A natural O-ring optimizes the dispersal of fungal spores

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The forcibly ejected spores of ascomycete fungi must penetrate several millimetres of nearly still air surrounding sporocarps to reach dispersive airflows, and escape is facilitated when a spore is launched with large velocity. To launch, the spores of thousands of species are ejected through an apical ring, a small elastic pore. The startling diversity of apical ring and spore shapes and dimensions make them favoured characters for both species descriptions and the subsequent inference of relationships among species. However, the physical constraints shaping this diversity and the adaptive benefits of specific morphologies are not understood. Here, we develop an elastohydrodynamic theory of the spore's ejection through the apical ring and demonstrate that to avoid enormous energy losses during spore ejection, the four principal morphological dimensions of spore and apical ring must cluster within a nonlinear one-dimensional subspace. We test this prediction using morphological data for 45 fungal species from two different classes and 18 families. Our sampling encompasses multiple loss and gain events and potentially independent origins of this spore ejection mechanism. Although the individual dimensions of the spore and apical ring are only weakly correlated with each other, they collapse into the predicted subspace with high accuracy. The launch velocity appears to be within 2 per cent of the optimum for over 90 per cent of all forcibly ejected species. Although the morphological diversity of apical rings and spores appears startlingly diverse, a simple principle can be used to organize it.

1. Introduction

Spore dispersal is the primary determining factor for the range and distribution of fungi in nature. The importance of understanding this process in detail has been highlighted in recent years by an unprecedented number of fungal diseases, which have caused some of the most severe die-offs and extinctions ever witnessed in wild species \([1]\) and are increasingly considered a worldwide threat to food security \([2]\). An effective control of these emerging diseases is possible only if we can understand and control how they propagate.

The defining feature of the largest fungal phylum, Ascomycota, is the ascus, a fluid-filled sac from which spores are ejected. Ejection is powered by a build-up of osmotic pressure \([3]\), which forces spores through a ring or hole at the tip of the ascus, after a critical pressure is reached \([4]\). Ascus and spore morphologies are highly variable and have been an essential element of species descriptions for more than 200 years \([5,6]\). Since spores are the primary agents of dispersal, these morphologies also play a critical role in the ascomycete life cycle: most fungi grow on highly heterogeneous landscapes, and to persist a fungus must move between disjoint patches of habitat \([7]\), thus effective dispersal is critical to the fitness of an individual.

To reach dispersive air currents, spores must be launched with enough speed to cross the stagnant air layer around the fungus, the fluid mechanical boundary layer. Although typical boundary layer thicknesses are around 1 mm \([8]\), a spore’s small size (approx. 10 \(\mu\)m) causes rapid deceleration after
launch, meaning that it must be launched at very high velocity even to travel a very small distance, and the likelihood of effective dispersal is directly correlated to the thickness of boundary layer that the spore is able to cross [9].

The critical role of the apical ring in spore dispersal caused speculation about whether the diverse morphologies of the spore ejection apparatus are tuned to allow effective dispersal. Buller [10] proposed a relationship between the dimensions of the apical ring and the size of the spore, ostensibly to prevent spores from tumbling during flight. Ingold [7] thought spores would be shaped to maximize the force used by apical rings to push on them. But, surprisingly, the individual geometric dimensions of apical rings and spores critical to these hypotheses are either very weakly or not correlated.

Here, we resolve this discrepancy by demonstrating a strikingly tight coupling between the size of the spore and a nonlinear function of multiple dimensions of the apical ring. The relationship is suggested by physical constraints on spore ejection: the requirement to efficiently convert the potential energy stored in the ascus to kinetic energy of the spore. The apical ring is an elastic seal, and distorts significantly when the spore, which is lubricated by a thin fluid layer, passes through it. The basic physical principles governing this kind of process were discovered 50 years ago, in the study of elastomeric seals and O-rings used to control fluid flow in engines, pipes and other engineering applications [11]. By adapting these theories to the fluid mechanics of spore ejection, we demonstrate that although there are at least five independent dimensions to the morphological diversity of spores and apical rings, the need to minimize energy losses during ejection restricts spore and ascus morphologies to a one-dimensional subspace, where the dimensions of a spore and its apical ring are tightly coupled.

We test this theory using published electron micrographs of apical rings and spores [12–19] and a recently published ascomycete phylogeny [20], which identifies two potentially independent groups of species with spores singly ejected through apical rings. Quantitative descriptions of spores and apical rings at a high resolution are available for 45 species, with dimensions of the spore and apical ring characters varying over one order of magnitude. Nonetheless, the observed variation is confined to the predicted one-dimensional subspace with surprising accuracy: energy losses are held within 2 per cent of the theoretical optimum.

