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TOPOLOGICAL MODELS IN BIOLOGY†

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INTRODUCTION

THE PROBLEM of Morphogenesis—broadly understood as the origin and evolution of biological structures—is one of the outstanding questions in present day Biology. Many experimental attempts have been made to elucidate the cause of morphogenetic processes in Embryology, Development, Regeneration, etc. Some of them have been partially successful. For instance, as a typical example, let us consider the well-known fact of orientation of a plant toward light (*positive phototropism*); here, the physiologists have been able to characterise a chemical substance, *an auxin*, which inhibits the growth of the stem when under light. In such a case, the immediate causative agent and a satisfactory local explanation have been found. But, in most cases, when one tries to get beyond the first causative factor, the experimentalist gets lost in the seemingly infinite multiplicity of possible causes, and the bewildering variety of intermingled reactions which have to be considered. Most people—in this situation—satisfy themselves by vague appeals to differential action of genes, decoding of genic DNA ... and so on.

There is little doubt, in fact, that the problem is essentially of a theoretical, conceptual nature. Granted that all local morphological or physical phenomena inside a living being occur according to a local biochemical determinism, the problem is to explain the stability and the reproduction of the global spatio-temporal structure *in terms of the organization of the structure itself.* There appears to be a striking analogy between this fundamental problem of theoretical Biology and the main problem considered by the mathematical theory of Topology, which is to reconstruct a global form, a topological space, out of all its local properties. More precisely, a new mathematical theory, the theory of *Structural stability*—inspired from Qualitative Dynamics and Differential Topology—seems to offer far reaching possibilities to attack the problem of the stability of self-reproducing structures, like the living beings. But—at least in the author's opinion—the validity of this type of dynamic description exceeds by far the biological realm, and may be applied to all morphological processes—whether animate or inanimate—where discontinuities prohibit the use of classical quantitative models. It should be noted, in that respect, that any morphological process involves by definition some discontinuity of the phenomenological properties of the medium

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studied: this explains why Morphogenesis—whether in Biology, like in Development—or in inanimate nature, like for crystal growth—has up to now resisted all attempts of classical mathematical treatment:a ny quantitative model, using explicit equations, involves necessarily analytic, hence continuous functions. The only partial exception to this statement is the theory of *shock waves* in Fluid dynamics, where some local equations of propagation may be established, but here again, complicated problems like the behaviour of interacting shock waves may be solved only empirically [1]. In all these situations, a new mathematical theory, nearer to the qualitative thinking of the topologist than the quantitative estimates of classical analysis, seems particularly relevant.

§1. THE MATHEMATICAL THEORY OF STRUCTURAL STABILITY

A. Notion of Dynamic System

Suppose we put in a box B k chemical substances $s_1, s_2, \dots, s_k$, at concentrations $x_1, x_2, \dots, x_k$. Because of the reactions taking place between these substances, their concentrations x_i vary according to a law which we may write:

$$dx_i/dt = X_i(x_j, \tau, t) \tag{1}$$

where t denotes time, τ some external parameter like temperature ... In such a case, a state of the system is described by a system of $(k+2)$ parameters (x_i, t, τ), i.e. by a point in $(k+2)$-dimensional euclidean space $\mathbf{R}^{k+2}$, which is the "phase space" M of our system. The right hand side X_i of (1) define in M a vector field X. Provided this vector field satisfies some regularity conditions (for instance to be differentiable), then we may—at least locally—integrate the differential system (1) and get equations:

$$x_i = h_i(x_i^0, \tau, t) \tag{2}$$

describing the evolution of the system as a function of the initial data x_i^0. This general picture applies to practically all known systems of any nature whatsoever, provided they are directed by a local determinism. The most outstanding example of this model has been given by Celestial Mechanics, with Newton's Gravitation Law defining the right-hand side of (1) in the phase space (q_i, p_i) of positions and momenta. The differential model (M, X) offers the ultimate motivation for the introduction of quantitative models in Science. Nevertheless, its use is fraught with grave difficulties:

1°) Despite the widespread belief to the contrary, there are very few natural phenomena which allow a precise mathematical description, for which the right hand side of (1) is "exactly" known and given by explicit formulae. Gravitation and classical electromagnetism are practically the only cases to fulfil this requirement. In most other cases, the right hand side of (1) is known only approximately through empirical formulae.

2°) Even if the right hand side of (1) is explicitly given it is nevertheless impossible to integrate formally the system (1). To get the solution (2), one has to use approximating procedures.

For these two reasons, one has to know to what extent a slight perturbation of the right hand side of (1) may affect the global behaviour of the solutions (2). To overcome—at least partially—these difficulties, Henri Poincaré introduced in 1881 a radically new approach, the theory of "Qualitative Dynamics" [2]. Instead of trying to get explicit solutions of the system (1), one aims for a global geometrical picture of the system of trajectories (2) defined by the field X. If this can be done, one is able to describe qualitatively the asymptotic behaviour of any solution. This is in fact what really matters: in most practical situations, one is interested, not in a quantitative result, but in the qualitative outcome of the evolution (Will the bridge stay or break down?). Thus, qualitative dynamics, despite the considerable weakening of its programme, remains a very useful—although very difficult—theory.

B. Structurally Stable Dynamical Systems

A new development occurred in 1935 with the introduction by the Soviet mathematicians Andronov and Pontrjagin of the concept of *structurally stable dynamical system*. The dynamical system (M, X) is said to be *structurally stable*, if, for a sufficiently small perturbation δX of the vector field X, the perturbed system $(M, X + \delta X)$ is, roughly speaking, topologically isomorphic to the unperturbed system (see Figs. 1 and 2 for examples). An outstanding question was then to characterize the structurally stable systems for a given space M, and to know if they are *dense*, that is, if any differential system in M can be approximated by

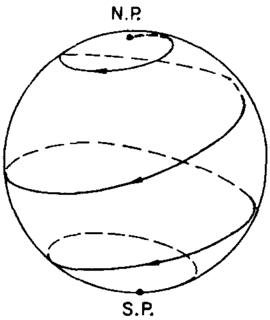

FIG. 1. Example of a structurally stable system on the two-sphere $x^2 + y^2 + z^2 = 1$.

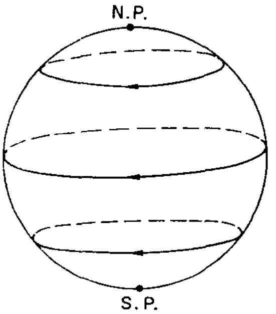

FIG. 2. On the same sphere, the vector field defined by $dz = 0$ is not structurally stable; a small deformation of the form $z = -\varepsilon^2$ transforms it in the field of Fig. 1.

a structurally stable one. These difficult questions were recently solved affirmatively for dim $M \leq 2$ by M. Peixoto; for dim $M \geq 4$, S. Smale showed that structurally stable systems may not be dense (see [2] and [3]).

