

The late Paleozoic ecological-evolutionary laboratory, a land-plant fossil record perspective

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INTRODUCTION

In this essay we examine the fossil record of land plants, focusing on the late Paleozoic. We explore the nature of this record in terms of what is preserved, where, why and with what biases.

And as a consequence, how it can be used to answer questions posed at various spatial and temporal scales, what cautions we must consider when interpreting it, and what surprises it may hold. Generally speaking, the record of terrestrial plants is rich and reveals clear directional trends in phenotypic complexity, biodiversity, and ecosystem organization. It also has reasonably well understood taphonomic biases. It must be used with considerable caution, however, when researching time and location of evolutionary innovations and the development of ecological structure and interactions.

THE LATE PALEOZOIC LABORATORY

Earth experienced a 70-million-year period of intermittent glaciation (Montañez and Poulsen 2013) from the middle Mississippian to early Permian. This interval is characterized by 10^5 -year glacio-eustatic cycles (Heckel 2008), superimposed on longer, 10^6 -year scale intervals of global warming and cooling (Birgenheier et al. 2009). These are further superimposed, in the equatorial regions, on a long-term, 10^7 -year scale trend of warming and increasing aridity (Montañez et al. 2007, Tabor and Poulsen 2008). Consequently, the world of the time had many similarities to that of today, captured in the fossil and geological records. The Earth's continental landmasses, however, were aggregated into the supercontinent of Pangea, which differed greatly from today's high elevation world of dispersed continents (Figure 1).

The Pennsylvanian and Permian are known for vast coal deposits, which formed in extensive peat swamps. In the tropics, these wetlands were populated by old, evolutionarily conservative plant lineages, the subjects of dioramas in natural history museums and illustrations in nearly every paleo-textbook. At the same time, however, large areas of the tropics harbored more evolutionarily derived plants adapted to seasonal drought (e.g., DiMichele 2014). There were also distinct north- and south-temperate floras segregated into wetland and drought tolerant assemblages, but subject to strong seasonal temperature contrasts (Rees et al. 2002). Such areas also tended to be populated by more derived evolutionary lineages.

Our understanding of the origin and spread of major late Paleozoic plant groups is based on these patterns of ecosystem-scale and biogeographic-scale patterns. Some of the groups originating in the late Paleozoic are still important today, such as conifers. Others, now extinct or diminished, dominated many pre-angiosperm, Mesozoic ecosystems. These include cycadalean, peltaspermalean, and corystospermalean seed-plants and ferns such as the osmundaleans and primitive filicaleans (Lidgard and Crane 1990). Until recently, many of these groups were thought to have had Mesozoic or latest Paleozoic origins. Over the past few decades, however, some have been found in Paleozoic deposits, often as isolated occurrences, suggesting that significant evolutionary innovation took place in parts of the terrestrial landscape poorly represented in the fossil record. This is not a matter for despair, however. Such patterns may mean we cannot easily or confidently “stack up” the record for a direct, temporal reading. Nonetheless, through linkage of sedimentological and ecological factors to patterns of spatial and temporal plant distribution, we can still infer a lot about the locus and nature of the evolutionary process.

THE OVERPRINT OF TAPHONOMY

Rule #1: Plants are crystalized climate

“Ja, man kann die Pflanzendecke das kristallisierte, sichtbar gewordene Klima nennen, in dem sich so manche Züge deutlicher zeigen als in den Angaben unserer Instrumente.”

Wladimir Köppen (1936, p.6)

This may be translated: “Yes, **one may call vegetation materialized, visible climate**, in which quite a few climate traits are more readily discernible than in the readings of our instruments”, or, the part in bold above, somewhat more graphically as “plants are crystalized visible climate” (Claussen 1998). There are few more compelling rules for understanding the fossil record of land plants. And it is safe to assume that terrestrial plants have conformed to this axiom since their earliest appearances, which should strongly condition our interpretations of their spatial and temporal distributions and evolutionary patterns.

