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A NONLINEAR ANALYSIS OF A MECHANICAL MODEL FOR BIOLOGICAL PATTERN FORMATION*

P. K. MAINI†‡ AND J. D. MURRAY†

Abstract. This paper studies a simplified but biologically relevant version of a mechanical model for morphogenesis proposed by Oster, Murray, and Harris [*J. Embryol. Exp. Morph.*, 78 (1983), pp. 83–125]. A nonlinear bifurcation analysis of the partial differential system is presented. In the one-dimensional version, the derivation of the amplitude equation involves a nonstandard element. The analysis of a caricature of the two-dimensional system predicts the formation of rolls and hexagons. The biological significance of these results to feather germ formation is briefly discussed.

Key words. biological pattern formation, bifurcation theory, mechanical models

AMS(MOS) subject classification. 92.

1. Introduction. Several models have been proposed to describe pattern formation in early embryonic development. Most consist of reaction-diffusion systems which, in the appropriate region of parameter space, bifurcate from an initial homogeneous steady state and evolve to an inhomogeneous steady state (for example, Turing (1952), Murray (1977), (1981a), (1981b), Meinhardt (1982)). Cells interpret the concentration of chemical in some way and differentiate accordingly, thus leading to pattern; this is the essence of Wolpert's (1969), (1981) "positional information" concept.

An alternative approach to pattern formation in embryology has been made by Oster, Murray, and Harris (1983), Murray and Oster (1984a), (1984b), Oster, Murray, and Maini (1985) based on the mechano-chemical properties of embryonic cells and tissue. Section 2 contains a brief derivation of a simple version of the model equations (see Oster et al. (1983) for fuller details). In § 3 we carry out a nonlinear bifurcation analysis on the model. Using small parameter expansions, multi-time scales, and the method of balancing harmonics, we derive an amplitude equation for the inhomogeneous steady state. The asymptotic technique requires a nonstandard approach. In § 4 we investigate regular two-dimensional patterns in a caricature of the model analyzed in § 3. We conclude (§ 5) that nonlinear analysis predicts patterns in the appropriate parameter space in one dimension, and the formation of rolls and hexagons in two dimensions. We briefly discuss the biological significance of these results to feather germ formation in chicks.

2. Mechanical model equations. Mesenchymal cells in the dermis of the developing embryo exert large traction forces which deform the cross linked fibrous substratum, the extracellular matrix (ECM), on which they move (Fig. 2.1). The model is based on the three field variables:

$n(\underline{x}, t)$ = density of mesenchymal cells at position \underline{x} and time t .

$\rho(\underline{x}, t)$ = density of extracellular matrix at position \underline{x} and time t .

$u(\underline{x}, t)$ = displacement at time t of a material point of ECM initially at \underline{x} .

The full model equations are given in Oster et al. (1983). As we shall study a simplified version of the original model in this paper, here we only give the simpler system.

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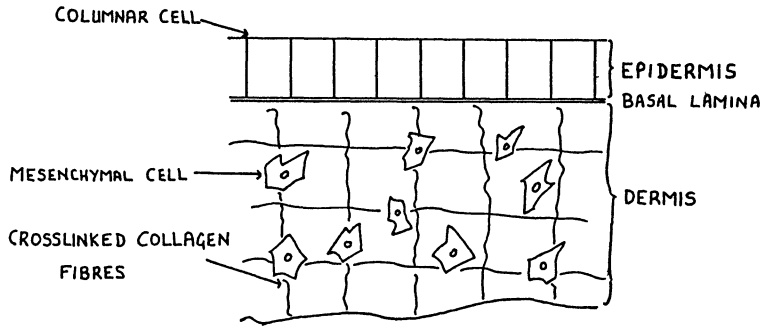


FIG. 2.1. Diagrammatic representation of chick epithelium at day six. The epithelium is composed of two layers; an epidermis consisting of columnar cells, and a mesenchymal dermis, connected by anchor filaments. The dermis consists of mesenchymal cells in a jelly-like matrix, the extracellular matrix (ECM), which is composed of cross linked collagen fibres capable of exerting elastic forces (Trinkaus (1984)). The cell tractions deform the matrix and eventually lead to an aggregate of dermal cells known as a papilla. The mechano-chemical interaction between the dermis and epidermis leads to epidermal aggregates called placodes which, together with the papillae, form primordia, or feather germs, which eventually form feathers. The model presented here is concerned only with the formation of dermal aggregates.

