Palaeobotany: the rise of the Earth's early forests

Rare fossil forests are the best evidence for the ecology of the pioneering large land plants that transformed the Earth system and the terrestrial environment. A new study reveals a spectacular, remarkably extensive early fossil forest in China and sheds light on the evolution of key rooting systems.

The rise of land plants, which became well established during the Devonian Period (419-359 million years ago), is a key episode in the history of life. The evolution of moderate to large sized plants had profound influence on many aspects of the Earth system, including atmospheric composition, the hydrological cycle, sediment transport and the nature of the sedimentary rock record, and albedo and global temperatures, arguably creating the modern Earth. However the ecology of the early forests remains poorly understood. A new study by Wang and colleagues [1] in *Current Biology* documents an incredibly rare Devonian fossil 'forest', the first known in Asia, which sheds light on the global spread of forest ecosystems, their ecology, and the development of wetland plants.

The Devonian Period is for botanists what the Cambrian (541-485 Ma) is for zoologists. From almost nothing appeared a large diversity of forms and taxonomic groups. But unlike marine organisms, land plants faced the challenge of adapting to a new environment, out of water. Initial assembly of the characters required to adapt to a harsh, desiccating, nutrient and buoyancy-poor medium (e.g. strengthened water conducting cells and other structural tissues, cuticle, stomata, sporangia producing spores, rhizoids) was followed by an extended time in which land plants grew in complexity and size with the acquisition of further characters (ribbed and divided vascular columns, lateral branching, further differentiation of organs including leaves and complex roots, secondary growth of tissues most noticeably wood) culminating in the appearance of seed plants towards the end of the Devonian [2]. Other than the dramatic inception of flowering plants more than 200 million years later, plant innovation was more or less done.

One deservedly famous fossil deposit is the Early Devonian (ca. 410 Ma) Rhynie Chert from Scotland, in which an entire ecosystem is preserved in a silicified hot spring deposit [3]. The small plants, invertebrate land animals, fungi and cyanobacteria were almost instantly petrified, and have been preserved in astonishing detail. A chance discovery, with patience and decades of study, reveals the ecology of an entire early terrestrial ecosystem. But this ecosystem was only a few centimetres high allowing it to become completely submerged in the shallow volcanic waters.

Going forward into the Mid Devonian, plants became larger and more complex, and would have naturally broken into isolated organs, which got mixed together, transported and then compressed in sediment to form a carbon imprint. Small patches of the more resistant tissues, such as xylem, might have been infilled with rapidly forming pyrite, allowing some insight into the anatomy. Many attempted reconstructions of the earliest trees might be described as 'hopeful monsters', not because of their evolutionary status, but because they were chimeras; optimistic constructs of unrelated plant organs joined together to form bizarre looking plants that only existed in the minds of the palaeobotanists that sketched them. Visual representations of the Middle Devonian landscapes and vegetation made for books and museum dioramas were reliant on these monstrous reconstructions, and show the plants as isolated specimens within what are effectively Devonian botanical gardens. Little evidence of actual ecology is apparent, nor is crucial information such as habitat preference expressed [4].

Fortunately much progress has been made in recent years. In terms of understanding the body plan and growth of major plant groups, breakthroughs in plant reconstructions have come from both anatomical clues which have allowed for example the trunks and leafy branches of the woody tree *Archaeopteris* to be united [5], or the extensive ground-running rhizomes and leafless branches of the aneurophytaleans [6], and also from spectacular discoveries of almost complete large plants, particularly the cladoxylopsids [7, 8].

Direct evidence for early forest ecology, in the form of fossil trees rooted in ancient soil, is much more rare. In the famous Mid Devonian Gilboa fossil forest, New York, the large rooted bases of cladoxylopid trees have woody rhizomes of aneurophytalean progymnosperms running between them [6]. In deposits of a similar age from nearby localities the earliest much branched rooting systems of *Archaeopteris* can also be found [9]. *Archaeopteris* went on to be the dominant tree of the Late Devonian epoch, but direct information about the spacing of early *Archaeopteris* trees is not yet documented in such detail [9, 10].