In the Pennsylvanian-Permian, perhaps the best examples of this are the striking differences in taxonomic composition among equatorial Euramerican, equatorial Cathaysian, south-temperate Gondwanan and north-temperate Angaran assemblages (Figure 1, Wnuk 1996). At a spatially more refined level, several compositionally distinct biomes have been recognized in the Euramerican floral realm, each associated with physical indicators of greater seasonal dryness (Falcon-Lang and Bashforth 2004, Tabor et al. 2013). Within the best known of these biomes, the wetlands, environmental preferences have been determined for particular taxa or lineages (e.g., DiMichele and Phillips 1996a) that can be traced back to the earliest radiations of terrestrial plants (Bateman et al. 1998).

The other fundamental controls

There are other important taphonomic factors that strongly influence interpretation of the land-plant macrofossil record (Gastaldo and Demko 2011). Taphonomic



Figure 1: The Late Paleozoic supercontinent, Pangea. Four major floral zones are indicated, tropical Euramerica and Cathaysia, and temperate Angara and Gondwana. Paleogeography after Scotese (1997)

rule #2 is that short-term preservation of plant remains is most likely to occur under a background of perhumid to wet sub-humid conditions (terminology of Cecil 2003), though dry sub-humid and even arid climates may harbor some habitats where preservation is possible.

Taphonomic rule #3 is that plant macrofossils rarely can be recycled by reworking. Impressions or fragile coalified compressions are easily destroyed, exceptions being wood or wood-like resistant tissues. Thus, the plant macrofossil record preserves fine levels of temporal resolution and high stratigraphic integrity. In practice, however, a collection of plant fossils is usually analytically time averaged by sampling (Behrensmeyer et al. 2000). This happens mostly because of the difficulty of tracing a “T⁰” time

horizon (Johnson 2007) laterally for any distance unless it is tied to an “event” of determinable short-term duration, say an ash fall (Wing et al. 1993; Opluštil et al. 2014). Parautochthonous and some allochthonous assemblages generally represent either members of the same community or plants that lived in close proximity to the depositional environment, in time and space.

Rule #4: Plant organic matter will be destroyed rapidly by the combined actions of physicochemical (e.g., mechanical breakage, fire, slow oxidation) and biotic agents (e.g., microorganismal decay, roots), particularly if on or above the soil surface, or in the soil vadose zone of water table fluctuation (Gastaldo and Demko 2011). Consequently, most of the plant macrofossil record represents

