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THE EVOLUTION OF THE FIRST FORESTS IN THE DEVONIAN*

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In recent years much new data have been obtained regarding the earliest trees, and their ecology in early forest ecosystems. Aspects of this new data are summarised below, concentrating on the Mid Devonian and earliest Late Devonian, c. 390–380 million years ago, before the dominance of *Archaeopteris*. The arborescent cladoxylopsids, archaeopteridaleans and lycopsids are considered, as well as the recumbent but large woody aneurophytes. Until now, cladoxylopsid dominated forests, cladoxylopsid/aneurophyte forests, early *Archaeopteris*, and lycopsid forests are the four forest types identified, largely on the basis of near coastal, wet environments. True *in situ* fossil forests are extremely rare during this time interval. Future research aims to identify further forest types, to better understand their relationship to palaeogeography and sedimentary environment, and to spread the understanding of early forests beyond the Old Red continent.

Keywords: *palaeobotany, forest ecology, Lycopsida, Aneurophytales, Archaeopteridales, Cladoxylopsida.*

ЭВОЛЮЦИЯ ПЕРВЫХ ДЕВОНСКИХ ЛЕСОВ

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В последние годы получено много новых данных о самых ранних в истории Земли древесных растениях и их экологии в ранних лесных экосистемах. Эти новые данные кратко изложены ниже, с акцентом на среднедевонские и самые ранние позднедевонские (390–380 млн лет назад) растения, до господства *Archaeopteris*. Рассматриваются древовидные кладосилеевые, археоптерисовые и плауновидные, а также стелющиеся по земле крупные древесные аневрофитовые. До настоящего времени были идентифицированы четыре типа лесов — с преобладанием кладосилопсид, леса кладосилопсид/аневрофитовых, ранние *Archaeopteris* и леса плауновидных растений, в основном представители прибрежных влажных сред обитания. Настоящие инситуные ископаемые леса этого возраста встречаются исключительно редко. Будущие исследования направлены на выявление новых типов лесов и на лучшее понимание их связи с палеогеографией и условиями осадконакопления, а также на выявление ранних лесов за пределами Древнего красного материка.

Ключевые слова: *палеоботаника, экология леса, Lycopsida, Aneurophytales, Archaeopteridales, Cladoxylopsida.*

Introduction — what is a Devonian forest?

It is generally agreed that the evolution of land plants in the early part of the Palaeozoic, and of vascular plants in particular, had a profound effect upon the Earth System.

The first vascular land plants were very small and were simple dichotomously-branching axial systems with very limited rooting structures, if any. By the Early Devonian (see Figure 1 for timescale), plants with advanced branching patterns, sometimes sturdy upright main axes and small amounts of secondary xylem tissue (wood) [7] had evolved in the euphyllophyte clade, as well as herbaceous forms of lycopsid.

Early Devonian plants with a protostele and little if any secondary wood, and a main stem of only perhaps 25 mm, such as *Pertica*, would have been unable to support more than 2–3 m of main stem before bending under their own weight. While these plants certainly had an effect on important Earth System parameters, including flood plain stability and weathering of soils [20], it was not until the evolution of trees that the magnitude of the impact of plants really began to accelerate [13].

In the euphyllophyte clade trees might be defined as substantial plants with a woody self-supporting upright

main axis. In the lycopsids arborescent forms generally have a self-supporting main stem strengthened by secondary tissues (largely cortex or bark rather than wood) [11] supported by a branched rhizomorph or cormose base with rootlets.

The Forestry Department of the Food and Agriculture Organization of the United Nations (Global Forest Resources Assessment 2010) defines a tree as a ‘woody perennial plant with a single main stem... having a more or less definite crown’, and a forest as ‘Land spanning more than 0.5 hectares with trees higher than 5 meters and a canopy cover of more than 10 percent, or trees able to reach these thresholds *in situ*.’ National criteria may vary to include trees of as little as 1.3 m height (Estonia) and may include such plants as palms and bamboo [8]. Some of these criteria may be difficult to determine on the basis of fossil plants and limited outcrops. For example, the area of crown of a small arborescent lycopsid is hard to evaluate, especially on the basis of preserved stumps. Therefore, in terms of fossil forests over the past 390 million years, with a greater variety of tree-formed plant morphologies and anatomies, it is clear that a slightly broader definition can be accepted.

