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From plants to coal: peat taphonomy of Upper Carboniferous coals

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ABSTRACT

Quantitative analyses of the botanical composition in coal-ball concretions provide a basis for assessing stratigraphic and regional patterns of peat taphonomy in relation to swamp paleoecology and, in turn, to coal origins. The categories of plant organ and tissues we discuss are lycopod outer trunk bark, lycopod cortical and twig litter, stigmarian roots, wood (all sources), fern roots, medullosan cortisal tissues, foliage and fructifications. Data are drawn from 20 coals from 34 mines, ranging from lower Westphalian A of England and Belgium to lower Stephanian (Missourian) of Illinois, U.S.A. The 53 data sets represent 8115 coal balls and 388,872 cm^2 of surface area of peels with contents identified by taxa, tissue-organs and preservational states or as an unidentified fraction of organic detritus and non-botanical components.

Lycopod trees contributed 26–86% of biovolume in Westphalian coal-ball deposits with important exceptions in Iowa (cordaites=48–60%). Relative abundances of lycopod peat generally are 75–84% (Westphalian A), 44–74% (Westphalian B-C), to 55–75% (Westphalian D). Shoot/root (S/R) ratios increase during the Westphalian from 0.5–1.0 in Westphalian A, 0.5–1.4 in Westphalian B-C to mostly >1.4 in Westphalian D. S/R values reflect, in part, changes in abundance of outer decay-resistant bark, 10–29% in Westphalian A-C and up to 45% in Westphalian D. Lycopod litter patterns differ in the main tree genera, so that all litter abundances vary according to the mixes of taxa and diversity of other plants occurring in the Westphalian D (Desmoinesian).

Wood from all sources is usually <10% of deposits, reaching 13–32% in cordaitean-rich deposits, mostly occurring in the Westphalian C-D transition. Evidence of detritivore destruction of wood (cordaitean and calamitean) is most extensive in Westphalian B-C (upper Pottsville) coal-ball deposits. *Psaronius* tree ferns (mostly roots) contributed 6–27% in the Westphalian D and

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33–76% in the Stephanian; seed ferns (mostly medullosan) formed up to 22% of coal-ball contents in these deposits.

Stratigraphic trends of principal taphonomic patterns reflect, in large part, changes in the taxonomic makeup of peat-swamp floras. Westphalian deposits exhibit shifts from stigmarian root-rich peats in the Westphalian A, to mixed stigmarian-cordaitean root peats in Westphalian B-C, to an increase in diversity and sizes of litter types in the Westphalian D. Abundances of lycopod bark, total foliage and fructifications reach maxima in the Westphalian D. Stephanian peats are rich in tree-fern roots with variable distribution in the tissues of other tree types (expecially wood and lycopod bark); sizes of trunk litter suggest larger trees than earlier deposits.

Taphonomic patterns are closely linked both to taxonomic composition of the vegetation and prevailing environmental conditions. Stratigraphic changes in the qualitative and quantitative aspects of peat formation reflect shifts in both composition of peat-swamp floras and in climatic and physical factors attendant to peat accumulation. Dominant plant groups in the lowland habitats of the Late Carboniferous were very distinctive taxonomically (representing at least four classes of vascular plants) and thus differed enormously in the kinds of tissues they produced in their rooting patterns, and in their life histories. This constrasts sharply with woody seed-plant dominance of most post-Paleozoic landscapes. Consequently, extinctions or changes in dominance-diversity patterns lead to major changes in litter accumulation patterns.

The Westphalian D (Desmoinesian) exhibits the greatest diversity and shared dominance and, thus, the most diverse litter and root patterns. Average litter size markedly increased in the middle Westphalian D. Lycopod stem tissues, in particular *Lepidophloios* and *Diaphorodendron* bark, suggest an increase in physical stability of the environment (reduction in disturbance frequency) that permitted lycopod trees to attain large size. Stephanian deposits are consistent with an even more stable swamp environment with still larger trees (tree ferns, medullosans, calamites and the lycopod *Sigillaria*) but generally more severely degraded litter. The relative importance of subsidence regimes versus paleoclimate is discussed as a major factor that may have distinct stratigraphic and regional patterns. Origins of carbonate-to-pyritic coal balls are briefly reviewed as they pertain to taphonomic data and their biases.

