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Fossil evidence of tylosis formation in Late Devonian plants

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Tyloses are swellings of parenchyma cells into adjacent water-conducting cells that develop in vascular plants as part of heartwood formation or specifically in response to embolism and pathogen infection. Here we document tyloses in Late Devonian (approximately 360 Myr ago) *Callixylon* wood. This discovery suggests that some of the earliest woody trees were already capable of protecting their vascular system by occluding individual conducting cells.

Tyloses are protoplasmic inflations formed by parenchyma cells into the lumen of neighbouring conducting cells[1,2]. They extend through the pit pair and can completely fill the lumen of the conducting cell. The mechanisms underlying tylosis formation remain largely unresolved[3,4], but it is generally accepted that they represent a response to embolism and have a major role in blocking air-filled conducting cells. Moreover, tylosis formation is among the earliest processes in the compartmentalization of decay in trees[5], which can delay the spreading of pathogens. Tyloses in fossil plants therefore provide direct insights into the evolution of one of the most important mechanisms with which plants protect their vascular systems from biotic and abiotic stresses.

Structurally preserved fossils provide evidence that tylosis formation occurred in most lineages of vascular plants as early as the Mississippian (~350 Myr ago (Ma))[6]. However, the oldest fossils interpreted to represent vascular plant conductive elements (tracheids) are dispersed microscopic tubes from the latest Silurian (~430 Ma)[7], and the first record of secondary xylem (wood) comes from the Early Devonian (410 Ma)[8–10]. By the Middle Devonian, many plants possessed wood[11] in which the arrangement of conducting cells and parenchyma could, in theory, have allowed the formation of tyloses. The development of larger and more complex plant bodies during the later Devonian, along with the evolution of leaves and more extensive root systems[12,13], probably increased the risk of embolism in the vascular system. There is also evidence from the Devonian of the existence of various vascular plant–fungal interactions, possibly including wood decay[14,15]. It is therefore surprising that no tyloses have been hitherto reported in plant fossils older than the Mississippian.

The lack of documented evidence of tyloses in early vascular plants has spurred us to specifically look for these structures in structurally preserved Devonian woods. We found that many early woods are fossilized in a manner not conducive to the preservation (in a recognizable form) of delicate parenchymatous structures, including tyloses. Nevertheless, we discovered evidence of early stages of tylosis formation in one pyritized wood from the Upper Devonian (Famennian, ~360 Ma) of Sandeel Bay, County Wexford, Ireland.

This wood consists of tracheids and small parenchymatous rays (Fig. 1); distinct growth-ring-like zones of tracheids with reduced radial diameters are indicative of intermittent periods of less favourable growth conditions (Fig. 1a). The radial tracheid walls show groups of pits separated by unpitted areas, a feature typical of *Callixylon*, the wood of the archaeopteridalean progymnosperms (Fig. 1c)[16] (see also Methods). The rays are 1–2 cells wide and 1–15 (usually less than 10) cells high in tangential section (Fig. 1d) and are abundant, and each xylem tracheid is in contact with many ray parenchyma cells. Conspicuous bubble-like outgrowths of ray cells into the lumen of adjacent tracheids occur in one area of a longitudinal section (Fig. 1e–k). Although they appear darker than the surrounding parenchyma cells, we interpret these outgrowths as tyloses rather than gum deposits, on the basis of their regular outline, their physical connection to the rays and the presence of several translucent examples (Fig. 1k). The majority of the tyloses are spheroidal (Fig. 1e,f), in some cases constricted at the base (probably corresponding to their passage through the pits connecting rays and tracheids); others are more flattened (Fig. 1h,i). Still others completely occlude the tracheid (Fig. 1g). Several tyloses commonly emerge from a single ray, in places evident along both sides of the ray in tangential sections (Fig. 1j). No evidence of tylosis formation was observed in any other structurally preserved plant fossil from the Sandeel Bay locality.

