Commentary

Climate–vegetation models bring fossil forests back to life

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Footnotes

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Globally widespread forests first arose in the Pennsylvanian subperiod, some 300 to 320 Ma, populated by bizarre tree-sized club mosses, ferns, sphenophytes, and gymnosperms (1). At this time, most of Earth's landmasses were fused together as Pangaea, gripped by the late Paleozoic ice age, and subject to glacial–interglacial cycles (2). The compacted remains of the forests that densely covered this partially frozen supercontinent are widely preserved, and in the best-explored tropical realm form economic coal measures (3). Knowledge of the so-called Pennsylvanian coal forests has been literally mined from Earth's surface through 200 y of hard labor in the coalfields of Appalachia, the Ruhr, and South Wales, among many other places (3). These hard-won fossil discoveries reveal that primeval vegetation choked almost every conceivable terrestrial environment from boggy deltas (3) to rugged mountain terrains (4). Especially tantalizing is the localized preservation of whole forested landscapes, allowing scientists to walk for miles through the coalified stands of upright fossil trees (5). Yet, despite being entombed with such remarkable fidelity, Pennsylvanian forests remain deeply mysterious ecosystems, lacking even remotely close living relatives for comparison. In PNAS, Matthaeus et al. (6) develop sophisticated vegetation–climate models that elegantly fuse traditional fossil data with fundamental plant physiology to bring these long-dead forests back to life. Quite unexpectedly, their wide-ranging findings identify frost tolerance as a key factor in controlling Pennsylvanian forest dynamics and distribution, with episodic frost dieback disturbing cycles of runoff, erosion, and weathering at a global scale. They further hypothesize that enhanced frost tolerance, which arose in early conifers, may have simultaneously conferred drought adaptation, paving the way for conifer dominance in the hot and arid Mesozoic that followed the cool Paleozoic.

Pennsylvanian forests have always evoked a sense of wonder among the students of Earth history. W. G. Chaloner FRS (1928–2016), one of the great paleobotanists of recent times (7), frequently encouraged his graduate students to consider the Pennsylvanian time period for their theses, arguing that these extinct ecosystems were so bafflingly different from extant forests that an aspiring scientist must work from first principles to reveal their structure and function. In PNAS, Matthaeus et al. (6) follow this logic perfectly, applying process-based plant physiology to improve understanding of Pennsylvanian ecosystems (and it is perhaps no coincidence that coauthor McElwain was Chaloner's last student). In **AQ6** doing so they identify frost tolerance as a key factor. Frost is, of course, one of the major limiting processes on forest growth today, delineating the tree line and constraining tree productivity between latitudinal and altitudinal boundaries (8). Yet, as frost damage is such an ephemeral process, with very low preservation potential in the plant fossil record, never before have Pennsylvanian paleobotanists seriously considered its significance, despite widespread geological evidence for contemporaneous glaciation (2, 3). By deploying GENESIS V3 general circulation models of Pennsylvanian climate, well-constrained by geological data, what Matthaeus et al. (6) have now done is to demonstrate that frost was a globally widespread process, occurring both during glacial and interglacial climate phases and widely impacting the tropical belt. By synthesizing all that is known about 1) the hydrologic conductivity of Pennsylvanian tree trunks, based on wood anatomy, 2) potential for evapotranspiration, based on stomatal arrays preserved on leaf cuticles, and 3) the leaf-area index based, in part, on direct measurements of leaf carbon:nitrogen ratios, they have quantified frost tolerance in Pennsylvanian forests, revealing that most tree species were intolerant of cold snaps below −4 °C.

