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Foldable structures and the natural design of pollen grains

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Upon release from the anther, pollen grains of angiosperm flowers are exposed to a dry environment and dehydrate. To survive this process, pollen grains possess a variety of physiological and structural adaptations. Perhaps the most striking of these adaptations is the ability of the pollen wall to fold onto itself to prevent further desiccation. Roger P. Wodehouse coined the term harmomegathy for this folding process in recognition of the critical role it plays in the survival of the pollen grain. There is still, however, no quantitative theory that explains how the structure of the pollen wall contributes to harmomegathy. Here we demonstrate that simple geometrical and mechanical principles explain how wall structure guides pollen grains toward distinct folding pathways. We found that the presence of axially elongated apertures of high compliance is critical for achieving a predictable and reversible folding pattern. Moreover, the intricate sculpturing of the wall assists pollen closure by preventing mirror buckling of the surface. These results constitute quantitative structure-function relationships for pollen harmomegathy and provide a framework to elucidate the functional significance of the very diverse pollen morphologies observed in angiosperms.

harmomegathy | inextensional deformation | thin shell theory | elasticity

Harmomegathy (1) is the characteristic folding of pollen grains to accommodate the decrease in cellular volume due to water loss. The partial desiccation of the pollen grain following its release from the anther results in the grain falling into a dormant state that ensures the cellular material survives until the pollen grain reaches the stigma of a flower. Upon capture by the stigma, the pollen grain is once again exposed to a humid environment, resumes its hydrated condition, and harmomegathy is reversed (2, 3). The apertures on the pollen surface provide the main routes for exchange with the environment (3) and serve as exit points for the pollen tube. The structure of the pollen wall is designed to allow the apertures to fold inwardly during harmomegathy thus reducing the rate of water loss. Therefore, harmomegathy can be interpreted as an elegant solution to two conflicting demands on the pollen grain—the requirement to maintain routes of exchange between the grain and the environment and the need to limit the desiccation of the cellular material (Fig. 1A).

The pollen wall has a complex composite structure (Fig. 1B). The outer layer known as exine is rich in sporopollenin—a stiff, chemically resistant, and water impermeable biomaterial. The cellulosic intine forms a compliant, water permeable layer that lies just inside the exine and is firmly attached to it. The intine is only exposed at the apertures where the exine is interrupted (Fig. 1B). The number, arrangement, and shape of the apertures greatly influence the pollen grain folding pathway (4–7). During dehydration, aperture pollen grains become increasingly elongated, with the aperture margins approaching each other so that the pollen grain becomes effectively sealed (Fig. 1C and D). The compliant apertures provide preferred sites of invagination that guide the folding. On the other hand, pollen grains that lack

elongated apertures respond to desiccation by forming depressions on the exine whose number and location can vary greatly (Fig. 1E and F). The importance of wall structure in guiding harmomegathy was recognized as early as 1883 (8), and although more recent work has reinforced this idea (5, 9, 10), there is still no theory to support the many claims about the function of the pollen wall as a harmomegathic apparatus. Here, we provide a first detailed quantitative analysis of the structure-function relationship for pollen harmomegathy.

Results and Discussion

To understand how the different folding pathways emerge, we must consider the mechanical response of a closed shell to a reduction of its volume. Exact solutions for large deformation of a shell are difficult to obtain. However, it is possible to derive approximate solutions to the problem based on geometric considerations only. Central to our approach is the classic result for thin-walled shells that bending deformations (i.e. changes in the surface curvature) are energetically more favorable than stretching deformations (11). Thus, closed-form approximate solutions for large deformation of thin shells can be found by considering inextensional (bending-only) deformations of the initial geometry.

Pogorelov (11) showed that for a closed convex surface such as a sphere the only possible inextensional deformation is a mirror reflection of a segment of the surface about a dissecting plane. This solution provides a good approximation of the folding pathway observed in porate and inaperturate pollen grains (Fig. 1E and F). By virtue of being a bending-only deformation of the original surface, one can surmise that mirror buckling is a minimal energy solution for pollen folding when large apertures are absent as demonstrated for nonbiological systems (12). In closed shells with finite wall thickness, pure bending is not possible without some stretching. Since stretching is energetically costly, it is concentrated along ridges and cusps (11–13) as those observed in the pollen grains of *Aristolochia* and corn (Fig. 1E and F).

Applying these considerations to aperture pollen grains, we would expect the harmomegathic wall deformation to be primarily accommodated by bending of the thin but stiff exine, with most of the stretching being concentrated at the apertural site where the exine is reduced or completely absent. To test this prediction, we used environmental scanning electron microscopy to observe the folding pathway in lily (*Lilium longiflorum*) and *Euphorbia milii* pollen (Fig. 2A and D (see Movies S1 and S2 for the folding process)). The apertural and interapertural regions differ

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six nearest neighbors, except for the inevitable 12 points for spherical topologies which have only five neighbors. To test whether the fivefold "defects" of the tessellated mesh have an effect on the folding pathway, we performed simulations changing their position on the model pollen grain and found that there was little variation in the results, the most important difference being a slight asymmetry of the in-rolled margins of the aperture.