Cell conservation:

$$(2.1a) \quad \partial n / \partial t + \nabla \cdot [n \partial \underline{u} / \partial t] = 0.$$

Mechanical force balance:

$$(2.1b) \quad \nabla \cdot [\mu_1 \partial \mathbf{e} / \partial t + \mu_2 \partial \theta / \partial t \mathbf{I} + \{E / (1 + \nu)\}(\mathbf{e} + \nu^* \theta \mathbf{I}) + \tau n (\rho + \beta \nabla^2 \rho) \mathbf{I}] = s \underline{u} \rho.$$

Matrix conservation:

$$(2.1c) \quad \partial \rho / \partial t + \nabla \cdot [\rho \partial \underline{u} / \partial t] = 0$$

where $\mathbf{e} = [\nabla \underline{u} + \nabla \underline{u}^T] / 2$ is the linear strain tensor, $\theta = \nabla \cdot \underline{u}$ the dilatation, \mathbf{I} the unit tensor, and $\mu_1, \mu_2, E, \nu, \nu^*, \tau, s,$ and β are nonnegative parameters which we describe below.

We briefly motivate the various contributions to (2.1a)-(2.1c).

Cell conservation. The equation for cell conservation is of the form

$$(2.2) \quad \partial n / \partial t = -\nabla \cdot \underline{J}_n,$$

where \underline{J}_n is the cell flux through a volume element of matrix and we assume that at the pattern formation stage cell proliferation is negligible as appears to be the case from experimental observations. The cell flux, \underline{J}_n , is composed of a number of terms (see Oster et al. (1983)). In this paper we only deal with the convective flux since experimentally this seems to be the major contribution to cell movement. The convective velocity is $\partial \underline{u} / \partial t$ so the flux term is

$$(2.3) \quad \underline{J}_n = -n \partial \underline{u} / \partial t.$$

Substituting (2.3) into (2.2) gives (2.1a).

Mechanical force balance. We are dealing with a system with low Reynolds number (Purcell (1977), Odell et al. (1981)), so the viscous and elastic forces dominate the inertial terms and cell motion instantly ceases when the applied forces are switched off. Therefore, the mechanical force balance equation is

$$(2.4) \quad \nabla \cdot \sigma + \rho \underline{F} = \underline{0}$$

where σ is the stress tensor and \underline{F} the body force.

We model the cell-matrix composite as a linear, isotropic, viscoelastic material with stress tensor

$$\sigma = \sigma_{\text{matrix}} + \sigma_{\text{cell-matrix}}$$

where

$$(2.5a) \quad \sigma_{\text{matrix}} = \underbrace{\mu_1 \partial \mathbf{e} / \partial t + \mu_2 \partial \theta / \partial t \mathbf{I}}_{\text{viscous}} + \underbrace{[E / (1 + \nu)](\mathbf{e} + \nu^* \theta \mathbf{I})}_{\text{elastic}}$$

$\theta = \nabla \cdot \underline{u}$, the dilation, E is Young's modulus, μ_1 and μ_2 the shear and bulk viscosities, respectively, ν the Poisson ratio, $\nu^* = \nu / (1 - 2\nu)$, and \mathbf{I} is the unit tensor (see, for example, Landau and Lifshitz (1970)).

The stress exerted by the contractile forces of the cells on the matrix is taken as

$$(2.5b) \quad \sigma_{\text{cell-matrix}} = \tau n [\rho + \beta \nabla^2 \rho] \mathbf{I}$$

where τ and β are both nonnegative. The $\beta \nabla^2 \rho$ term accounts for long-range traction forces (cf. long-range diffusion).

