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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

24 spores. Here we show that much of the sophistication of this ejection mechanism, and
25 the basis for its efficiency, lie in the two very different time scales associated with the
26 sporangium closure. The simple structure of the sporangium belies the complexity of its
27 action (Fig. 1A). Central to the ejection process is the annulus – a row of 12-13 cells
28 that forms a crest to one side of a spherical capsule enclosing the spores. As the annulus
29 cells lose water by evaporation, their thickened radial walls are forced closer together
30 while lateral walls collapse internally (Fig. 1B, movie S1). The whole annulus is thus
31 bent out of shape much like an accordion in the hands of a musician. The strong change
32 in curvature (Fig. 1B&D) forces the opening of the sporangium at the stomium, thus
33 exposing the spores. All the while, water tension builds in the cells of the annulus [3, 4].
34 When the tension reaches a critical value (approximately -9 MPa [5]), cavitation occurs
35 within adjacent cells [6] (Fig. 1C&S2, movie S2&S3). The annulus then closes by about
36 30-40% within about 10 μ s, leading to a quick release of the energy stored in the
37 annulus and expulsion of the spores at an initial velocity of up to 10 m.s⁻¹ [7]. This
38 corresponds to an acceleration of approximately 10⁵ g. This first phase is followed by a
39 comparatively slow relaxation to a 85 % closed configuration in a few hundreds of ms.
40 We interpret the two time scales as a fast inertial recoil of the annulus followed by a
41 slow poroelastic dissipation [8] of the energy remaining in the annulus. The annulus
42 walls are constituted of a tight network of cellulose fibers surrounded by water that
43 flows to conform to their relative displacements. The tiny size of the pores [9] and thick
44 wall [10] induce strong viscous losses (from Darcy's law) that dramatically slow down
45 the annulus motion. This dynamics can be described using a generalized viscoelastic
46 Maxwell model that fits our data very well and integrates all the physical forces at play
47 (see Fig. 1E&S3). The measured and predicted time scales are in good agreement both

48 for the inertial (respectively $25\mu s$ and $27\mu s$) and the poroelastic regime (respectively
49 $5.8 ms$ and $3 ms$). The coexistence of these two widely different timescales allows the
50 sporangium to release its spores efficiently without the use of structural elements to
51 arrest the recoil motion.

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

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57 **References and Notes**

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74 **Supporting Online Material**

75 Materials and Methods

76 Fig. S1 to S4

77 Captions for Movies S1 to S4

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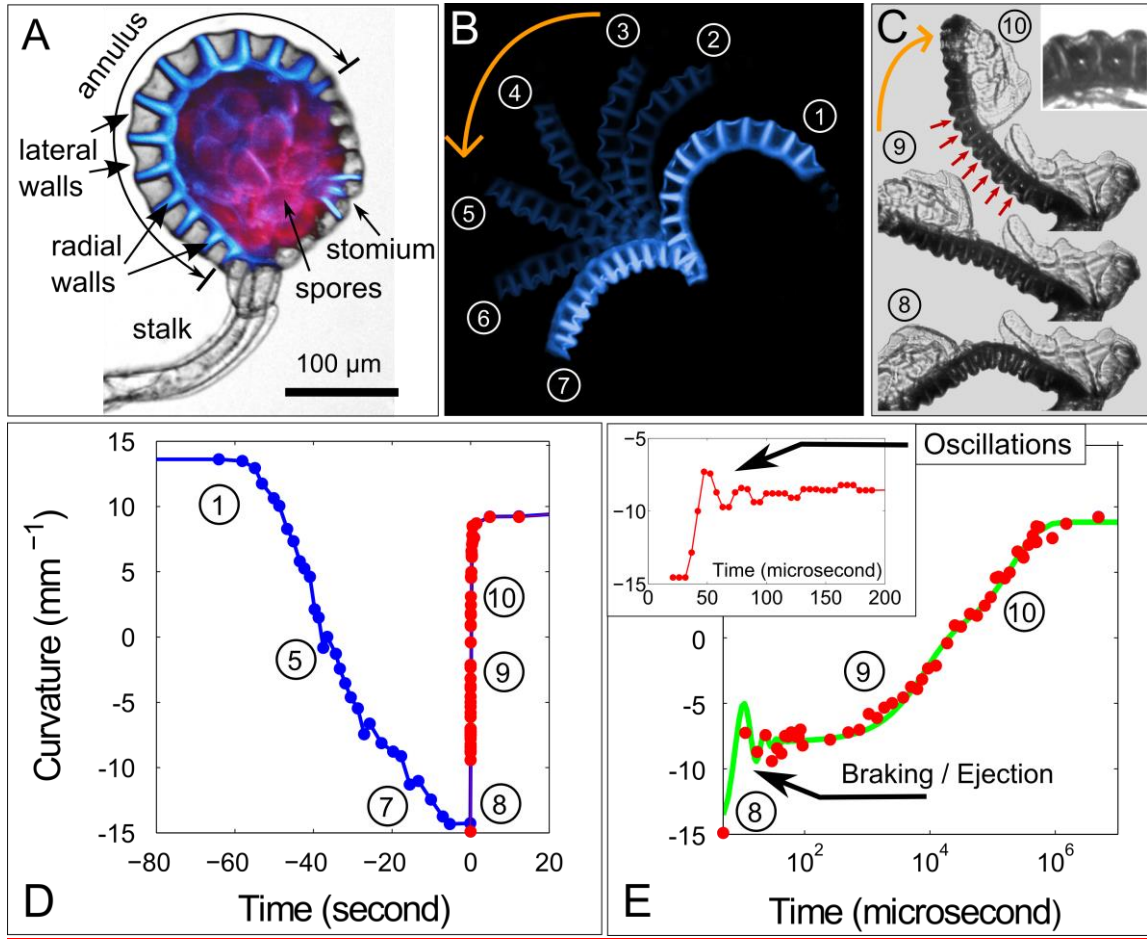
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82 **Caption for Fig.1:** (A) The sporangium of *Polypodium aureum*. Annulus geometry
83 during sporangium opening in (B) and in (C) just prior to cavitation, 0.4 ms and 40 ms
84 after cavitation. Note the seven cells that have cavitated (red arrows).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

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