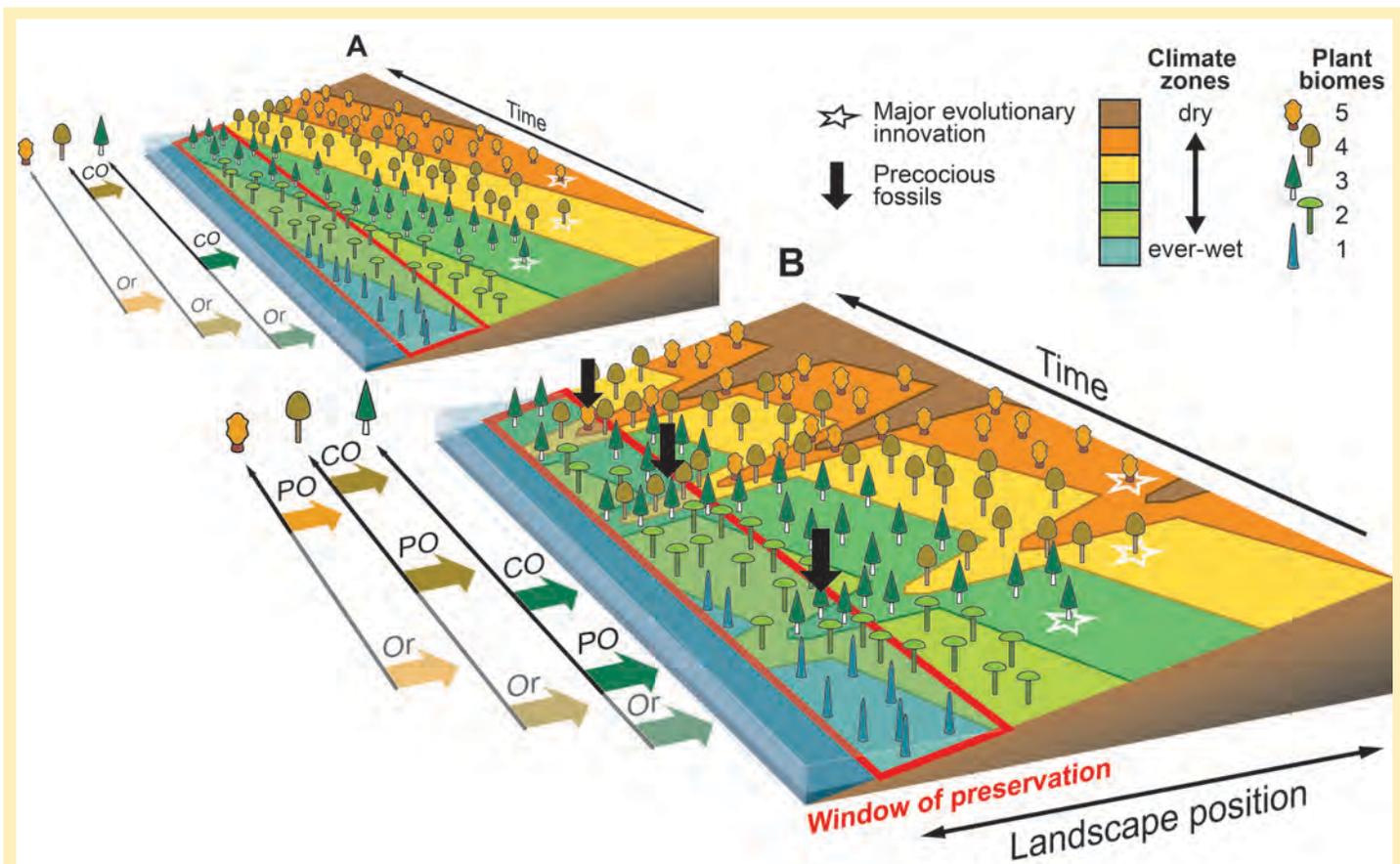


Figure 2: Plant evolutionary innovation and environment, Late Paleozoic. A. General pattern based on an early, incomplete knowledge of the fossil record. Major evolutionary innovations appear in stressful, extrabasinal habitats and track climate changes, moving into basinal habitats, where preservational potential is highest, during the progressive global warming and drying of the late Paleozoic. B. Emerging pattern with an increased sampling of the fossil record. Seemingly precocious floras change our general view depicted in A. Precocious appearances reflect climate oscillations and accompanying tracking by plants, bringing new forms initially temporarily into the window of preservation during drier episodes. Or – origination of clades forming new plant biomes outside the window of preservation, PO – precocious occurrence of fossil floras, CO – common occurrence of fossil floras.

wetland assemblages or vegetation fringing standing water bodies, growing within channels or on wet floodplains (Scheihing and Pfefferkorn 1984), where chances of preservation are highest.

Rule #5: Most deep-time, fossil-plant accumulations will be confined to what were, at the time, actively subsiding basins. Even if preserved for the short-term, organic deposits must be protected from decay on intermediate time scales of thousands to tens of thousands of years to permit sufficient subsidence and burial below the level of active erosion. Intermediate-term preservation is most likely where ocean transgressions or inland water bodies could flood the site of burial. This must be followed or accompanied by tectonic creation of accommodation

space, permitting deeper burial and protection from erosion on million-year time scales. Thus, except in unusual tectonic circumstances (e.g., Opluštil 2005), the late Paleozoic terrestrial record contains primarily lowland deposits, leaving much room for speculation about what was going on evolutionarily and ecologically elsewhere.

