

Surprisingly complex community discovered in the mid-Devonian fossil forest at Gilboa

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The origin of trees by the mid-Devonian epoch (398–385 million years ago) signals a major change in terrestrial ecosystems with potential long-term consequences including increased weathering, drop in atmospheric CO₂, modified climate, changes in sedimentation patterns and mass extinction^{1–3}. However, little is known about the ecology of early forests or how changes in early terrestrial ecosystems influenced global processes. One of the most famous palaeontological records for this time is the ‘oldest fossil forest’ at Riverside Quarry, Gilboa, New York, USA, discovered in the 1920s^{4,5}. Hundreds of large *Eospermatopteris* sandstone casts, now thought to represent the bases of standing cladoxylopid trees⁶, were recovered from a horizon that was originally interpreted as a muddy swamp. After quarry operations ceased, relatively minor outcrops of similar fossils at nearby localities have provided limited opportunities to evaluate this pervasive view using modern methods^{7,8}. In 2010, removal of the quarry backfill enabled reappraisal of the palaeoecology of this important site. Here we describe a 1,200 m² map showing numerous *Eospermatopteris* root systems in life position within a mixed-age stand of trees. Unexpectedly, large woody rhizomes with adventitious roots and aerial branch systems identified as aneurophytalan progymnosperms run between, and probably climb into, *Eospermatopteris* trees. We describe the overall habit for these surprisingly large aneurophytaleans, the earliest fossil group having wood produced by a bifacial vascular cambium. The site also provides evidence for arborescence within lycopsids, extending the North American range for trees in this ecologically critical group. The rooting horizon is a dark grey sandy mudstone showing limited root penetration. Although clearly belonging to a wetland coastal plain environment⁹, the forest was probably limited in duration and subject to periodic disturbance. These observations provide fundamental clarification of the palaeoecology of this mixed-group early forest, with important implications for interpreting coeval assemblage data worldwide.

Tree-sized plants become evident in the fossil record in the Middle Devonian. The oldest (primarily from the Eifelian–Givetian ages) belong to the order Pseudosporochnales (class Cladoxylopsida). These plants possess a strong central trunk bearing a crown of ephemeral non-leafy branches and have an overall form that looks much like a modern palm or tree-fern¹⁰. Recent evidence unites the long-enigmatic *Eospermatopteris* stump casts from Riverside Quarry, Gilboa (Givetian age) with pseudosporochnalean crown and branch compressions of the genus *Wattieza*⁶. Although the group has almost worldwide distribution, little is currently known about its morphological variation, phylogenetic relationships or occurrence in specific palaeoenvironments. As a result, Goldring’s iconic “oldest fossil forest” (ref. 5) continues to exert great influence. She described trees “resting in and upon shale” representing “muds in which the trees stood”, with bases that were “bulbous, as might be expected of certain trees growing under swampy conditions”⁵. By the late Middle Devonian (Givetian), pseudosporochnaleans were joined by the order Archaeopteridales (class Progymnospermopsida)¹¹.

Demonstration of a bifacial vascular cambium producing wood, leaves, extended development by means of buds¹², and possibly more deeply penetrating roots, has led to the hypothesis that archaeopteridaleans mark the beginning of another type of forest in the Devonian that is different from the water-restricted *Eospermatopteris*^{1,13}. However, both groups are commonly found together in variable lithologies within the North American Catskill sediment complex¹⁴ and elsewhere, with little to suggest spatial or environmental separation of the plants.

In spring 2010, backfill at Riverside Quarry was removed, exposing the highwall and extensive quarry floor at the original 292.6-m (960-ft) elevation for a few weeks, before refilling. The highwall section consists of several massive fine sandstone beds that are 0.2–0.8 m thick, with one thin wedge of shale (Supplementary Figs 1 and 2). Two sandstone moulds left by *Eospermatopteris* casts collected in the 1920s occur at the 296-m (972-ft) level⁴. Both moulds show attached roots forming a loose root mantle within the enclosing sandstone, passing outwards, downwards and partly penetrating a palaeosol below (Fig. 1a).

