Commentary

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Close observation of a common fern challenges long-held notions of how plants move. A commentary on 'Fern fronds that move like pine cones: humidity-driven motion of fertile leaflets governs the timing of spore dispersal in a widespread fern species'

James E. Watkins Jr[1,*] and Weston L. Testo[2,3]
[1]Department of Biology, Colgate University, Hamilton, New York, USA, [2]University of Gothenburg, Gothenburg, Sweden and [3]Gothenburg Global Biodiversity Centre, Gothenburg, Sweden

***Corresponding author details:** James E. Watkins, jwatkins@colgate.edu

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For centuries, careful study of the natural history of plant species has played a fundamental role advancing botanical knowledge, forming the basis for transformative hypotheses and highlighting novel, exciting avenues of research. It is hard to overstate the extent to which the descriptions of Caldas (González-Orozco *et al.*, 2015) and von Humboldt (Romanowski and Jackson, 2009) on the distribution of plants along elevational clines in the Andes informed our collective understanding of how climate and geography shape species distributions. Similarly, Darwin's observations of plant movement (Darwin, 1880) formed much of the basis of our modern understanding of phototropism, much as the careful records of Edgar T. Wherry and Warren H. Wagner Jr on the morphology and ecology of Appalachian spleenworts (*Asplenium*, Aspleniaceae) helped focus our awareness of how hybridization and polyploidy shape the course of plant evolution Wherry, 1925; Wagner, 1954). Indeed, it is difficult to imagine what the field of pollination biology would be today without countless hours of observation and careful note taking by thousands of botanists, from Mayan agriculturalists, to Edmond Albius and Charles Darwin. If 'standing on the shoulders of giants' made possible Isaac Newton's contributions to maths and science, the advances of today's and tomorrow's botanists rest upon the shoulders of countless natural history observations.

In recent decades, we have witnessed a fundamental shift in how we conduct much of our research, driven mostly by technological and methodological advances that have enabled us to analyse more data, faster. Today, articles are published regularly that synthesize datasets and analyses that would have been hard to fathom in the not very distant past: phylogenies built with hundreds of loci and tens or hundreds of thousands of taxa, macroecological datasets built from millions of herbarium specimens, and imaging techniques such as microCT and optical vulnerability that have revolutionized how we study plant anatomy and ecophysiology. These new capabilities have captured our attention – as they should! – and enabled us to pursue novel and exciting research directions. Unfortunately, the era of big data has coincided with a decline in the attention paid to natural history studies and whole-organism approaches to botanical research. In many ways, this shift in the relative prominence of research approaches reflects important progress in how we conduct science: we live in a time of unparalleled advancement in our knowledge of many aspects of plant ecology and evolution. At the same time, one wonders: what might we learn if we spent more time actualyy looking at the plants that we study.

A new study by Suissa (2022) in this issue of the *Annals of Botany* provides us with an excellent example of how careful observations of plants in the field can provide novel insights into their form, function and evolution. The findings of this study, which examines the timing and mechanisms of spore dispersal in the sensitive fern, *Onoclea sensibilis*, are noteworthy both because they challenge our current understanding of how plants move and because they were documented in such a widespread, common and recognizable species. Native to eastern North America and north-eastern Asia, this species is particularly abundant in the north-eastern USA and adjacent parts of Canada, where it fills wet roadside ditches, spreads throughout open wetlands and inhabits low areas in back gardens. For many of us, *O. sensibilis* is one of the first fern species that we learn to identify, on account of it being found so commonly, and its distinctive yellow-green sterile leaves and unusual fertile leaves that resemble bunches of small grapes held high above the rest of the plant. These fertile leaves, which are highly sclerotized and can persist for up to 3 years, are familiar to almost anyone – botanist or otherwise – who has walked through wetlands within the range of *O. sensibilis* in the winter, when they are the sole visible part of the plant. We have known for at least a century that these leaves overwinter and release their spores in late winter and early spring, just as snow begins to melt (Hartt, 1925). This unusual phenology is thought to facilitate dispersal and provide its gametophyte with a competitive advantage by promoting germination when soil is wet and other species have not yet started their seasonal growth. Surprisingly, although this unusual reproductive strategy has been carefully documented for many years, the mechanisms that enable *O. sensibilis* to bear its senescent fertile leaves through winter and then disperse upon snowmelt has remained a mystery.