This generally negative answer to the problem of the density of structurally stable systems shows only that the notion of structurally stable systems is still too fine to be really useful. A further weakening of the notion is obtained by the following consideration: as already remarked, the most important feature of a solution (2) of the system (1) is its asymptotic behaviour for t tending to $+\infty$. It may happen, for instance that the representative point $h(t)$ tends toward a point q, which is an *equilibrium position* of the system. If this point q is such that the trajectory of any point near q goes to q, and no trajectory leaves q, we shall say that q is an *attractor* of the system (stable equilibrium). This attractor is said to be *structurally stable* if any perturbation —sufficiently small—of the given system contains an attractor q' near to q. For some vector fields, like the gradient fields, almost any trajectory goes to an attractor—in general a point which is structurally stable. One may conjecture that for almost any field on a space M, almost any trajectory goes to an attractor—which may be a more complicated geometric object, like a closed trajectory, a torus, or an even more complicated set, but which is nevertheless structurally stable. We might consider, finally, only those systems which have a finite set of structurally stable attractors. There are good reasons [3] to believe that this is finally the useful notion, and that any system may be approximated by one of this standard type. For any such system, let $A_1, A_2 \ldots A_r$ be its attractors. To any attractor A_i we associate the set $B(A_i)$ of trajectories tending to A_i, the "*basin*" of A_i. Almost all of the space M is partitioned into the basins $B(A_i)$, and the geometry of these basins characterizes entirely the qualitative behaviour of the system [4]. In the simplest cases, like the gradient fields, the basins are separated by piecewise differentiable hyper-surfaces (like the crest line in a geographic map separating the basins of two rivers) and these separatrices are structurally stable (see Fig. 3); but, in other situations, the basins may be-

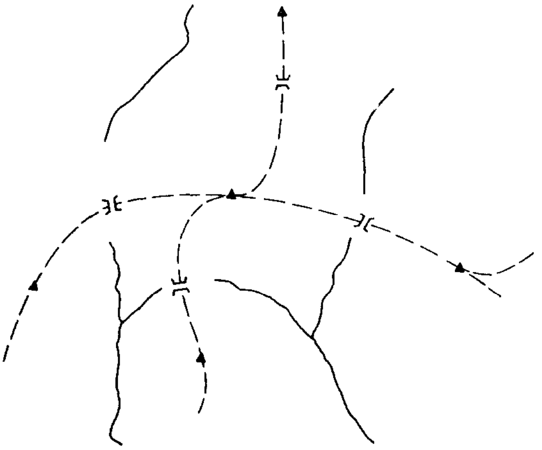

FIG. 3. The crest line (divide), dashed, separating the basins of two rivers is a piecewise differential curve (having eventually cusps at the generic vertices (summits)).

come intermingled in a very complicated, structurally unstable way. If so, the final evolution starting from a point adherent to these basins may be practically indeterminate, and this in a "structurally stable" way, see Fig. 4. This shows the philosophically important fact that a deterministic system may exhibit, in a "structurally stable way", a complete indeterminancy in the qualitative prediction of the final outcome of its evolution [5]. In such a case, we may speak about a "choice" of the system between the two outcomes, or of a conflict, of a "flight" between the two attractors. We will return to this point later.

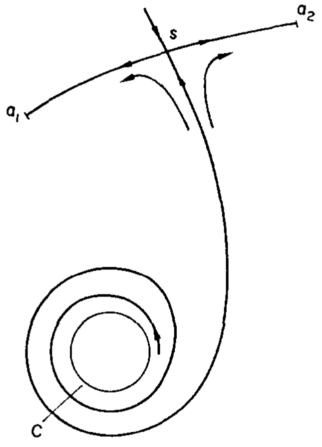

FIG. 4. Example of intermingled basins: the separatrix arriving at a saddle point s tends to limit cycle C. Any point of C is adherent to the two basins of the attractors a_1, a_2 connected to s.

C. Structurally Stable Mappings

In many cases, the description of a physical process by a dynamical system (M, X) is unnecessarily complicated, and we may—at least locally—parametrize the states of the system by a set of mappings $U \xrightarrow{g} W$ (U, W Euclidean spaces), which we may suppose to be differentiable. For instance, if the vector field X is a gradient field, we may consider instead of X the associated potential function V: $X = -\text{grad } V$, where V is a real valued function on M, $V: M \to \mathbf{R}$. Suppose we perturb the given mapping g. We may ask whether the perturbed mapping has the same form, the same "topological type" as the initial mapping. This gives rise to the problem of stability of differentiable mappings, object of current work among mathematicians [6]. We shall discuss here a special case of the problem, which seems to offer many applications: this is the case of an isolated singularity of a potential function V.

First, let us recall that a singular point of differentiable real valued function V of n variables $x_1, x_2, \ldots, x_n$ is a point where all partial derivatives of first order $\partial V/\partial x_i$ vanish. (For the dynamical system defined by $X = -\text{grad } V$, these points are equilibrium positions of the system.) The first question is: when is such a singular point structurally stable?

Mathematically, the answer is quite easy: a singular point m_0 of V is structurally stable if and only if the rank of the mapping defined by $(x_1, x_2, \ldots, x_n) \rightarrow \partial V/\partial x_1, \partial V/\partial x_2, \ldots, \partial V/\partial x_n$ is equal to n at m_0, that is, if the hessian $|\partial^2 V/\partial x_i \partial x_j|$ does not vanish. In such a case the point is said to be a *non degenerate critical quadratic point*, which means that the quadratic part in the Taylor expanison of V at m_0 is non-degenerate. Around such a point, there exists a local system of (curvilinear) coordinates, in which V is expressed as a quadratic form $\sum_{i=1}^{n} (\pm) X_i^2 = V - V(m_0)$ [7].

If the singular point m_0 is non-structurally stable, two cases may occur: let us perturb V by adding an arbitrary function δV such that it and all its derivatives $\partial_\omega \delta V/\partial x_\omega$ of any order are small. Either we may get an infinite number of topological types for the germ of the perturbed function $V + \delta V$; or we can get only a finite number of them. In the first case, the singular point is said to be of *infinite codimension*, in the second, of *finite codimension*. For instance, in one variable, the "flat" singular point $V = \exp(-1/x^2)$ is of infinite codimension, as one may approximate it by a function presenting an arbitrary high number of bumps (take for instance $\delta V = \exp(-1/x) \cos nx$, $x > 0$). The singular point $V = x^3$, on the other hand, is of finite codimension (one), as any perturbation of x^3 is either of the topological type of $x^3 - x$ (curve with a bump), or $x^3 + x$ (curve without bump). (cf. Figs. 5, 6a and 6b). There exists a precise algebraic criterion which tells whether or not a singular point is of finite codimension [8].

D. Universal Unfolding of a Singularity

For a singular point of finite codimension $V(x)$ at $x = 0$, there exists a k-dimensional family of deformations, which is in some sense universal with respect to all possible deformations of V: If

$$V = V(x) + u_1 g_1(x) + u_2 g_2(x) + \cdots u_k g_k(x), \qquad u_j \in \mathbf{R}, j = 1, \ldots, R$$

is this universal family, any perturbation of V, of the form $G(x, t)$, with $t \in \mathbf{R}^s$ and $G(x, 0) = V(x)$ may be obtained, up to topological equivalence, by a mapping $t \rightarrow u$ in this universal family. For instance, if $V = x^3$, its universal unfolding family is $V = x^3 + ux$.

This universal family is called—for obvious intuitive reasons—the *universal unfolding* the singularity $V(x)$, which we call—by analogy borrowed from embryological induction—the *organizing centre* of the family. The dimension k of the universal unfolding is the *codimension* of the singularity $V(x)$.

This notation of universal unfolding plays a central role in our biological models. To some extent, it replaces the vague and misused term of "information", so frequently found in the writings of geneticists and molecular biologists. The "information "symbolized by the degenerate singularity $V(x)$ is "transcribed", "decoded", or "unfolded" into the morphology appearing in the space (u) of external variables which span the universal unfolding family of the singularity $V(x)$.

