



Research papers

Calamitalean “pith casts” reconsidered

William A. DiMichele^a, Howard J. Falcon-Lang^{b,*}^a Department of Paleobiology, NMNH Smithsonian Institution, Washington, DC 20560, USA^b Department of Earth Sciences, Royal Holloway, University of London, Egham, Surrey TW20 0EX, UK

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ABSTRACT

Sediment-cast calamitalean axes in growth position are one of the most common fossils in the Pennsylvanian coal measures. In this paper, we challenge the long accepted position that these fossils represent “pith casts”. If correct, the hypothesis would require the sediment-cast pith to have been surrounded by a cylinder of secondary xylem during life, which later decayed away. However, sedimentary layers and structures developed around upright calamitaleans indicate that fluid flow was interacting directly with the preserved surface of the stem, not a hypothetical woody cylinder that lay external to it. Furthermore, stem diameter–density data for calamitalean stands already lies at the self-thinning threshold, and if actual stem diameters were significantly greater than preserved diameters, this threshold would be significantly exceeded. We also note that measured diameters for upright sediment-cast calamitaleans are more similar to stem diameter data for anatomically preserved calamitalean axes than for pith diameter data from the same axes. Our findings indicate upright calamitaleans are in fact stem casts and their preservation involved a two-stage process. First, stems were buried in flood-deposited sediments, creating a mold of the external surface of the plant. Second, following near-total decay of the axis, which may have occurred in a matter of weeks under tropical conditions, further sedimentation infilled the mold, forming a cast. As such, the preservation of upright calamitaleans was identical to that for arborescent lycopsids, which are commonly found in the same beds. That said, we stress that *some* transported sediment-cast calamitalean axes preserved in fluvial channel facies are certainly “pith casts” in the traditional sense, however, their morphologies differ from those specimens traditionally called “pith casts”. In this context, axes were buried in a single phase of sedimentation under energetic flow conditions, resulting in the pith becoming sediment-filled. However, intriguingly, a review of such genuine pith casts shows that only a tiny proportion preserves large woody cylinders surrounding the pith. This is not a taphonomic feature, but reflects our contention that the great majority of floodplain-based calamitaleans were reed-like plants with relatively small amounts of secondary xylem. Woody calamitaleans, including large tree forms, are documented almost exclusively from petrifications, and thus from peat-forming environments (coal balls) and, more rarely, floodplain settings under exceptional conditions of preservation (volcanogenic deposits, for example). These may be difficult to recognize in adpression preservation due to the masking, by wood development, of node-internode features. The differing architectures may reflect adaptations to disturbed and undisturbed environments, respectively.

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1. Introduction

Calamitaleans, relatives of modern *Equisetum* (the “horse-tail” or “scouring rush”), are one of the most commonly encountered groups of fossil plants of Pennsylvanian and Permian age (Cleal and Thomas, 1994). Comprising typically disconnected organs, including foliage, stems, reproductive structures, and roots, they may be preserved as adpressions, sediment-casts, and petrifications. One of the most compelling types of calamitalean fossil – and one that has caught the imagination of many paleontologists, professional and amateur – is the preservation of upright stems evidently in growth position

(T⁰ assemblages), and buried in a geological instant (e.g., Dawson, 1851; Scott, 1978; Gradzinski and Doktor, 1995; Calder et al., 2006; Falcon-Lang, 2006; DiMichele and Falcon-Lang, 2011; Fig. 1). These upright stems are almost always preserved as sediment-casts of some sort, retaining three-dimensional attributes and showing on their outer surfaces the distinctive nodes and ribbed internodes characteristic of the sphenopsid clade, looking superficially like giant *Equisetum*. Such sediment-casts also commonly are found in horizontal position, sometimes clearly flattened in place and buried during floods, but not infrequently showing some transport from their site of growth.

Whether in growth position or transported, the three-dimensional casts are generally referred to as “pith casts”, reflecting a belief that they are casts of the internal hollow pith area that is a key characteristic feature of the equisetalean clade. The origin of this taphonomic

* Corresponding author.

E-mail addresses: dimichel@si.edu (W.A. DiMichele), h.falcon-lang@es.rhul.ac.uk (H.J. Falcon-Lang).

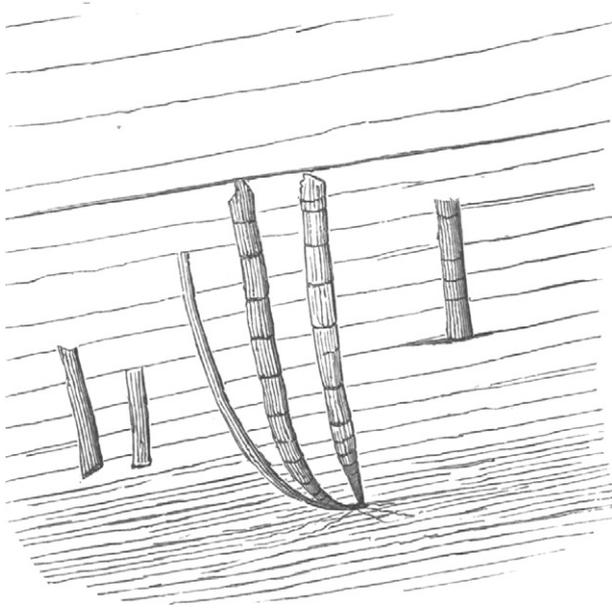


Fig. 1. A field sketch of a stand of sediment-cast calamitaleans, preserved in growth position in the Middle Pennsylvanian Pictou Group of Nova Scotia, Canada (reproduced from Dawson, 1851).

model may be traced to a collaboration between E.W. Binney and J.D. Hooker, in the course of their pioneering work on coal balls (Hooker and Binney, 1854). In a letter dated August 25, 1854, Hooker described the concept to his close friend, Charles Darwin (Letter 1581, www.darwinproject.ac.uk), as follows: “I spent a day at Manchester with Binney at Fossil plants, a study I hate & despise & am always sneaking after all the same. I think we have proof positive now that all Calamites are mere casts of piths! I am glad of it for the Survey people used always to laugh at us for maintaining that we did not know that Calamites was an identifiable vegetable form – The fact is that the striæ are the impressions of the interspaces between the medullary rays, & the scars are points at which bundles go from a pseudo-medullary sheath through the woody wedges to the bark.”

The calamitalean stem, like that of all members of the Equisetalean clade, is organized on a body plan of distinctly separate nodes and internodes, with all leaves and lateral appendages borne in whorls, in

most cases at the nodes. This is reflected in the anatomy of the plant. The stem has a central pith that is lined along its external margin by parenchyma but is hollow in the center through the internodal regions. At the nodes, the pith becomes solid, consisting of drum-head-like plates of parenchyma, termed nodal diaphragms (Fig. 2A). Surrounding this pith region is a ring of primary vascular bundles, each of which contains a distinctive carinal canal, surrounded by primary xylem (Fig. 2B). From each primary xylary bundle, a wedge of secondary xylem develops, the extent of which is variable. In specimens with thick wood, the individual bundles fuse laterally with adjacent bundles after some distance to form a solid ring of wood. This wood generally retains wide parenchymatous rays separating the wedges developing from each primary xylem bundle.

In their landmark textbook, Taylor et al. (2009) have described how this anatomical structure might result in the distinctive “pith casts” preserved in the fossil record. We quote them here because their exposition spells out the taphonomic implication of the pith cast hypothesis very clearly. “Pith casts of calamites were formed by sediments that filled the hollow central canal [i.e. the pith] and solidified before the more resistant tissues of the stem, such as the primary and secondary xylem, were broken down by various biological agents. Following the decay of the remainder of the axis, additional sediment filled in around the cast, thus resulting in a mold-cast preservation type. The structural organization of a calamite stem includes wedges of primary xylem that extended into the central canal [pith], with broad channels of parenchyma representing the vascular rays between. On the surface of a pith cast, these appear as a series of ribs and furrows – furrows mark the former position of the primary xylem wedges, whereas ribs correspond to the vascular rays between them” (Taylor et al., 2009, p. 350).

