Review of Palaeobotany and Palynology 173 (2012) 1–14

Contents lists available at SciVerse ScienceDirect

Review of Palaeobotany and Palynology

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

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

ARTICLE INFO

Article history:
Received 12 December 2011
Received in revised form 30 January 2012
Accepted 31 January 2012
Available online 12 February 2012

Keywords:
Calamites
pith cast
fossil forest
plant taphonomy
fossilization
Late Paleozoic

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 petrifactions, and thus from peat-forming environments (coal balls) and, more rarely, floodplain settings under exceptional conditions of preservation (volcanigenic 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.

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 petrifactions. 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 (T^0 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).

0034-6667/$ – see front matter
doi:10.1016/j.revpalbo.2012.01.011

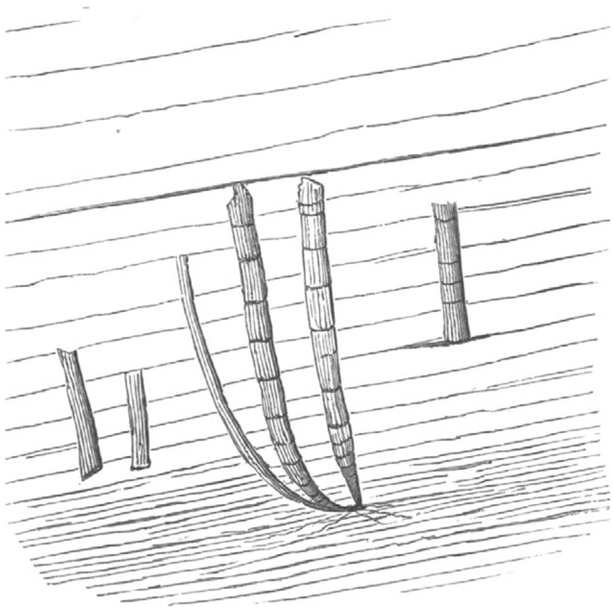

Fig. 1. A field sketch of a stand of sediment-cast calamitaleans, preserved in growth position in the Middle Pennsylvanian Pictou Group of Nova Scotia, Canada (reproduced from Dawson, 1851).

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 drumhead-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

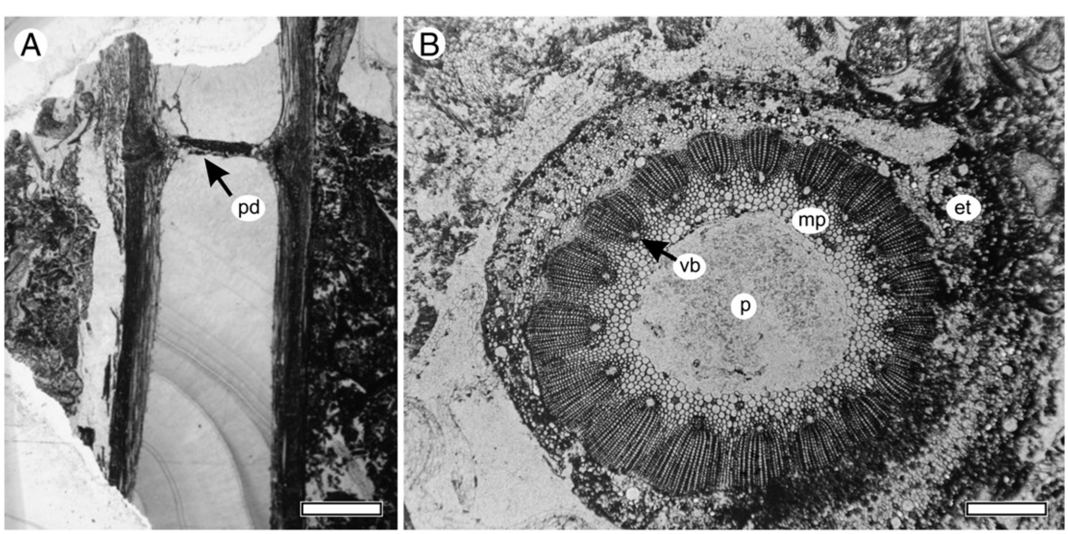

Fig. 2. General anatomy of calamitaleans. A) Longitudinal section of a calamitalean axis showing a solid pith diaphragm (pd), from a specimen from the Lower Pennsylvanian, Lancashire, England (courtesy of Hans Steur). B) Cross section of a Lower Pennsylvanian calamitalean axis from Yorkshire, England, 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).