It is not too difficult a task to find all possible singularities $V(x)$ of finite codimension not exceeding four. These singularities are important, because they may appear on our

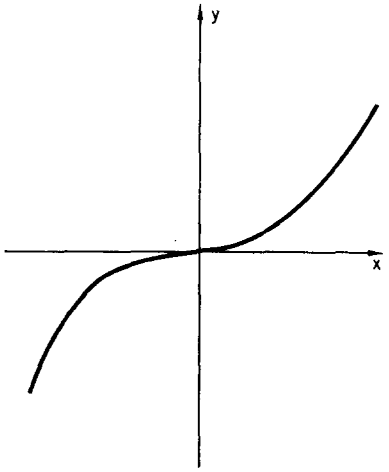

FIG. 5. $v=x^3$.

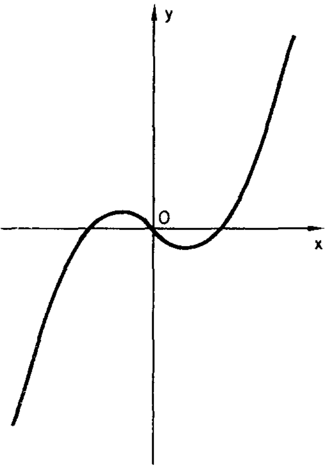

FIG. 6a. $y=x^3-x$.

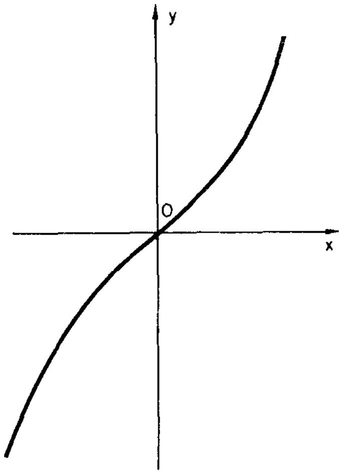

FIG. 6b. $y=x^3+x$.

space—time in a structurally stable way. They give rise to what we call the "elementary catastrophies", when we interpret them as describing dynamical fields on our space—time, as explained below. Here is the list of these singularities, with their dynamical interpretation in every day language.

These "elementary catastrophies" describe also the structurally stable singularities presented by *wavefronts*, or more generally any propagative process directed by a variational principle, like Fermat's principle in Classical Optics. This is why it is possible to realize them as singularities of caustics of light rays (see Plates I–IV).

TABLE OF ORDINARY CATASTROPHIES ON FOUR DIMENSIONAL SPACE–TIME

	Codimension	Name	Organizing centre	Universal unfolding	Spatial interpretation	Temporal interpretation
Dimension one	0	Simple minimum	$V=x^2$	$V=x^2$	A being An object	To be To last
	1	The fold See Fig. 8	$V=x^3/3$	$V=x^3/3+ux$	The boundary The end	To end To start
	2	The cusp (Riemann–Hugoniot catastrophy) See Plate I, Figs. 9a, 9b, 10a, 10b	$V=x^4/4$	$V=x^4/4+ux^2/2+vx$	A pleat A fault	To separate To unite To capture To generate To change
	3	The swallow's tail See Plate II, Fig. 11	$V=x^5/5$	$V=x^5/5+ux^3/3+vx^2/2+wx$	A split A furrow	To split To tear To saw
	4	The Butterfly Fig. 12	$V=x^6/6$	$V=x^6/6+x^4/4+ux^3/3+vx^2/2+wx$	A flake A pocket A scale (of a fish)	To fill To empty } (a pocket) To give } To receive
Dimension two	3	The hyperbolic umbilic See Plate III, Fig. 14	$V=x^3+y^3$	$V=x^3+y^3+w\,xy-ux-vy$	The crest (of a wave) The arch	To break (for a wave) To collapse To engulf
	3	The elliptic umbilic See Fig. 15	$V=x^3-3xy^2$	$V=x^3-3xy^2+w(x^2+y^2)$ $-ux-vy$	The needle The spike The hair	To drill } (a hole) To fill } To prick
	4	The parabolic umbilic See Plate IV; Fig. 16 a–e	$V=x^2y+y^4$	$V=x^2y+y^4+wx^2+ty^2-ux-vy$	The jet (of water) The mushroom The mouth	To break (for a jet) To open } (the mouth) To close } To pierce To cut, to pinch To take, to eject To throw

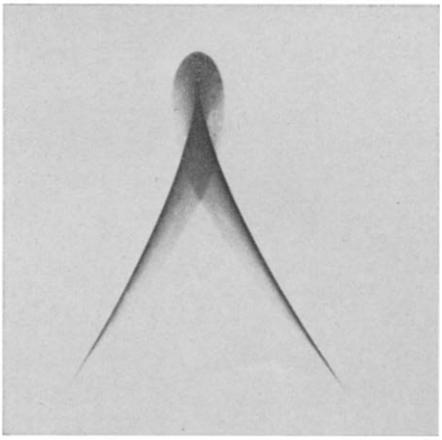

Plate I. Cuspidal caustic. (Riemann–Hugoniot catastrophy.)

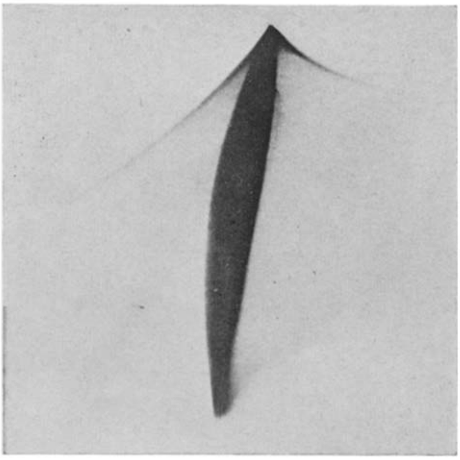

Plate III. Hyperbolic umbilic.

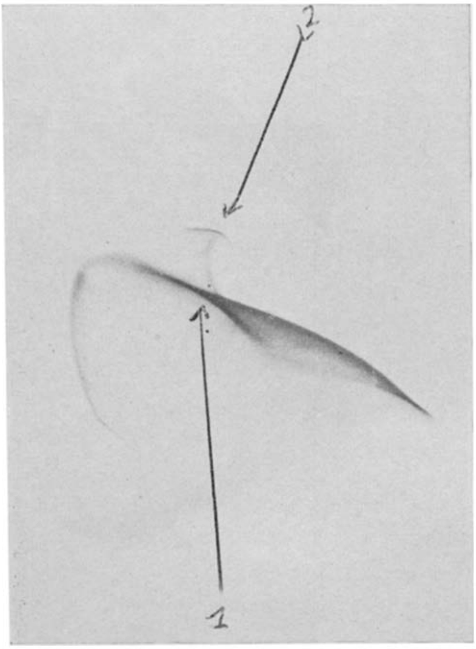

Plate II. A swallow's tail (arrow 1). A hyperbolic umbilic may be seen at the extremity of arrow 2.

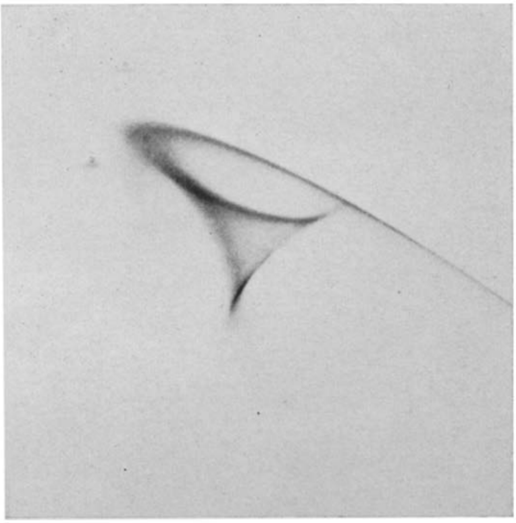

Plate IV. A deformation of a parabolic umbilic.