To be absolutely clear, in order to form such “pith casts” of upright, autochthonous stems, sediment is envisioned to have surrounded and, sometime during or after burial, infilled the partially hollow central portion of a stem. Following decay of the wood, the space created is inferred to have been infilled by further sedimentation. The resulting outer surface of the cast is thus supposed to show the inner surface of the pith. As Taylor et al. (2009) imply some of the support for this viewpoint comes from the well-known form of most anatomically preserved calamitaleans, which have a circumferential ring of secondary xylem, outside the pith and primary vascular system. Such wood buries the mostly hollow pith region and would have provided a means for the stem to stand erect and resist collapse as it was

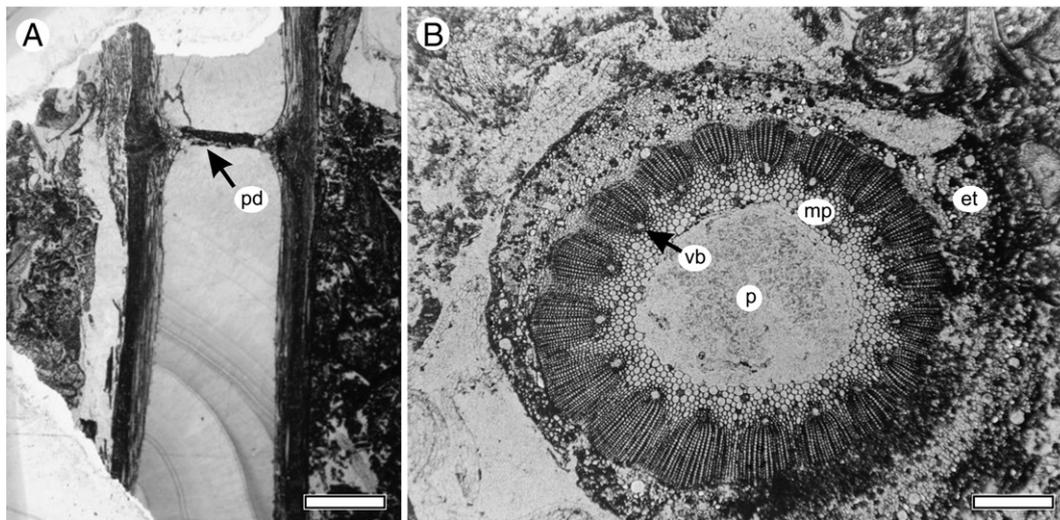


Fig. 2. General anatomy of calamitaleans. A) Longitudinal section of a calamitalean axis showing a solid pith diaphragm (pd), from a specimen from the Lower Pennsylvanian, Lancashire, England (courtesy of Hans Steur). B) Cross section of a Lower Pennsylvanian calamitalean axis from Yorkshire, England, showing the characteristic structure of the hollow pith (p) with marginal parenchyma (mp), surrounded by a ring of vascular bundles (vb) containing carinal canals and minimal extraxylary tissue (et) (Copyright, British Geological Survey, photograph number: P685958).

buried by the weight of flood-borne sediment. Numerous examples of such woody calamitalean stems are known from coal-ball permineralizations collected directly from coal beds, silicified nodules, or trees preserved as petrifications in ash beds (e.g., Fig. 3; Williamson and Scott, 1895; Anderson, 1954; Andrews and Agashe, 1965; Rößler and Noll, 2006).

However, the occurrence of a woody cylinder also raises a problem for the traditional taphonomic model because, if correct, the preserved pith cast ought to be surrounded by a thick covering of wood and bark, which is not seen in the many examples of upright calamitaleans that we have observed. In the traditional model, summarized by Taylor et al. (2009), this problem is solved by the later decay of the wood and a secondary phase of sedimentation infilling the gap. Seward (1898) also seems to have been well aware of this problem, but attempted to resolve it in a different way, by assuming that the wood had been compressed to a negligible thickness. In this regard, he argued that “a zone of wood 27 mm in thickness is reduced in the process of carbonisation to a layer 1 mm thick” (p. 366). However, it is uncertain whether burial would result in the kind of lateral compressive force to achieve this effect, and certainly not without significantly deforming the sediment-cast as well.

The presumed existence of a layer of wood and bark is similarly problematic for interpreting transported “pith casts”. Where these horizontally disposed stems occur in parautochthonous associations in flood-basin shales, they may show varying degrees of infilling by mud, and may lie atop one another in thick mats. In most instances, the stems are surrounded by a thin coaly rind with the external features of ribbing and nodes variably, but usually fairly clearly, visible. Where horizontally disposed stems occur in channel sandstone bodies, they are usually more dispersed, but also can comprise more concentrated assemblages. In both these instances, it is perplexing why the presumed “pith cast” is visible and not deeply buried in the secondary xylem layer, unless the fossils were somehow fractured along the contact zone between the pith and wood. Yet even if this had fortuitously (and repeatedly) occurred, one would also expect to see a section through the wood, lying either side of the pith. And it seems unreasonable to assume that horizontally disposed calamitalean stem remains were transported as sediment-filled “pith casts”, which would have been too fragile to survive transport as bed load in moving water.

In this paper, we argue that the great majority of sediment-cast calamitaleans, both autochthonous and allochthonous, do not represent internal “pith casts” at all but, in fact, external stem casts very similar to the stem casts of arborescent lycopsids, with which they commonly co-occur (DiMichele and Falcon-Lang, 2011; Gastaldo, 1986); we know of no cases where these lycopsid tree casts have

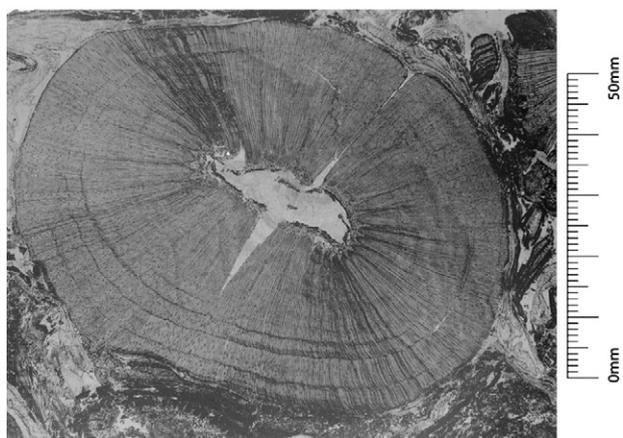


Fig. 3. A Lower Pennsylvanian calamitalean axis from Lancashire, England showing development of a relatively thick (~30 mm) woody cylinder (Copyright, British Geological Survey, photograph number: P685953).

been referred to as “pith casts”. This is not a new idea, but one implicitly accepted by some of the earliest investigators of calamitalean forests (Dawson, 1851, 1868, 1892).

Like the lycopsids, the sediment-cast calamitalean stems and, importantly for our argument, subterranean rhizomes, can show varying degrees of external decay, corrosion or abrasion. Perhaps best illustrated by Weiss (1884), there are clear examples showing that the layers of bark and perhaps secondary tissues found external to the typically ribbed pith cast were very thin, at most, and easily removed or decayed (Fig. 4). In other instances, these tissues appear to be variously compressed against the ribs such that the ribbing is clearly visible through the bark, again indicating that they were veritable “skins”, thin and ephemeral (Fig. 5).

These two plant groups, the calamitaleans and the arborescent lycopsids, in contrast to the many other kinds of plants common in Carboniferous and Permian deposits, appear indeed to have had hollow cavities in the stems, especially in the lower parts, during life, as a result of their fundamental architecture and an anatomy that permitted inside-out decay. In addition, they populated the wetter, low-lying parts of landscapes, including channel margins and intra-channel bars, likely to attract sediment-laden floods (DiMichele and Falcon-Lang, 2011). Furthermore, they were exceptionally well anchored in the substrate, unlike contemporary tree ferns or pteridosperms, either by extensive stigmarian rhizomorphs, or by development from subterranean rhizomes (Fig. 6), and thus were capable of remaining erect when inundated by flood-borne sediments. And finally, they possess unusually diagnostic external morphologies, rendering them easily and immediately recognizable.

These characteristics facilitated the peculiar mold-cast taphonomy that has so often preserved them in growth position. However, rather

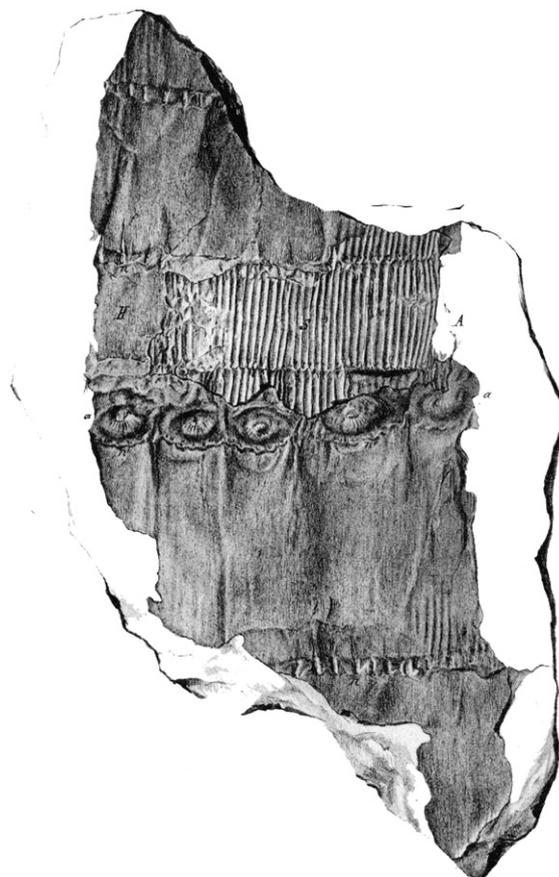


Fig. 4. A *Calamites* from the Stephanian C of Wettin near Halle/Saale, Germany showing the exterior markings of pith (nodes and internodes) covered by a thin “skin” of surrounding tissue. Reproduced from Weiss (1884, plate I, fig. 1). Scale: 77 mm diameter at node labeled a.



