67. A Partial Differential Equation for a Model of Morphogenesis

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§ 1. **Introduction.** R. Thom ([1], p. 176) proposed a model to explain the gastrulation of the Amphibia. Let $C^{\infty}(R^k)$ be the space of C^{∞}-functions on R^k, let D^3 denote the three dimensional ball in R^3 and let T be the axe of time. His static model is a mapping $F: D^3 \times T \to C^{\infty}(R^k)$. In the space $C^{\infty}(R^k)$ there is a subset Σ of functions which are not stable. This set is called the bifurcation set. The inverse image of this set $F^{-1}(\Sigma)$ (or its subset) is called the catastrophe set. According to his catastrophe theory, F is transversal to the bifurcation strates and the catastrophe set is a stratified set such that any point of the set has a neighbourhood which is isomorphic to elementary catastrophes.

In his book [1], he tries to explain the gastrulation of the Amphibia by a static model whose organizing center is a swallow's tail.

In this paper a partial differential equation on the sphere S^2 is studied. For some initial data, the solution generates a shock wave which is just R. Thom described in his book, and that the solution is stable under the perturbation of the initial data and the equation.

Next, a static model is constructed out of the partial differential equation and the initial data. The catastrophe set of this static model simulates the gastrulation of Amphibia.

It is quite interesting that in our model, the gradient of animal-vegetative potential and the initial data which has a peak in the area of the gray crescent play the essential role.

The role which is played by a swallow's tail in Thom's model is played by a cusp in our model.

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§ 2. **Quasi-linear partial differential equation on S^2.** Let S^2 be the unit sphere $S^2=\{x \in R^3 \mid |x|=1\}$. S^2 is a Riemannian manifold with Riemannian metric g induced from the standard inner product of R^3. Let $b: S^2 \to R$ be a C^{∞}-function on S^2. At each point $x \in S^2$, the Riemannian metric g gives an isomorphism of the cotangent space $T_x^*S^2$ and the tangent space T_xS^2. Define the gradient vector field ∇b of b as follows. For each point $x \in S^2$, ∇b_x is the vector which corresponds to the convector db_x, the exterior derivative of b, i.e. ∇b_x is the unique vector such that for any vector v in T_xS^2, $g(\nabla b_x, v)=db_x(v)$. Let $A: R \to R$ be a smooth function such that the second order derivative is strictly positive $A''(u)\geqslant\varepsilon>0$. Let $a(u)=A'(u)$. Let T denote the axe of time and let its coordinate t. Let $\langle\ ,\ \rangle$ denote the Riemannian metric, i.e. $\langle v_1, v_2\rangle=g(v_1, v_2)$.

Consider the Cauchy problem for the following partial differential equation,

$$\frac{\partial u}{\partial t}+\langle\nabla A(u), \nabla b\rangle=0 \tag{1}$$

where u is the unknown function $u: S^2\times T\to R$, with initial condition $\phi: S^2\times 0\to R$, and ∇ denotes the gradient vector field with respect to S^2. The equation (1) is also written as

$$\frac{\partial u}{\partial t}+a(u)\langle\nabla u, \nabla b\rangle=0\ . \tag{2}$$

The equation tells that the value of u depends only on the initial data on the trajectory of the vector field ∇b which runs through the point.

§3. The equation on the trajectory. Let a one-dimensional submanifold L of S^2 be a trajectory of the gradient vector field ∇b. Parametrize the trajectory by the length. Let l denote the length of the trajectory L. Then the parametrization is a mapping of the open interval $I_l=(0, l)$ to L.