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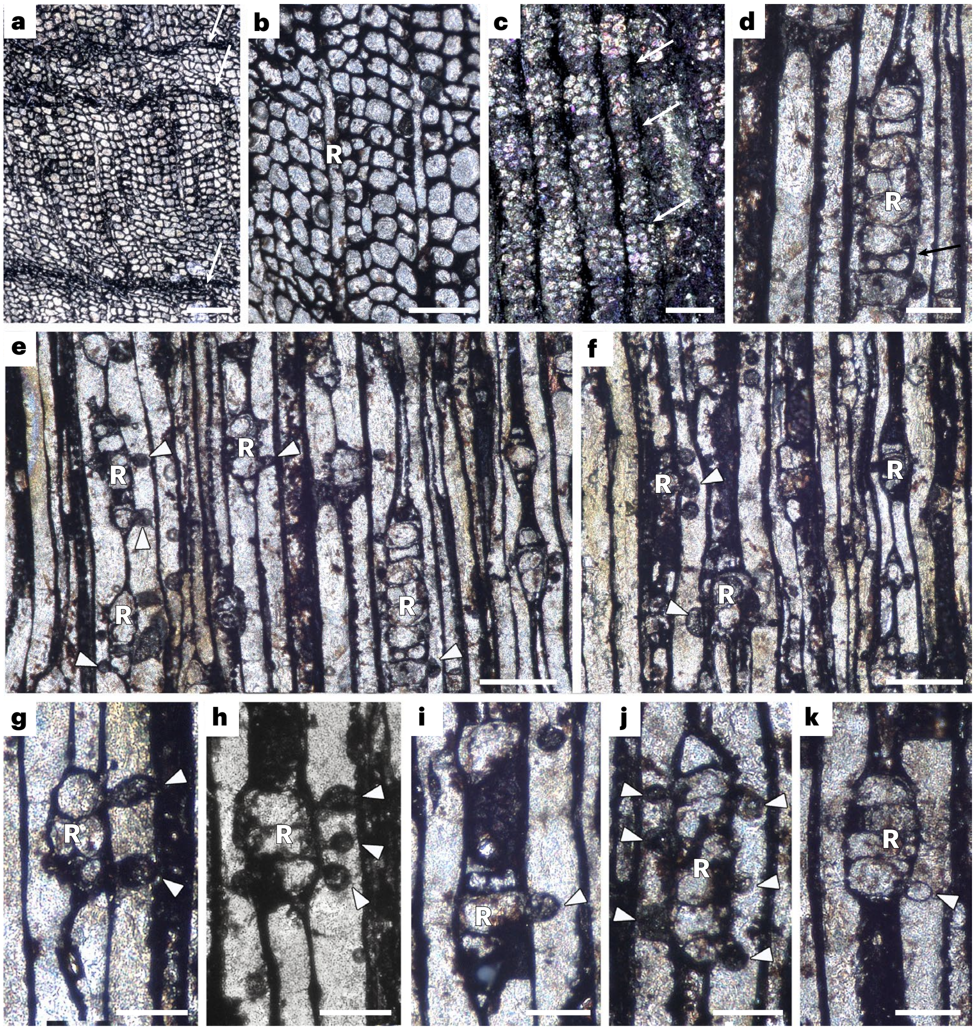

Fig. 1 | Late Devonian *Callixylon* wood containing tyloses. a, Transverse section, showing growth ring boundaries (white arrows). **b**, Detail of a transverse section with two rays. **c**, Radial longitudinal section, showing groups of pits separated by unpitted areas (white arrows) typical of *Callixylon*. **d**, Tangential longitudinal section of a ray containing what appear to be ray tracheids (black arrow). **e**,**f**, General views of areas with abundant tyloses. **g**, Tyloses entirely blocking a conducting cell. **h**, Ray with several small outgrowths (developing tyloses) into an adjacent tracheid. **i**, Small outgrowth from a ray cell into a tracheid. **j**, Ray with tyloses on both sides. **k**, Tylosis lacking dark content (translucent). All images were selected from the direct observation of preparations of a single fossil (no. HH5) under the microscope: **a**,**b**, slide HH5-B-CT1r; **c**, HH5-E (surface of specimen); **d**–**g**,**j**,**k**, slide HH5-D-G1r; **h**, slide HH5-D-G1v. A general view of slide HH5-D-G1r is provided in the Supplementary Information. Scale bars: **a**, 200 μm; **b**, **e**, **f**, 100 μm; **c**, **d**, **g**–**k**, 50 μm. R, ray. The arrowheads indicate tyloses.

