnants in artificially flooded lakes), and based on the often monotonous compositional patterns and frequent lack of ground-cover plants, possibly involve differential decay and disappearance of a considerable percentage of the original vegetation (DiMichele *et al.* 2009). The uncertainties characteristic of these kinds of settings do not mean they are useless as snapshots of ancient forests, only that they must be studied with due care given to the sedimentary context of the fossil vegetation.

Most of the examples of in place vegetation that we encountered in the literature are from wetlands or wetter parts of dryland environments. Such settings are the most likely sites of attraction for sediment-laden waters or were near or even below mean water table and thus conducive for short-term preservation. In Pennsylvanian age wetlands, such occurrences most frequently involve peat and clastic swamps. In dryland settings, they most commonly represent within-channel deposits (Bashforth *et al.* 2010, 2011), particularly of braided streams where vegetation may have colonized abandoned segments of the main river channel system or may have grown along channel margins. Calamites are a common element of such wet areas within dryland settings. Some taphonomic factors are magnified in drylands and may select against preservation. For example, the unlikelihood of burial occurring in a sub-vadose environment contributes to organic oxidation in the short term, even if the deposit was buried rapidly and in a long-term tectonic setting favouring burial. Dryland Pennsylvanian age trees are typically woody and decay completely rather than leaving standing hollow cylinders within and around which sediment may accumulate. Finally, unless in low spots on a seasonally dry or arid landscape, sediment thicknesses would need to be considerable to avoid preferential erosion, thus selecting against preservation of vegetation living on interfluvies or extensive, well-drained parts of alluvial plains.

In the end, T^0 assemblages, like so many other kinds of fossil plant deposits, can be used most effectively if they are brought to bear on specific ecological or evolutionary questions, their strengths and weaknesses clearly considered (and spelled out; Bennington *et al.* 2009). When examined and considered in light of a particular ecological question, they may provide unparalleled information on plant spatial distribution, tree size, the distribution of ground cover, or the relationships among organs previously known only in fragmentary, dispersed states. When found

in a stratigraphic series, such as that at Joggins, Nova Scotia, the *in situ* forests can demonstrate change or conservatism of spatial patterns within particular habitat types. We note that there have been numerous reports of 'erect trees' over the past 200 years, mostly descriptive. They have contributed to our understanding of many aspects of the geological record and the ecologies of ancient vegetation. Yet much remains to be evaluated in light of sedimentology and taphonomy, interpreted ecologically, and applied to our broader understanding of ecological dynamics.

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