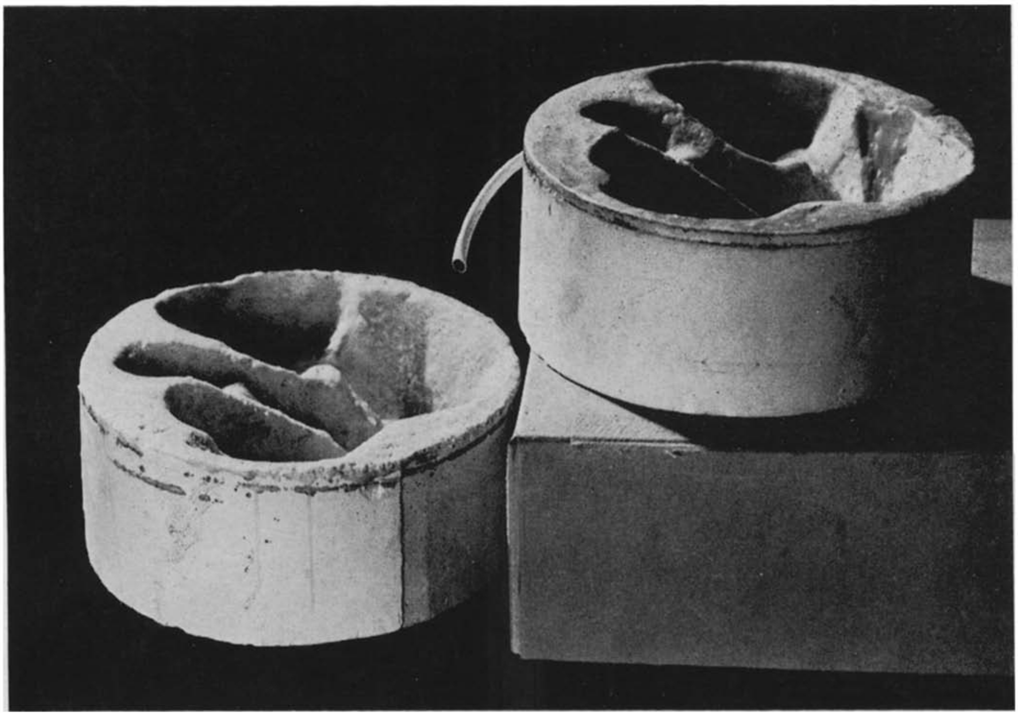

Plate V. The hydraulic model of the epigenetic landscape.

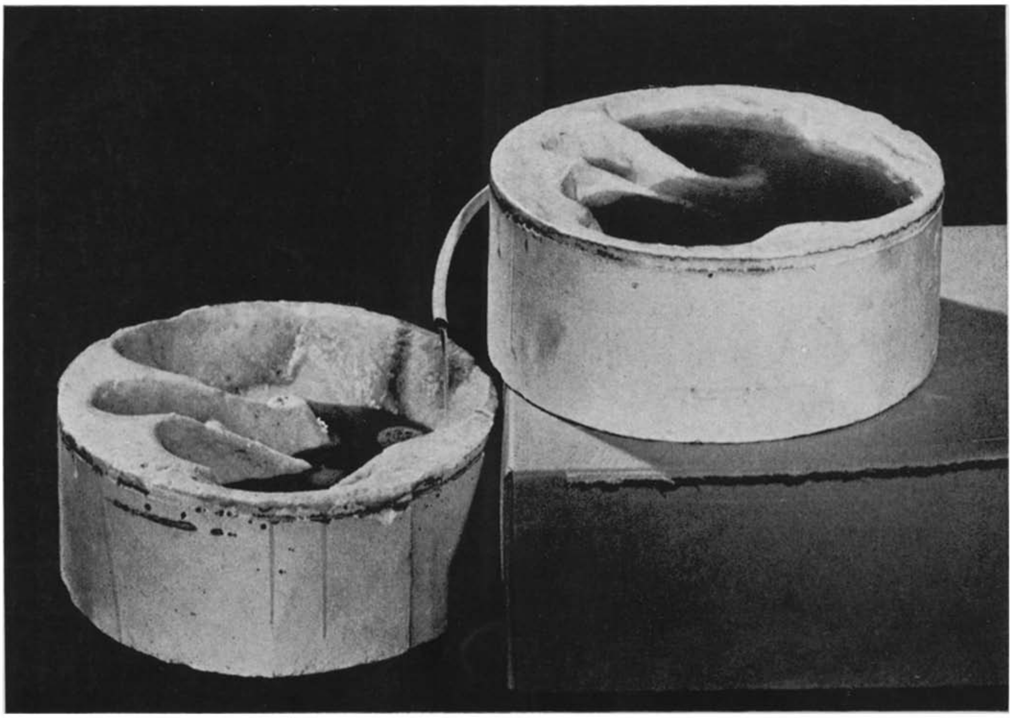

Plate VI. The hydraulic model of reproduction. (The clay models were kindly built by M. Marcel Froissart.)

§2. DETERMINISM AND STRUCTURAL STABILITY

The hypothesis that external phenomena are subjected to a rigid determinism is more an epistemological postulate than a proved fact. Not only because of quantic indeterminism: many situations in the macroscopic world exhibit a kind of very high instability: an infinitesimal change of the initial data may cause an enormous change in the following evolution. As a typical example, let us consider the "bathtub experiment": in a perfectly cylindrical bathtub, filled with water perfectly at rest, what occurs if we open the plug at the bottom? Water begins to spin in a cyclonic movement, the sense of which is practically indeterminate (Many factors have been invoked to determine it: residual motion of water; movement of the air at the surface; Coriolis effect due to the Earth's rotation... and so on.) In such a situation, the final state exhibits less symmetry than the initial data: a *breaking of symmetry* does occur. It is quite clear, for "*a priori*" reasons, that any phenomenon exhibiting such a breaking of symmetry cannot be given any deterministic, formalizable model. One may still say that the initial data were not perfectly symmetrical; but proving the deterministic character of the process may well be an *undecidable* question, just as the non-contradiction of arithmetic is undecidable.

Contrary to these highly unstable situations, there are many cases where the determined character of a process is experimentally obvious; this occurs for processes described by "well posed problems" in Analysis, where the evolution is a continuous function of the initial data; this may occur also for morphogenetic processes, described by a set of discontinuities in the properties of the medium. If such is the case, if the given morphology exhibits stability properties with respect to small variations of the initial data, we shall say that the process is the support of a *morphogenetic field*, or to use a word coined by C, H. Waddington [9] that the process is described by a *chreod*. With this definition, there is no mystery at all in the notion of morphogenetic field: it only expresses the fact that a given process gives rise to a fixed morphology—defined once and for all by a model associated to the field—and this in a structurally stable way. This definition may be put in a precise mathematical form [10] involving the topological notion of homeomorphism.

For any natural morphological process, it is very important to isolate first those parts of the process which are the support of morphogenetic fields, to find out the *chreods* of the process. They form kinds of islands of determinism, separated by zones of instability or indeterminacy. That such a presentation is possible, amounts to say that the morphology is more or less *describable*. In fact, almost any natural process exhibits some kind of local regularity in its morphology, which allows one to distinguish recurrent identifiable elements denominated by words. Otherwise the process would be entirely chaotic, and there would be nothing to talk about. (*Turbulence* in Hydrodynamics might be an example of the last kind, and one knows the difficulty met just in *describing* the process.)