Archaeopteridales is a Middle–Late Devonian group of progymnosperms—extinct plants that had a gymnosperm-like wood but reproduced via spores[16]. Archaeopteridalean trees produced a large amount of wood, formed a deep and complex root system, and had true leaves, making them the first trees with a 'modern' vegetative body[12,17]. Recent studies of their hydraulic properties suggest that archaeopteridalean wood had a conductivity comparable to that of extant conifers, with some plasticity provided by variations in the size of the conducting cells and rays[18,19]. Like extant trees, archaeopteridaleans were susceptible to wood-decaying fungi that invaded their vascular system[14]. By the Late Devonian, these trees were a major component of ecosystems worldwide, having been reported from the palaeotropics to the high latitudes of Gondwana[20]. This wide latitudinal and geographic range implies that the group was able to adapt to very diverse growth conditions. The ability to protect the vascular system from biotic and abiotic stresses by occluding (some of) the conducting cells may therefore have been an important advantage. The depositional environment of the anatomically preserved plants at Sandeel Bay has been interpreted as a cut-off channel chute of a meandering river near the coast[21], within a dry tropical area located at a palaeolatitude of about 15° S[22]. Growth-ring-like zones in the archaeopteridalean woods from this deposit suggest that the trees were exposed to periodic shifts from favourable to less favourable growth conditions. It is likely that there were episodes of drought governed by variations in the water table that could have caused embolism in certain regions of the wood and led to tylosis formation. The fact that most tracheids are not completely blocked indicates that the specimen depicts an early stage in this process. This discovery illustrates how structurally preserved fossils can provide snapshots of plant physiology in deep time and allow us to piece together episodes in the evolutionary history of key biological processes. Moreover, it provides further evidence of the antiquity of tylosis formation in plants and suggests that the emergence of this capacity could have been linked to the evolution of larger plant bodies with a more complex organization. As soon as plants had evolved a water-conducting system[11,12], they had also created a gateway through which physical (that is, embolism) and biological (that is, pathogens) threats could spread. Early vascular plants were perhaps able to mitigate this drawback simply through their small size and the short lifespan of their structures. However, as soon as plants grew larger, an effective system of protection of the vascular system became essential[23], with tylose formation being an integral component.

Methods

Age of the fossil wood and the sedimentological and floristic context

The specimen was collected in 2021 at Sandeel Bay on Hook Head peninsula, Wexford County, Ireland. Outcrops containing Late Devonian plant macrofossils in this area belong to the Harrylock Formation[24] (Supplementary Fig. 1a), which incorporates fluvial sediments deposited in a proximal alluvial plain setting. Anatomically preserved specimens occur as pyritic permineralizations in grey–green mudstones, which also contain compressions, dispersed spores and cuticles (Supplementary Figs. 1b and 2). The miospore assemblage at Sandeel Bay is assigned to the LL Miospore Biozone of latest Famennian age[24]. New findings in 2021 of *Retispora lepidophyta* (Kedo) Playford 1976 and *Vallatisporites pusillites* (Kedo) Dolby and Neves 1970 in the layers containing the macrofossils (Supplementary Fig. 2h,j) confirm their age as latest Famennian. Other permineralized plants recovered from the source deposit of the specimen with tyloses include axes of the lycopsid *Wexfordia hookense* (Matten) Klavins 2004 at different developmental stages[25,26] (Supplementary Fig. 2a), together with axes and wood with the typical *Callixylon* Zalessky 1911 anatomy of archaeopteridalean progymnosperms[16]. *Callixylon* was first reported from this locality by Klavins[21], who also described an anatomically preserved branch assigned to *Archaeopteris* cf. *hibernica*. Newly collected specimens from this locality include the first anatomically preserved *Archaeopteris* roots (Supplementary Fig. 2d–g). Finally, Klavins[21] reported three different types of pyritized seeds, which indicate the presence of seed plants in the palaeoenvironment. Palaeosol layers at Sandeel Bay contain traces of relatively deep and branched root systems that could belong to *Archaeopteris* and/or seed plants.