In our simulation, all key geometrical parameters were measured directly (see above). However, the Young's modulus of sporopollenin and the cellulosic intine are not known except for one measurement for the exine of ragweed pollen (21). We set the Poisson ratio to $\nu = 1/3$, leaving us with one free parameter in the model, the ratio of the Youngs modulus of the intine E_I and exine E_E . The simulations presented in this work were performed at a small intine to exine bending modulus ratio $\kappa_I/\kappa_E < 0.015$. To determine how sensitive the pollen grain folding is to the value of the Youngs modulus, we performed numerical simulations for an ellipsoidal pollen grain for various modulus ratios and compared the optimum sealing states, defined as the folded geometry that minimizes the distance of the apertural margins at the equator. We found that the folded shape is robust over a wide range of modulus ratios (see *SI Text*).

The bending (H_b) and stretching (H_s) energies of the tessellated pollen were calculated using a mass-spring model with the spring rest lengths and angles chosen so that the initial pollen geometry is stress free. This choice was dictated by our observations that isolated wall fragments retain the geometry of the hydrated condition, despite the absence of cellular material (22). The discretized stretching energy of the pollen grain, modeled as a thin elastic shell is

$$H_s = \frac{1}{2} \sum_{\langle ij \rangle} \epsilon_{ij} (|\vec{r}_i - \vec{r}_j| - \rho_{ij})^2, \quad [2]$$

where \vec{r}_i is the position of the nodes of the mesh, ρ_{ij} is the equilibrium length of the bond joining nodes i and j , and the summation ($\langle ij \rangle$) is over adjacent vertices (15, 23). The equilibrium lengths were chosen to relax the strains associated with the 5-fold coordinated points and suppress spurious buckling transitions (24). Depending on whether the bond of the pair ij is assigned to the aperture or interapertural region of the wall, the discretized stretching modulus takes the values ϵ_I and ϵ_E , respectively.

The discretized bending energy is

$$H_b = -\frac{1}{2} \sum_{\langle kl \rangle} \kappa_{kl} \cos(\theta_{kl} - \theta_{kl}^0)^2, \quad [3]$$

where θ_{kl} is the angle between the normals of adjacent triangular faces k and l of the tessellated surface, whereas θ_{kl}^0 is the equilibrium angle determined by the spontaneous curvature, that is the shell curvature at the initial stress free state. The parameter κ_{kl} is proportional to the bending rigidity of the

surface and, similar to the stretching modulus, takes the value κ_E at the exine and κ_I at the aperture.

To enforce self-avoidance of the shell during the deformation, the nodes of the shell were assigned a "hard core" repulsive potential with range equal to one third of the average tether length. To impose the fixed volume constraint, we added a quadratic term of the form

$$H_V = \lambda(V - V_0)^2, \quad [4]$$

where V is the volume of the pollen and V_0 is a target volume (25).

Pollen dehydration proceeds over a period of 1 min or more. Inertial effects are thus unimportant and the folding is dominated by energetics. The equilibrium volume of the pollen grain depends on the atmospheric humidity (26), which provides a fixed volume constraint. The shape of the folding pollen grains should be determined by minimizing the total elastic energy $H_s + H_b$ for the fixed volume. The shell shape that minimized the sum of the elastic energy and the volume constraint term was found using either an adaptive step gradient descent or conjugate gradient scheme. The parameter λ was initially chosen sufficiently small to allow convergence and gradually increased until $(V - V_0)/V < 10^{-5}$ (25).

Appendix

The Gaussian curvature of a doubly curved surface is the product of the two principal curvatures, c_s and c_θ , where s and θ are the meridional and azimuthal coordinates. The meridional curvature is $c_s = -r''/(1 - r'^2)^{1/2}$ and the circumferential curvature is $c_\theta = (1 - r'^2)^{1/2}/r$ where r is the distance from the axis of rotation and the prime and double prime denote the first and second derivatives with respect to the arclength s . The Gaussian curvature of the surface is thus $K(s) = c_s c_\theta = -r''(s)/r(s)$. During folding, the Gaussian curvature must be preserved. This property can be used to predict families of surfaces that are isometric. According to the definition above, the family of surfaces $r(s, t) = \alpha(t)r_0(s)$ all share the same Gaussian curvature $-r_0''(s)/r_0(s)$. Here α is a parameter greater than zero that allows a gradual transition between the different surfaces. When the angular displacement changes inversely with α allowing the closure of the pollen grain, the parameter α does not appear in the first fundamental form (14). Thus, this family of curves represents a pure bending transformation.

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