We assume that the cell-matrix composite is attached elastically to a subdermal layer in the skin. We model this, in the simplest possible way, as a linear elastic spring with spring constant $s (> 0)$. Thus the body force, \underline{F} , is

$$(2.6) \quad \underline{F} = -s \underline{u}.$$

Matrix conservation. The equation for matrix conservation is

$$\partial \rho / \partial t = -\nabla \cdot \underline{J}_\rho + S(n, \underline{u}, \rho),$$

where \underline{J}_ρ is the flux and $S(n, \underline{u}, \rho)$ the secretion rate.

The matrix moves only due to the contractile forces exerted by the cells, that is, by convection. At the stage in development we are concerned with, matrix secretion is negligible. Hence the equation for matrix conservation is

$$(2.7) \quad \partial \rho / \partial t = -\nabla \cdot [\rho \partial \underline{u} / \partial t]$$

convective flux

3. One-dimensional nonlinear analysis. In Murray and Oster (1984a), (1984b), we nondimensionalized the full original model system and carried out a linear stability analysis about the steady state $n = \rho = 1$, $\underline{u} = 0$. In this paper we examine the nonlinear behavior of the simpler model (2.1) in one dimension, namely,

$$(3.1a) \quad \partial n / \partial t + \partial / \partial x (n \partial u / \partial t) = 0,$$

$$(3.1b) \quad \partial^3 u / \partial x^2 \partial t + \partial^2 u / \partial x^2 + \tau \partial / \partial x [n(\rho + \beta \partial^2 \rho / \partial x^2)] - s u \rho = 0,$$

$$(3.1c) \quad \partial \rho / \partial t + \partial / \partial x (\rho \partial u / \partial t) = 0,$$

where we have rescaled time by dividing through by $\mu (= \mu_1 + \mu_2)$ and the remaining parameters by dividing through by $(1 + \nu^*)$.

The dispersion relation is

$$(3.2) \quad \sigma(k^2) = -[\beta \tau k^4 + (1 - 2\tau)k^2 + s] / k^2,$$

where

$$\begin{pmatrix} n' \\ u' \\ \rho' \end{pmatrix} \propto \exp[\sigma(k^2)t + i\mathbf{k} \cdot \underline{x}],$$

with n' , u' , and ρ' small perturbations from the steady state $n = \rho = 1$, $u = 0$. Figure 3.1 illustrates its behavior as τ increases.

We take τ as the bifurcation parameter. If τ is slightly greater than τ_c , the uniform steady state will be linearly unstable to random perturbations and the fastest growing unstable wave number is k_c (Fig. 3.1). To examine the behavior of the full nonlinear system near the bifurcation point, we set $\tau = \tau_c + \varepsilon^2 \delta$, where $0 < \varepsilon \ll 1$ and $\delta = \pm 1$.

Expanding σ about (k_c^2, τ_c) in a Taylor series we have

$$(3.3) \quad \sigma(k_c^2, \tau_c + \varepsilon^2 \delta) = \sigma(k_c^2, \tau_c) + \varepsilon^2 \delta \left. \frac{\partial \sigma}{\partial \tau} \right|_{k_c^2, \tau_c} + O(\varepsilon^4)$$

↙
↘
0

and the exponential growth term is $\exp [O(\varepsilon^2)t]$ which suggests the usual long time scale $T = \varepsilon^2 t$. As k_c is the fastest growing wave number we assume that it will be the dominant spatial term on the long time scale. We also assume that temporal changes occur only on the long, or slow, time scale T . To investigate the nonlinear behavior of (3.1) therefore, we ignore the fast time variable, t , and use the method of balancing harmonics. To this end we substitute