A very small number of fossil forests are known where

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the bases of multiple Devonian trees or clearly recognisable rooting systems are preserved *in situ*, likely by a single depositional event, such as levee breach, debris flow or storm-driven influx of coastal sediment. Here inference from incorporated or nearby megafossil assemblages might be used to reconstruct the above ground part of the trees and thereby the structure, spacing and ecology of the forest at time of burial. Such fossil forests are a considerable step forward in understanding individual forests and forest ecologies, and these examples might act as models for understanding the more common diverse fossil assemblages that are not found *in situ*. No Devonian forests preserved by ash falls are yet known.

Earliest forests (cladoxylopid dominated)

The earliest assemblage of tree-formed plant fossils is from Lindlar in Germany, and dates from the mid Eifelian (see Figure 1). The fossils are preserved in a shallow marine deposit, transported by a high energy catastrophic coastal event, possibly a tsunami [9]. The best fossils come from a single lens exposed in the high wall of the quarry in the 1960s and collected and described by Schweitzer, and more recently in the 2010's by Giesen and colleagues, although further good fossils were also collected from a neighbouring quarry. The flora is subject to reassessment in the light of modern knowledge of Mid Devonian plants, and the discovery of many articulated large specimens. The taxa described as *Calamophyton* and *Duisbergia* by Schweitzer have now been reassembled into a single plant, *Calamophyton* [9] which forms the dominant element of the flora. Complete specimens are known of 2 m length (height), but based on the size of the branches against abscised examples found elsewhere it was suggested that these are only small to medium sized trunks compared with their potential size.

Calamophyton is recognised as an early member of the pseudosporochnalean cladoxylopsids, the oldest known vascular plant type to reach sizable tree form. These plants are characterised by a trunk which has a large pith, and the vascular system comprises numerous strands of xylem arranged in a ring, surrounded by parenchymatous cortex. Lateral branches have a characteristic digitate branching habit carrying small non-laminate appendages, and were abscised as the broad crown of the trunk grew upwards (Figure 2). Giesen and Berry [9] interpreted *Calamophyton* to have secondary growth based on analysis of the dimensions of the suite of specimens recovered, suggesting an ontogenetic sequence. More recently Xu et al. [19] have shown that late Devonian cladoxylopsids, preserved in silica, grew by adding wood around the circumference of each of the xylem strands, by proliferation of parenchymatous tissues between the strands, and changes in the geometry of the entire vascular system. Cladoxylopsids apparently evolved a unique and well-engineered way of growing to tree size quite different from other woody trees, and formed the backbone of forest ecology from early Mid Devonian through to the early Late Devonian (Figure 1).

Calamophyton is the dominant element in the Lindlar flora, although other cladoxylopsids from the site are presently being described. Because neither *in situ* trunks nor palaeosols with tree bases have been found, Lindlar is not a true fossil forest. We do not know the spacing of the *Calamophyton* trees, nor their relationship to other plants, so the reconstruction of a stand shown in Figure 2 is necessarily illustrative rather than factual, but is based

on the known closeness of spacing of cladoxylopid bases (at Gilboa — below) and the short length of the branches. A small amount of the aneurophyte *Rellimia* is also known at Lindlar but has not been described in detail.

The Gilboa forest (cladoxylopid/aneurophyte association)

Although known since 1860s all previous work on the fossil trees and forest of Gilboa, New York State, USA, has been superseded by modern investigations. Riverside Quarry, Gilboa is critical because it is the oldest known site from which multiple *in situ* tree bases have been described.