Take a point p in L and define a local coordinate (x, y) around p so that the family of curves $y=$constant are trajectories of ∇b and the family of curves $x=$constant are local level manifolds of b, and that $\left|\frac{\partial}{\partial y}\Big|_p\right|=1$. Then vectors $\frac{\partial}{\partial x}\Big|_p$ and $\frac{\partial}{\partial y}\Big|_p$ make an orthonormal basis of T_pS^2. Therefore the gradient vector at p is expressed as

$$\nabla b_p=\frac{\partial b}{\partial x}(p)\frac{\partial}{\partial x}\Big|_p+\frac{\partial b}{\partial y}(p)\frac{\partial}{\partial y}\Big|_p\ ,$$

but by the definition of the local coordinate, $\frac{\partial b}{\partial y}(p)=0$. Hence the equation (2) is transformed into a quasi-linear equation on $I_l\times T$,

$$\frac{\partial u}{\partial t}+a(u)\frac{\partial b}{\partial x}\frac{\partial u}{\partial x}=0\ . \tag{3}$$

As p may be any point in L, the equation (2) is equivalent to (3). This argument is good wherever $\nabla b\neq 0$. Where $\nabla b=0$, the equation tells that u remains constant there.

Next, we transform the equation into a conservation law. Take a point p_0 in $I_l=(0, l)$. Define a diffeomorphism h of I_l into R by

$$h(x)=\int_{p_0}^{x}\frac{dx}{\dfrac{\partial b}{\partial x}}.$$

As $\dfrac{\partial b}{\partial x}$ is of constant signature on I_l, $\dfrac{dh}{dx}$ never vanishes.

Let I_h denote the image $h(I_l)$ in R. We denote the coordinate of I_h by ψ. Note that

$$\frac{\partial u}{\partial x}(x)=\frac{\partial(u\circ h^{-1})}{\partial\psi}(h(x))\cdot\frac{\partial h}{\partial x}(x).$$

Let $\tilde{u}=u\circ h^{-1}$, $\tilde{u}: I_h\times T\to R$. Then the equation (3) is transformed into a quasi-linear equation

$$\frac{\partial\tilde{u}}{\partial t}+a(\tilde{u})\frac{\partial\tilde{u}}{\partial\psi}=0 \tag{4}$$

that is to say

$$\frac{\partial\tilde{u}}{\partial t}+\frac{\partial}{\partial\psi}A(\tilde{u})=0\ , \tag{5}$$

This equation is well known. In particular, for an initial data $\phi: I_h\to R$, if there is a point x_0 in I_h such that

$$\phi'(x_0)<0,\quad \phi''(x_0)=0,\quad \phi'''(x_0)>0 \tag{6}$$

then at time $t_0=-\dfrac{1}{a'(\phi(x_0))\phi'(x_0)}$, at $x_0+a(\phi(x_0))t$, it generates a shock wave.

Remark. The argument above is good also for any Riemannian manifold. The weak solutions of (5) make a global solution of (1), because we have transformed only by changes of local coordinates.

§ 4. Construction of a model for morphogenesis. We construct a model which will generate a 'blastopore'. For the functions $A: R\to R$ and $a: R\to R$, take the simplest functions $A(u)=\dfrac{1}{2}u^2$ and $a(u)=u$ so that $a'(u)=1>0$.

Let $b: S^2\to R$ be the animal-vegetative potential, i.e. a smooth function on S^2 with two non-degenerate critical points. For example, $b(x)=x_3$, $x=(x_1,x_2,x_3)\in R^3$, $S^2=\{x\in R^3\,|\,x_1^2+x_2^2+x_3^2=1\}$, in this case, the point $(0,0,1)$ corresponds to the vegetative pole and $(0,0,-1)$ to the animal pole. Trajectories of the gradient vector field are the longitudes.