Of approximately 30 new *Eospermatopteris* casts retrieved from the backfill, two specimens remain encased within the casting sandstone with their flat to shallowly convex bottoms exposed and their roots still attached (Fig. 1b and Supplementary Fig. 8). Numerous and conspicuous raised mounds of radiating roots delimit the original, and still largely intact, forest palaeosol surface on the quarry floor (Fig. 1c and Supplementary Figs 3–11). Root mounds occur over most, if not all, of the quarry floor and contact of palaeosol with the overlying sandstone responsible for *Eospermatopteris* casts is clearly observed at the base of the highwall. We conclude that the root mounds on the quarry floor and exposed cast bottoms described above represent matching counterpart surfaces. Approximately 1,200 m² of the palaeosol surface was pressure-washed and plan-mapped, and this showed a total of 486 objects including root mounds, horizontal stems and aerial plant fragments (Fig. 2). The basic features of this survey and of the criteria that we used for recognizing different plants are described here and in the Supplementary Information.

Approximately 200 root mounds in the mapped region unquestionably mark locations of *Eospermatopteris* casts that were originally removed from the site. The best-preserved examples typically exhibit a circular densely imbricate skirt of unbranched lateral roots 1–2 cm in diameter radiating from a raised rim and central basin corresponding respectively to the widest diameter and bottom of the originally seated cast. The rim, approximately 0.2–1.9 m in diameter, suggests outward displacement of soil by each tree base during growth. The central basin often shows a radiating pattern of grooves with circular depressions, which correspond to roots descending directly into the quarry floor. Although most root mounds represent single individuals, some more extensive mounds exhibit multiple circular to elliptical basins each with a raised rim suggesting the presence of two or more intertwined individuals or genetically related ramets sharing a common root mass (Supplementary Fig. 6). One specimen (Supplementary Fig. 7) was evidently toppled and shows the base of a horizontal trunk and a root mass oriented at right angles to their typical appearance on the quarry

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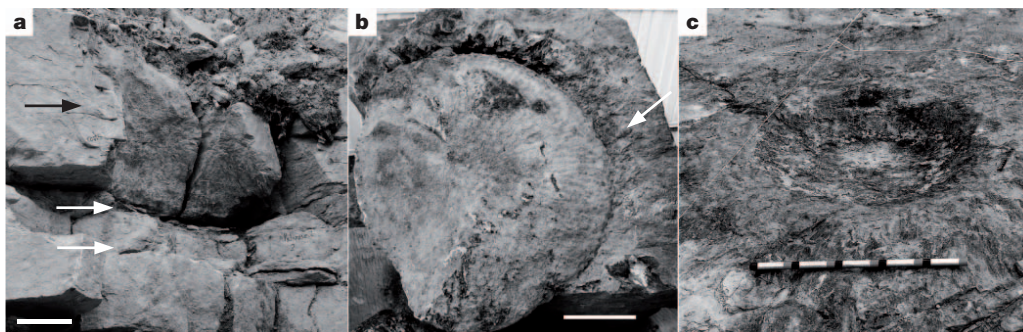


Figure 1 | *Eospermatopteris* cast, moulds and root system, Riverside Quarry, New York, USA. **a**, Mould in quarry highwall showing casting sandstone (black arrow) and the vertical extent of rooted palaeosol (white arrows) with both levels containing attached roots. Scale bar, 20 cm. **b**, Bottom of newly recovered cast with attached roots diverging into casing sandstone

(arrow; New York State Museum (NYSM) 18055). Scale bar, 20 cm. **c**, Forest palaeosol horizon on quarry floor showing raised rim, central basin and extensive rooting system; the surface equivalent to the counterpart of the cast shown in **b**. Entire scale bar, 50 cm.

floor. Heterogeneity in spacing of *Eospermatopteris* trees is evident along with a size variation consistent with individuals of different ages.

A surprising second tree-sized member of this assemblage is represented by straight to curved horizontal stems that are as much as 15 cm in diameter, probably greatly exceeding 4 m in length (Figs 2 (arrows **b** and **h**) and 3a, and Supplementary Figs 16–20). In a small number of cases, segments of stem are enveloped by numerous unbranched lateral organs that are approximately 5 mm in diameter, interpreted as roots (Fig. 3b). Surfaces of stems are unique in the quarry in having a 1–3-mm thick outer carbon layer together with an orthostichous pattern of circular to transversely elongate depressions, or corresponding knobs permineralized by pyrite. The permineralizations show fragmentary evidence of original tissues consistent with broken branch

bases oriented at right angles to the main stem preserved long after they originally functioned (Fig. 3c, d and Supplementary Figs 12–15). Secondary xylem is abundant, often interdigitating with carbon on the surface. In a transverse view of the branch bases, narrow vascular rays extend outward in radial files from secondary xylem to the vascular cambium, and beyond to sclerenchymatous elements of secondary phloem. The cortex consists of thin-walled parenchyma and clusters of sclereids. In the samples recovered so far, three- or four-ribbed protostelic configuration of the primary xylem (Fig. 3c, d and Supplementary Fig. 12) allows us to identify these within the order Aneurophytales (class Progymnospermopsida)^{15,16}. This interpretation is strongly supported by complementary compression evidence from a specimen originally collected by Goldring (Fig. 3e and Supplementary