Each of the taxa mentioned above are members of the Euphyllophyte clade [2]. Lycophytes are the sister group to Euphyllophytes, and despite only representing a fraction of one percent of living plant diversity, have an heroic evolutionary history. Early forms were herbaceous , and recently it has been shown that roots had an independent origin in lycophytes [11].The oldest and only previously known Devonian fossil lycophyte forest is that from the very beginning of the Late Devonian recently described from Svalbard [12]. Notable in comparison to the known cladoxylopsid and *Archaeopteris* forests was the very close spacing of the slender, small lycophytes growing in dense monospecific stands. The bases of these trees were somewhat enlarged, with flat bases, covered in small rootlets.

In the present paper [1], Wang et al. describe a spectacular new forest of lycophyte trees that extends over a large area of active quarries in Xinhang Town, Anhui, China, allowing the changing exposure to be monitored over several years. This forest dates from the very end of the Devonian, perhaps 20 million years younger than the Svalbard lycophyte forest. An outstanding feature is that this fossil assemblage allows not only for the bases and roots of the trees to be studied *in situ*, but the fallen remains of the upper parts of the trees have also been preserved. Usually when Devonian tree bases are found, one has to look elsewhere for fossils representative of the upper parts of the tree, and to make reconstructions of the whole plant based on circumstantial evidence and inference. Trees at many stages of growth have been found, only a few with trunks more than 10 cm in diameter. In common with many tree formed lycophytes these examples have a long unbranched trunk with simple dichotomous branching at the top, yielding an unfussy crown with dangling terminal cones, and are covered with small tapered leaves, or the scars from which the leaves abscised.

The other notable feature of the fossils is underground: this new lycophyte has the earliest known attached unequivocal stigmarian rooting system. This is a remarkable organ, that probably lives on in a reduced form as the base of *Isoetes*, comprising larger roots and laterally attached small rootlets [13]. Older Chinese small upright lycophytes have dichotomous roots only [14], and those from the Svalbard forest [12] and the 'Naples Tree' [15] from New York have expanded, bulbous (cormose) bases which bear rootlets. Another from Pennsylvania had four distinct basal lobes with rootlets [16]. However the base of the new fossil tree divides into four equally spaced extended rhizomorphs which each branch dichotomously, and to which are attached laterally narrow rootlets. Over time these simple structures developed in size such that by the late Carboniferous Period (Pennsylvanian) (c. 320-310 Ma) they could structurally support the first giant wetland trees (up to 50 m high) [13, 17]. Stigmarian rooting systems were by this time supremely adapted to living in waterlogged oxygen poor soils and swamps, where the chances of the fallen tree's structural carbon being protected from decay in the accumulating peat was high. Thus lycophytes form the bulk of the Carboniferous tropical wetland coal deposits which fuelled the industrial revolution across Great Britain, Europe and the United States. This has influence on atmospheric CO_2 concentrations, both in the Carboniferous, and because of industrial processes, in the present day.

Like the older Svalbard lycophyte forest, the Xinhang forest grew on the palaeoequator, and is only found away from it now because of plate tectonics. Fortunately this small sample of tropical Devonian lycophyte forests can be expanded from study of the dispersed spore record associated with coal deposits [18]. As well as providing a snapshot of a single ecosystem, the fossils also highlight the transition to a true stigmarian rooting system within the lycophytes. Although a coastal setting is interpreted for Xinhang [1], it would be interesting to know further details of the environments, sediments and soils in which this transition took place. The quantity of well preserved fossils also suggests that further investigation could be made of the development and ontogeny of these plants, perhaps even with respect to the speed of growth, from which inferences can be made about the impact of tropical forests on atmospheric CO_2 levels [19, 20], and the contribution of tree lycophytes to the onset of the first ice age on a forested Earth.

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Figure:

Summary of the known stratigraphic ranges (vertical lines) of Devonian forest types and form of Devonian forest trees (not to scale). Time in millions of years before present. Data from [1], [6], [7],[9], [10], [12].