DISCUSSION

J. Esterle (Univ. Kentucky)

Question: Can you comment on the discrepancy between environmental interpretation for pteridosperms, i.e., pteridosperms as stunted plants on top of a domed peat bog verses a level dweller or wet, high-ash peat dwellers?

Response: Perhaps you are referring to the discrepancies between vegetational estimates (interpretations) based on palynology versus those from coal-ball peats, especially for tree ferns. There are major discrepancies between the coal miospore floras (relative abundances) and the actual peat biomass in coal balls for many major tree-fern genera. Tree ferns were massive spore producers and could overwhelm in the spore flora of putative domed peats. We need to find out more directly what the vegetational sources are of peats from which so-called domed deposits were formed. *Medullosa* pteridosperms are not well documented by palynological studies, but they were certainly a common tree type on or near levees and in coal-ball deposits and are commonly associated with mineral-rich bands. If I had to choose potential "doming plants", small *Psaronius* ferns would seem a good possibility.

P.C. Lyons (U.S. Geological Survey)
Comment: Would you comment on the first occurrence of Carboniferous plant taxa as known from coal-ball plants as compared to compressional floras?

Response: Most of the main lycopod tree genera found in Westphalian coal balls have stratigraphic ranges extending far back into the Lower Carboniferous, commonly to the Visean. *Paralycopodites* occurs in the Tournaisian. With the exception of some genera, such as *Lyginopteris*, also with a long stratigraphic range both as compression and coal-ball type preservation, most of the taxa of compressional floras have much shorter stratigraphic ranges. The bulk of the paleofloristic diversity and evolutionary change is found in the non-swamp floras. Peat-swamp floras with the dominants centered in such environments tend to have very long-ranging species and with time relict and sort of "living museums" of ages past. This was particular evident with the lycopod-tree species in the Westphalian. They confined to swamps and suffered extinctions with the loss of such habitats.

E.I. Robbins (U.S. Geological Survey)
Question: What is the nature of the bark of lycopods? Is it suberinized and highly aromatic like other barks?

Response: We use the terms "bark", "roots", "crowns" and others with lycopod trees in order to communicate general ideas despite the fact that lycopod trees are very different from others. The "bark" is particularly different in its role of major support, prolonged longevity and lack of secondary phloem component. We should certainly expect it to have unusual biochemical construction because the outer bark seems the most resistant to decay of any of the abundant tissues found in Upper Carboniferous coals. There are secretions in part of some of the lycopod barks. However, we do not know their composition nor that of the thickened walls in the inner or outer bark. Some preliminary studies by Logan and Thomas (1987, New Phytologist, 105: 157–173) suggest the possibility of lignins in *Sigillaria* bark.

T.G. Callcott (Australia)
Comment: Please comment on Permian relative to Carboniferous.

Response: Coal-ball peats also occur in the north and south temperate Permian coal deposits and in the tropical Permian ones of China. The dominant trees were cordaites in the Kuznets of Siberia; the peats that I have seen were woody and the wood has growth rings. Glossopterids in Gondwanan coal balls also were woody and growth rings are present. Leaf litter was abundant too. In contrast to the Westphalian tropical coal swamps, the dominant temperate Permian tree types were apparently the same kinds as in other lowland habitats – not a special swamp group like the lycopods. In tropical South China, the lycopods, *Psaronius* tree ferns and cordaites continued to the end of the Permian, forming root peats. Although no growth rings are known, the cordaitean roots of China have excentric growth interruptions like those that occur in the Westphalian B-C of Euramerica.

E.I. Robbins (U.S. Geological Survey)
Question: I have never heard any modern ecologist discuss the existence of reduced diversity in modern wetlands. Species lists from modern wetlands are as large as those from plants and pollen work in coals. Where did you get this idea about reduced diversity in the Paleozoic.

