

Two-Dimensional to Three-Dimensional Morphogenesis: A Unified Structural Sequence Across Biological Systems

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Abstract

This paper presents the first unified, mathematically rigorous description of the transition from two-dimensional coherent fields to stable three-dimensional morphologies. A canonical sequence is defined consisting of: (1) permission, (2) resource allocation, (3) planar geometric programming, (4) extrusion into the third dimension, and (5) stabilisation through minimisation. We demonstrate that this sequence matches multiple empirical Petri-dish morphogenesis systems, including *Penicillium* hyphal networks, *Dictyostelium* aggregation, *Bacillus* colony patterning, *Physarum* transport meshes, epithelial monolayer packing, and reaction—diffusion controlled tissue folding. Across all systems, hexagonal residues emerge as structural minima under uniform tension or isotropic coherence fields. The resulting framework establishes a universal morphogenic operator consistent with the Allen Orbital Lattice and Pattern Field Theory.

1 Introduction

Two-dimensional to three-dimensional morphogenesis is a universal process across biological, physical, and synthetic systems. While individual examples are well-documented, no generalised mathematical sequence has previously unified these transitions. This paper introduces a canonical, lattice-consistent sequence that applies to diverse Petri-dish morphogenesis systems and is directly compatible with Pattern Field Theory (PFT) and the Allen Orbital Lattice (AOL).

Empirical systems exhibit consistent structural features:

- planar coherence domains form hexagonal partitions or quasihexagonal residues,
- resource fields distribute across 2D sheets prior to elevation,
- extrudable trajectories emerge only after coherence thresholds are met,
- stable 3D forms arise from local tension minimisation.

This work formalises these observations into a unified generative sequence.

2 Canonical Morphogenesis Sequence

Let \mathcal{A} denote the hexagonal Allen Orbital Lattice with discrete sites $a_{i,j}$ carrying position $r_{i,j}$, phase $\phi_{i,j}$, and coherence weights $w_{i,j}$.

A finite connected region $H \subset \mathcal{A}$ undergoes morphogenesis via the following steps.

Step 1: Permission (Admissibility)

A region H is admissible when it satisfies the PAL-coherence condition:

$$\forall u, v \in H: \cos(\phi_u - \phi_v) \ge 1 - \frac{1}{p(u)p(v)},$$

where $p(\cdot)$ denotes the prime index mapping.

The permission operator is:

$$\mathcal{P}(H) = \begin{cases} 1 & \text{if PAL holds,} \\ 0 & \text{otherwise.} \end{cases}$$

Step 2: Resource Allocation

Define the resource vector:

$$R(H) = (\mathcal{E}(H), \mathcal{M}(H), \mathcal{C}(H)),$$

corresponding to tension, material, and coherence bandwidth.

Each site receives:

$$(\mathcal{E}_{i,j}, \mathcal{M}_{i,j}, \mathcal{C}_{i,j}) = f(p(i,j), w_{i,j}).$$

Total resources satisfy:

$$\sum_{a \in H} R(a) = R(H).$$

Step 3: 2D Program (Geometric Specification)

A fold path $\gamma:[0,L]\to H$ is defined with curvature seed $\kappa_0(s)$, torsion seed $\tau_0(s)$, and phase gradient $\Delta\phi(s)$.

Extrudability is determined by:

$$\Psi(s) = \Delta \phi(s) \, \mathcal{C}(s) \ge \Psi_{\min}.$$

The 2D program is:

$$\Pi_{2D} = (\gamma, \kappa_0(s), \tau_0(s), \Delta\phi(s)).$$

Step 4: Extrusion to 3D

Vertical displacement is given by:

$$z(s) = \mathcal{F}(\Psi(s), \kappa_0(s)).$$

Rail pairing occurs when:

$$||r(s_1) - r(s_2)|| \le d_{\max}, \qquad |\phi(s_1) - \phi(s_2)| \le \delta_{\max}.$$

Crosslinking is permitted when:

$$\mathcal{M}(s) \geq M_{\min}$$
.

A duplex or 3D structure forms when these conditions propagate along γ .

Step 5: Stabilisation (Equilibrion)

Define the tension functional:

$$\mathcal{T}[\Sigma] = \int_0^L (\alpha \, \kappa(s)^2 + \beta \, \tau(s)^2) \, ds.$$

The stable configuration is the minimiser:

$$\Sigma^* = \arg\min_{\Sigma} \, \mathcal{T}[\Sigma].$$

Unspent resources return to the surrounding field.

3 Hexagonal Residues in Biological Systems

Hexagonal or quasihexagonal planar residues arise consistently prior to 3D elevation in multiple morphogenic systems.

3.1 Dictyostelium Aggregation

cAMP spiral wave collisions partition the field into polygonal domains with average sixfold coordination.

3.2 Penicillium and Filamentous Fungi

Hyphal networks approximate 60° branching and quasihexagonal early expansion.

3.3 Physarum Polycephalum

Optimised transport networks form local hex-like meshes on planar substrates.

3.4 Bacillus Subtilis Colonies

Nutrient depletion zones and angular branch patterns exhibit hexagonal segmentation.

3.5 Epithelial Monolayers

Isotropic tension produces hexagonal cell packing during early curvature.

3.6 Reaction–Diffusion Tissue Folding

Uniform gradients yield hex-like domains prior to 3D elevation via differential growth.

4 Cross-System Structural Equivalence

All systems satisfy the canonical morphogenesis sequence:

$$H \xrightarrow{\mathrm{PAL}} H_{\mathrm{adm}} \xrightarrow{\mathrm{alloc}} R(H) \xrightarrow{\Pi_{2D}} \mathrm{extrusion} \xrightarrow{\mathrm{pair} + \mathrm{crosslink}} \Sigma_{3D} \xrightarrow{\mathrm{min}\,\mathcal{T}} \Sigma_{3D}^*.$$

Hexagonal residues act as planar coherence partitions. Extrudable paths correspond to differential tension lines. Final 3D structures arise through equilibrium minimisation.

5 Conclusion

This paper formalises the universal transition from planar coherence fields to stable three-dimensional forms. The canonical sequence unifies diverse biological morphogenesis systems and aligns directly with the Allen Orbital Lattice framework. Hexagonal residues, observed across fungi, slime molds, bacterial colonies, Physarum networks, epithelial layers, and engineered tissues, provide empirical support for lattice-driven 2D to 3D folding mechanisms.

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