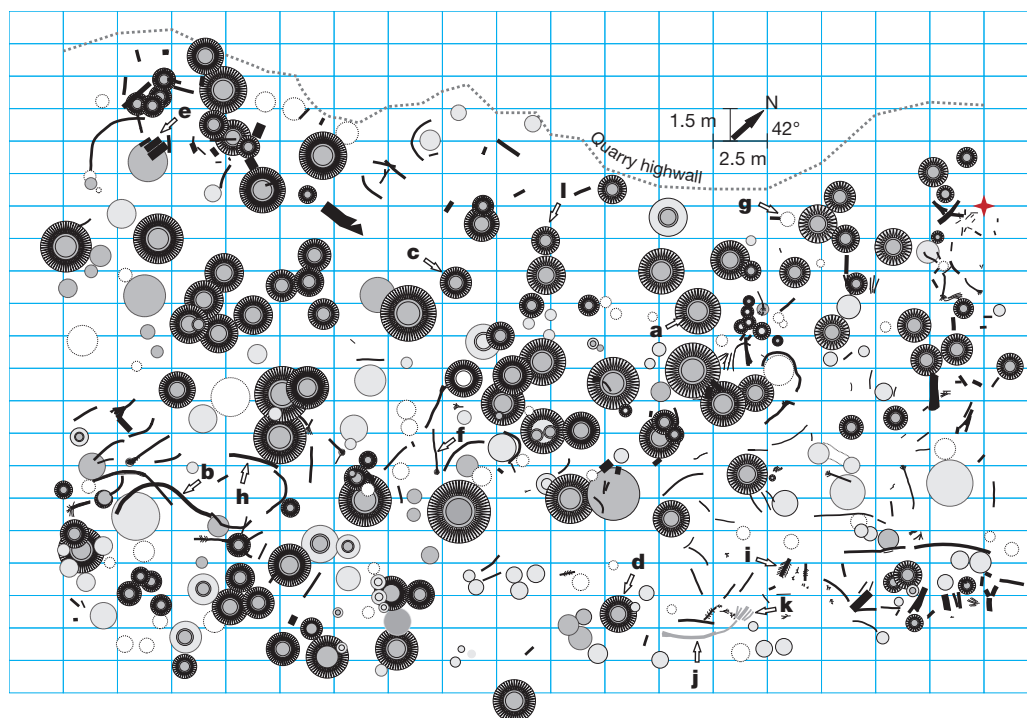


Figure 2 | Plan map of part of the quarry floor showing original rooting horizon. *Eospermatopteris* root mounds indicated with different levels of confidence. Dark shading, high confidence; light shading, intermediate confidence; dashed circles with no shading, low confidence. Radiating lines, radiating pattern of roots associated with root mound; central double circle, approximate diameter of central basin; outer circle, entire diameter of observed

root system. Aneurophytalean main stems and other linear stem fragments are shown in black. Lycopsid main stem (arrow **j**) and probable distal branches (arrow **k**) are grey. The approximate position of the quarry highwall is indicated by a dotted line; the georeference point (see Supplementary Discussion) is indicated by a four-point star. Arrows **a**–**l**, plants that are shown in Figures or in the Supplementary Information.