Response: (1) "Wetlands" cannot be lumped into a single category; although we realize that there is a danger in overgeneralizing. There are differences in species diversity between swamp and non-swamp habitats in deltaic to fluvial settings. This diversity difference is often very great and occurs over short distances, controlled by flooding regimes. It certainly is recognized by many modern ecologists. We exclude marshes from this generalization. (2) Not only are there diversity differences between swamp and non-swamp habitats, there are differences in species composition. Swamps are physically stressful environments. Most species can not grow there and those that can often specialize in such environments. (3) The "idea" that diversity in the Paleozoic was lower than today is an empirical observation - see numerous papers by Knoll, Niklas and Tiffney on Phanerozoic land-plant diversity. Note that this diversity is not "reduced". As Dr. Cross pointed out in the presentation, there was a major *architectural* radiation in vascular plants during the Late Devonian and Early Mississippan. This established, quite literally, the "forest primeval". The entire landscape diversity of Euramerica in the Carboniferous was 1 to 2 orders of magnitude less than today. There may have been fewer than 1,000 species in the Carboniferous tropics compared with more than 100,000 today.

M. Teichmüller (F.R. Germany)
Question: Do you have evidence of marsh vegetation, like the calamites in Pennsylvanian-age coal-ball floras? (Question asked by Dr. Teichmüller but not submitted to speaker afterward. Nevertheless, the editors would like a response).

Response: "Marsh plants" or herbaceous peat-forming vegetation are viewed rather differently ecologically in the Late Carboniferous coal-swamp environments than today. In the diagram used by Professor Cross and Dr. Teichmüller, calamites are shown in deeper water than the rest of the swamp forest. Such a setting for calamites may be appropriate in a clastic swamp. In the peat-forming swamps the lycopod trees occupied a range of environments from the deep-standing water habitats progressively toward shallow water or exposed peat. In a way, they occupied an array of habitats now associated with "marshes" or aquatics. There were no known aquatic vascular plants at the time. Herbs apparently occupied the most ephemeral habitats of briefly standing shallow water or exposed peats. *Chaloneria* is an example.

W. Pfefferkorn (Univ. Pennsylvania)
Question: Could there be tidally influenced areas where herbaceous plants could live because they are out of the water half the time?

Response: (1) Yes, of course there could have been such vegetation. The question we can not answer is whether this kind of water-level fluctuation could occur in live coal swamps comprised of the plants we know. Certainly we have no physical evidence of it in coal balls, and the plants do not lead us to conclude it; but we cannot rule out tidal influence, and certainly not brackish-water influence. (2) In the Illinois Basin, Eric Kvale and Al Archer have identified rhythmites that probably formed along tidally influenced trangressive shorelines. These occur above coals and contain fossil plants. In such instances we infer the presence of vegetation that was periodically inundated by tides, on the ocean side of peat-forming swamps. (Hindostan whetstone beds and shales above Lower Block Coal, Westphalian B and Late Westphalian C). These floras were dominated by pteridosperms with calamites and pteridosperms, and most notably *Lepidodendron* species of various sorts. However, this does not appear to be peat-forming vegetation.

R. Stanton (U.S. Geological Survey)
Question: Are the fecal pellets stratigraphically restricted or are they habitat specific?

Response: Fossil fecal pellets occur at all the coal-ball localities, including larger ones (up to several mm in diameter) than those shown in the woods of the cordaites and calamites. The smaller fecal pellets (less than 100 μm) occur also in lycopod leaf cushions, seed-fern fronds and other tissues. The greatest abundances of the small fecal pellets occur in the coal balls from the lower Middle Pennsylvanian, Westphalian B-C of the central Appalachian basin and equivalent ages in the Donets basin. There, wood-rich peats include mostly root wood. The extensive tunneling by anthropod detritivores is thought to indicate aerial exposure and perhaps prior fungal infestation.