Semantic Models

This decomposition of a morphological process taking place on an euclidean space $\mathbf{R}^m$ can be considered as *a kind of generalized m-dimensional language*; I propose to call it a "*semantic model*".

In fact, our usual language is nothing but a *semantic model of dimension one* (the time), the *chreods* of which are the *words* (spoken, or written).

Given such a "semantic model," then two kinds of problems may be considered:

i) To classify all types of chreods, and to understand the nature of the dynamic processes which insure their stability.

ii) A process involving several chreods is in itself structurally unstable (otherwise it would be covered by a unique over-chreod); but, frequently, one has to deal with an *ensemble* of processes of the type studied. Then, generally, there are some associations of chreods which appear more frequently than others. One may speak, in that case, of a *multi-dimensional syntax* directing the semantic model. The problem is then to describe this syntax, to formalize it in the same way as one may formalize grammatical rules in linguistics.

To do that, one needs to build, first a dictionary of chreods, second what the linguists call a "corpus" of the given language; it is the task of the experimentalist to give this "corpus" in the case of natural morphological processes, and to extract from it statistical data. This is in fact what quantitative biologists do in forming statistics of morphological processes; physicists do the same in their scattering experiments in Elementary Particle Physics. The problem of interpreting these data, and to extract out of them a formal theory seems to be—in general—of the utmost difficulty: it amounts to deciphering an entirely unknown language.

Going back to the first problem, what would be its interpretation in usual linguistics? This would be the famous problem of Plato's Cratylus, to understand how the phonetic structure of a word proceeds from its meaning. One knows that, in that case, the relation between the structure of a word and its meaning is very remote, darkened as it is by the effect of a long history. In many natural phenomena—especially of the inanimate nature—such an arbitrary coding is not to be expected, and one might hope to read more or less directly from the internal structure of the chreod the qualitative dynamic which insures its stability. In Biology the situation is somewhat intermediate: in some cases, the dynamical interpretation of a morphological process is fairly easy; in other cases, the weight of the past manifests itself by submitting the process to *genetic constraints*, which makes the dynamical interpretation more difficult and sophisticated.

§3. THE GENERAL DYNAMIC MODEL

B. Bifurcation and Catastrophies

Let U be a domain in space-time in which some natural process takes place; we admit that all possible local states of the process can be parametrized by points of a manifold M, and that the local evolution around a point $u \in U$ is described by a vector field $X(u)$ in M, varying slowly with u. Then, the local dynamic around u reaches a structurally stable attractor (a stable regime), and stays there for u varying in U, until we reach a point in u where this attractor breaks down through the variation of the dynamical system $X(u)$; the final state is then captured by another attractor (the "basin" of which is adherent to the vanishing basin of the destroyed attractor). We get in U a "shock wave" separating the two regimes, which defines in U morphology to be studied.

This shows that, in such a model, the fundamental phenomenon to be studied is the destruction of a structurally stable attractor by variation of the vector field. This is the object of a part of qualitative Dynamics named—after Henri Poincaré—*bifurcation theory*; this theory is far from being well known from a mathematical point of view. The morphological effect of such a change in local regime I propose to call a *catastrophy*. Our main postulate is that any morphology can be attributed to such a bifurcation phenomenon, whatever may be the nature of the ambient medium, and the physical nature of the forces acting in the local dynamic. Explanations of this kind (with the local metabolism as local dynamics) were put forward for cellular differentiation by C. H. Waddington and Max Delbruck around 1940 [11]. But the great forerunner in this field of ideas is d'Arcy Thompson [12], whose famous treatise "On Growth and Form" contains a wealth of examples and ideas which still have to be explored and developed from the mathematician's point of view.

B. Catastrophies and Morphogenetic Fields

It remains now to explain how bifurcation theory of dynamical systems may lead to the notion of "*morphogenetic field*," of a *chreod*. Here, the intuitive notion is that even *bifurcation, and catastrophy may occur in a structurally stable way, according to a fixed algebraic model* given by theoretical considerations. This is true at least of the most simple type of catastrophies—which we call *ordinary catastrophies*—by contrast to *generalized catastrophies* to be described later.

In the actual state of the mathematical theory, the study of bifurcation—and the following catastrophies—can be done only when the local dynamic (M, X) is a gradient dynamic. In that case, the theory of bifurcation reduces to the theory of structurally stable mappings, and the notion of the "universal unfolding" of a singularity of the potential may be applied. On the universal unfolding space (spanned by the external variables u_i) we get a system of shock waves describing the conflict between the attractors (minima of the potential of the internal dynamic (M, X)). One gets this system by applying the somewhat arbitrary—but easy—rule known as "Maxwell's convention": On any point u of the unfolding space U, the dominating regime corresponds to the absolute *minimum of the potential* V. By this rule, we may associate to any singularity of the potential $V(x)$ of finite codimension a "*universal catastrophy set*" K defined in the unfolding space U with the singularity $V(x)$ as *organizing centre*. If in some domain W of space-time $\mathbf{R}^4$, the local internal dynamic has the singularity $V(x)$ at a point $w \in W$, then—in general—the associated morphology is given by a mapping h of the domain W into the unfolding space U, and we may suppose this map to be in general position—transversal to the universal catastrophy set K. Then the morphology which appears around w in W as a result of the bifurcation $V(x)$ is the counter-image $h^{-1}(K)$. Roughly speaking, the morphology having $V(x)$ as organizing centre is given by the universal model K; there exists around w a *morphogenetic field*, a *chreod* which describes the induced morphology. As the set K has a relatively simple topology—a polyhedral structure—the induced morphology is itself relatively simple: this is the case of "*ordinary catastrophies*."

In order that such a process takes place, a preliminary condition has to be satisfied:

the external variables u_i of the unfolding space must have some local realization as coordinates in W. This requires that the domain W be *polarized* by local agents. The necessity of a preliminary polarization in a tissue support of a morphogenetic field is a postulate of *Child's gradient theory* in Embryology [13]. Our model justifies entirely this point of view.

When the domain W is not sufficiently polarized, then the mapping h may not be a transversal to K; then, the induced morphology $h^{-1}(K)$ may be quite complicated: we get what I call a "*generalized catastrophy.*" A generalized catastrophy is characterized by a very complicated topology involving ramifying domains into smaller and smaller pieces (or, conversely, the condensation into isolated clumps of a dust of very fine particles). Such generalized catastrophies appear as a rule in all symmetry-breaking processes, and they are in general structurally unstable (although the final state of the catastrophy may be very well determined) (see Fig. 7).

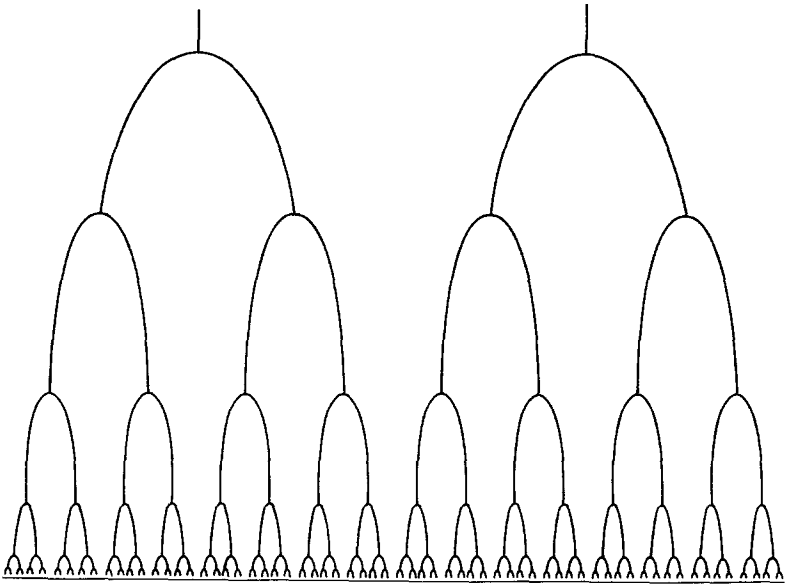

FIG. 7. Scheme for a generalized catastrophy.