That fossil floras occur throughout most of the Phanerozoic is empirical documentation that there is potential for the preservation of plant remains when the conditions are right. Conditions for intermediate and long-term burial of epicontinental sediments (e.g., Davies and Gibling 2013) are favorable in Pennsylvanian-Permian basins, leaving a reasonably good record. Within these deposits, organic remains of plants from

wetlands and localized high-moisture habitats are best represented, including swamp, peri-lacustrine, lagoonal fringe, coastal mudflat, floodplain and stream corridor habitats.

From a climatic perspective, the best record of lowland vegetation comes from times of perhumid to wet sub-humid climate, which most favor the first step of fossilization: short-term preservation. Due to unfavorable conditions for short-term preservation, the plant record from dry sub-humid to arid conditions is very limited. There are also few records of true “upland” floras, those from continental interiors or other places where erosion was the dominant sedimentological force on intermediate and long-term, million-year time scales.

WHAT'S HAPPENING "OUT THERE" AND HOW DO WE KNOW?

Due to the climatic and taphonomic factors discussed above, much of the natural experimentation that characterized Paleozoic plant evolution seems to have occurred outside of areas or time windows with the best chances for preservation. These include basins during the times they experienced climates unfavorable for short-term preservation and extrabasinal regions, lowland and true upland (Pfefferkorn 1980). How can we tell if major evolutionary breakthroughs occurred in such places? Fortunately, plants faithfully reflect climate. Because climate is generally insensitive to tectonic regime, particularly subsidence, basins are sometimes subject to drier climate at the same time they experience conditions conducive to intermediate-term preservation. When that happens, plants from habitats that rarely become fossilized will appear as isolated, seemingly anomalous occurrences.

Stratigraphic anomalies

There has long been attention, particularly among marine invertebrate biostratigraphers, to occurrences of taxa outside of previously known temporal ranges. Given such names as "Lazarus" taxa (Jablonski 1986) for those appearing well beyond inferred range termini, equally important are cameo appearances well before known ranges. In either case, these appearances strongly imply significant biases in the record or in the patterns of organismic distribution on the landscape. Such evidence is particularly powerful where the occurrences straddle extinction boundaries, indicating unsuspected earlier existence and/or survival in unseen areas. Regarding plant evolution, precocious occurrences may indicate evolutionary innovation at times and in places outside of our detection abilities, and can carry significant implications regarding climate and habitat.

Precocious occurrences: Methuselah taxa

Of greater interest than Lazarus taxa, from an evolutionary perspective, are precocious taxonomic occurrences, millions to tens of millions of years preceding otherwise well-established ranges. Unexpectedly "old" occurrences like these lead us to suggest the term "Methuselah" taxa for those with a much older origin than assumed possible, given the bulk of earlier existing observations. Upon re-evaluation of all data, the epithet 'precocious' really only exists in the eye of the myopic beholder, and turns out to mean nothing more than "inconceivably old", just like Methuselah in Hebrew Scripture. In the plant fossil record, these Methuselah genera and species typically occur in seasonally dry environments, often in deposits sandwiched among those with typical wetland floras. They also are composed of or contain many derived elements of evolutionary lineages, implying a linkage between environmentally "peripheral" habitats and major innovation in plant evolution (DiMichele and Aronson 1992).

Among the most noteworthy Methuselah occurrences is the callipterid peltasperm *Dichophyllum* (Cover, 1), from the early Late Pennsylvanian of Kansas (Cridland and Morris 1963). This occurrence, in a seasonally dry, channel complex (Feldman et al. 2005), falls within the midst of the Midcontinent USA coal measures and is conifer-dominated; an assemblage quite unlike that of shales associated with surrounding coal beds. This occurrence caused considerable debate about the age of the deposit, leading some biostratigraphers to argue for Permian age (e.g., Bode 1975). Since this time, other Late Pennsylvanian callipterid occurrences have been documented, but these are rare and none are as old as this.