Fossil preparation and observation

The fossil is approximately 17 cm long and 2–3 cm wide and consists of seven consecutive portions of a single axis. Selected axis portions were prepared at UMR AMAP in 2022 according to the following protocol. They were embedded in epoxy (DBF, Escil), and transverse and longitudinal sections 1–2 mm thick were subsequently cut with an Isomet 1000 diamond saw and polished on both sides. To improve contrast, the sections were then etched following a modified version of the protocol for pyrite permineralizations published by Stein and collaborators[27]. They were initially etched in 70% nitric acid (HNO_3) heated to 70 °C for 60–90 seconds. After neutralization in sodium hydroxide (NaOH), they were additionally etched in 37% hydrochloric acid (HCl) for a few seconds, neutralized and then etched again in 5–10% HCl before being rinsed in water and let to dry. Selected sections were mounted on glass slides and observed in reflected light. Due to the distortion of the wood, there was no good-quality view of the radial pitting on the mounted sections. Photographs of the radial pitting (Fig. 1c) were thus taken directly on the surface of fragment HH5-E after a fracture in the radial plane. All photographs were taken with a Keyence VHX 7000 digital microscope and the associated software (VHX-7000 main software and VHX-7000 communication software). Composite figures were assembled in Adobe Photoshop v.21.2.2 (Adobe Inc., San José, CA, USA). In slide numbers, such as HH5-D-G1, the first part refers to the specimen number (5), the second to the part of the specimen (D) and the last to the section (G1). The letters r or v in the photographs indicate the side of the wafer that was photographed (recto, bearing the number, or verso).

Systematic affinity of the wood

The systematic affinity of the specimen was determined on the basis of wood anatomical traits in longitudinal and transverse sections. Although no primary tissues are preserved, the presence of wood tracheids with groups of radial pits separated by unpitted areas on their radial walls is a distinctive feature of the fossil genus *Callixylon*, which represents the wood of archaeopteridalean progymnosperms[16]. Other woody plants discovered from the source layers of the specimen described here are lycopsids, which clearly differ from *Callixylon* in the radial pitting (Supplementary Fig. 2c). Seed plants, currently evidenced from this locality only on the basis of the seeds described by Klavins[21], are not known to produce wood with unpitted areas on the radial walls. Species of *Callixylon* are distinguished on the basis of differences in certain wood anatomical features, such as ray width and the presence, abundance and distribution of ray tracheids[28]. Rare ray cells with thicker walls and a squarish outline in the new specimen (for example, Fig. 1d) could correspond to ray tracheids. However, the preservation of the specimen prevents a confident assignment at the species level.

Interpretation of the outgrowths as tyloses

An alternative interpretation of the bubble-like outgrowths views them as partly coagulated (due to water loss) cell contents of the ray cells that have oozed out into adjacent tracheids as a result of the pyritization process. Strongly arguing against this interpretation are the facts that (1) similar structures have not been observed in any other pyrityzed wood from the Sandeel Bay site, and (2) the occurrence of outgrowths is limited to one particular region of the specimen that does not differ from the rest in regard to preservation. Small, circular structures lacking a clear connection to parenchyma cells could also correspond to tyloses, but they could also be gum or other organic residues.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data that support the findings of this study are included in this published article and its Supplementary Information files. A high-resolution image of the section showing tylosis from Supplementary Fig. 3 is also available on Figshare at https://doi.org/10.6084/m9.figshare.21572448.v1. The fossil and associated slides are currently on loan at UMR AMP Montpellier and accessible under specimen number HH5 (for Hook Head No. 5). This material and other fossils illustrated in the supplementary figures will ultimately be deposited in the Trinity Geological Museum, Trinity College Dublin, Dublin, Ireland, once the study of the assemblage is completed.