Fig. 1. Schematic timeline of known Devonian forest types against geological ages (Period, Epoch, Age, numerical age (Ma)). Modified after Berry [2]

Рис. 1. Схематическая временная шкала известных девонских типов лесов в зависимости от геологического возраста (период, эпоха, относительный и абсолютный возраст) по К. М. Берри [2]

Fig. 2. Reconstruction of stand of *Calamophyton* (cladoxylopid) trees (2–3 m high) based on fossils from Lindlar, Germany (Mid Eifelian age) [9]. Credit Peter Giesen

Рис. 2. Реконструкция древостоев *Calamophyton* (cladoксилопсид) (высотой 2–3 м) на основе окаменелостей из Линдлара, Германия (средний эйфель) [9]. Питер Гизен

It is of late Givetian age (Figure 1), and the environment of deposition was considered as very close to the sea [3]. Investigation in 2010 of the floor of Riverside Quarry, which had been cleared during work to reconstruct the Gilboa reservoir dam, showed that cladoxylopsid trees were the dominant element of the Gilboa forest [15]. Tapered tree bases were preserved as sandstone casts. Measurement of the tree bases extracted from the quarry showed them to be up to 1 m in diameter. Discovery of a laterally compressed incomplete trunk 6 m long with a 47 cm diameter base at the nearby but slightly younger (early Frasnian) South Mountain locality [16], together with an isolated crown, allowed the whole plant to be reconstructed without ambiguity, and the genus to be established as *Wattieza*, a pseudosporochnalean cladoxylopsid. The height of the largest specimens, with bases double the diameter, cannot be established.

The exposed quarry floor allowed the relatively close spacing of the cladoxylopsid trees to be determined. Also present on the forest floor were long thick woody rhizomes, up to 15 cm in diameter and several meters long, which were shown to belong to an aneurophytalean progymnosperm [15]. Progymnosperms were capable of growing secondary xylem and phloem from a bifacial cambium and reproduced with dispersed spores. The aneurophyte was reconstructed with lots of branches attached, which have been found detached in great numbers in the Gilboa sandstone.

The association of dominant cladoxylopsids with more or less ground running aneurophytes, reconstructed in Figure 3, was also found in transported assemblages at the Belgian locality of Goé, of latest Eifelian age, interpreted as a near shore marine depositional environment [3]. This suggests that this forest type persisted over a period of at least 6 million years in certain environments (Figure 1), perhaps associated with coastal settings.

Lycopsid forests

Early forms of upright standing lycopsids, known from the Mid and early Late Devonian of China, may have had dichotomous rooting systems homologous to the rootlets of Carboniferous *Stigmaria* [10]. In the earliest tree-like forms known from Euramerica, from Svalbard, rootlets were attached to a cormose, or enlarged rounded, base. Outcrops of the early Frasnian Plantekløfta conglomerate allowed the spacing of monospecific stands of *Protolepidodendropsis* to be determined [4]. These small trees, with basal diameters up to about 20 cm, grew very close together in life (Figure 4). Because of the abundance of remains of the same trees lower down in the sedimentary sequence, it is likely that such stands of trees were present in Svalbard during the late Middle Devonian (late Givetian) as well. In New York, USA the Frasnian age Naples Tree had a similar habit to *Protolepidodendropsis*, but a different pattern of leaf cushion/bark [18]. Remains of fallen or transported lycopsid trunk(s) were found in one small patch on the floor of the Gilboa forest floor [15].

In Xinhang, Anhui Province, China, an *in situ* forest of small lycophytes has recently been described [17], again with very close spacing of the bases, which are generally of smaller diameter than the Svalbard ones. The forest dates from the very end of the Devonian, perhaps 20 million years later than Svalbard. Most interesting about this new discovery is that this is the oldest occurrence of well-preserved *Stigmarian* rooting systems, in which four dichot-

Fig. 3. Reconstruction of forest showing upright cladoxylopsid trees (up to at least 8 m) and recumbent aneurophytaleans, from Gilboa, New York (Late Givetian age) [15]. Credit Frank Mannolini, New York State Museum

Рис. 3. Реконструкция леса с вертикальными кладоксилопсидными деревьями (до 8 м) и лежащими аневрофитолями из Гильбоа, Нью-Йорк (поздний живет) [15]. Фрэнк Маннолини, Музей штата Нью-Йорк

Fig. 4. Reconstruction of forest of lycopsids with cormose bases and attached rootlets, from Munindalen, Svalbard (early Frasnian age) [4]. Credit Berry

Рис. 4. Реконструкция леса ликопсид с основаниями и прикрепленными корнями из Муниндалена, Шпицберген (ранний фран) [4]. К. М. Берри

omously branched rhizomorphs are subtended by dichotomous rootlets which leave characteristic round scars. This is a feature of the trees of the major Carboniferous coal forests. The environment of both the Svalbard and Xinhang forests are believed to be wet, in an inland fault-bounded basin in Svalbard, and in a coastal setting in Xinhang [4, 17].