Several other noteworthy examples of Methuselah occurrences include: (1) Four species of the corytosperm *Dicroidium*

from the late Permian of Jordan (Cover, 2), then equatorial Pangea, in a floodplain deposit formed under seasonally dry climate (Kerp et al. 2006). This genus is a characteristic element of late Early to Late Triassic high-latitude Gondwanan floras. (2) *Dioonitocarpidium*, a cycad-like reproductive structure typical of the Late Triassic and Early Jurassic of central Europe (Cover, 3). It occurs in a late early Permian deposit from Texas, in association with a peculiar assemblage, deposited under seasonally dry climate (DiMichele et al. 2001). (3) Voltzian conifers, a derived group (Cover, 4), also occur in seasonally-dry habitats of the Texas late early Permian (Looy 2007, Looy and Stevenson 2014). Their earliest prior occurrence was late Permian of central Europe. (4) The seed-bearing structure of highly derived, typically Mesozoic Peltaspermales has been reported from isolated occurrences in latest Pennsylvanian equatorial regions of Europe and North Africa (Kerp et al. 2001), and the early Permian of China (Liu and Yao 2000) and the Urals (Naugolnykh and Kerp 1996, Kerp 1996). The species, *Peltaspermum retensorium*, was found at several localities in the same Angaran horizon, a chance basinal occurrence of a rarely found "upland" plant associated with a flora indicating seasonal moisture stress. (5) Another peltasperm, *Germaropteris martinsii*, from dryland settings of late Permian age (Lopingian) of Central and Southern Europe (Kustatscher et al. 2014), was recently reported from early Permian seasonally dry deposits in southern France (Galtier and Broutin 2008) and from allochthonous offshore settings in Texas, presumably derived from coastal, mangrove-like habitats (Erik Kvale, personal communication, 2014 – specimens examined by Kerp and DiMichele). Other precociously appearing conifers include (6) the "Mesozoic" genus *Podozamites* from seasonally dry early Permian deposits of Texas (DiMichele et

al., 2001) and Late Pennsylvanian of New Mexico (Mamay and Mapes 1992). (7) Walchian conifers, rare but known from the Late Pennsylvanian equatorial regions (e.g., Kerp 1996, Hernandez-Castillo et al. 2001), have been reported from Middle Pennsylvanian age localities, two in the Illinois Basin, a sinkhole in limestone at the basin margin (Plotnick et al. 2009) and a channel fill within a seasonally dry landscape (Falcon-Lang et al. 2009), and two from allochthonous deposits in New Mexico (Lucas et al. 2013). (8) A number of genera reported from the early Permian seasonally dry habitats of southwestern Euramerica, most notably *Comia*, *Supaia* and *Compsopteris*, are both significantly more abundant and have much broader distributions in the late Permian of Angaraland and Cathaysia (Mamay et al. 2009, Halle 1927). (9) The enigmatic gigantopterids, abundant in the late Permian of China occur in early Permian seasonally dry environments of southwestern Euramerica (DiMichele et al. 2005), the Arabian Peninsula (Berthelin et al. 2003), Sumatra (Booi et al. 2009) and Venezuela (Ricardi-Branco 2008).

PRECOCIOUS OCCURRENCES AND PLANT EVOLUTION

Three patterns stand out when considering the significance of precocious, Methuselah occurrences. (1) These taxa nearly always appear in deposits formed under seasonally dry background climates, even if the fossils themselves are from wet substrate sites, consistent with constraints on short-term preservation. (2) The taxa are almost always among the more derived members of their respective evolutionary lineages at some taxonomic level. (3) The earliest host deposits tend to be “one-offs” – single deposits or thin stratigraphic horizons – found in basinal lowlands or in allochthonous, offshore deposits, reflecting taphonomic controls.