This recognition of frost tolerance as a key factor in influencing Pennsylvanian forests is an extremely surprising result; however, like all fundamental discoveries, with hindsight these remarkable findings appear obvious. In Pennsylvanian times, fossils confirm that forests grew widely across the vast supercontinent of Pangaea, not just is the warm tropics (present-day Europe and North America) but also in the southern polar latitudes (South America, Australia, India, Africa, and Antarctica) (3). The vegetation that once grew close to the southern icecaps, and whose remains occasionally occur in fjord deposits (9), comprise woody glossopterid trees that surely were subject to very hard frosts. However, direct fossil evidence for frost damage in Pennsylvanian forests (and those of early Permian age that coincided with the last stage of the late Paleozoic ice age) is absent, even in these most sensitive ice-margin areas (10), let alone in the tropics (1). Counterintuitively, this absence of fossil evidence may actually support the veracity of Matthaeus et al.'s modeling (6), however, rather than contradict it. Frost damage is only developed in trees that survive and recover from frosts, whereas among intolerant plants (including all neotropical trees) frost is immediately lethal, resulting in no anatomical wound response (11). The absence of evidence of frost damage may therefore indicate that many Pennsylvanian tree species were only weakly frost-tolerant and were likely killed by plunging temperatures.

Frost was not simply a disturbance process in Pennsylvanian forests, however; it also may have profoundly driven evolution and ecological innovation. Fossil data show that early conifers (and their coniferopsid allies) were the trees most closely associated with mountainous terrains of the tropical belt (4) and, like the high-latitude glossopterid forests, must have been similarly subject to intense frosts. Studies of modern trees show that features such as dense woods and a leaf-dropping habit may confer considerable resilience to frost (11). Two key features of some Pennsylvanian coniferopsids (Fig. 1) are their pycnoxylic woods characterized by very small tracheid diameter and their deciduous phenology (12), which likely facilitated frost tolerance at much lower temperatures compared with most other contemporaneous evergreen species constructed of manoxylic tissues (1). An intriguing possibility is that frost may have selected for traits that coniferopsids could have simultaneously deployed to optimize drought survival, and it is noteworthy that early conifers are associated not just with cold high-altitude settings but also the most arid regions of Pangaea (13). As Matthaeus et al. (6) hypothesize, such adaptive synergies may have underpinned the subsequent 150-My dominance of conifers as global climate became hotter and more arid in the Mesozoic Era.