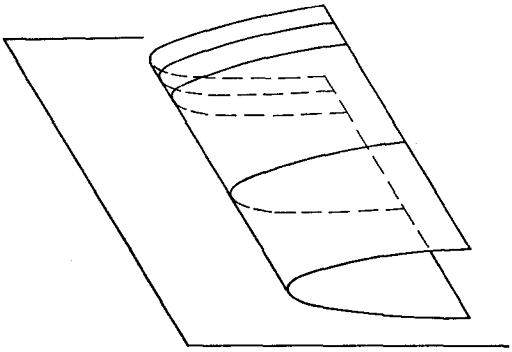

FIG. 8. Ordinary fold.

When the internal dynamic is not of gradient type, the theory of bifurcation is practically unknown. Nevertheless, one may expect that the gradient-like situation keeps some validity, with the restriction that generalized catastrophies may occur even in polarized media.

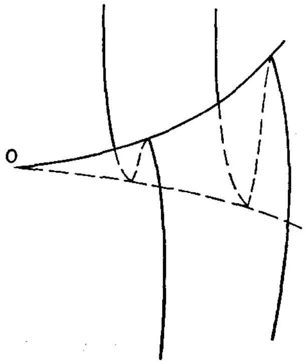

FIG. 9a. Cusp or Riemann–Hugoniot catastrophy.

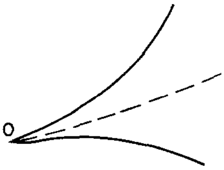

FIG. 9b. The universal catastrophy set of the Riemann–Hugoniot type (shock wave with free edge)

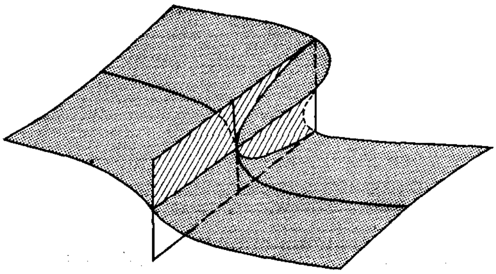

FIG. 10a

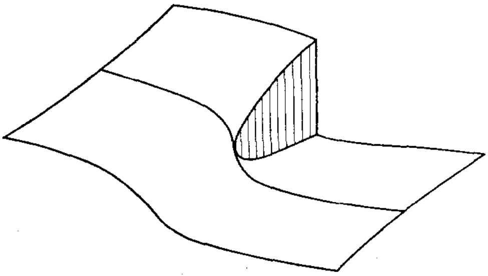

FIG. 10b

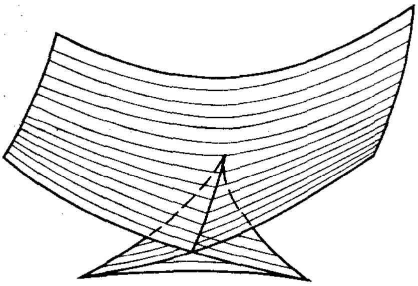

FIG. 11. Swallow's tail.

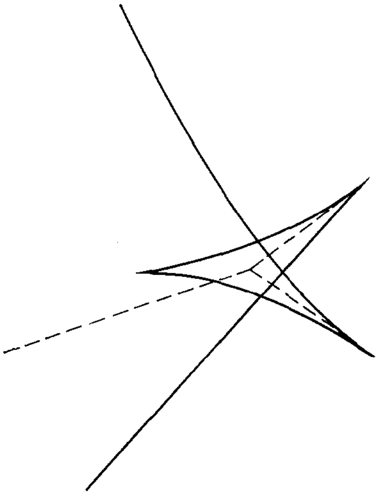

FIG. 12. Most complicated plane section of the universal unfolding of the "Butterfly" singularity. Dashed, the universal catastrophy set.

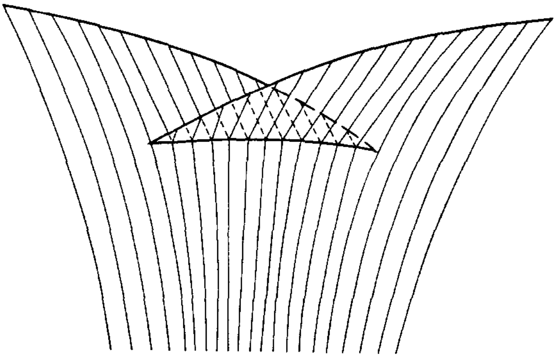

FIG. 13. Universal catastrophy set associated to the "Butterfly" singularity: exfoliation of a shock wave.

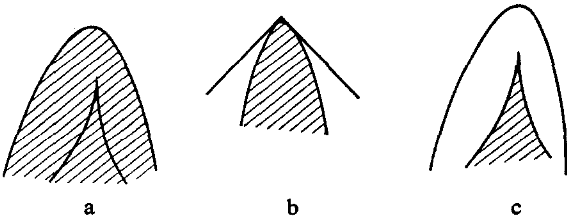

FIG. 14. Sections of the universal unfolding of the hyperbolic umbilic. Hatched; domain of a stable regime.

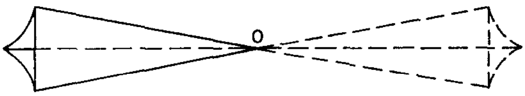

FIG. 15. Universal unfolding of the elliptic umbilic. Dashed; limiting surface of an unstable regime.

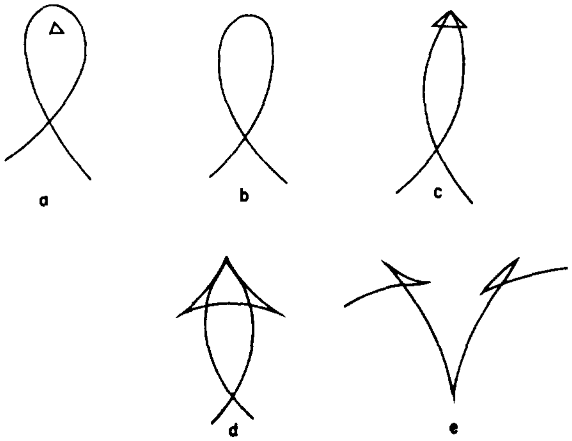

FIG. 16. Some plane sections of the universal unfolding of the parabolic umbilic.

The list of "ordinary catastrophies" on our space-time $\mathbf{R}^4$ plays, I believe, a very important role in the interpretation of natural morphological phenomena, whether living or non-living. The catastrophies of internal dimension two, the so-called *umbilics*, have a directing role in the "breaking" phenomena in Hydrodynamics (*breaking of waves*; *breaking of jets*). In Biology, they govern—I believe—the morphology of engulfing phenomena like phagocytosis, neurulation ... and, in reproduction, the emission and spreading of gametes.

C. The Reconstruction of the Organizing Centre

There is still an algebraic phenomenon which we have to describe before introducing our biological models. This is the "*structurally stable reconstruction of an organizing centre.*" Let us consider the cusp $4u^3 + 27v^2 = 0$ of the Riemann–Hugoniot catastrophy: $V(x) = x^4/4$, the unfolding of which is $V(x) = x^4/4 + ux^2/2 + vx$.