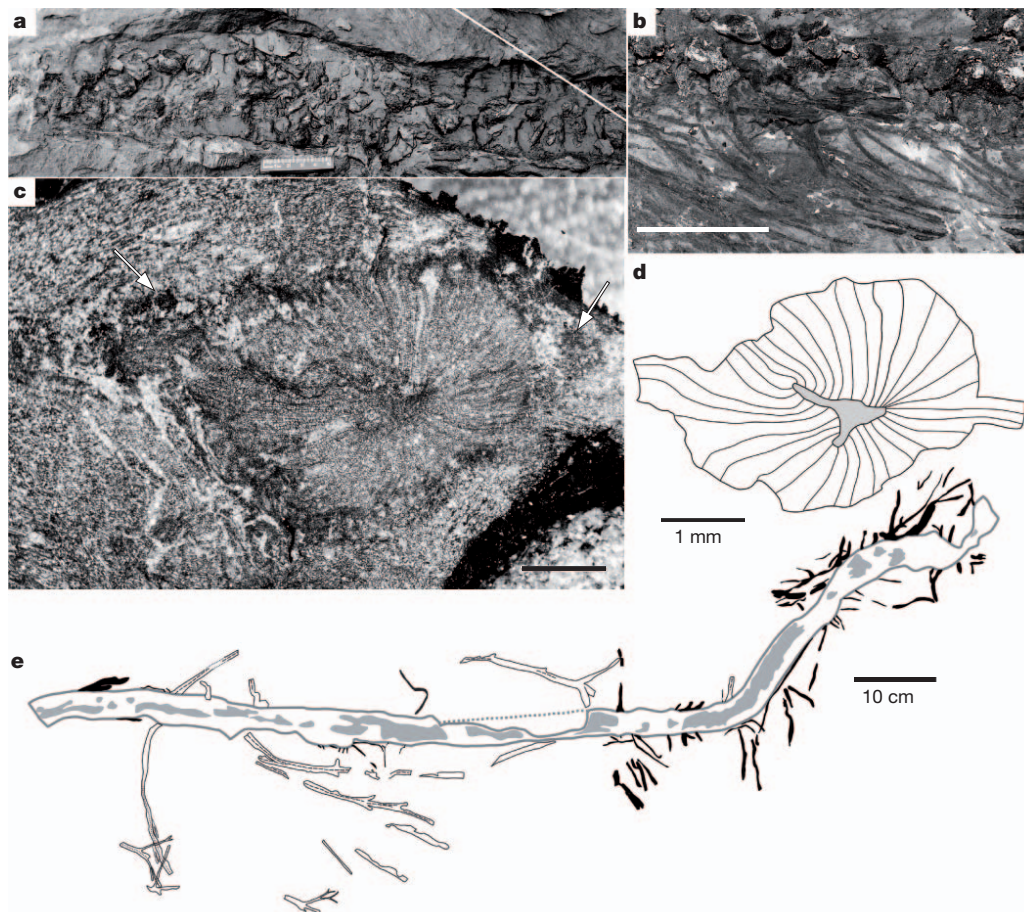


Figure 3 | Aneurophytalean rhizomes. **a**, Large specimen showing abundant carbon and several depressions, or knobs partially permineralized with pyrite. White line, part of the grid system for the map constructed in the field. Scale, 5 cm. **b**, Rhizome collected by Goldring (NYSM 6575) showing numerous attached roots. Scale bar, 10 cm. **c**, Transverse section of branch base showing primary xylem, secondary xylem, secondary phloem and remnants of cortex

(arrows), all embedded in extensive secondary xylem of the main stem (NYSM 18056). Scale bar, 1 mm. **d**, Interpretation of the lateral branch xylem in **c** showing probable three-ribbed primary xylem (shaded). **e**, Interpretation of rhizome originally collected by Goldring (NYSM 18051), showing attached and associated aerial branches in outline, attached roots in black and thick carbon on rhizome in grey.

Figs 21 and 23), also from Riverside Quarry. In this specimen a main stem shows similar orthostichous knobs bearing numerous roots of different sizes. Removal of sandstone reveals attached aerial branches that in turn bear dichotomous appendages mostly in an opposite, probably decussate, pattern that is consistent with the aneurophytalean genus *Tetraxylopteris*¹⁷.

Clustering of aneurophytaleans is conspicuous in Fig. 2, with some stems describing arcs around, and others running directly towards or away from, apparently established *Eospermatopteris* root mounds, and several stems appearing to end abruptly on an *Eospermatopteris* mound, near its rim. These findings suggest a rhizomatous habit for the plant with definite interaction between the aneurophytaleans and already established upright *Eospermatopteris* trees. It seems possible, perhaps likely, that the aneurophytaleans used the *Eospermatopteris* trees for support. Taken together, the observations suggest a new whole-plant concept for at least one member of the Aneurophytales as a large, woody, scrambling to lianaceous plant bearing adventitious roots and three-dimensional aerial branch systems functioning as frond-like ephemeral modules. These modules comprise the bulk of described evidence for this group to date^{16,17}.