Fig. 5. A specimen of *Calamitina paucirama* Weiss from near Jedlina Zdroj (formerly Charlottenbrunn), Lower Silesia, Poland. An upright stem showing a thin layer of external tissue still visible, strongly adpressed against ribs beneath. Small ovals at nodes are interpreted as leaf scars and large ovals as branch scars. The lines beneath branch scars appear to be deformations on the surface of the specimen, possibly taphonomic in origin. Reproduced from Weiss (1844, plate XI, fig. 1). Scale: 40 mm diameter axis.

than the pith being generally filled first, resulting in an internal pith cast, we argue here that the stems were initially buried by sediment. The buried stem then decayed in the moist tropical climate, leaving a mold of the external surface, which was subsequently cast by a later phase of sedimentation. Sediment-cast calamitaleans are, therefore, stem casts and not generally pith casts.

2. Sediment-cast calamitaleans in growth position

As already discussed, according to conventional thinking based on permineralized calamitalean axes (Anderson, 1954; Andrews, 1952; Cichan and Taylor, 1983), upright stems in growth position were woody in life, to some degree, and represent only sediment-cast pith regions, their surfaces reflecting the outer margin of the pith area. This model raises three initial questions, which allow the “pith cast hypothesis” to be critically tested. (1) How do measurements of pith and stem diameter in anatomically preserved axes compare with measurements of the presumed “pith casts”? (2) Given the



Fig. 6. A specimen of *Calamites (Stylocalamites) suckowii* Brongniart from the Orzesze (formerly Orzesche) Mine in Upper Silesia, Poland, showing a horizontal rhizome and vertical side shoots. Secondary rootlets can be seen in various states of preservation attached at the nodes on both the rhizome and the upright shoots. Reproduced from Weiss (1884, plate IV, 1). Scale: horizontal axis is 69 mm diameter at widest point.

typical close proximity of standing casts, just how thick could the woody cylinder have been if it were present during life? (3) If there was a woody cylinder of considerable thickness surrounding the primary body and hollow pith, which later decayed away, to what extent is this supported by sedimentological evidence?

2.1. Comparison of sediment-cast dimensions with anatomically preserved calamitaleans

As an initial test of the “pith cast hypothesis”, we collated data on the diameter of sediment-cast calamitalean upright stems, and the diameter of the piths and stems of anatomically preserved calamitaleans (Fig. 7). Sediment-cast diameters were obtained from two field studies undertaken over a 15 year period by one of us (HFL): the two intervals investigated comprised the Early Pennsylvanian Joggins Formation of Nova Scotia, Canada, a predominantly wetland coastal plain succession ($n = 65$; Falcon-Lang et al., 2006) and the Early Pennsylvanian Tynemouth Creek Formation of New Brunswick, Canada, a mostly dryland alluvial plain succession ($n = 143$; Falcon-Lang et al., 2010). Only sediment-casts that were nearly three-dimensional were measured; however, as most of these axes showed some compression, both the long and short diameters were measured, and the median value obtained.

For permineralized calamitaleans, data were collated from publications (e.g., Anderson, 1954; Andrews, 1952; Cichan and Taylor, 1983; Reed, 1952; Rößler and Noll, 2006, 2007; Scott et al., 1997; Wang et al., 2006), online museum collections with reliable scale bars (e.g. <http://geoscenic.bgs.ac.uk/asset-bank/action/viewHome>), and online fossil shops, using the same measurement protocols. However, in this case, both pith diameter and stem diameter were measured, and Pennsylvanian ($n = 14$) and Permian ($n = 22$) datasets were kept separate. In most cases, stem diameter was taken as the diameter of the secondary xylem, as extraxylary tissues commonly are not preserved. No attempt was made to control the position in the tree; however, in order to partly exclude lateral branches and the upper parts of trunks, only axes with a diameter > 20 mm were selected for study.

The two Canadian field studies show that calamitalean sediment-casts have diameters in the range of 20–160 mm. However, over 80% of records we examined are in the range of 40–70 mm diameter with a mean for all datasets of 59 mm ($n = 208$). In addition, we have noted, on various field excursions, prostrate axes up to 200 mm (e.g., DiMichele et al., 2010), although flattening may have enlarged some of these. Furthermore, older published literature suggests a

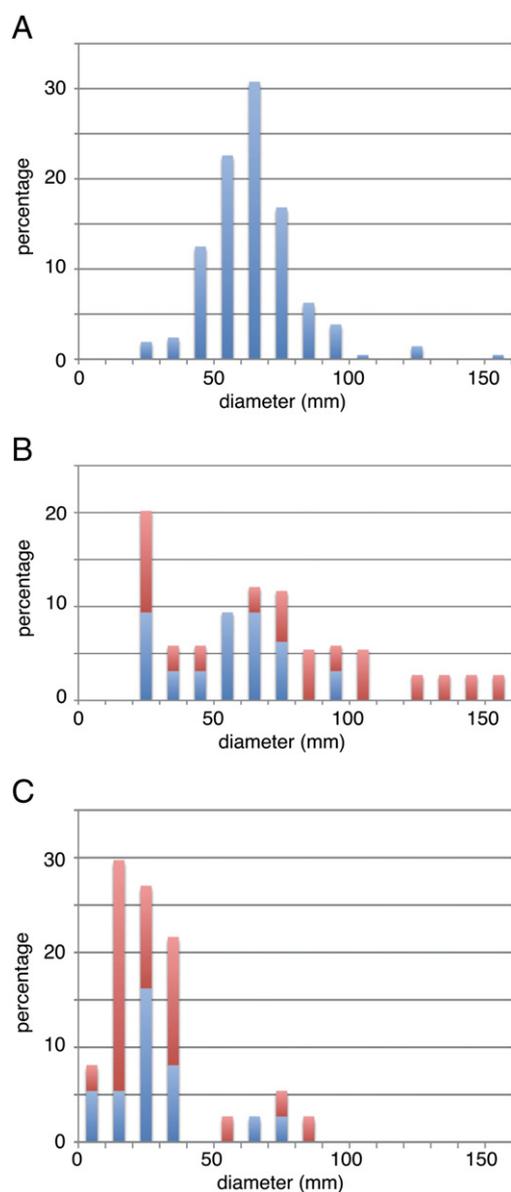


Fig. 7. Calamitalean diameter data. A) Diameter of pith casts in growth position in the Lower Pennsylvanian Joggins and Tynemouth Creek formations of Canada; B) Stem diameter in anatomically preserved calamitaleans, subdivided by Pennsylvanian occurrences (blue) and Permian occurrences (red); C) Pith diameter in anatomically preserved calamitaleans, subdivided by Pennsylvanian occurrences (blue) and Permian occurrences (red). See text for explanation.

very small number of larger (up to 650 mm) calamitalean axes (e.g., Renault, 1893–1896). Overall, our findings are fairly similar to an earlier compilation by Kidston and Jongmans (1917), who concluded that most calamitalean casts were in the range of 50–200 mm diameter.

For anatomically preserved axes, pith diameter ranges from 9 to 75 mm (mean 29 mm) and stem diameter from 23 to 90 mm (mean 52 mm) for Pennsylvanian data ($n = 14$). In contrast, while Permian axes ($n = 22$) have similar-sized piths (9–82 mm; mean 28 mm), stem diameter is rather larger (20–160 mm; mean 81 mm). Furthermore, the ratio between stem: pith diameter ratio and is 2.53 and 2.96 for Pennsylvanian and Permian datasets, respectively. In preparing these statistics, we excluded three very large stems (600 mm, 240 mm and approximately 250 mm) with relatively small piths (15 mm or less) recently described from the Early Permian of Chemnitz, Germany (Rößler and Noll, 2006) and the Late Permian of southwest China (Wang et al., 2006), whose inclusion would have significantly skewed the results.

We are cognizant of potential difficulties in comparing measurements of sediment-cast specimens with anatomically preserved specimens. The former mostly come from occurrences in growth position and represent the basal part of trunks, whereas the latter may include material from the basal or upper trunk, and even large lateral branches (>20 mm diameter). Nonetheless, some conclusions may be drawn. Clearly the modal size of sedimentcast axes (40–70 mm) is much more closely similar to the mean size of Pennsylvanian and Permian stem diameters (52 mm and 81 mm, respectively) than it is to mean pith diameters (29 mm and 28 mm diameter, respectively). Furthermore, pith diameters above 40 mm have been reported only rarely (5 out of the 36 specimens in our datasets) and dimensions never exceed 82 mm. Yet, sediment-casts are dominantly in this larger size range and may be up to double the diameter of the largest documented pith dimensions. This initial analysis suggests that upright sediment-cast calamitaleans are stem casts not pith casts.

2.2. Tree proximity, stand density and the self-thinning threshold

A second approach to testing the “pith cast hypothesis” is to consider the density of calamitalean forests. Whereas upright stem casts of calamitaleans can occur singly, they more frequently occur in quite dense stands. One of the best sites for observing upright calamitalean forests in plan view is the Gardner Creek section of the Early Pennsylvanian Tynemouth Creek Formation of New Brunswick, Canada (Fig. 8; Falcon-Lang, 2006). Measurements of seven separate fossil horizons indicate densities ranging from 4 to 9 stems per m^2 and a mean sediment-cast diameter of 62 mm (Falcon-Lang, 2006, and unpublished data). In the Early Pennsylvanian Joggins Formation of Nova Scotia, Canada (Falcon-Lang et al., 2006), similar bedding plane exposures indicate calamitalean densities on the order of 2 to 13 stems per m^2 with a mean stem diameter of 53 mm (Falcon-Lang, 1999).

