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The Fern Sporangium: A Unique Catapult — Source link

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The fern sporangium: a unique catapult

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Spore dispersal in plants and fungi plays a critical role in the survival of species and is thus under strong selective pressure. As a result, various plant and fungal groups have evolved ingenious mechanisms to disperse their spores effectively [1, 2]. Many of these mechanisms use the same physical principles as man-made devices but often achieve better performance. One such dispersal mechanism is the cavitation-triggered catapult of fern sporangia. The sporangia open when dehydrating and use the stored elastic energy to power a fast closure motion that ultimately ejects the spores. The beauty of this dispersal mechanism and similarity with medieval catapults has not escaped notice [1]. All man-made catapults are equipped with a crossbar to stop the motion of the arm midway. Without it, catapults would launch their projectiles right into the ground. This “crossbar” is conspicuously missing from the sporangium, suggesting that it should simply speed up to its closed conformation without ejecting the spores. Here we show that much of the sophistication of this ejection mechanism, and the basis for its efficiency, lie in the two very different time scales associated with the sporangium closure. The simple structure of the sporangium belies the complexity of its action (Fig. 1A). Central to the ejection process is the annulus – a row of 12-13 cells that forms a crest to one side of a spherical capsule enclosing the spores. As the annulus cells lose water by evaporation, their thickened radial walls are forced closer together while lateral walls collapse internally (Fig. 1B, movie S1). The whole annulus is thus bent out of shape much like an accordion in the hands of a musician. The strong change in curvature (Fig. 1B&D) forces the opening of the sporangium at the stomium, thus exposing the spores. All the while, water tension builds in the cells of the annulus [3, 4]. When the tension reaches a critical value (approximately -9 MPa [5]), cavitation occurs within adjacent cells [6] (Fig. 1C&S2, movie S2&S3). The annulus then closes by about 30-40% within about 10 μs, leading to a quick release of the energy stored in the annulus and expulsion of the spores at an initial velocity of up to 10 $m.s^{-1}$ [7]. This corresponds to an acceleration of approximately 10^5 g. This first phase is followed by a comparatively slow relaxation to a 85 % closed configuration in a few hundreds of ms. We interpret the two time scales as a fast inertial recoil of the annulus followed by a slow poroelastic dissipation [8] of the energy remaining in the annulus. The annulus walls are constituted of a tight network of cellulose fibers surrounded by water that flows to conform to their relative displacements. The tiny size of the pores [9] and thick wall [10] induce strong viscous losses (from Darcy's law) that dramatically slow down the annulus motion. This dynamics can be described using a generalized viscoelastic Maxwell model that fits our data very well and integrates all the physical forces at play (see Fig. 1E&S3). The measured and predicted time scales are in good agreement both for the inertial (respectively $25\mu s$ and $27\mu s$) and the poroelastic regime (respectively $5.8\ ms$ and $3\ ms$). The coexistence of these two widely different timescales allows the sporangium to release its spores efficiently without the use of structural elements to arrest the recoil motion.

It is striking that a dozen cells placed in a row can fulfill all the functions of a medieval catapult including the motive force for charging the catapult (water cohesion), energy storage (annulus wall), triggering mechanism (cavitation), and returning motion arrest (poroelastic behavior of the annulus wall).

References and Notes

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Supporting Online Material

Materials and Methods

Fig. S1 to S4

Captions for Movies S1 to S4

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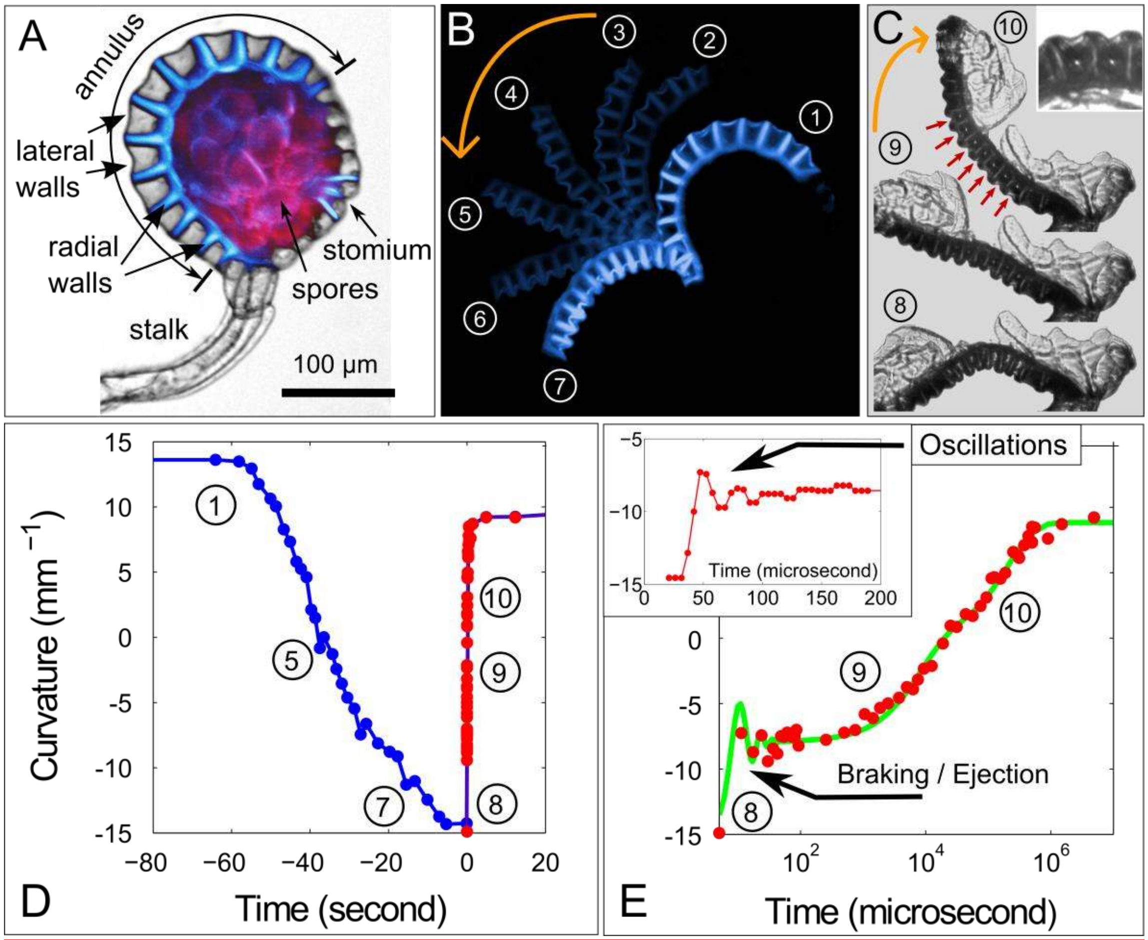
Caption for Fig.1: **(A)** The sporangium of *Polypodium aureum*. Annulus geometry during sporangium opening in **(B)** and in **(C)** just prior to cavitation, 0.4 ms and 40 ms after cavitation. Note the seven cells that have cavitated (red arrows). **(D)** Annulus curvature during the opening (blue) and closing (red) phases. **(E)** The closing phase in log-linear scale revealing the poroelastic relaxation, the green line represents the fit from our model. The numbers correspond to frames in (**B**) and (**C**). Insert: expended view of the inertial oscillations.


A
annulus
lateral
walls
radial
walls
stomium
spores
stalk
100 µm
B
C
Oscillations
Time (microsecond)
Curvature (mm −1)
Time (second)
Braking / Ejection
D
E
Time (microsecond)