Inside the cusp $4u^3 + 27v^2 < 0$, we have two stable regimes in competition, corresponding to two minima of the V function. Let us admit now that the local dynamic admits some component in the external variables $U = U_0$, $V = V_0$, in particular at the local attractors: to each stable regime corresponds in the (u, v) plane a vector field V, V'. Let us suppose that these vector fields are like in Fig. 17: for the dominating regime in $v > 0$, we have V_0

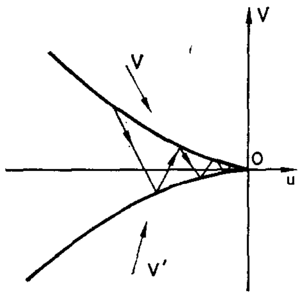

FIG. 17. Stable reconstruction of the organizing centre (Riemann–Hugoniot catastrophy).

negative, and conversely. Put U_0 positive for both V and V'. Then, if the initial position is inside the cusp, the representative point goes to 0, by a succession of oscillations with reflexion on the branches of the cusp. (Here we admit, contrary to "*Maxwell's convention,*" that each local regime persists till its complete breaking (perfect delay).) (Cf. Fig. 17).

We believe that this gives a very simplified model of what occurs in gametogenesis, where the organizing centre of the complete somatic structure is reconstructed in the egg.

§4. BIOLOGICAL MODELS

A. The Static Model

We admit that all possible local states of the metabolism in a living being can be parametrized by a function space, more precisely a set of potentials $V: M \to \mathbf{R}$. In this function space $L(M; \mathbf{R})$, there exists a point which represents the "germinal state," represented by the most degenerate potential $w \in L(M; \mathbf{R})$. Suppose w admits at a point $O \in M$ an isolated singularity of finite codimension. Let U be the universal unfolding space of this singularity. Then development of the egg may be described by a mapping $F: B^3 \times T$ of the 3-cell $B \to U$ (called the "wave of growth") which meets transversally the catastrophy set K in U. As soon F_t meets some components of K, new cellular differentiations appear. After some time, when maturity is reached, some part of the image $F_t(B^3)$ gets back to the organizing centre w by a structurally stable process, describing (without the complication of sexuality) the formation of gametes. See Fig. 18 for a global picture.

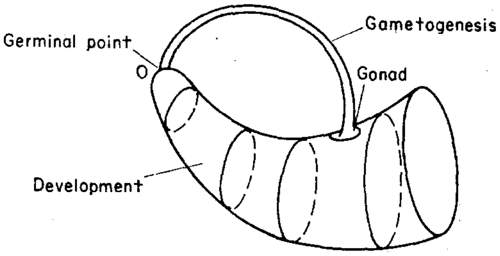

FIG. 18

A more refined model may be defined as follows (Fig. 19). The organizing centre O is never realized in any point of the organism; the space U is multiplied by an auxiliary coordinate y playing the role of a momentum. Put $x = |F|$, distance to w in U. Then the wave of growth F describes a kind of circle of centre O in Oxy (like the trajectory of a one-dimensional oscillator in phase space (x, y)). The half circle $x < 0$ represents the haploid states (gametes), $w(x = 0, y = 1)$ is the fertilization of the egg. The quadrant $x > 0, y > 0$ represents development; the point $x = 1, y = 0$, sexual maturity. The quadrant $x > 0, y < 0$ gametogenesis, and the point $x = 0, y = -1$, meiosis. Such a model may give some answer to the trick question, which started first, the hen or the egg? In fact, the "orgaizing centre" of the whole structure is out of the figure, and we may consider some pathological processes, like cancer, to be a kind of approximate realization of this organizing centre. (Circle c of Fig. 19).

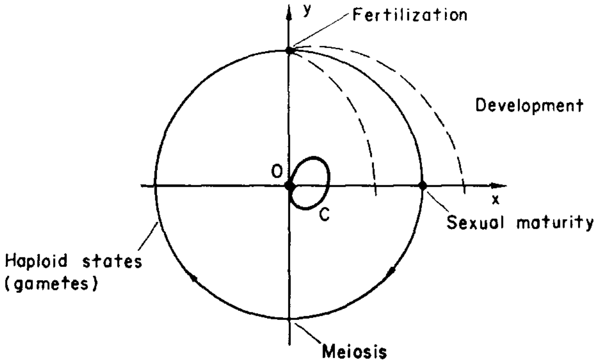

FIG. 19

The main defects of this model are first its imprecision, second, to attach a static character to the local regimes, although they are obviously of metabolic nature.

B. The Metabolic Model: Figure of Regulation

The global homeostatic properties of the metabolism of any living being may be given the following geometric interpretation: let W be an Euclidean space representing the mean states of the organism. Suppose we submit the organism to a stimulus s; then the representative point goes to a point $s_t \in W$, and then (if the stimulus is strong enough—but not so strong as to immediately kill the animal), the metabolism gets into an excited regime; as a result, a correcting vector field Z describing a reflex r appears in W which brings the representative point back to the "ground zone" G of W, zone of rest, where the excited regime disappears in favour of a normal regime; hence Z also vanishes. There exists a fundamental correspondence $s \rightarrow r(x)$ which associates to any stimulus a correcting reflex (or a sequence of them). This whole structure can be generated by a unique "organizing centre" in a multidimensional space and is called the *figure of regulation* (see Fig. 20 for a two-dimensional scheme).

The main postulate of our model is the following: if we describe—in a convenient function space, the metabolism of the young blastula cell—or the metabolism of the gametocytes—primitive germ cells—then the geometric picture defined by the regulation of this metabolism *simulates* (in a sense [14] which can be made mathematically precise) the *figure of regulation of the whole organism.* As soon as development proceeds, this figure becomes too complicated to be stable. Some cells—those near the "animal pole" of the egg—specialize in s-states; those near the vegetative pole specialize in r-states; in advanced animals (Vertebrates), the s-cells lose any regulative power, and become nervous cells: neurons, having lost their regulative abilities, keep track of everything happening to them, a very important property for the future organ of memory. The main physiological field, involve at the adult stage a complete sequence of ordered chreods: for instance an alimentary

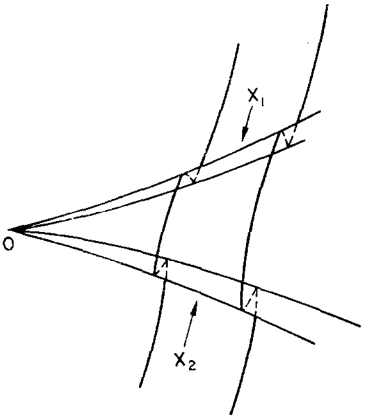

FIG. 20. Two-dimensional representation of the figure of regulation. X_1, X_2 ; correcting vector fields. 0, organizing centre.

reflex implies the following sequence: seeing a prey; capturing it; bringing it to the mouth; eating it; motor and glandular activities of the digestive tract. All this sequence is represented, at the blastula stage, by a preferential oscillation $s \rightleftarrows r(s)$ in the metabolism, which keeps going to some extent even after differentiation. When later in development two tissues carrying such a truncated oscillation come into contact, a biochemical resonance ensues, and a local regime arises through interaction (*embryological induction*): the corresponding catastrophy builds then an organ of this chain of reflexes. Conversely, in gametogenesis, all these oscillations disappear successively with the vanishing amplitude of the metabolism; when such an elementary oscillation vanishes, it gives rise to the condensation of a genic material, the "biochemical vibrations" of which restore the oscillation after fertilization. This is the general scheme, which we cannot develop here at a greater length [14]. The mitotic cycle itself may be described in the same way.