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Author contributions

A.-L.D. and C.J.H. initiated the research project. A.-L.D., C.P. and T.D. participated in the fieldwork during which the material was collected. M.R. prepared the sections. A.-L.D. and M.R. photographed the sections. A.-L.D., C.J.H. and M.K. analysed the data with input from T.D. and C.P. C.P. analysed the sedimentological context and prepared the spores and cuticles illustrated in the supplementary figures. A.-L.D. and M.K. prepared the paper with contributions from all co-authors.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41477-023-01394-0.

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	All photographs were taken with a Keyence VHX 7000 digital microscope and the associated software ("VHX-7000 main software" and "VHX-7000 communication software"). Composite figures were assembled in Adobe Photoshop 21.2.2.
Data analysis	No software was used for data analysis

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Reporting on sex and gender	not applicable
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Ethics oversight	not applicable

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Ecological, evolutionary & environmental sciences study design

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Study description	An analysis of the anatomy of a late Devonian fossil wood showing the oldest evidence of tylosis formation
Research sample	The specimen studied is one of several fossils collected in the same fossiliferous horizon. It is a small piece of pyritized fossil wood about 17 cm long and 2-3 cm in diameter that has been prepared as thin-sections for microscope observation.
Sampling strategy	All the fossil plant found in the fossilliferous horizon were collected. The one specimen showing the evidence of tylosis formation was discovered while looking at the thin-sections of all the fossils.
Data collection	The data consists of the thin-sections of the fossil and of the images of the thin-sections. Images of the thin-sections were taken with a Keyence VX 7000 electronic microscope and the associated software by ALD and MR
Timing and spatial scale	non applicable
Data exclusions	non applicable
Reproducibility	non applicable
Randomization	non applicable
Blinding	non applicable

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Field conditions were mild and did not impact fieldwork or specimen condition
Location	The specimen was collected at Sandeel Bay, on the Hook Head peninsula, Wexford County, Ireland (52°09'41.1"N 6°52'56.5"W)
Access & import/export	No specific permit was needed; Trinity College Dublin is a Public Authority ,which does not require a permit under the Activity Requiring Consent. The project and fieldwork were conducted with researchers from Trinity College Dublin, Ireland (CJH and TD) and all specimens and associated slides will be deposited in Trinity Geological Museum, Trinity College Dublin, Dublin, Ireland
Disturbance	Disturbance risk was assessed as very low prior to collecting. Fossils were collected either (A) as loose pieces or on the surface of the

Disturbance	rocks, or (B) by hammering with geological hammers and chisels to a maximum depth of about 40-50 cm to extract plant fossils embedded in the sediment. The activity took place on already exposed rocks of a cliff sides(no plant/soil removal). Fossil collection was entirely mechanical (no chemicals used) and the impact on the coastal environment extremely limited.

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Specimen provenance	The specimen was collected at Sandeel Bay, on the Hook Head peninsula, Wexford County, Ireland. No specific permit was needed; Trinity College Dublin is a Public Authority, which does not require a permit under the Activity Requiring Consent.
Specimen deposition	The specimen is currently on loan at UMR AMAP Montpellier France (publicly accessible) and will ultimately be returned to Ireland to be deposited in the Trinity Geological Museum, Trinity College Dublin, Dublin, Ireland, once the other specimens have been studied.
Dating methods	non applicable

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Ethics oversight	no ethical approval was required

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