$$(3.4) \quad \begin{aligned} n(x, T, \varepsilon) &= 1 + \sum_{j=1} \varepsilon^j \{A_j(\varepsilon, T) \cos jk_c x + D_j(\varepsilon, T) \sin jk_c x\}, \\ u(x, T, \varepsilon) &= \sum_{j=1} \varepsilon^j \{B_j(\varepsilon, T) \sin jk_c x + E_j(\varepsilon, T) \cos jk_c x\}, \\ \rho(x, T, \varepsilon) &= 1 + \sum_{j=1} \varepsilon^j \{C_j(\varepsilon, T) \cos jk_c x + F_j(\varepsilon, T) \sin jk_c x\} \end{aligned}$$

where

$$T = \varepsilon^2 t, \quad A_j(\varepsilon, T) = \sum_{i=0} \varepsilon^i A_j^i(T),$$

with similar expressions for B_j , C_j , D_j , E_j , and F_j . We substitute these into (3.1) and equate coefficients of ε . This leads to a hierarchy of linear equations for the coefficients $A_j^i(T)$, $B_j^i(T)$, $C_j^i(T)$, $D_j^i(T)$, $E_j^i(T)$, and $F_j^i(T)$ which we can solve. To lowest order in ε , we have

$$(3.5) \quad \begin{aligned} d/dT \{A_1^0(T) + k_c B_1^0(T)\} &= 0, \\ k_c \tau_c A_1^0(T) + (k_c^2 + s) B_1^0(T) + k_c \tau_c (1 - k_c^2 \beta) C_1^0(T) &= 0, \\ d/dT \{C_1^0(T) + k_c B_1^0(T)\} &= 0 \end{aligned}$$

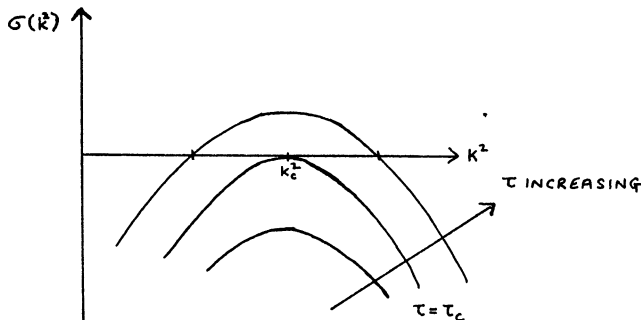


FIG. 3.1. Behavior of the dispersion relation (3.2) for fixed β and s as τ , the bifurcation parameter, increases. For $\tau < \tau_c$, the uniform steady state $n = \rho = 1$, $u = 0$ (in nondimensional form) is stable to random spatial perturbations. For $\tau = \tau_c + \varepsilon^2 \delta$ ($0 < \varepsilon \ll 1$, $\delta = 1$), the uniform steady state is unstable and the spatial disturbance with wave number k_c grows fastest, where $k_c^2 = (s/\beta\tau_c)^{1/2}$ and $\tau_c = [1 + s\beta + \{(1 + s\beta)^2 - 1\}^{1/2}]/2$.

and a similar set of equations for $\{D_1^0(T), E_1^0(T), F_1^0(T)\}$. To simplify the analysis we shall only consider $\{A_j^i(T), B_j^i(T), C_j^i(T)\}$ for the remaining calculation. The analysis may be repeated exactly for $\{D_j^i(T), E_j^i(T), F_j^i(T)\}$.

Order ϵ^2 terms give

$$\begin{aligned}
 & d/dT\{A_2^0(T) + 2k_c B_2^0(T)\} + k_c A_1^0(T) dB_1^0(T)/dT = 0, \\
 & 2k_c \tau_c A_2^0(T) + (4k_c^2 + s)B_2^0(T) + 2k_c \tau_c(1 - 4\beta k_c^2)C_2^0(T) \\
 (3.6) \quad & = -k_c \tau_c(1 - \beta k_c^2)A_1^0(T)C_1^0(T) - \frac{1}{2}sB_1^0(T)C_1^0(T), \\
 & d/dT\{C_2^0(T) + 2k_c B_2^0(T)\} + k_c C_1^0(T) dB_1^0(T)/dT = 0.
 \end{aligned}$$