Archaeopteris forests

Archaeopteris a genus of progymnosperm (Archaeopteridales) with substantial upright woody trunk. Its leafy fronds first appear in mid to late Givetian age sediments, although its microspore is known from closer to the beginning of the Givetian. It became extinct about the Devonian/Carboniferous boundary, giving it a temporal range of about 25 million years, and has been presumed to dominate forests in all but the earliest parts of the Late Devonian. Most detailed information about its structure and branching comes from the latest Devonian, and it has been reconstructed with a conifer-like habit [1]. Details and reconstructions of the earliest forms of *Archaeopteris* are still uncertain. Most critical for the point of view of this summary is the question if the Mid Devonian *Archaeopteris* trunks supported large woody long-lived boughs, or were merely the point of attachment of leafy, short-lived fronds. Substantial bases of *Archaeopteris* trees, including the

proximal parts of the major roots, are known from the Famennian of the Donetz Basin (Figure 5) [14].

In Svalbard, small early Frasnian *Archaeopteris* tree bases have been found *in situ* in small outcrops away from the lycopod stands [4]. In New York, drifted *Archaeopteris* fronds [5] attached to bigger axes are found in association with similarly transported large cladoxylopsid trees [16] at the South Mountain locality of early Frasnian age. It may be that *Archaeopteris* was as capable of growing with cladoxylopsids as aneurophytes were at Gilboa.

Roots with morphologies attributed to *Archaeopteris* are known through much of the Givetian-Famennian terrestrial deposits of New York [6, 12]. However only parts of the rooting systems are known, and detailed plan mapping of large areas remains to be published [13].

Conclusions and Future Directions

The evidence assembled in recent years, centred on Euramerica, suggests that only a small number of the potential associations of plant types that formed forests in the Devonian Era (Figure 1) have yet been discovered. This is not surprising given the exceptionally rare occurrences of fossil forests and palaeosol deposits where root morphologies can be interpreted in terms of taxonomy. The key types of trees that formed forests were the pseudosporochnalean cladoxylopsids, the lycopsids, the archaeopteridaleans and the recumbent woody aneurophytales. Initially cladoxylopsids were the dominant trees, joined by aneurophytales and then *Archaeopteris*. *Archaeopteris* then became the dominant forest tree. Lycopsids seem to have lived in the wettest environments, perhaps with less interactions with the other trees from their beginnings. Further fossil forest types are in course of being described [2]. Naturally, we also need to spread this work to other continents where rich deposits of Mid Devonian to early Late Devonian plants are known, particularly in China where work to date largely concerns the taxonomy of individual plants.

For the fossil forest types so far described in detail, it is clear that they (unsurprisingly) mainly reflect wet, near coastal environments, and the diversity of large plants growing on dryer soils has not yet been explored. With the recognition of different early forest types, it becomes critical to make in depth sedimentological analysis to determine environmental control on forest types, to evaluate palaeogeographic and climate parameters to understand their distribution, and to provide accurate biostratigraphic control to understand their spread. Palynology, as a proxy for vegetation, is a further important line of evidence for the spread of forests (see e. g. Marshall and Tel'nova, this volume).

We can also hope for even more spectacular preservation of fossil forests, perhaps preserved in volcanic ash, where we might determine how other important, but often more fragile, plant groups, such as zosterophylls, herbaceous lycopsids, iridopteridaleans and stenokolealeans, might fit into the presumed understory component of Devonian forests.

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Fig. 5. Base of *Callixylon trifilievii* (trunk of *Archaeopteris*) from the Late Devonian (Famennian) of Donetz Basin [14]. Komarov Botanical Research Institute, St. Petersburg (courtesy S. Snigirevsky)

Рис. 5. Основание *Callixylon trifilievii* (ствол *Archaeopteris*) из позднедевонских (фаменских) отложений Донецкого бассейна [14]. Ботанический научно-исследовательский институт им. Комарова, Санкт-Петербург (предоставлено С. Снигиревским)

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