A universal relationship between plant metabolism and the spatial distribution of trees in three dimensions has been posited for modern multi-species forests composed of individuals of different ages (Enquist and Niklas, 2001; Enquist et al., 2009; West et al., 2009). An even-aged forest composed primarily or entirely of a single species is a special case of this more general relationship, which presumably applies to ancient forests as well. One expectation, termed “self-thinning” is that tree density declines as tree diameter, and hence biomass, increases, a function of the fact that trees compete for limited resources (sunlight, water, soil nutrients), and as they mature, uncompetitive neighboring trees die off (e.g., Silvertown and Doust, 1993). Consequently, when diameter–density data for modern forests are plotted, it is possible to ascertain the upper threshold for stem diameter at a given density (e.g., Cao et al., 2000). This relationship has been questioned for some clonal plants but studies show that it does apply to



Fig. 8. Example of a bedding surface in the Lower Pennsylvanian Tynemouth Creek Formation, New Brunswick, Canada, for which calamitalean density data were obtained. Diameter of upright trees is ~50 mm, for scale.

woody, tropical species with perennial life-histories, while at the same time annual plants may not follow the self-thinning trajectory (e.g., de Kroon and Kalliola, 1995; Peterson and Jones, 1997). Thus, given the woody and presumed perennial nature of calamitalean clones (recognizing that not all calamitalean species were clonal), we believe we can safely assume that the self-thinning laws apply. Our Pennsylvanian calamitalean forests from Canada already lie more or less on the self-thinning threshold, if not above it, representing trees with the maximum possible stem diameter for the extremely high densities measured.

However, if these sediment-cast axes represent only part of the tree diameter in life, how might this affect our calculations? As noted above, the ratio between pith diameter and stem diameter is 2.53 and 2.96 for Pennsylvanian and Permian calamitaleans showing anatomical preservation. As such, if we add wood to a typical 60 mm diameter “pith cast” we might infer that it must have represented, in life, a tree with a diameter in the range of 152–178 mm. Applying these “corrected” diameters to our high density stands would push these forests significantly above the self-thinning threshold, in other words being impossibly dense stands for the inferred mean diameter (Fig. 9). It is possible, though not likely, that extinct trees with unusual architectures, like the calamitaleans, may have had quite different self-thinning thresholds than the conifers and dicots on which the modern analysis is based. Greater uncertainty may lie in the realm of how such clonal trees would compete for resources with their non-clonal neighbors – as individual trees? Allowing for these important caveats, this density: diameter analysis further challenges the concept that upright calamitaleans are pith casts of trees that were much more substantial in life.

A more straightforward piece of evidence that leads to exactly the same conclusion is the observation of adjacent sediment-cast calamitaleans that are in very close proximity to one another. For example, in the Tynemouth Creek Formation, there are several examples of adjacent axes in growth position that, in plan view, either touch one another or are spaced only a few millimeters apart. In related examples seen in vertical section from the same site, calamitalean axes are commonly observed budding off from a parent rhizome, forming a dense

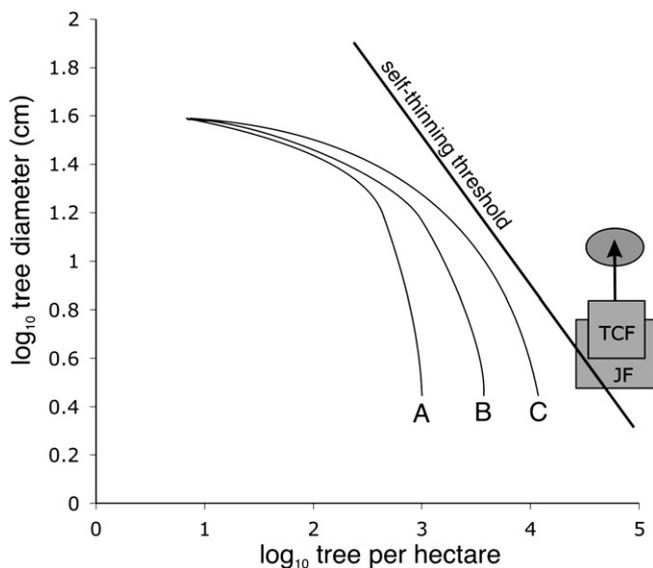


Fig. 9. Log-transformed relationship between tree density and tree diameter based on modern forestry observation showing the self-thinning threshold, and data for three forests of varying initial density: medium-density stand A (1000 trees per hectare, tph); high density stand B (4000 tph); extremely high density stand C (10,000 tph). Figure and dataset modified after Cao et al. (2000). Data for calamitalean stands in the Lower Pennsylvanian Tynemouth Creek (TCF) and Joggins (JF) formations are plotted, together with “adjusted” values assuming that real tree diameter is 2.5 times larger than observed diameter. Unadjusted calamitaleans lie on or near the self-thinning threshold, but adjusted stands significantly exceed it.

“bush” (Fig. 10), a pattern reported relatively commonly in the literature (e.g. Dawson, 1851; DiMichele et al., 2009; Fig. 1). The only credible interpretation of this phenomenon is that the preserved axis diameter observed today is the same, or at least nearly the same, as in life.

2.3. Relationship of upright calamitaleans to sedimentary layers

A third way to test the “pith cast hypothesis” is to examine the relationship of upright sediment-cast axes to entombing sedimentary layers and structures. If we maintain that such calamitaleans are casts of the “pith”, then the following seem to be the rarely stated assumptions: (1) The axis would need to have been open to the penetration of sediment, basically through its entire preserved length, meaning that the nodal diaphragms (which partitioned the pith in life) either would have to have been gone prior to, or were breached during, sediment filling. (2) The fully buried axis would have needed support for an open central cavity to become filled by sediment, meaning either by a rind of mechanically strong tissue (secondary xylem) or by burial in sediment deposited before or during central cavity filling. Thus, the stem most likely would have been either partially or fully buried by sediment prior to, or contemporaneously with, the infilling of the pith area. (3) The rind would (a) have had to undergo decay subsequent to burial, in order to allow surrounding sediment to lie in direct contact with the pith cast, or (b) need to have been highly compacted against the pith cast after burial, remaining only as a thin layer (the contention of Seward, 1898).

If the organic material sometimes found adherent to the “pith” cast were the result of compaction of the rind (wood and parenchyma) with only minimal decay, then the degree of compaction would need to have been considerable. As noted above, some compression specimens (e.g., Figs. 5–6) show that tissues outside the distinctly ribbed portions of the stem were very thin. In woody permineralized specimens, secondary xylem of typically 10–30 mm radius (Anderson, 1954; Cichan and Taylor, 1983; Wang et al., 2006) has been reported, requiring compaction of perhaps 20:1 or more to account for the thinness of the rinds observed on most calamitalean casts. Were this to have been the case, the great differences in compaction ratios between organic material and siliciclastic sediment must be considered (Nadon, 1998). Plant material compacts between 10:1 and 80:1, by some estimates (e.g., Winston, 1986), whereas the compaction ratios of siliciclastic sediment are approximately 2:1 for siltstone and close to zero for sandstone, both of which commonly entomb and cast calamitalean stems. Thus, whether the rind decayed or whether it was compacted, the expectation is that one should see a distinct zone of sediment



Fig. 10. Two calamitalean axes budding off a “parent” axis in the Lower Pennsylvanian Tynemouth Creek Formation, New Brunswick, Canada. This is evidence that these plants were of the same diameter in life, as preserved today. Hammer for scale is 0.4 m long.

between the outer edge of the “pith” cast and the inferred original outer edge of the stem.

If the entombing sediment were stiff (had “set up”) before the hypothetical decay or compression of the rind began, there ought to be evidence for a cavity remaining after decay of the rind tissue. Thus, as Taylor et al. (2009) have stressed, an upright calamitalean “pith cast” should show clear evidence for a double-filling event: the first stage involving filling of the hollow pith area, and the second the filling of the hollow left by decay or partial decay of the rind tissue. This should be detectable on outcrop as one or more concentric fillings around the “pith cast”, in total radius equal to the thickness of the original organic rind. Such filling sediment possibly would be distinct from the general sediment of the deposit, in terms of color, texture, or bedding. On the other hand, if the sediment entombing the exterior of the full stem were still in a fluid or semi-fluid state, some deformation of that sediment around the central “pith” cast might be expected as the organic rind either decayed or compacted. At least a few examples of these hypothetical relationships should have been noted in the literature, given the observational powers of most field geologists; however, to our knowledge, none have, though there are many examples where undeformed laminae truncate directly against upright calamitalean stems (Fig. 11).