This pattern may be contrasted with

Paleozoic wetland communities dominated by evolutionarily less-derived lycopsids, pteridosperms, marattialean tree ferns, cordaitaleans and sphenopsids. These floras show long-term compositional conservatism and intra-assemblage species turnover strongly constrained by evolutionary-lineage ecological centroids (DiMichele and Phillips 1996b), a pattern reflective of “phylogenetic niche conservatism” (e.g., Prinzing 2001; Wiens 2004). Such conservatism led Knoll (1985) to refer to swampy lowlands throughout geological history as “museums”. They are characterized by long-term persistence of ecological organization and evolutionary innovation and of taxonomic composition and ecomorphic characteristics. When disrupted by major environmental disasters, they are recolonized from “outside” species pools, restructured and, subsequently, again demonstrate conservatism for millions of years.

When considered together we draw two conclusions from these patterns (summarized in Figure 2). First, evolution of major body-plan innovations (meaning ancestor-descendant divergence reflected in higher, traditional-Linnean ranks) occurred more commonly in environments that were environmentally challenging to established plant lineages and unfavorable for organic preservation on the short-term and intermediate-term time scales. Such environments, likely, were of initially low diversity and encompassed new and different resources that were available for use. Increasing drought and temperature stress, in particular, may have simultaneously limited range expansion of existing plants and created opportunities for innovation. Initially permissive, survival likelihood of variant forms was enhanced due to relaxed natural selection. Second, we first see the results of such innovation when environmental change in the lowlands, caused by increased seasonality of rainfall and perhaps temperature, permit these lineages to move into and

occupy basinal areas temporarily. Based on the low number and typically singular appearance of Methuselah taxa we infer that conditions permitting their basinward biogeographic shifts most often occurred at times when intermediate-term preservation was unlikely. This makes them rare to start with, and the deposits difficult to find, even if present, thus causing initial myopia in the eye of the paleobotanical beholder (i.e. the pattern seen within the window of preservation in Figure 2 A). In the longer-term, evolutionarily derived lineages became dominant in basinal lowlands. They did so not by *displacing* the incumbent, ancestral forms, but by *replacing* them as long-lasting environmental change opened basins to long-term colonization (DiMichele and Bateman, 1996). Consequently, whenever fossiliferous sites are found outside of preservation-friendly regions or in settings of generally drier climates, seemingly precocious occurrences will result (Figure 2 B). Plants appearing well before previously known stratigraphic ranges should be expected rather than considered anomalous.

We interpret these patterns to suggest that the window for innovation in ecologically permissive environments is brief and the survival of new forms declines as resource pools are occupied (e.g. in the extreme, Valentine 1980; DiMichele and Bateman, 1996). Intrabiome and intra-species-pool turnover tend to be dominated by niche-conservatism and within-clade, near ancestor-descendant replacements, reflected by paired intra-generic extinction and origination. The result is minor compositional fluctuation at the level of the dominant lineages through time during which assemblages became hide-bound and niche construction (Odling-Smee et al. 2013) was a rare phenomenon. The existing hegemony was broken-up by periodic, extrinsically induced disruptions (i.e., Vermeij 1993).

We also note an inversion between the generalized evolutionary patterns in

marine invertebrates and land plants. The onshore-offshore pattern of evolutionary innovation and radiation in marine invertebrates (Jablonski et al. 1983) actually may contribute to high amounts of Lazarus taxa. There, heterotroph innovations occur in shallow marine environments within the window of preservation followed by radiation outside this window into the deep. Lazarus taxa wander back into the preservational window after ecological crises. Exactly the opposite happens with autotrophs in the terrestrial realm. Major innovations happen outside the window of preservation, with subsequent migration, and sometimes radiation into the window following environmental change. So one can expect this process to produce the opposite of Lazarus taxa, the apparent precociously appearing Methuselah taxa.

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