By assembling data on species where there is no selective pressure to maximize ejection velocity, because spores are dispersed using different mechanisms, for example insect vectors, we test whether genetics are a constraint on morphology. In fact, these species have very different apical ring and spore shapes, suggesting natural selection is the force maintaining collapse into the one-dimensional subspace for species with functional apical rings.

2. Results

2.1. Fluid mechanics of spore and apical ring coupling

Figure 1 shows a representative context in which spore ejection occurs. The sporocarps of a fungus are scattered on a host (e.g. the stalk of a plant, figure 1a). These structures are produced by the fungus with the sole purpose of dispersing the spores. Within each sporocarp, there can be hundreds of asci, each generally containing eight spores (figure 1b). When the spores in an ascus are mature, osmoles are produced, leading to water influx into the highly elastic ascus, resulting in a significant increase in volume and pressure [4]. When the osmotic pressure \( p_0 \) inside an ascus is sufficiently high, the spores are singly ejected into the surrounding air.

The speed \( U \) at which a spore is launched depends critically on energy losses during ejection. If the osmotic pressure were entirely converted to kinetic energy, the spore would be ejected at an ideal velocity

\[
U_{\text{ideal}} = \sqrt{\frac{2p_0}{\rho_s}},
\]

where \( \rho_s \) is the density of the spore and \( p_0 \) is the overpressure in the ascus.

However, the ideal launch velocity is necessarily degraded by both friction and fluid loss as the spore moves through the apical ring (figure 1c–f). The apical ring consists of an elastic material with thickness \( b \) and height \( h \). The size of the opening of the apical ring before the spore starts to pass through it, \( d \), is much smaller than the width \( W \) of the spore. During the ejection of the spore, the apical ring is strongly deformed, and there is a thin layer of fluid with viscosity \( \mu \) and density \( \rho \), separating the apical ring from the spore.

Energy losses arise from two different processes occurring in this lubricating fluid layer of thickness \( h_0 \): first, there is friction between the spore and the apical ring, owing to the viscous force in the fluid gap \( F \sim W \mu d^2 \), opposing the motion of the spore moving with velocity \( U \). The total energy dissipated is then \( E_{\text{friction}} = FL \), the product of this
viscous force with the distance that the spore moves when the force is acting, which is the length \( L \) of the spore. The second energy loss arises because the pressure in the ascus, and thus the main accelerating force, decreases while the spore and lubricating fluid leave the ascus. If ascus pressure and volume are proportional, the energy lost due to fluid leaving the ascus is proportional to the kinetic energy, 
\[
E_{\text{fluid}} = \rho W h_l L^2,
\]
up to a constant parametrizing the ratio of ascus volume before ejection to spore volume. If \( h_l \) is large, the energy loss is dominated by the fluid flow through the gap, while if \( h_l \) is small, the energy loss is dominated by friction. The minimal total energy loss \( E_t = E_{\text{fluid}} + E_{\text{friction}} \) occurs if \( E_{\text{fluid}} \approx E_{\text{friction}} \) and thus if the physical gap thickness is close to the optimal value \( h_0 \), with
\[
h_0 = a \sqrt{\frac{\mu}{p \ell}} = a \left( \frac{\mu(x)}{(2 \rho h_0 \ell)^{1/2}} \right),
\]
where in the second equality, we have assumed that the energy dissipation is sufficiently small that \( U \approx U_{\text{dissip}} \) with \( \rho_s \approx \rho \). The proportionality factor \( a = 0.45 \) can be found by explicitly integrating the equations of motion for the spore, as demonstrated in the electronic supplementary material. Figure 2a shows a plot of the energy dissipated as a function of \( h_0 \) following from this more complete analysis.

2.2. The fluid layer thickness \( h_0 \)

What physical mechanism determines \( h_0 \)? During spore ejection, the apical ring undergoes a strong deformation to allow the spore to pass, and this deformation causes a restoring elastic pressure to push against the spore. On the other hand, within the fluid gap there is viscous pressure caused by the fluid motion itself. The fluid layer thickness \( h_0 \) is determined so that these two pressures exactly balance. The layer thickness \( h_0 \) thus depends in a non-trivial fashion on all of the parameters of the problem outlined thus far: the dimensions and elastic modulus \( E \) of the apical ring, the viscous forces acting in the thin fluid layer and the size of the spore.