2.4. Vegetation-induced sedimentary structures

A fourth test of the “pith cast hypothesis”, and one closely related to that discussed above, is the occurrence of what has been termed vegetation-induced sedimentary structures (VISS) by Rygel et al. (2004). These comprise sedimentary structures generated by the

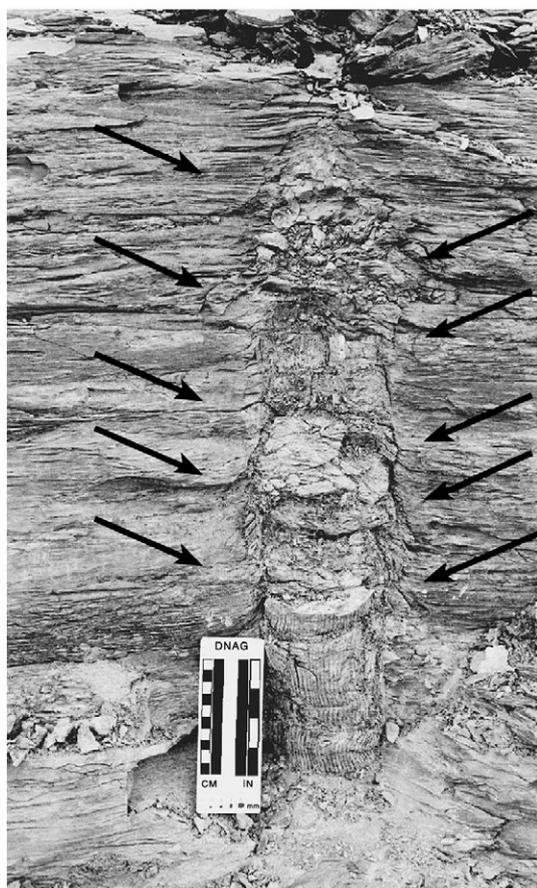


Fig. 11. A Lower Pennsylvanian calamitalean tree buried in tidalites in Alabama, USA (reproduced from Gastaldo et al., 2004) with arrows highlighting rhythmites (scale in cm). Note that the laminations are upturned and truncate directly at the edge of the upright stem.

fluid flow around an obstacle such as, in this case, an upright calamitalean tree (Fig. 12). Such structures might include laminations that dip towards the trunk (centroclinal cross-stratification; Leeder et al., 1984), formed as a result of the acceleration of water around the tree, which generates scours that are subsequently draped when the flow wanes. Another style of VISS is the occurrence of laminations that are upturned towards the tree and record mounding of sediment against the obstacle at times of relative low flow velocity. Of key importance is that close examination of these features demonstrates that (1) laminations and structures truncate directly against the edge of the preserved sediment-cast tree and (2) they indicate that fluid flow was interacting directly with the preserved surface of the stem not a hypothetical woody cylinder that lay external to it.

Thus, all these discussions lead us to infer that sediment-cast calamitaleans in growth position are either (1) external stem casts or (2) pith casts of an architectural variety that had only a very small amount of secondary xylem and whose outer surface more or less corresponded to the preserved surface of the sediment-cast. Our literature review indicates that anatomically preserved calamitaleans typically had a variably thick cylinder of secondary xylem, generally favoring the former hypothesis. However, an exceptional 75 mm diameter stem described by Anderson (1954), which showed a 65 mm diameter pith and only ~5 mm radius of secondary xylem development, also offers some support for the latter hypothesis. It is possible that such a “reed-like” calamitalean could hypothetically generate pith casts with minimal sediment disturbance due to compression and decay of outer layers. Nonetheless, it should be possible to distinguish between external stem casts and internal pith casts based on the structures preserved.

2.5. Could upright calamitaleans be “pith casts” of reed-like plants?

If sediment-cast calamitaleans are pith casts of reed-like plants, then the cast is a mold of the outer surface of the pith. However, in contrast, if sediment-cast calamitaleans are stem casts then the features preserved reflect the structure of the outer surface of the plant stem or some of the layers immediately beneath that outer surface (analogous to the “decortication” stages of arborescent lycopsid stems). Yet, here lies the problem because, as Taylor et al. (2009, p. 350) note, “the impression of the outer surface of the xylem cylinder and the pith cast look almost identical, even in the alternation of ribs and furrows at the node”. Nonetheless, close examination of the carbonaceous rind that commonly surrounds sediment-cast calamitaleans should allow internal and external casts to be distinguished.

Although these rinds are usually quite thin (<1 mm), they more commonly than not show diagnostic features suggestive of the outer surface of the stem (ribs, nodes, branch scars, even attached lateral branches in whorls, locally with attached stroboli or leaves; Figs. 13–15), although such features may be dampened on some specimens (Fig. 5), due to the exposure of underlying tissues, such as a thin layer of wood. However, coaly organic matter frequently adheres to the indentations between the ribs, indicating that the organic mantle of the stem reflects such architecture from its inner to its outer surface, and that such stems had limited wood development.

A comparison with stem casts of arborescent lycopsids is useful at this point to illustrate how a decayed external surface of a trunk might show composite features from different internal tissues. Most commonly, the outer surface of the stem preserves the characteristic leaf cushions on the external side of the coaly rind, so there is no question that the outer surface of the stem is in view, even if the carbon has been lost from the immediate surface of the leaf cushions. However, in contrast, in some *Sigillaria* specimens, the diagnostic paired to fused parichnos aerating strands may instead appear on the outer margins of sediment-filled casts (Fig. 16), reflecting the deeper internal surfaces of the preserved bark, and suggesting a considerable amount of external tissue decay prior to burial of the stem

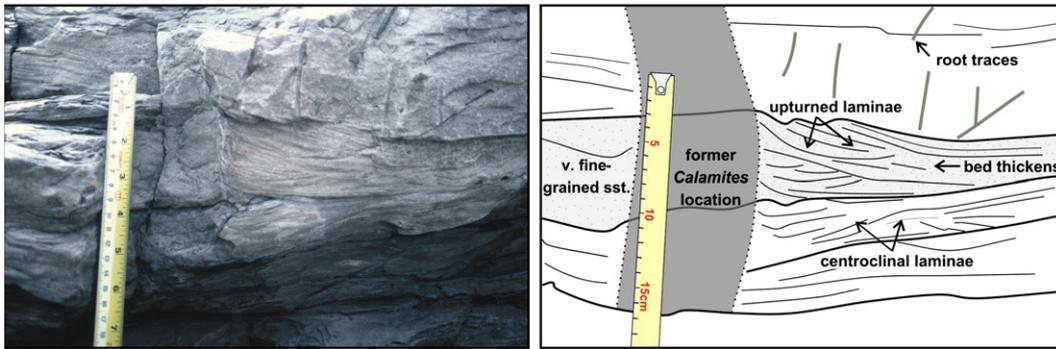


Fig. 12. Vegetation-induced sedimentary structures (VISS) surrounding an upright calamitalean tree in the Lower Pennsylvanian Joggins Formation, Nova Scotia, Canada (reproduced from Rygel et al., 2004, fig. 10).

externally and filling of the interior hollow area with sediment. Thus, the occasional presence of features such as infranodal canals on the surface of sediment-cast calamitaleans does not falsify the hypothesis that these are external stem casts. Even if these plants were reed-like, with relatively little wood development, they are still preserved as external stem casts.

2.6. Casts of rhizomes

Among the most significant challenges to the “pith cast hypothesis” are horizontal, likely subterranean rhizomes. Weiss (1884, his plate IV, 1) illustrates a nice example of such a specimen (reproduced here as Fig. 6). Although slightly flattened, it is cast with sediment, has roots at the nodes on both sides, indicating that it was subterranean at the time of death and preservation, and has carbonized remains of tissue adherent to the ribbed surface, through which the ribs are clearly visible. In addition, it bears two upright axes, each of which also bears roots at the nodes, indicating that they, too, were embedded in the sediment at the time of casting.

It stretches credulity to imagine that this, or other specimens like it, are casts of pith regions of an originally much larger, woody axis. The presumed woody rind would have had to decay below ground without leaving a noticeable cavity in the original sediment (nor would there be an obvious way to fill such a cavity were it to have

developed), or have been compressed to a tissue-paper thin layer through which the ribs could show. In addition, the roots are attached to the specimen directly at the nodes, both on the horizontal axis and on the attached upright axes, suggesting little or no tissue beyond the surface of the modern-day cast (the interpretation we prefer). Alternatively, one might presume either that a now-missing woody rind decayed while leaving intact the roots, around which wood would have developed as cambial activity proceeded, or that the wood was compressed to a thin sheet while, at the same time, the roots that passed through it were uncompressed or minimally compressed.