Parametrize $S^2-\{(0,0,-1)\cup(0,0,1)\}$ by the longitude $\theta\in R/2\pi Z$ and the latitude x, $-\dfrac{\pi}{2}<x<\dfrac{\pi}{2}$, so that $b(x,\theta)=\sin x$. Then $\dfrac{\partial b}{\partial x}=\cos x$, $I_l=\left(-\dfrac{\pi}{2},\dfrac{\pi}{2}\right)$, $I_h=(-\infty,\infty)$. Take $p_0=0\in I_l$.

$$h(x)=\int_0^x\frac{dx}{\cos x}=\log\left(\tan\left(\frac{x}{2}+\frac{\pi}{4}\right)\right).$$

Next, define a function $\chi: R \to R$ such that $\lim_{\psi \to \pm\infty} \chi(\psi)=0$, $\chi(\psi) \geqslant 0$ and that there is a unique point $\psi_0 \in R$ which satisfies $\chi'(\psi_0)<0$, $\chi''(\psi_0)=0$, $\chi'''(\psi_0)>0$ and $\psi_0>0$. For example $\chi(\psi)=\exp(-\psi^2)$.

Define the maps $\chi_{\rho,\sigma}: R \to R$ for $\rho, \sigma \in R$ by

$$\chi_{\rho,\sigma}(\psi)=\rho\chi(\sigma\psi).$$

Then at time $t(\rho, \sigma)=-\dfrac{1}{\chi'_{\rho,\sigma}\left(\dfrac{\psi_0}{\sigma}\right)}=-\dfrac{1}{\rho\sigma\chi'(\psi_0)}$ the solution of the equation (5) with initial condition $\tilde{u}(\psi, 0)=\chi_{\rho,\sigma}$ breaks and generates a shock wave at $\dfrac{1}{\sigma}\left(\psi_0+\dfrac{-\chi(\psi_0)}{\chi'(\psi_0)}\right)$. Let $S^1=R/2\pi Z$ be the circle of longitudes. Define a map $\gamma: S^1 \to I_l$ so that the graph of γ is the set of end points of blastopore at each time. Define also a map $\tau: S^1 \to T$ so that for each longitude $\theta \in S^1$, $\tau(\theta)$ is the time when the end point of the blastopore passes. The image of the graph map $id_{S^1} \times \gamma \times \tau: S^1 \to S^2 \times T$ defines a circle C in $S^2 \times T$. (Cf. R. Thom [1] p. 177.)

Define maps $\sigma: S^1 \to R$ and $\rho: S^1 \to R$ by

$$\sigma(\theta)=\frac{\psi_0-\dfrac{\chi(\psi_0)}{\chi'(\psi_0)}}{h\circ\gamma(\theta)},$$

$$\rho(\theta)=-\frac{1}{\tau(\theta)\sigma(\theta)\chi'(\psi_0)}.$$

Finally define the initial condition $\phi: S^2 \to R$ by

$$\phi(x, \theta)=\chi_{\rho(\theta),\sigma(\theta)}(h(x))$$

and $\phi((0,0,1))=\phi((0,0,-1))=0$. For this initial data, the equation (1) will generate a gastrulation of type C.

§ 5. The relation between our model and Thom's static model. D. Schaeffer [2] defined a static model for conservation laws such that the catastrophe set of the static model is just where the shock wave runs. Our static model is slightly modified so as not to decay when $t \to 0$.

First, define a static model on $S^1 \times I_l \times T$, i.e. a field of smooth maps $F: S^1 \times I_l \times T \times R \to R$ by

$$F(\theta, x, t, u)=u \cdot a(u)-A(u)-\frac{1}{t}\int_{h(x)}^{h(x)-a(u)t} \phi_\theta(v)dv,$$

where ϕ_θ is the restriction of the initial data ϕ,

$$\begin{tikzcd} S^2 \arrow[r, "\phi"] & R \\ S^1 \times I_l \arrow[u] & I_h \arrow[l, "(\theta, h^{-1})"] \arrow[u, "\phi_\theta"'] \end{tikzcd}.$$

For a bounded time interval no phenomenon occurs at both poles so that this static model can be extended over $S^2 \times T$. The catastrophe set of this model corresponds to our shock wave.

References

[1] R. Thom: Stabilité structurelle et morphogénèse (1972). Benjamin.
[2] D. Schaeffer: A regularity theorem for conservation laws (to appear).