Secular terms appear at order ϵ^3 in (3.1b). Suppressing these gives the condition

$$\begin{aligned}
 (3.7) \quad & -k_c^2 dB_1^0(T)/dT - k_c \delta\{A_1^0(T) + C_1^0(T)\} + \beta \delta k_c^3 C_1^0(T) \\
 & + k_c \tau_c(2\beta k_c^2 - \frac{1}{2})A_1^0(T)C_2^0(T) + \frac{1}{2}k_c \tau_c(\beta k_c^2 - 1)A_2^0(T)C_1^0(T) \\
 & - \frac{1}{2}s\{C_1^0(T)B_2^0(T) - B_1^0(T)C_2^0(T)\} = 0.
 \end{aligned}$$

Standard nonlinear analysis simply requires successive suppression of secular terms. However, with the structure of our equations this is not sufficient to determine the amplitude equation. We have to use an *integrated* form of the conservation equations. Integrating the first and third of (3.5) we have three simultaneous inhomogeneous equations for $A_1^0(T)$, $B_1^0(T)$, and $C_1^0(T)$, namely,

$$\begin{aligned}
 (3.8) \quad & A_1^0(T) + k_c B_1^0(T) = \gamma_1^0, \\
 & k_c \tau_c A_1^0(T) + (k_c^2 + s)B_1^0(T) + k_c \tau_c(1 - \beta k_c^2)C_1^0(T) = 0, \\
 & k_c B_1^0(T) + C_1^0(T) = \gamma_3^0
 \end{aligned}$$

where γ_1^0 and γ_3^0 are constants depending on the initial conditions. The system (3.8) is degenerate and has a nontrivial solution if and only if

$$[k_c^2(1 - \tau_c) + s]\gamma_3^0 + k_c^2 \tau_c \gamma_1^0 = 0,$$

that is, there is a constraint on the initial conditions. This is only to be expected because of the intimate relationship between u and ρ ; that is, the initial random perturbations in the matrix density from the uniform steady state ($\rho = 1$) automatically give rise to the displacements (u) of the material points of the ECM. The correlation between the two is given by the above constraint. Thus an initial perturbation of the system (2.1) cannot be random in all variables n , u , and ρ . Once ρ is perturbed, u is determined (and vice versa). Mathematically, other initial conditions are possible but are not of biological interest.

Integrating the first and third of (3.6), we obtain

$$\begin{aligned}
 (3.9) \quad & A_2^0(T) + 2k_c B_2^0(T) = \{A_1^0(T)\}^2/2 + \gamma_1^1, \\
 & C_2^0(T) + 2k_c B_2^0(T) = \{C_1^0(T)\}^2/2 + \gamma_3^1
 \end{aligned}$$

where γ_1^1 and γ_3^1 are constants.

To simplify the analysis we shall consider initial perturbations to be $O(\epsilon^3)$; thus $\gamma_1^0 = \gamma_3^0 = \gamma_1^1 = \gamma_3^1 = 0$. From (3.8) and the integrated form of (3.6), we can solve for $B_1^0(T)$, $C_1^0(T)$, $A_2^0(T)$, $B_2^0(T)$, and $C_2^0(T)$ in terms of $A_1^0(T)$ and, substituting into (3.7), we have the usual Landau equation

$$\begin{aligned}
 (3.10) \quad & d/dT\{A_1^0(T)\} = \delta X A_1^0(T) + Y\{A_1^0(T)\}^3 \\
 & \text{where } X = (2\tau_c + 1)/2\tau_c, \quad Y = (14\beta\tau_c s + 24\tau_c - 63\beta s - 12)/72\beta s
 \end{aligned}$$

Table 3.1 summarizes the behavior of the amplitude equation (3.10).