2.7. Positive proof that sediment-cast calamitaleans are not pith casts

Positive proof that sediment-cast calamitaleans are not pith casts comes from a remarkable fossil preserved in seasonally dry red bed

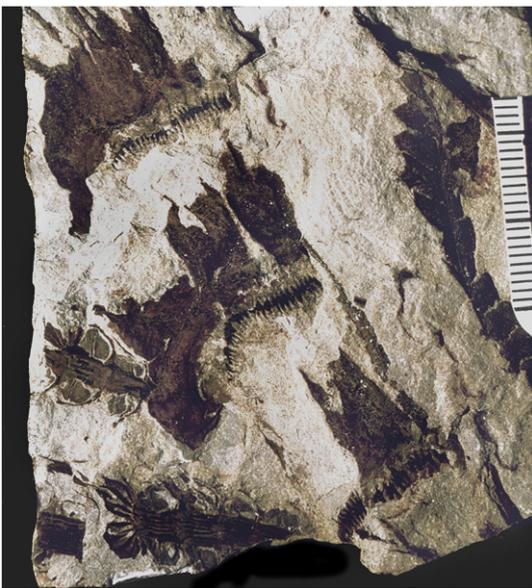


Fig. 13. A specimen of *Calamites multiramis* Weiss from Manebach, Germany showing lateral branches bearing strobili, accessioned in the Museum für Naturkunde der Humboldt-Universität zu Berlin (courtesy of Manfred Barthel, Berlin, Germany). Scale in mm (small divisions).



Fig. 14. A specimen of *Calamites ramosus* Artis from the Westphalian of Nowa Ruda (formerly Neurode), Lower Silesia, Poland, showing lateral branches and *Annularia* foliage, some of which may be still attached. This specimen was reproduced in Weiss (1884, plate V) and is in the collection of the Museum für Naturkunde der Humboldt-Universität zu Berlin (photo Hans Kerp, Münster, Germany).



Fig. 15. A specimen of *Calamites goeppertii* Ettingshausen from the mid-Stephanian of Reischbach, Saar, Germany, showing branch scars at the nodes (axis 60 mm diameter). This specimen is in the collection of the Laboratory of Palaeobotany and Palynology, Utrecht, Netherlands (photo, Hans Kerp, Münster, Germany).



Fig. 16. A Middle Pennsylvanian sediment-cast sigillarian lycopsid tree (*Syringodendron* sp.) buried in growth position at Jenlin strip mine, Indiana, USA. Note the paired parichnos scars in parallel bands indicating that the external leaf cushions had been sloughed off or decayed away prior to burial (DiMichele et al., 2009). Scale: upper trunk, 0.3 m diameter.

deposits in the Tynemouth Creek Formation of New Brunswick. Here, an upright calamitalean exposed in plan view appears to show a “wound” that allowed sediment to enter the pith at the time the stem was buried, forming a poorly preserved pith cast, but positioned inside the stem cast (Fig. 17). Presumably, this fossil formed by a three-stage process. First, the tree must have been wounded, creating a breach in its secondary xylem cylinder, i.e., an opening connecting the pith area to the outside (cf. Stopes, 1907). Second, the tree was buried in fine-grained sand, forming an external mold in the usual way, but with some sediment entering the pith through the opening afforded by the wound, creating an internal cast as well. It is possible that wounding and burial happened in the same flood event. Third, after the sediment-cast pith had hardened in the dry climate, the woody cylinder surrounding the pith decayed, and the hole it left behind itself became infilled with sand of a different character than that in which the stem was buried. Consequently, this extraordinary fossil

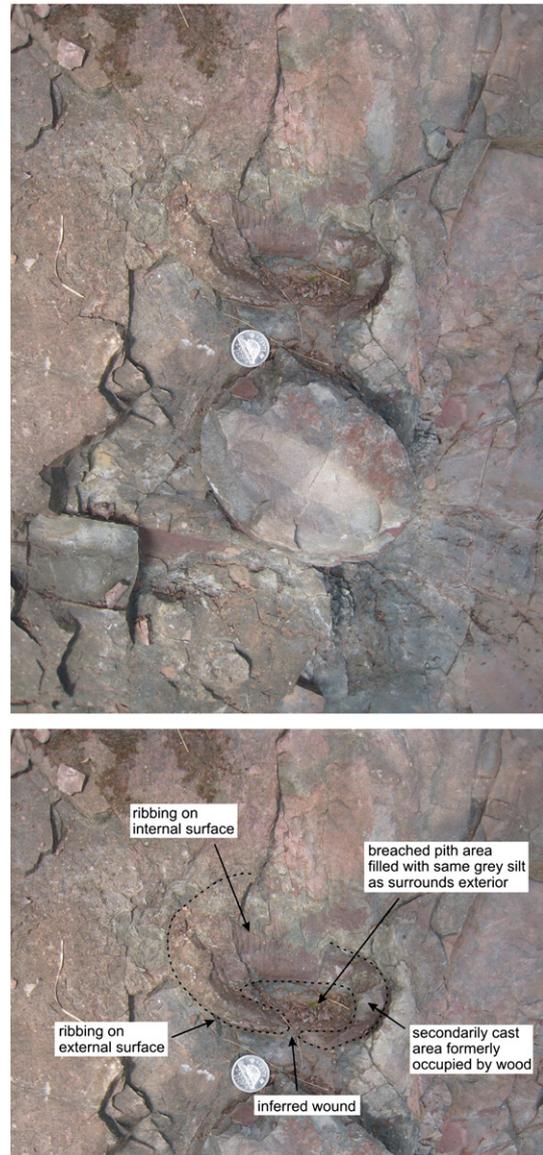


Fig. 17. The exception that proves the rule: a rare example of an external stem cast containing an internal pit cast from the Lower Pennsylvanian Tynemouth Creek Formation, New Brunswick, Canada. A) Two stem casts in growth position, observed in plan view, scale: coin 21 mm diameter. B) Annotated photo of the upper stem cast, scale: coin 21 mm diameter. This tree was apparently wounded, allowing sediment to fill the pith during the initial burial event. Later the secondary xylem decayed and the space was infilled by a second phase of sedimentation. Ribbed internodes are visible both on the outer surface of the pith cast, and also on the outer surface of the stem cast.

is a stem cast of the external surface but also contains a smaller internal cast of the pith cavity! Both external and internal surfaces preserve internodal ribbing.

The thickness of the sedimentary fill of what we infer is the decayed woody cylinder is only on the order of 7–10 mm radius in these specimens. This, in turn, supports the idea that sediment-cast calamitaleans were generally rather “reed-like” plants with a large pith cavity and relatively small amount of secondary xylem development. This reed-like architecture contrasts with the calamitaleans of undisturbed, Pennsylvanian peat-substrate environments (anatomically preserved in coal balls), which were mostly substantially more woody (typically >10–30 mm radius of wood; Anderson, 1954; Cichan and Taylor, 1983), with the exception of Anderson’s unusual reed-like form noted above. It also differs from certain Permian clades that developed gigantic woody trunks (radii up to 320 mm) and appear to have been adapted to more water-stressed settings (Barthel and Rößler, 1996; Kerp, 1984; Naugolnykh, 2005; Rößler and Noll, 2002).

2.8. A model for the formation of upright sediment-cast calamitaleans

Without having first-hand observations of the process of preservation of sediment-cast calamitaleans in growth position, we offer the following model as a likely explanation accounting for most of the observations seen on outcrop:

- (1) Those calamitaleans most commonly preserved as sediment-casts are associated with facies representing disturbed environments, along river banks or on floodplains. Most of these species were small and slender, much like over-sized *Equisetum* in terms of their growth architecture. They were not extensively woody, being supported by relatively small amounts of secondary xylem, or none at all, and therefore probably were of fairly limited stature.
- (2) The habitats of the Pennsylvanian sediment-cast calamitaleans were predominantly fluvial and prone to flooding. These floods rapidly buried whole stands of trees. In some instances the plants were able to recover from the floods and re-grow, as in the example presented by Gastaldo (1992). In other cases, the plants were killed, the stems broken open or sheared off, and then filled with sediment from the surrounding environment, especially if it were still flooded. In some instances, they were cast with similar sediment brought in by a later, but nearly contemporaneous flood. Because calamitaleans, like modern equisetaleans, had plates of parenchymatous tissue, like drum heads, spanning the nodal regions (Fig. 2A), these must have been decayed prior to infilling, either in life or after death, or destroyed mechanically during sediment entry.
- (3) Most upright calamitalean stems demonstrate some degree of departure from vertical (e.g., Appleton et al., 2011, fig. 10), as if they were pushed by currents bringing in the sediment in which they were buried, or by the weight of the sediment itself, were it to have come in preferentially on one side of the stem (Fig. 18). This implies that these plants were not able to stand upright in the face of floodwaters to the same degree as the basal portions of lycopsid trees. The latter were firmly anchored to the substrate by their stigmarian rooting systems and appear to have been stiffly vertical in their construction, held so by the well documented periderm/bark that provided the main support structure of the stem (e.g., Philips and DiMichele, 1992). The flexibility of the calamites further supports the idea that they were reed-like with minimal supporting woody tissue.
- (4) Preservation at an angle also suggests that filling of the stem cavity, in most instances, would have happened after the



Fig. 18. A Middle Pennsylvanian sediment-cast calamitalean axis preserved in growth position in Indiana, USA. The specimen is inferred to have been tilted at a low angle by floodwaters during burial (DiMichele et al., 2009). Rock hammer for scale, 22 mm in width at blunt end.

upright stems were stabilized by a surrounding mass of sediment, with exposed parts broken off or decayed sufficiently to permit entry of sediment to the hollow central areas. This calls either for two sedimentation events, not unlikely if the environments of preservation were being inundated actively (e.g., Gastaldo, 1992, for example), or for the stems to be broken off during active burial so that sediment could both surround them and enter the hollow central area (with due consideration given to the presence of nodal septa, mentioned above).