At this quarry site we also found a single horizontally preserved tree clearly representing an arborescent member of the class Lycopsidea (club mosses)^{18,19} (Fig. 2, arrows j and k). An obliquely preserved main trunk that is greater than 11 cm in diameter is smooth with broad longitudinal ridges and curved over 3.9 m of preserved length (Supplementary Fig. 25). Distally, a 15-cm-diameter main trunk is

surrounded by four to six smaller axes of 4.5–8.5 cm in diameter (Fig. 4, and Supplementary Figs 26 and 27). However, the overall plant architecture is unclear. Both trunk and axes are covered with the same

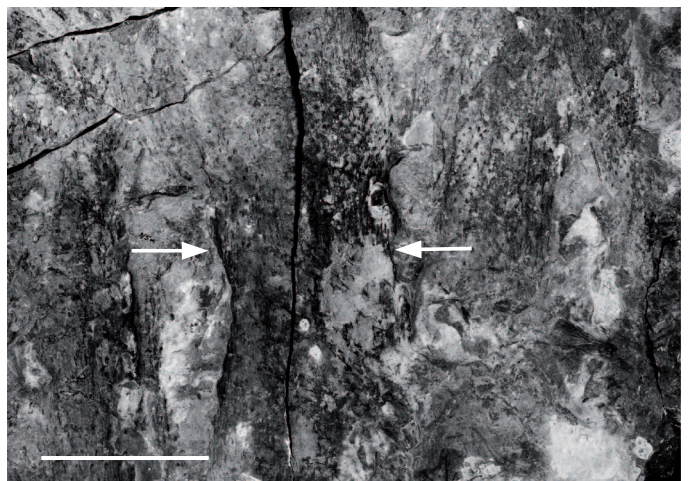


Figure 4 | Arborescent lycopsid. Upper portion of tree (arrow k in Fig. 2), including the main stem (occupying the width between the arrows) and smaller stems with similar leaf bases that probably represent distal portions of the main stem or lateral branches (NYSM 18053). Scale bar, 10 cm.

distinctive pattern of large attachment scars showing remnants of distal laminae; we can therefore confidently identify these fossils as lycopsids. Previous studies have reported abundant small lycopsids at Riverside Quarry and other Catskill localities^{20,21}, but none have been as large as this one. This record pre-dates the previous earliest (Frasnian age) lycopsid trees in North America²².

The remarkable *in situ* preservation of the Gilboa forest rooting horizon substantially enhances our understanding of this famous mid-Devonian 'earliest forest' terrestrial ecosystem. Rather than being a distinct muddy swamp containing a homogeneous stand of specially adapted *Eospermatopteris* trees, the site instead agrees sedimentologically with other exposures in the general vicinity^{23,24}, and with palaeobotanical evidence suggesting mixed assemblages worldwide²⁵. The location of this site was probably near an ancient shoreline during an interval of relatively high sea-level^{26,27}. Low-angle cross-bedded sandstones in the Gilboa region containing several *Eospermatopteris* levels suggest that the site was formed by recurrent, marine-influenced and possibly catastrophic, processes with a relatively high frequency of disturbance. Drab colour and high organic content of the forest palaeosol at Riverside Quarry indicates elevated water tables. Pyrite in aneurophytaleans, probably related to the presence of woody tissues, suggests concurrent or early diagenetic anoxia. All of this contrast with the predominantly red vertisols, which are also commonly observed in the Catskill complex. However, both facies are widespread and neither argues for a specific palaeoenvironmental reconstruction²⁸.

From one remarkable site, we now know that at least three major types of trees occurred in close proximity in a mixed, probably disturbed, wetland assemblage, with archaeopteridaleans absent at the scale of our map. We suspect that the sizes that were reached by the plants most probably relate to the rate of growth and frequency of reproduction permitted by disturbances, rather than reflect more regional environmental factors. From accumulating palaeobotanical evidence, we suggest that the very large but non-woody *Eospermatopteris* was probably hollow, reed-like and potentially fast-growing. This tree may have been capable of rapid establishment and, owing to the construction of sizeable root masses, contributed substantially to local substrate stability. Scrambling aneurophytaleans were also large, but woody, possibly longer-lived and potentially the greater contributor to global sedimentary carbon. Both plants bore leafless branch systems, suggesting only partial forest shade, and are commonly found together in Middle Devonian deposits today, probably as cast-off modular detritus. The apparent difference in growth form between rhizomatous aneurophytaleans and conifer-like archaeopteridaleans may signal some type of habitat specialization, but probably within a proximate wetland setting. Arborescent mid-Devonian lycopsids, now clearly present in mid-Devonian early forests, do not yet seem to be associated with coal-forming environments such as are typical for the Carboniferous period. Substantially modifying the image originally provided by Goldring⁵, we now glimpse a diversified early landscape already reflecting at least some of the complexity of later terrestrial ecosystems.

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