Figure 3.2 illustrates the $\beta - s$ parameter space wherein the cell density evolves to the bounded steady state $n = 1 + \epsilon(X/|Y|)^{1/2} \cos k_c x$.

TABLE 3.1
Behavior of $A_1^0(T)$ from (3.10).

	$Y < 0$	$Y > 0$
$\delta > 0$	A_1^0 evolves to $(X/ Y)^{1/2}$	$A_1^0 \rightarrow \infty$
$\delta < 0$	$A_1^0 \rightarrow 0$	Threshold in $A_1^0(0)$ $A_1^0(0) < (X/Y)^{1/2} \Rightarrow A_1^0 \rightarrow 0$ $A_1^0(0) > (X/Y)^{1/2} \Rightarrow A_1^0 \rightarrow \infty$

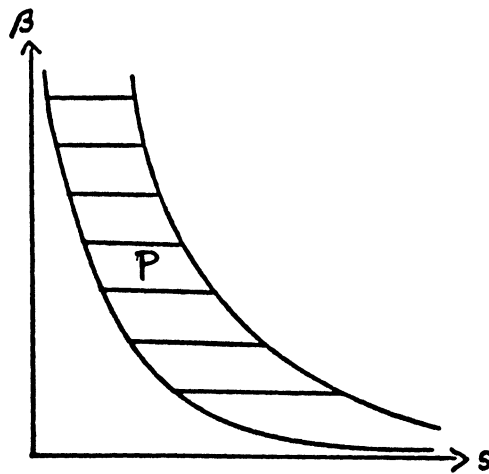


FIG. 3.2. β - s parameter space (P) where $A_1^0(T)$ ((3.10)) evolves to a bounded steady state (see Table 3.1).

If we do not make the assumption that the initial perturbations are $O(\epsilon^3)$ then we have the perturbed version of the above amplitude equation, namely,

$$(3.11) \quad d/dT\{A_1^0(T)\} = C_0 + \delta(X + X_0)A_1^0(T) + Z_0\{A_1^0(T)\}^2 + Y\{A_1^0(T)\}^3$$

where C_0 , X_0 , and Z_0 are functions of γ_1^i and γ_3^i , $i = 0, 1$ and the homogeneous steady state bifurcates to a heterogeneous steady state dependent (continuously) on initial conditions. Equation (3.11) is a simple ordinary differential equation which may be analyzed in the usual way, giving rise to results which are slightly different from those summarized in Table 3.1 for (3.10). For example, in the case $\delta < 0$, $Y < 0$, the solution to (3.10) becomes unbounded. In (3.11), however, the possibility exists of a small stable steady-state solution, depending on the values of γ_j^i , $i = 0, 1, j = 1, 3$. The γ_j^i are initial conditions and will be determined from a previous developmental process. Thus the model suggests that the process of development may lead to a variation in pattern, depending on the previous developmental phase.

4. Two-dimensional nonlinear analysis. To investigate the nonlinear behavior of the model in two dimensions is clearly a very complex problem. Experimental observations indicate that \underline{u} and $\nabla \cdot \underline{u}$ are small. Therefore we may simplify the analysis (with biological justification) and consider a caricature of the above model in two dimensions.

We linearize the conservation equations for n and ρ about the steady state $n = \rho = 1$, and integrate to give

$$(4.1) \quad n = 1 - \theta, \quad \rho = 1 - \theta$$

where $\theta = \nabla \cdot \underline{u}$, the dilation. As n and ρ are necessarily nonnegative we assume $\theta < 1$, that is, we are dealing with small strains; this is justified from biological observations.