- (5) The thin outer rind of tissues (primary vasculature and a thin woody layer) was then coalified and compressed. However, due to its initial thinness this compaction did not lead to significant distortion of sediment against the outer surface of the stem. The outer surfaces of these stems preserved the nodal morphology, internodal ribbing and appendicular scars at the nodes typical of this clade, though these may have been accentuated as the organic rind decayed revealing the internal layer, or as it compacted and vitrified in its compression against the sediment-cast.

3. Horizontally disposed stems and stem casts

Horizontally disposed, addressed remains of calamitalean stems are far more common than autochthonous remains found in upright posture. These vary from (par)autochthonous, where they were knocked over and buried nearly in place by floods, to allochthonous, transported some distance from their site of growth. In all instances, the stem remains may be accompanied by some degree of decay and disarticulation. And not all specimens have a sediment-cast pith region preserved. The degree of flattening, therefore, can be considerable, resulting in an effectively two-dimensional fossil. Most commonly, such addressed, prostrate remains have an organic rind similar to that found on upright stems. Thus, even though these remains have a different taphonomic history from upright cast stems, many of the same problems are faced regarding interpretation of the organic rind and sediment-cast central area, if one exists.

3.1. Critique of current thinking about prostrate calamitalean stems

In the literature, horizontally disposed calamitalean stems are not differentiated from upright, autochthonous stem remains, both referred to as “pith casts.” This interpretation raises some serious matters with regard to a model of formation. The clearest articulation of a

sedimentary model is that of [Gastaldo et al. \(1989\)](#), who considered addressed stem remains to have two distinct components. The first was the infilling of the hollow central cavity by sediment, deposited either from suspension or bed load. This is necessarily followed by a separate, temporally later event, the decay and/or coalification of the tissues external to the pith cast.

The first of these assumptions seems essentially irrefutable. Addressed calamitalean remains frequently have a core of sediment, of variable thickness, generally identical in grain size, color, and bedding/lamination to the sediment that surrounds and entombs the stems. In this situation, the stems were certainly hollow at the time of burial and the sediment surrounding them, carried in the ambient aqueous environment, mostly likely was deposited contemporaneously with that within their hollow centers (whether that took place in one or more depositional events). Consider also the following observations that characterize most of these specimens: (1) the stems are generally fully buried in that sediment, (2) their hollow core fillings are usually only wafers and not complete round pith region casts, or there is no pith cast at all, and (3) there is no reported evidence of infaunal activity within the central sediment if present (as noted by [Gastaldo et al., 1989](#), for the infilling of a Holocene woody log). These factors combine to suggest that complete burial of such specimens took place during the transport and burial event, in most instances. In other words, it was only the rare, exceptional specimen that lay open on the surface or at the bottom of a stream, fully or partially exposed, accumulating sediment through multiple floods over an extended period of time. In most cases such pith-area filling as did occur (zero to some) was contemporaneous with burial of the stem remains.

Far more problematic is the second part of the model, which, although articulated clearly by [Gastaldo et al. \(1989\)](#), is an implicit inference in all studies of these remains, from the earliest conception of the pith cast interpretation. Its fundamental assumption is that a woody rind surrounded the pith area, that this rind decayed or was compressed, and that the external morphology of the specimen reveals the internal characteristics of the outer surface of the pith. As discussed for upright stem remains, this interpretation requires that the ribs of the fossil stem, which are inferred to represent the manifestation of the carinal canals and any surrounding sclerenchymatous or primary xylem tissue, somehow retain rigidity while woody secondary tissues outside of them decay and collapse. Where there is a coalified layer outside of the sediment-cast, such tissues external to the pith must have completely collapsed against a rigid frame, such that they take on its form. It would have to be true, then, if the form of these coalified compressions were to reflect the inner part of the pith cavity, that the form of the pith was created by the strength of the tissues immediately surrounding the hollow pith area, because the classic node–internode form and internodal ribs can be seen even in specimens where there is no sedimentary filling of the pith region. In such simple compressions, supposed external surface form of the “pith” remains visible on the outside of the axis, in the organic compression.

Using this model, it becomes essentially impossible to explain the ribbed, nodal architecture seen on mats of calamitalean stems ([Fig. 19](#)), deposited in the same sedimentary event, especially examples where none have sediment-cast “piths” ([Fig. 20](#)). Such mats require that the external tissues of each stem decay back to the pith margin, the stems then deflating upon one another. It requires that smaller axes with attached foliage and branches, on which ribs and nodes are clearly visible ([Fig. 21](#)), somehow undergo differential decay of (woody) tissues external to the pith, but not of the foliage and branches ([Figs. 13–15](#)). And it is doubly difficult to explain how such axes could form in those instances where there is no evidence of a sedimentary wafer in the hollow, central, pith region.

Finally, calamitalean stem compressions are common components of addressed megaflores in which the remainder of the assemblage is



Fig. 19. Addressed, and partially sediment-cast calamitalean axes arranged in dense, randomly orientated prostrate accumulations; Baker Coal, Middle Pennsylvanian, Indiana, USA. Ruler for scale divided into one-inch intervals (courtesy of Scott Elrick, Illinois State Geological Survey).

enriched in foliage and axes of pteridosperms and ferns, axes of lycopsids, and organic debris of various kinds and sizes. Why, one might ask, should the organic exteriors of calamitaleans be preferentially decayed under such circumstances while the organic matter derived from virtually every other plant group is not decayed ([Fig. 22](#))? This is especially highlighted by the case of sediment-filled lycopsid stems and stigmarian roots (again, never referred to as “pith casts”), but which are often preserved with partial sediment infills, around which the stem has collapsed under sediment pressure following burial.

3.2. A model for the formation of prostrate, addressed calamitalean axes

In keeping with the model proposed by [Gastaldo et al. \(1989\)](#), we interpret prostrate calamitalean stems to have formed by burial in sediment, much like other parautochthonous to allochthonous organic plant remains. (1) This formation may have been effected simply by



Fig. 20. Mat of calamitalean axes without sediment-cast central areas. USNM Specimen 528424, USNM locality number 40005, late Virgilian (Stephanian C), Late Pennsylvanian, Markley Formation, North-central Texas, USA. Scale in mm (small divisions).

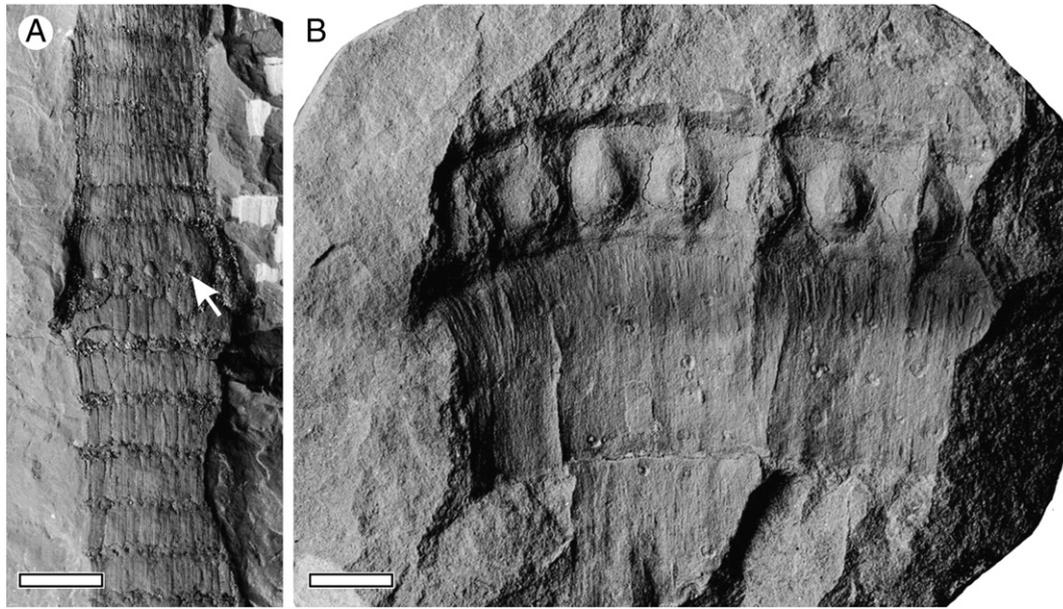


Fig. 21. Prostrate calamitanean axes showing demonstrably external features from the Lower Pennsylvanian of Yorkshire, England. A) Calamitanean showing leaf scars and whorled branch scars (arrow) at nodes, from Royston, Yorkshire, England; scale: 8 mm (Copyright, British Geological Survey, photograph number: P685992); B) Close-up of whorled branch scars on a specimen from Adeer Pit, Ayrshire, Scotland. That this is the external surface of the plant is demonstrated by the occurrence of attached spirorbids, an aquatic invertebrate, scale: 8 mm (Copyright, British Geological Survey, photograph number: P687965).

the burial and compression of the stem, without any infilling of its pith by sediment. (2) On the other hand, sediment infilling of a hollow central area may have occurred to varying degrees, measurable by the degree of flattening of the stem and the thickness of the sediment wafer that fills its central area. (3) Such internal sediment, when present, is most often identical to the sediment that entombs the total the fossil assemblage, including the calamitanean stems. This strongly suggests that the sediment entered a broken or fragmentary calamitanean stem at the time of burial. Not ruled out is the possibility that some prostrate calamitanean stems could have had their hollow central areas fully or partially filled by multiple flood/sedimentary events, were they to have lain exposed or partially buried on a surface or subaqueously, but such instances appear to be rare, given the lack of reports of sedimentary indicators of this kind of filling. (4) The buried stems, including their relatively thin external

tissue layers, are compressed in the same way that other compression fossils are in the assemblage of which they are a part. (5) The external features of these stems do not result from decay of tissues external to the pith. As with upright stems, they are reflective of the external morphology of the stem during life. Their external surfaces do not reflect the morphology of the outer margin of the pith, brought-out or enhanced by decay of exterior tissues and the processes attendant fossilization and compression.