This gap in our knowledge was the impetus for Suissa's study, which seeks to understand two fundamental questions about sensitive fern reproduction: first, how does the species so effectively disperse its spores from dead leaves; and second, how does it manage to maintain its spores over the winter? To appreciate the relevance of these questions, it is worth considering our general understanding of how different lineages of plants leverage structural features to facilitate dispersal. Across seed-free land plants, there are numerous examples of dispersal via hygromorphy – the movement of dead tissues by changes in humidity. These passive dispersal mechanisms include the movement of peristome teeth in mosses (Gallenmüller *et al.*, 2018), spore ejection from lycophyte eusporangia (Webster, 1995), the movement of elaters on the spores of *Equisetum* (Marmottant *et al.*, 2013) and, perhaps most conspicuously, the catapulting leptosporangium that defines the leptosporangiate ferns (Noblin *et al.*, 2012), a clade that includes *O. sensibilis*. Notably, all these examples of hygromorphy are restricted to single cells or a small number of cells (e.g. the annulus of a leptosporangium).

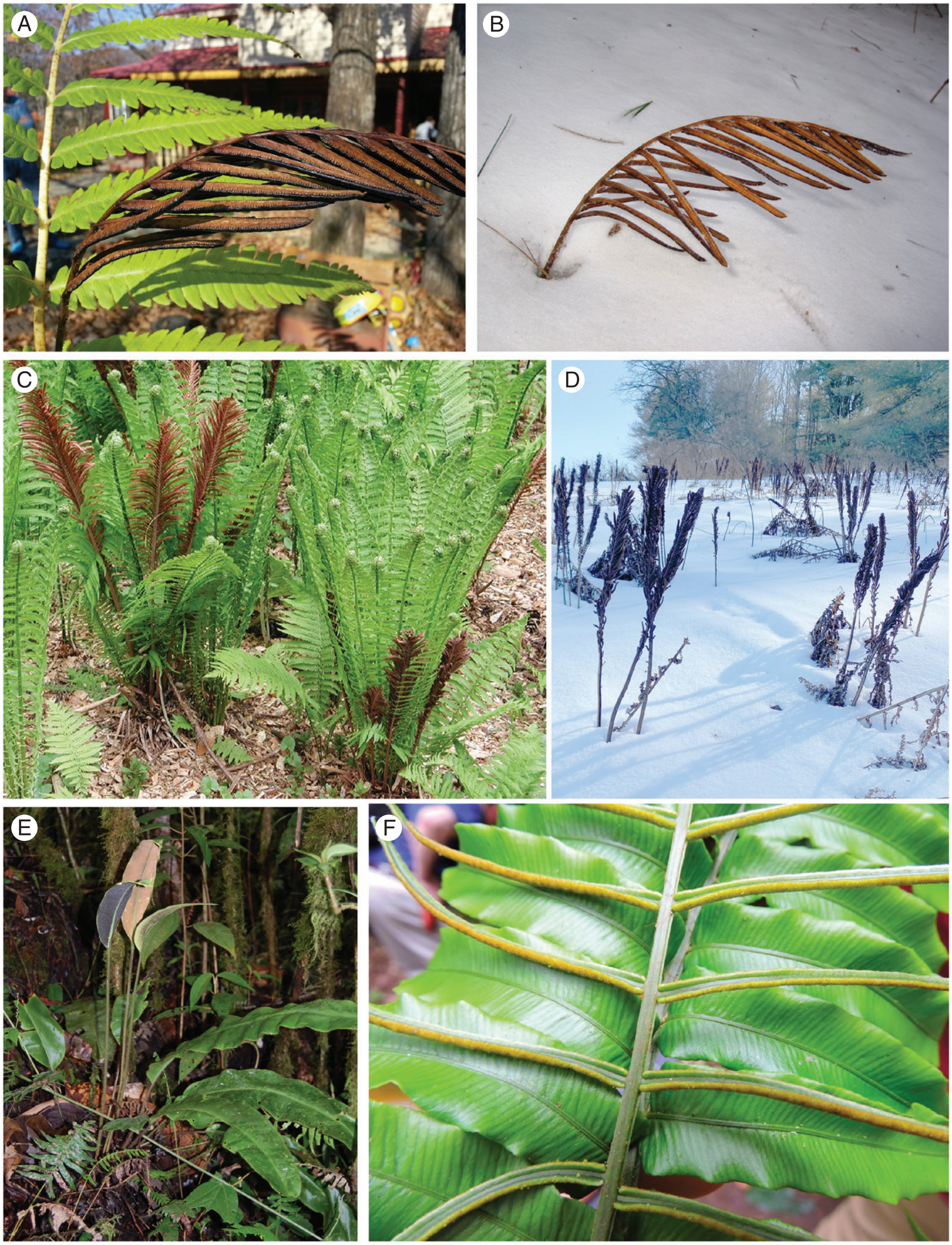

Fig. 1. All known temperate species of the Onocleaceae make overwintering fertile fronds. For example, the temperate *Pentarhizidium orientalis*, an Old World native, produces fertile fronds in the summer (A) that overwinter (B) and probably release spores the following spring. A similar pattern occurs in the New World temperate *Matteuccia struthiopteris* (C and D). It is probable that these species use similar patterns of humidity-driven movement to release their spores. Fertile–sterile dimorphism is common in ferns, but it is unlikely that such movement is employed by all such taxa. For example, taxa in (E) *Elaphoglossum* and (F) *Lomariopsis* produce achrostichoid sori with sporangia openly exposed, with no evidence of pinnae movement. Photo courtesy of (A) D. Chimitov, (B) O. Diras and (C) R. Moran.

Large-scale hygromorphic movement involving large numbers of cells and multiple tissue types is known in gymnosperms, (e.g. pine cone scales), and any array of angiosperms, from the awns of geraniums to grasses. Much like seeds and pollen, large-scale hygromorphy has appeared to be unique to seed plants, at least until now.