Determining the dependence of the layer thickness \( h_0 \) on these parameters is a classic problem in elastohydrodynamics, and it was examined in the 1960s to understand the properties of engineering seals, for example, O-rings. The theoretical ideas worked out in this context are directly applicable to the present problem, and here we recapitulate the basic arguments [11,21,22] in the context of our system. Figure 1e shows the geometry of the contact, focusing on the edge of the apical ring where the spore enters from the ascus. The coordinate \( x \) parametrizes distance from the entry point, located at \( x = 0 \). Within the ascus, far from the spore entry point, the pressure is \( p \approx p_0 \) and the shape of the apical ring is undeformed.

First, it is convenient to consider what would happen if there were no fluid gap (\( h_0 = 0 \)), and no flow through the contact. In this case, the elastic distortions and pressures caused by the spore moving through the apical ring follow from Hertzian contact theory. The Hertz contact solution is completely specified by the local radius of curvature \( R \sim \ell \) of the contact region,1 and the resulting elastic deformation, implying that when \( x < 0 \),
\[
h(x) = \frac{\xi(x/\xi)^{3/2}}{3},
\]
whereas when \( x > 0 \), the pressure distribution for \( x/\xi \lesssim 1 \) obeys
\[
p(x) = E/\sqrt{x/\xi},
\]
where \( E \) is the elastic pressure exerted by the spore on the apical ring, well inside the contact (\( x/\xi > 1 \)). Since the ring deformation is dominated by the spore passing through it, we can neglect the deformation of the ascus wall for the elastohydrodynamic calculation. Under this assumption, we can approximate the apical ring as a circular cylinder with internal radius \( r_i = d/2 \) and outer radius \( r_o = d/2 + b \), subject only to an internal pressure \( p_i \). Owing to symmetry, the displacement of the ring depends only on the radial distance \( r \) from the centre line. Classical elasticity theory [23] dictates that the deformation is given by
\[
h = \frac{3}{2E} \frac{r_i^2 - r_o^2}{r_i^2} \frac{r^2}{r - r_i^2},
\]
where
\[
p_i = \frac{E}{3} \frac{r_i^2 - r_o^2}{r_o b}. \]

With the spore passing through the apical ring, the deformation of the inner surface of the ring is \( u(r) = W/2 \), implying the elastic pressure
\[
p_i = \frac{E}{3} \frac{r_i^2 - r_o^2}{r_o b} = E, \quad W = b(d + b),
\]
where \( E_s = 2/(1 - \nu^2)E = 8/3E \). Here, we have assumed that the apical ring is incompressible (Poisson ratio \( \nu = 1/2 \)), as are most biological materials.

With a fluid gap separating the apical ring from the spore, this purely elastic solution is modified. Dowson & Higginson [11] solved the coupled elastohydrodynamic problem by realizing that the fluid gap thickness \( h_0 \) itself only slightly increases the elastic distortion of the apical ring. The pressure distribution in the centre of the apical ring is thus still given by the Hertzian solution, scaling as \( p \sim E \sqrt{x}/\xi \) for \( x \lesssim \xi \). Similarly, away from the contact (negative \( x \) in figure 1e), the shape of the apical ring is mainly affected by the large elastic stresses within the contact, and so it is also given by the Hertzian solution, \( h \sim E \sqrt{x}/\xi^{3/2} \). However, there will be deviations near the entry point (\( x \approx 0 \)), where the fluid pressures created by the flow through the gap will significantly modify \( h(x) \).

Solving for \( h(x) \) in this regime requires coupling the viscous flow in the gap to the elastic deformation of the apical ring. Viscous forces imply that the pressure gradient in the gap is given by the Reynolds lubrication equation
\[
\frac{dp}{dx} = 6 \mu U \frac{h - h_0}{h_0}. \tag{2.5}
\]
A coupled solution to the elastohydrodynamic problem requires that the pressure distribution \( p(x) \) and the gap shape \( h(x) \) satisfy both the Reynolds equation (2.5) and the elastic equations.