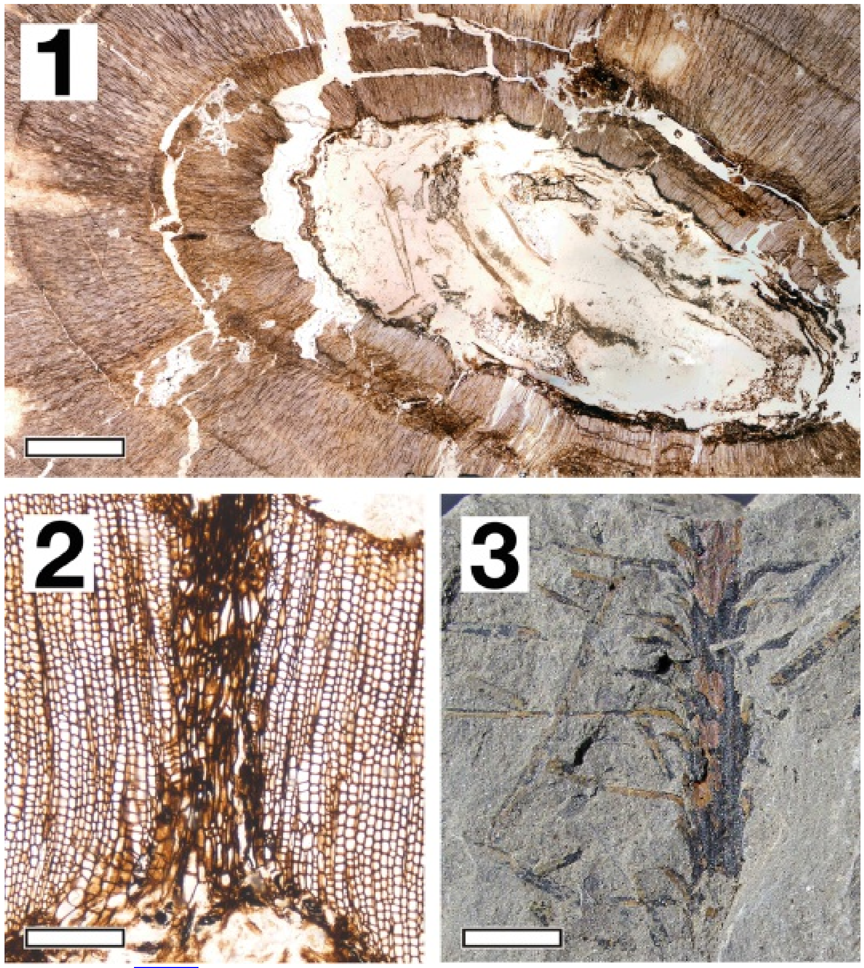

Fig. 1. Pennsylvanian AQ8 coniferopsids like *Giblingodendron* (12) grew in central tropical Pangaea in and around cold and arid **mountainous terrains.** ~~Its~~ This putative dicranophyll was characterised by a **dense pycnoxylic axis** with~~,~~ **small-diameter tracheids** (panel 1, scale 5 mm)**, a deciduous phenology** as ~~(~~**indicated by leaf traces abscised at the first ring boundary**~~)~~ (panel 2, scale 250 **µm), and needle-like shoots**, probably of *Dicranophyllum*-type (panel 3, scale 5 mm).~~, illustrated here,~~ These features **are consistent with its being a frost-tolerant specialist. Frost selection of traits may have also conferred adaptation to aridity, paving the way for early conifers to dominate the hot Mesozoic Era that followed, as hypothesized by Matthaeus et al. in PNAS (6).**

Significantly, it is in those Mesozoic ecosystems that we find the first unequivocal fossil evidence that conifers had evolved into frost-tolerant specialists par excellence. The most geologically durable evidence for frost damage in ancient ecosystems is the development of traumatic growth patterns in fossil wood. These so-called frost rings mostly occur in young stems when active cambial division is interrupted by episodes of ice nucleation and form as growing-season temperatures drop below freezing (11). Studies of dinosaur-haunted Mesozoic conifer forests that grew close to the Arctic and Antarctic poles (at paleolatitudes as high as 85°) reveal common frost rings, with one spectacular fossil trunk of a redwood conifer from Ellesmere Island recording no less than 15 sharp frost events in its first 40 y of growth (14). These data suggest that Mesozoic conifers were well-equipped to handle to the twin water stressors of aridity and frost, and this adaptive success was likely optimized through exposure to Pennsylvanian frosts.

Nonetheless, while early conifers were likely frost-tolerant specialists, most other tree species of the Pennsylvanian world appear to have possessed only a weak tolerance of frost, being vulnerable to cold snaps of less than −4 °C. The wider implications of such limited frost tolerance are explored as the final major theme of Matthaeus et al.'s PNAS paper (6). They infer that, through triggering frost dieback at a regional scale, even small climate fluctuations could have caused profound shifts in runoff, soil erosion, and weathering at a globally significant scale. Such effects would have been expressed most markedly in the sensitive tropical belt populated by the thermophilic coal forests, impacting the development of peat mires and the formation of economic coal seams, as well as disturbing the carbon cycle.

In PNAS, Matthaeus et al. (6) transform our understanding of Pennsylvanian forests in a genuinely surprising way. Through ingenious climate–vegetation models integrated with inferences of process-based physiology, they reveal that frost was a **AQ7** key process in influencing these ancient ecosystems, and they explore the major ramifications of this central finding for the evolution of life and the Earth system. In doing they breathe life into the coalified remains of long-dead fossils and shed a cold, frosty light on ancient forests.

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