If we replace the $s\underline{u}\rho$ term in the force balance equation by the linearized term $s\underline{u}$, substitute the linear approximations (4.1) for n and ρ into the resulting equation, and take the divergence, we finish up with an equation for θ , namely,

$$(4.2) \quad \nabla^2 \partial\theta/\partial t + \nabla^2 \theta + \tau \nabla^2 \{(1 - \theta)^2 - \beta(1 - \theta)\nabla^2 \theta\} - s\theta = 0$$

where we have used the identity

$$\nabla \cdot \underline{e} = \text{grad div } \underline{u} - \frac{1}{2} \text{curl curl } \underline{u}.$$

Clearly the dispersion relation for (4.2) is still (3.2) and, for $\tau > \tau_c$, the uniform steady state, $\theta = 0$, loses linear stability. To study the full nonlinear system, we substitute

$$(4.3) \quad \tau = \tau_c + \sum_{i=1} \varepsilon^i \tau^i, \quad \theta(\underline{x}, t) = \sum_{i=1} \varepsilon^i \theta_{i-1}(\underline{x}, t) \quad \text{where } 0 < \varepsilon \ll 1$$

into (4.2). As in the analysis in § 3, we equate coefficients of ε and the problem reduces to the solution of a hierarchy of linear equations. We follow in part the process used by Busse (1983).

The only regular patterns in the plane are rolls, triangles (hexagons), squares, and tessellations of these. Therefore we look for $\theta_0(\underline{x}, t)$ of the form

$$(4.4) \quad \theta_0(\underline{x}, t) = \frac{1}{2} a_1(t) \{(\cos(kx + ly) + \cos(ly - kx))\} + a_2(t) \cos 2ly$$

where the fastest growing unstable mode has wave number $K (= (s/\beta\tau_c)^{1/4})$ and $k^2 + l^2 = K^2$, $4l^2 = K^2$. Putting $a_1(t) = 0$, $a_2(t) = 0$, $a_1(t) = 2a_2(t)$ into (4.4) gives roll, rhombic and hexagonal patterns, respectively (Christopherson (1940)). On substituting the above form of $\theta_0(\underline{x}, t)$ into (4.2), we find that $\theta_1(\underline{x}, t)$ must have the form

$$\begin{aligned} \theta_1(\underline{x}, t) = & b_1(t) \cos 4ly + b_2(t) \cos(3ly + kx) + b_3(t) \cos(3ly - kx) \\ & + b_4(t) \cos 2(ly + kx) + b_5(t) \cos 2(ly - kx) + b_6(t) \cos 2kx \end{aligned}$$

where, on equating coefficients of ε^2 , we can find $b_i(t)$, $i = 1, 2 \dots 6$ in terms of $a_1(t)$ and $a_2(t)$; it is a simple but tedious calculation.

Taking powers of ε up to ε^3 into account, to suppress secular terms, $\dot{a}_1(t)$ and $\dot{a}_2(t)$ must satisfy the pair of ordinary differential equations,

$$(4.5) \quad \begin{aligned} K^2 da_1(t)/dt &= Xa_1(t) - Ya_1(t)a_2(t) - 2Za_1(t)a_2^2(t) - \frac{1}{4}(2Z + R)a_1^3(t), \\ K^2 da_2(t)/dt &= Xa_2(t) - \frac{1}{2}Ya_1^2(t) - Za_1^2(t)a_2(t) - Ra_2^3(t) \end{aligned}$$

where

$$\begin{aligned} X &= [(2\tau_c + 1)/2\tau_c] \{\varepsilon\tau_1 + \varepsilon^2\tau_2\} K^2, & Y &= (1/2\tau_c) \{\varepsilon\tau_c + \varepsilon^2\tau_1\} K^2, \\ Z &= (3\varepsilon^2/16\beta\tau_c) \{\tau_c - 1\}, & R &= (\varepsilon^2/36\beta\tau_c) \{6\tau_c - 5\}. \end{aligned}$$

For $\tau_1 > 0$ and ε small, X and Y are positive, and the sign of Z and R depends on the value of τ_c .