The value of \( h_0 \) is selected by the solution to this coupled elastohydrodynamic problem [11]. The dependence of \( h_0 \) on parameters follows from a scaling argument at \( x \approx 0 \) [21]. If \( \lambda \) is the length scale over which the pressure varies in the fluid gap, \( P \) is the pressure scale and \( H \) is the scale of the gap thickness, equation (2.5) implies \( P/\lambda \sim \mu U H^2 \). The lubrication solution must match the Hertz solutions, implying \( P \sim E \sqrt{\lambda/\xi} \) and \( H \sim \xi/\lambda \). Combining these relations, we find that
\[
h_0 = \beta H = E \xi/(U n) = \beta \left( \frac{E \xi^{3/2} \rho_0 d(d + b)}{\rho_0^{3/2} E W b d(b + b)} \right)^{1/5}, \tag{2.6}
\]
where \( K = E \xi/(U n) \) is the ratio of the elastic modulus to the viscous pressure created in the gap. The proportionality constant \( \beta = 1.42 \) requires the complete elastohydrodynamic solution, outlined in the electronic supplementary material. Figure 2b shows the exact gap height and pressure following from this complete elastohydrodynamic analysis. Note that in
as a function of the average gap thickness \( \bar{h} \) (equation (2.2)). The appropriate non-dimensionalization and numerical procedure are described in §4.1. Solid line and shading: results obtained for a realistic set of parameters \( (G,C, D = 0.79 \mu \text{m}^{-1}) \) and their expected variation, as described in the electronic supplementary material.

2.3. Optimality criterion

We can now combine the results of §§2.1 and 2.2 to define an optimal spore shooting apparatus. To minimize energy losses during spore ejection, the thickness of the fluid gap \( h_0 \) (equation (2.6)) determined by the elastohydrodynamic solution must be close to the optimal thickness of the fluid gap \( h^* \) (equation (2.2)). The equation \( h_0 = h^* \) implies the law

\[
W = \gamma = \frac{1}{2} \left( \frac{p_0}{E*} \right)^{3/2} \frac{d(d + 2b)^2}{b(d + b)\varepsilon},
\]

(2.7)

where \( \gamma = 0.371 \) (see the electronic supplementary material for derivation).

2.4. Testing the prediction with morphological data

Equation (2.7) implies a strong constraint coupling spore and apical ring morphologies: the spore diameter \( W \) should be linearly proportional to a single parameter \( S_r \), capturing the different dimensions of the apical ring,

\[
S_r = \frac{d(d + 2b)^2}{b(d + b)\varepsilon},
\]

(2.8)

if the material parameters of all species, most notably \( p_0 / E* \), are reasonably conserved. While theoretical considerations make it likely that both these values individually should be roughly constant across different species (see the electronic supplementary material), no experiments determining the elasticity of apical rings have been performed. The few available measurements of \( p_0 \) for different species indicate that this value might be roughly conserved [24].

To test our prediction, we compiled a library of over 1000 papers from the mycological literature, and searched them for high-resolution electron-micrograph images showing medial cuts of mature apical rings (see the electronic supplementary material for search rules and example images). We found data for 45 species in two classes (18 families), with a good coverage of the whole phylogeny of species whose spores are singly ejected through an apical ring (figure 3, classes and families where data were found are shown in colour). The phylogeny highlights the ubiquity of this trait in the ascomycetes (figure 3a), not only in two large classes (figure 3b,c) but also in more distant families (e.g. Peltigeraeacea and Geoglossacea), potentially indicating multiple independent origins of this trait. It also shows several loss events (represented by dashed lines), where species ejection spores through an apical ring evolved into niches where this trait conveyed no selective advantage and was eventually lost, both on the class level (e.g. Laboulbeniales, figure 3d) and family level (figure 3e).

From the images found with this search, we extracted the three independent dimensions of the apical ring \( (b, \ell \) and \( d \) relevant to our physical model, as well as the spore size \( W \). When available, morphological data were taken from the same publication, to limit the influence of intraspecies variability. If no spore size was reported or could be measured, it was taken as the average value reported in standard texts [25,26] (see the electronic supplementary material for details).

