

Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed
☐	☒ The exact sample size (<i>n</i>) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒ A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒ The statistical test(s) used AND whether they are one- or two-sided <i>Only common tests should be described solely by name; describe more complex techniques in the Methods section.</i>
☐	☒ A description of all covariates tested
☐	☒ A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒ A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒ For null hypothesis testing, the test statistic (e.g. <i>F</i> , <i>t</i> , <i>r</i>) with confidence intervals, effect sizes, degrees of freedom and <i>P</i> value noted <i>Give P values as exact values whenever suitable.</i>
☒	☐ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒ Estimates of effect sizes (e.g. Cohen's <i>d</i> , Pearson's <i>r</i>), indicating how they were calculated

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	Leaf samples were photographed with Canon EOS 5D Mark IV with a 100 mm macro lens or scanned with EPSON Perfection V600 Photo scanner. Thin section samples of extant fern petioles and fossil specimens were imaged using a Nikon Eclipse LV100ND compound microscope and Keyence VHX-7000 digital microscope. Automatic stitching in imaging software NIS-Elements and VHX were used to acquire large images.
Data analysis	Quantitative measurements on images were conducted using ImageJ (version 1.54f). All data analyses were carried out in R (version 4.4.0) within RStudio (2025.05.0). All codes used for this study are available in Edinburgh Datashare (https://doi.org/10.7488/ds/8198) for peer review and publication.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

The data of extant plants were produced in this study as described in methods and summarised in Table S1. The data of extinct plants from fossils are collected either from museum specimens in this study or from literature cited in the main text and summarised in Table S8. All data and code associated with this paper is either included in the paper or available on Edinburgh DataShare (<https://doi.org/10.7488/ds/8198>).

Research involving human participants, their data, or biological material

Policy information about studies with [human participants or human data](#). See also policy information about [sex, gender \(identity/presentation\), and sexual orientation](#) and [race, ethnicity and racism](#).

Reporting on sex and gender

Reporting on race, ethnicity, or other socially relevant groupings

Population characteristics

Recruitment

Ethics oversight

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	This study investigated the diversity and evolution of phloem in 26 extant fern species as well as eight extinct species of ferns and fern-like plants. We first carried out a comparative histological investigation of the conducting cells of the phloem, termed sieve elements, in 26 extant species, spanning 21 families and making over 18,000 measurements. All samples were taken from wild type plants. For 23 out of the 26 extant species, we sampled 3-6 individuals per species. For the other three species, either materials were limited or measuring of the sieve element was not feasible for multiple individuals. For these three species, data from one individual per species are collected. One healthy and matured leaf per individual was selected randomly from the living collections to represent the individual. In each leaf sample, over 50 measurements of sieve element radius were taken. We then carried out investigation on eight extinct species. Data from one fossilised petiole per species was collected except for <i>Sphallopteris schlechtendali</i> where two specimens were available. For each specimen, all possible measurements were taken and this provided more than 50 measurements of sieve element radius per species, except for <i>Sphenophyllum plurioliatum</i> where 12 sieve element were present in the specimen.
Research sample	The selected extant species covered 10 out of the 11 fern orders in the most up-to-date fern phylogeny. Species selection within each order depends on the availability of materials in Royal Botanical Edinburgh Living Collection (https://data.rbge.org.uk/search/livingcollection/) and in the Institute of Molecular Plant Sciences, University of Edinburgh. The selection of fossil specimens from literature based on the preservation of phloem cells and availability of high-quality cross-section images, which allow direct measurements of sieve element radius. Fossil specimens selected from museum collections are with good preservation of phloem cells and clear taxonomic identification.
Sampling strategy	To ensure the consistency of measurements, we first chose the petiole (stipe) of leaves (fronds), as this offered a standard landmark across ferns with very different habits. We then tested the variation in SE radius along the length of the petiole. For two species (<i>Polypodium vulgare</i> and <i>Pteris multifida</i>), we sampled at 1-cm intervals across the full length of the petiole and identified that SE radius varied along the length (Fig. S3). In both species we saw a similar trend where maximum SE radii corresponded to the mid-point of the petiole (MPOP) (Fig. S3). Based on this result we decided that for our overall analysis we would sample the MPOP in all 26 species.

To generate a realistic and robust dataset, a sampling strategy was developed based on quadrat sampling, in which five sampling squares were placed across the phloem area to capture more than 50 sieve elements on each image. To make ensure the sample size is sufficient and the sampling strategy is robust, we compared the datasets generated with our sampling strategy to complete datasets with all sieve elements measured. This was carried out for five species representing single (*Salvinia auriculata*, *Adiantum aleuticum*), double (*Asplenium viride*, *Onoclea sensibilis*) and multiple-symmetric (*Platycerium bifurcatum*) vascular bundle types (Fig. S4). The comparison between sampled datasets with full datasets show no significant differences (Kruskal–Wallis tests, p -value > 0.05, Fig. S4, Table S12) therefore the sampling strategy was applied to these vascular types.

Data collection	Data of measurements were collected from the images either produced in this study or from literature. Zishan Fu conducted all the sampling and data collection except that the images of a fossil species, <i>Sphallopteris schlechtendali</i> , were taken by Laura Cooper and Jeremy Wyman.
Timing and spatial scale	Mature ferns leaves were collected in summer 2022, 2023 and 2024. Only mature and healthy leaves were collected.
Data exclusions	For correlation analysis between sieve element radius and leaf or vascular traits, Linear-mixed models and principal component analysis, individuals without leaf or vascular trait data were excluded.
Reproducibility	All histological thin sections prepared for phloem trait measurements are held by the corresponding author and are available upon request. Images and codes generated for this study are available on Edinburgh DataShare (https://doi.org/10.7488/ds/8198).
Randomization	For extant species, healthy and matured leaves were selected randomly from living collections with clear taxonomic identification. For fossil specimens, the selection is based on preservation of phloem cells and clear taxonomic identification.
Blinding	Blinding is not relevant to this study because all the samples were collected from wild type plants without special treatments.
Did the study involve field work?	☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☐	☒ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☐	☒ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Palaeontology and Archaeology

Specimen provenance	The three fossils specimen used in this study are housed in the Hunterian, University of Glasgow and the Cockburn Museum, School of Geosciences, University of Edinburgh. The access to fossil specimens were granted by Neil Clark at the Hunterian and Gillian McCay at Cockburn Geological Museum.
Specimen deposition	The three fossils specimen used in this study are housed in the Hunterian, University of Glasgow and the Cockburn Museum, School of Geosciences, University of Edinburgh.
Dating methods	No new dating were done in this study.
☒ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.	
Ethics oversight	The access to fossil specimens were granted by Neil Clark at the Hunterian and Gillian McCay at Cockburn Geological Museum.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Plants

Seed stocks	Samples of extant species were collected from Royal Botanical Edinburgh Living Collection (https://data.rbge.org.uk/search/livingcollection/) and in the Institute of Molecular Plant Sciences, University of Edinburgh.
Novel plant genotypes	No genotype was identify in this study.
Authentication	No novel genotype was generated in this study.