We should note, independently of this model, that sediment-filled, prostrate “pith casts” in adpression preservation, must have formed *in situ*. It would be very difficult, indeed, to imagine that these plant fossils were first cast by sediment and then transported in water to their site of deposition. Issues of both flotation and survival of a sediment-cast in traction, in the bed-load fraction of a stream, would appear to rule out any such considerations.

In this model, we refer back to the comments of Rößler and Noll (2006) regarding the much greater-than-presently-appreciated diversity of the calamitaneans. As already discussed, it appears that the calamitaneans of highly-disturbed riparian environments may have been morphologically distinct from those of more stable peat-substrate habitats or long-persistent, low sediment flux, swampy sites. Repeated disturbance and burial (e.g. Gastaldo, 1986) favored those plants capable of recovering rapidly from such events.

3.3. Do genuine calamitanean pith casts exist? – Yes

All that said, there do appear to be rare examples of genuine pith casts preserved in the fossil record. In one case that we have documented above in the Lower Pennsylvanian Tynemouth Creek Formation, an autochthonous, upright stem has a sediment core that is different lithologically from the sediment between that core and the outer edge of the stem (Fig. 17). This appears to have formed by an initial infilling of a hollow central area, followed by decay of a woody zone with subsequent sediment infilling, fulfilling the expectations of the model of Taylor et al. (2009). The specimen still retains the outermost morphology of a calamitanean stem, however, reinforcing our argument that most stems of this size are stem, rather than pith, casts. Furthermore, the pith cast preserved in this example is somewhat unlike normal



Fig. 22. Calamitanean axes (two, in center of photograph), closely adpressed upon one another, showing clearly jointed and ribbed external morphology beneath thin, exterior layers of carbonized tissue. There is no evidence of a central filling by sediment. Note the co-occurrence of pteridosperm axes and *Neuropteris* foliage (middle and bottom) and marattialeean tree fern stem (top right). Immediate roof shales of the Springfield (No. 5) coal bed, late Desmoinesian age, Middle Pennsylvanian, Carbondale Formation, Indiana, USA. Rock hammer for scale, 22 mm in width at blunt end.

sediment-cast calamitaleans, being narrower with poorly developed nodes and internodes.

In addition we have observed several examples of prostrate stems that are demonstrably pith casts. These occur in the Lower Pennsylvanian Joggins Formation (Falcon-Lang et al., 2006) and above the Herrin Coal in Illinois (DiMichele et al., 2007). They comprise a sediment-filled central pith area surrounded by an external layer of woody tissue, the latter preserved in a flattened, adpressed state (Fig. 23). Therefore, rather than requiring a process of double-filling, there was but a single infilling event, followed by compaction of surrounding woody tissue into a thin sheet.

4. Discussion

The concept of the calamitean pith cast is venerable and of long standing. As already noted, it originated with Joseph Hooker at a time when he was fast rising to become one of the superstars of mid-Nineteenth Century science. With these credentials, it is unsurprising that the concept obtained mainstream acceptance. The pith cast hypothesis was, however, not universally accepted. William Dawson, one of the best-known Carboniferous palaeontologists of the Nineteenth Century, held a more nuanced view, writing that, “sometimes what we call a Calamite is a mere cast of its pith showing longitudinal striae and constrictions at the nodes. Sometimes we have the form of the outer surface of the woody cylinder, showing longitudinal ribs, nodes, and marks of the emission of the branchlets. Sometimes we have the outer surface of the plant covered with a smooth bark showing flat ribs, or almost smooth, and having at the nodes regular articulations with the bases of the verticillate branchlets, or on the lower part of the stem the marks of the attachment of the roots (Dawson, 1892, p. 122–123; many of the features that Dawson discusses are illustrated in Figs. 4–6, 13, 15, 20, 21). Dawson’s view is broadly consistent with our own position, although we believe that pith casts comprise the minority of such fossils.

However, while some Nineteenth Century scientists were aware that calamitean axes could be preserved as both as stem casts and pith casts, since the dawn of the Twentieth Century that nuance seems to have been lost. It is important to stress that we are not questioning the basic idea that the (partially) hollow central pith area of calamitean stems could, and frequently did, become cast by an influx of sediment. Our challenge is to the notion that such fossils represent only the central areas of once much larger diameter stems in which the pith region was surrounded by a thick mantle of various

tissues, mostly wood. Rather, we have argued that the common organic compressions and casts with an organic rind represent infilled stems, the external surfaces of which represent closely the external appearance of the plant in life. In this way, the calamitean stem cast parallels, but with much less interior decay (because of less original tissue mass along the inside of the hollow central area), the stem cast of a giant lycopsid tree, which no one would ever seriously consider calling a “pith cast”. In this sense, a pith cast is only part of the larger stem cast. The stem fossil, if cast, includes the coaly rind, part of original outer tissue, and the sediment-filled hollow central cavity cast, which may include both the original hollow pith area, and any area opened to infill by decay of the tissues lining the pith cavity, which must have been considerable.

As with most conventional wisdoms, when situations or conditions are encountered that do not fit the model, some head-scratching ensues generally followed by a digression explaining why the data are somehow flawed, thus preserving the truth as established by authority. An example of this is provided by Arber (1918), who puzzled about the absence of “infranodal canals” below the nodes in some calamitean specimens, traditionally thought to be pith casts. Arber concluded that, in fact, such specimens are not pith casts in the strictest sense, but “incrustations of surfaces that lay external to the pith” (Arber, 1918, p. 213), which he called “sub-medullary casts.” These sub-medullary casts supposedly resulted from “considerable decay” of the outer margin of the pith cavity prior to casting. Arber credits his insight to observation of a petrified stem in the collection of Dr. D.H. Scott, reflecting the unspoken certitude, well established by that time, that calamitean stems were universally woody. So, here is another example calling for decay of the tissues external to the pith, from the inside outward, yet still leaving the basic form of the pith, the ribs and nodes, visible. This explanation, on the surface of it, fails the test of “total evidence,” in that it explains one particular observation, the absence of small openings below the nodal plate in some calamitean stem fossils, while failing to account for many other factors, such as the widespread nature of this phenomenon, the need for partial decay of the most resistant parts of the stem, leaving the tissues most likely to decay behind (in tens of thousands of examples), or the occurrence of such morphologies in specimens that do not have cast central areas.

Our contention that most calamitean stem fossils represent external stem casts, in turn, implies that many of these flood-basin plants had a somewhat “reed-like” growth habit quite similar to modern *Equisetum*, with little development of secondary xylem. In contrast there are the large diameter stems of *Calamites gigas* (Kerp, 1984; Taylor et al., 2009, fig. 10.35), which have been interpreted as succulents, with specialized mechanisms for water storage, permitting them to live in dry environments (Barthel and Rößler, 1994; Rößler and Noll, 2002; see Naugolnykh, 2005 for an alternative interpretation), something quite different from the generally accepted conceptions of Carboniferous calamitaleans. Such growth morphologies are markedly different from the woody calamitaleans, which seem to have preferred swampy, stable substrates, both on peat and clastic soils, but were themselves diverse in size and form. Thus, a secondary insight, in agreement with Rößler and Noll (2006), is that the calamitaleans were much more diverse in terms of their growth architectures and phylogenetic diversity than is generally appreciated. Using due caution, we recognizing that not all calamitean axes represent stem casts or were reed-like in habitat, and that genuine pith casts do occur, the most unequivocal examples of which also show evidence for wood development. All such things considered, however, the adpression fossil record is dominated by the stem casts of reed-like calamitaleans.

Acknowledgments

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Fig. 23. A rare example of a genuine calamitean pith cast, surrounded by its adpressed outer woody cylinder, from the Lower Pennsylvanian Joggins Formation of Nova Scotia, Canada (courtesy of Melissa Grey, Joggins Fossil Institute, specimen number NSM008GF031.151). Scale bar in cm (numbered intervals).

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