Figure 4 shows the results of this analysis. Each data point represents one species from the classes highlighted in figure 3. The individual dimensions of the apical rings are not strongly linked to the dimensions of the spores for the same species. The spore width \( W \) does not correlate with \( \ell \) or \( b \) \( (R^2 = 0.11 \) and 0.10). The degree of correlation between \( W \) and \( d \) is higher \( (R^2 = 0.64) \), indicating that species with larger spores have apical rings with slightly larger diameters. By contrast, figure 4b shows the correlation of the spore radius with \( S_r \). The data collapse on a single straight line \( (R^2 = 0.84) \) is in excellent agreement with the theoretical expectation (equation (2.7)), with only one free parameter \( D = \gamma \mu^{3/2} (p_0/E*)^3 / (p_0p)^{1/3} = 0.79 \pm 0.06 \mu \text{m}^{1/3} \). If we assume \( \mu = 1000 \text{ kg/m}^3 \), \( \mu = 10^{-3} \text{ Pa} \), and \( p_0 = 2 \text{ atm} \), the predicted elastic modulus of the apical ring is \( E* \approx 1 \text{ MPa} \), consistent with the elastic moduli of soft biological materials [28]. To quantify energy losses within this system, figure 4b also shows contours (grey
Figure 3. Phylogenetic tree highlighting the 45 species used in this study (adapted from [20]). Classes and families with functional apical rings are in colour, those with non-functional rings are represented by grey dashed lines, and classes with other dispersal mechanism are shown in solid grey. (a) Cladogram of the entire ascomycete phylum, delineating classes. Clades with functional apical rings are the Leotiomycetes (blue), Sordariomycetes (red), Geoglossaceae (orange) and the Peltigeracea in the Lecanoromycetes (green). More detailed phylogeny of the Sordariomycetes (b) and of the Leotiomycetes (c) delineating families. The families of the species used in this study are highlighted. (d) Examples of apical ring geometries (not to scale) to illustrate morphological diversity (adapted from [12–19]). Scale bars represents substitutions per site.
shading) for spores attaining 99, 98 and 95 per cent of the maximum launch velocity, which can be obtained from a numerical integration of the equations of motion (see the electronic supplementary material). Nearly, all of the data fall within 2 per cent of the theoretical optimum.

3. Discussion

The collapse of morphological data suggests that spore launching apparatuses have evolved to maximize dispersal potential. A spore must escape its parent and if it can penetrate through the fluid mechanical boundary layer surrounding the sporocarp, it may be carried by the wind and achieve long-distance dispersal. After launch from the ascus, the velocity \(U(t)\) of a spore decelerates according to

\[
\frac{dU}{dt} = -\zeta U, \tag{3.1}
\]

where \(m\) is the spore mass and \(\zeta\) is the drag coefficient. This implies that the distance \(Z\) a spore ejected with initial velocity \(U_\text{ej}\) will travel is given by

\[
Z = U_\text{ej} \frac{m}{\zeta}. \tag{3.2}
\]

The larger the range \(Z\), the greater the variety of environments a spore can tolerate and still escape the boundary layer. We have previously shown the shape of spores (the ratio \(m/\zeta\)) is tuned to within 1 per cent of the theoretical optimum [29]; the present study demonstrates that the launch velocity \(U_\text{ej}\) is optimized to the same degree of precision by matching apical ring shape to spore size.

Our theory shows that gradients away from the optimum are steep—if a species moves off of the line in figure 3b, the energy dissipation penalty will be high, and the launch velocity \(U_\text{ej}\) will plummet.

The most striking feature of the data collapse shown in figure 4b is the large diversity of apical ring shapes captured by the model. Apical rings may be flat, thin, elongated or shallow, with only weak correlations between the different geometrical dimensions, as seen in figure 3d (\(R^2\) between 0.32 and 0.39), but in the right combination all morphologies are confined to the one-dimensional subspace of the theoretical prediction (equation (2.7)). It is worth noting that our analysis explains more of the variation in the dimensions \(W_d, d, \ell, b\) than traditional morphometric analysis using the first principal component (84 versus 64%). Principal component analysis finds the linear combination of parameters that best explains a wide variance. In contrast, equation (2.7) depends nonlinearly on all of the parameters, in a fashion predicted by our mechanical analysis of dissipation processes occurring during spore ejection (see the electronic supplementary material).

Morphologies may also be shaped by genetic constraints. To test whether genetics constrains fungi within the one-dimensional subspace, we explored the evolutionary trajectories of ascomycete species not subject to the selective force for range maximization. Several groups have evolved into niches where spore shooting is not critical to survival, because species use insects or other animals to disperse spores. Although nearly all of these species have completely lost the apical ring, the evolutionary residue of spore ejection is seen in a few genera, for example, Geospora. Species of Geospora do forcibly eject spores, but spores are ejected into a closed, subterranean sporocarp, where range maximization is irrelevant.

Using the same methodology described for the forcibly ejecting species (see the electronic supplementary material for details), we collected morphological data for 13 species with non-functional rings: seven are deliquescent, i.e. ascospores are not forcibly ejected because the ascus wall dissolves; five are cleistothelial, i.e. spores are released within an enclosed sporocarp; and one releases spores through a fissure in the ascus wall, and not through the apical ring. The spore and ring morphologies of nine of 13 species are far from the subspace occupied by spore shooting species (figure 5). So while over 90 per cent of all species with functional apical rings have morphologies within 2 per cent of the optimum, this is only the case for about 30 per cent of species with non-functional apical rings.