The system (4.5) has the following steady states:

$$(4.6) \quad \begin{aligned} \text{(I)} \quad & a_1(t) = a_2(t) = 0, \\ \text{(II)} \text{a, b:} \quad & a_1(t) = 0, \quad a_2(t) = \pm(X/R)^{1/2}, \\ \text{(III)} \text{a, b:} \quad & a_1(t) = 2a_2(t), \quad a_2(t) = [-Y \pm \{Y^2 + 4X(4Z + R)\}^{1/2}]/2(4Z + R), \\ \text{(IV)} \text{a, b:} \quad & a_1(t) = -2a_2(t), \quad a_2(t) = [-Y \pm \{Y^2 + 4X(4Z + R)\}^{1/2}]/2(4Z + R), \\ \text{(V)} \text{a, b:} \quad & a_1(t) = \pm 2\{X - RY/(R - 2Z)\}^{1/2}/\{R + 2Z\}^{1/2}, \quad a_2(t) = Y/(R - 2Z) \end{aligned}$$

where, for example, (II)a, b exist if and only if $\tau_c > 5/6$. To lowest order in ϵ , (III)a is $a_1(t) = 2a_2(t)$, $a_2(t) = [-Y_0 + \sqrt{Y_0^2}]/2(4Z + R) = 0$, where $Y_0 = \epsilon K^2/2$, and this is the same as (I). A similar argument can be applied to (IV)a and, in the following analysis, we shall not distinguish between states (I), (III)a, and (IV)a.

We analyze the stability of states (I)–(IV) in the usual way by calculating the eigenvalues (λ_s) of the appropriate matrix. This gives a quadratic in λ_s , with coefficients dependent on ϵ . To simplify the analysis, we approximate these coefficients to lowest order in ϵ . The results of the stability analysis are summarized in Table 4.1.

TABLE 4.1
Summary of linear stability analysis of steady states (I)–(IV) (see (4.6)) of the coupled ordinary differential equations (4.5). (See text for details.)

$\tau_c < 5/6$	$5/6 < \tau_c < 47/51$	$47/51 < \tau_c < 32/33$	$\tau_c > 32/33$
I unstable star			
(II)a, b do not exist	(II)a stable star (II)b saddle point		
(III)b and (IV)b unstable node		(III)b and (IV)b saddle point	(III)b and (IV)b stable node

Note that when the critical traction, τ_c , lies between 5/6 and 32/33, the only stable regular pattern is a roll, while for $\tau_c > 32/33$ rolls and hexagons are stable. In the latter case, the evolved pattern depends on initial conditions.

5. Conclusion. We have shown that, in a simplified version (2.1) of the model proposed by Oster, Murray, and Harris (1983), nonlinear analysis predicts one- and two-dimensional patterns in the appropriate parameter space. The one-dimensional analysis requires an integrated form of the conservation equations in order to get the amplitude equation. The two-dimensional analysis shows that rolls and hexagons are linearly stable in certain parameter regimes.

The model is based on the properties of cells in chick dermis and it is well known that the cells develop into an hexagonal array of aggregations on the chicken back during feather germ development (Davidson (1983a), (1983b)). Initially, a row of feather germs appears on the mid-dorsal line on the chick back. Subsequent rows appear laterally adjacent to this initial row with aggregates at interdigitating points, leading to a hexagonal pattern. We have shown that the model wherein convection is the major contribution to cell movement can give rise to such patterns in the dermis. In the case of the two-dimensional analysis, the pattern of dermal aggregates forms simultaneously. This sets up a pre-strain on the epidermis and if the mechano-chemical properties of the epidermis were to change in such a way that the epidermis became competent to form aggregations sequentially, then the feather germs (epidermal placode + dermal papilla) would appear to form sequentially (Murray and Oster (1984a), (1984b)). Note that the dermis controls the geometry of the feather germ pattern; this appears to be observed.

Numerical simulations (Perelson, Maini, Murray, Hyman, and Oster (1986)) of the full original model have shown the possibility of one-dimensional pattern in the

vicinity of the bifurcation, and the possibility of a sequentially organized hexagonal pattern in two dimensions, wherein an aggregation pattern of cells in one dimension imposes a strain field on either side causing neighboring aggregates to form at interdigitating points.

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