In this study, Suissa shows that pinnules of mature fertile leaves of *O. sensibilis* open and close in response to changes in humidity, showing both structural and functional similarity to hygroscopic structures previously known only from seed plants. Although the spores are viable by late summer, they are only released much later, once the majority of pinnules begin to open in late winter of the following year. During the summer, autumn and winter, these pinnules remain tightly wrapped around the sori; opening only becomes possible once the leaves begin to form sutures along a series of small abscission zones that occur between veins in the lamina. The opening of these sutures – themselves loosened by repeated fluctuations of humidity – allow the pinnules to move back and forth sufficiently to permit the release of spores. The movement itself is the product of elegant anatomical architecture: the internal structure of the pinnules combines microfibrils of varying cell wall thickness and orientation to form an antagonistic bilayer that functions like a bimetallic strip in a (mechanical) thermostat. As such, *O. sensibilis* manages to successfully disperse its spores not through the action of its leptosporangia (which are rather lackadaisical by fern standards) but by movement of its overwintered fertile leaves. Though this is the first documentation of such movement outside of seed plants, it is surely not the only fern species to utilize such dispersal mechanisms (see Fig. 1). Other members of the Onocleaceae, such as the ostrich fern (*Matteuccia struthiopteris*), also have overwintering fertile fronds that almost certainly engage in similar patterns of humidity-driven movement in order to release their spores. Many members of the Blechnaceae, a diverse, cosmopolitan fern family that is the sister group to Onocleaceae, bear similarly reduced fertile leaves and probably rely on hygromorphic leaf movement as well. Understanding the diversity of hygromorphic movements and structures, as well as their evolution across the land plant phylogeny will only be possible with sustained careful study like that of Suissa (2022).

In many ways, the elegant observations carried out by Suissa in this study engender the spirit of organismal curiosity demonstrated by a long tradition of botanists and naturalists. They also illustrate how combining basic organismal biology with new approaches and tools can enrich our fundamental understanding of plant biology and generate important advancements in the field. Without such an approach, we may never have known that the humble sensitive fern held such a secret!

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