These data confirm that the data collapse in figure 4b is not the result of genetic constraints: alternate morphologies are possible. In fact, the time of divergence from an ancestor with a functional apical ring is positively correlated with the
in substitutions per site) and the loss in range compared with an optimal to a 5% deviation from the optimum, which would contain all species (31,32) using ancestral character reconstruction. The grey band corresponds can be written in non-dimensional form as equation for the spore form a closed system of equations that equation (2.6), the pressure evolution equation, and Newton's logical trait evolution may provide valuable additional data where molecular clock models remain problematic, morpho-

donzing and shaping morphological diversity, which—even for dating species divergences.

Our model highlights the key role of physics in generating and shaping morphological diversity, which—even despite the emergence of molecular tools—remains a key to understanding the evolution of biodiversity.

4. Material and methods

4.1. Integration of equations of motion

If ascus pressure \( p_a \) and ascus volume covary linearly, then equation (2.6), the pressure evolution equation, and Newton’s equation for the spore form a closed system of equations that can be written in non-dimensional form as

\[
U \frac{dU}{dx} = 3X(1 - X)p_a - \frac{12G}{F} \left[ \frac{1}{5} \right] \left( \frac{X(1 - X)}{X} \right) \left( X(1 - X) \right)^{4/5}
\]

and

\[
\frac{dp_a}{dx} = \frac{48}{C} \left[ \frac{1}{5} \left( \frac{1}{X} - X \right) - \beta \frac{G}{F} \left[ \frac{1}{5} \right] \left( \frac{X(1 - X)}{X} \right) \right] \left( X(1 - X) \right)^{4/5}
\]

where \( X, U \) and \( p_a \) are normalized by \( L, U_0 \) and \( p_{fa} \) respectively. The value of \( U_0 = U(X = 1) \) after integration only depends on the three non-dimensional parameters \( G = h_a/W, \quad F = H/h, \quad \text{and} \quad C \), which is the ratio of ascus to spore volume before ejection (see the electronic supplementary material for details). In the physiologically relevant region of parameter space, the solution has a sharp optimum in \( F \), corresponding to the optimum in \( h \) shown in figure 2a.

4.2. Elastohydrodynamics

Near the entry point, elasticity theory [11] dictates that the gap thickness is related to the pressure distribution by

\[
h(x) = \frac{3}{4} \frac{E}{h_a} \int_{-\infty}^{x} dx \left( p_f(s) - p_{\text{Hertz}}(s) \right) \log \left| \frac{x-s}{\frac{r}{2}} \right|
\]

where \( h_{\text{Hertz}}(x) \) and \( p_{\text{Hertz}}(x) \) are the Hertz solutions and \( p_f \) is the solution to the Reynolds equation (2.5). We require \( p_f(x) \sim p_{\text{Hertz}} \) far from the entry point, i.e., as \( x \) becomes large. For this to happen, the gap thickness must asymptote to a constant value \( h \rightarrow h_0 \). We solve equation (4.13) iteratively at every point \( x \) along the contact profile (for details, see the electronic supplementary material) to compute the pressure and hight profile shown in figure 2b.

This research was supported by the National Science Foundation through the Harvard Materials Research Science and Engineering Center (DMR-0820484) and the Division of Mathematical Sciences (DMS-0907985), by the National Institute of General Medical Sciences (GM-086763), by a Marie Curie IO Fellowship within the 7th European Community Framework Programme to A.S., and by a fellowship from the Alfred P. Sloan Foundation to M.R. M.P.B. is an investigator of the Simons Foundation.

We thank the Harvard Botany Libraries for their help and M. Mani, T. Schneider and D. Pfister for useful discussions and comments. We also thank three anonymous referees for their positive and extremely helpful feedback that significantly improved the quality and clarity of this paper.

Endnotes

1The local radius of curvature is approximately \( \ell \) as a result of the spore being much larger than the apical ring. We obtain the proportionality constant by data analysis as illustrated in the electronic supplementary material.

2Experimental evidence shows that ascus pressure and volume do covary during spore ejection [30] and linear covariance is most plausible given the material properties of the ascus in the relevant parameter regime (see the electronic supplementary material). For a different functional relationship, our model still predicts \( W \propto S_r \), however, the interpretation of the constant of proportionality, and thus our prediction for the elastic modulus of the ring, would change.

References