C. Spatio-temporal Development

The preceding models tried to describe only the "internal biochemical" variations of the local metabolism, and not the spatio-temporal morphology they cause. In order to describe this morphology—at least qualitatively—one makes the relatively mild assumption: to any stable local regime, there corresponds in three-space a propagation of the corresponding tissue described by a variational principle of the " Lagrangian" type (each regime having its own lagrangian). Then the successive evolution will be described by a kind of wave-front, and this wave-front may present singularities of the type described by our " elementary catastrophies"—at least initially. Quite frequently, because of the polarization of the tissue, these geometric catastrophies are coupled to biochemical ones, and give rise to new differentiations. For instance gastrulation in the Amphibian egg is an ordinary catastrophy, defined by a circle (closed curve) of "swallow's tails" (queue d'aronde) separating ectoderm from endoderm (Fig. 21); the primitive streak, in Bird's embryos, may also be interpreted by the formation of a double line limited by two "swallow's tails" separating ectoderm from mesoderm) (Fig. 22). Of course, the early delamination of hypoblast and epiblast—in Birds and Mammals—has to be considered as a generalized catastrophy, due to the insufficient polarity of the tissue when it starts (manifesting probably an increasing power of regulation for these eggs). Later on, genetic constraints do appear, the first of which is bilateral symmetry; its "organizing centre" is chord formation, and its effect is very strong on the dorsal s-directed tissues; it disappears finally on the ventrally located organs, like the heart and digestive tract. The mathematical theory of these constraints is more sophisticated: one may express it roughly by saying that the "external (unfolding) coordinates of a chreod C_1 play the role of internal variables for the succeeding chreod C_2.

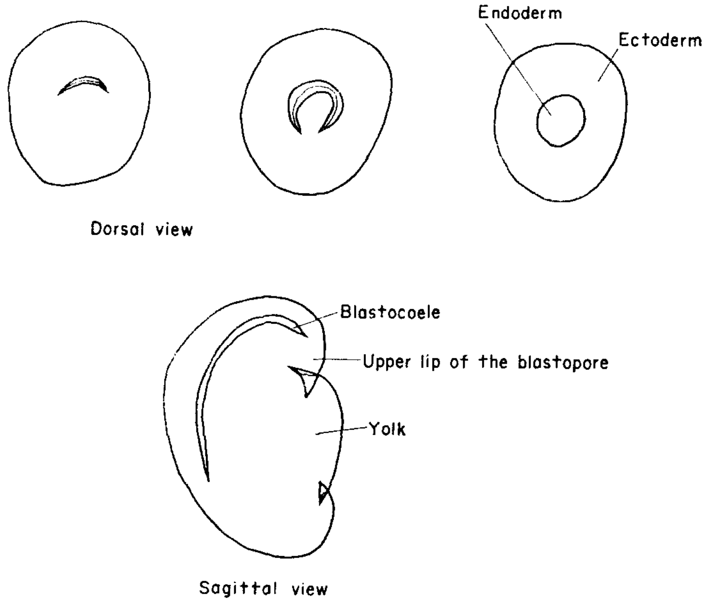

FIG. 21. Amphibian gastrulation. (Theoretical scheme.)

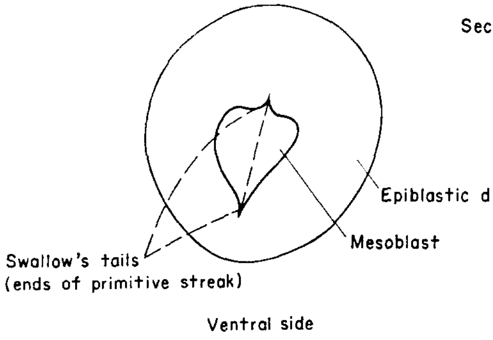

FIG. 22a

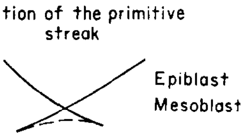

FIG. 22b

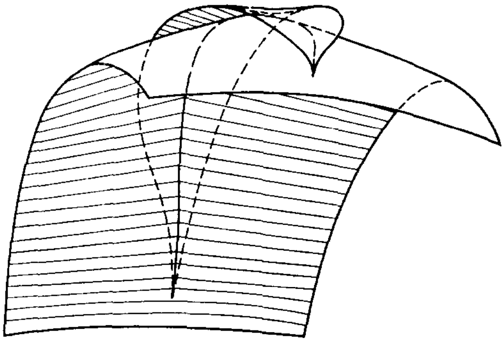

FIG. 22c. View of the theoretical surface associated to a couple of swallow's tails.

Such a rule introduces degeneracies of a more complicated type (singularities of composed mappings), and leads to a more complex morphology. This may explain why, finally, we get chreods which are subjected to a relatively precise metric control as in bones and eye formation.

D. The Hydraulic Model

The following model has been inspired by an idea given by C. H. Waddington [16], the idea of the *epigenetic landscape*; C. H. Waddington proposed to look at the development in Embryology as the trajectory of a material point in a "landscape" where valleys define the main paths of development. Here, we propose—according to our Lagrangian way of describing development, to regard it as being locally given by the propagation of a wave-front in a three-dimensional domain. More precisely, if development is given by a function of the type $S(x, y, z) = t$ (where S defines some kind of "action"), we construct a 4-dimensional landscape by putting a height coordinate $u = S(x, y, z)$, and then, we consider the level varieties of the u function. We may materialize the model in three-space by shrinking the number of independent variables from three to two. We realize then a kind of potential well, the bottom of which is the germinal point $u = 0$. We then flood this well by pouring water in it. The shore of the lake so obtained describes the spatial development of the embryo; there are three main valleys in the geography of the potential well corresponding to the three main layers; ectoderm, mesoderm, endoderm. The ectoderm valley communicates with the "neutral lake," describing the formation of the neural plate; the endoderm valley with the sinuous meanders of the digestive tract. And so on: each layer, having its own Lagrangian, has a specific slope in the well. Another interest of this model is to make possible a representation of (vegetative) reproduction. High above the mesoderm valley, is a suspended lake symbolizing the gonad. Now suppose we have two exemplars M_1, M_2 of our potential well, M_1 being above M_2. Suppose at the bottom of the gonad there is a small pipe pouring above the germinal point of M_2. Then, if we fill M_1 till the level of the gonad is reached (sexual maturity), water will pour from M_1 to M_2, thus describing the development of a progeny child from M_1. (In fact, in the Mammals, the pipe connecting M_1 to M_2 has a kind of anatomical realization in the umbilical cord.) See Plates V and VI. Despite the obvious shortcomings of this model (due to shrinking of dimensions, and also to the fact that singularities of wave-fronts are not singularities of level varieties of a function), it gives some reasonable intuition of the global dynamic of reproduction in the living beings. It may also—to some extent—represent Regeneration phenomena for species like Planarians, with a high regenerative capacity.

E. Physiological Fields

The notion of chreod has obvious applications in Physiology, where it may replace the classical notion of "Physiological field." In fact, when development is viewed as a whole, physiology is nothing but the final stage of the unfolding of embryological fields; in particular, the internal variables of nervous activities (i.e. the exciting rate of neurons) can be identified with the "external" variables of the developmental fields: as an example, the firing of motoneurons causes the extension or contraction of muscles, a specific spatial variation of muscular tissue. Among all physiological fields, those having their support in neuronic, hence mental activities, are the most interesting. A model due to C. Zeeman [17] explains how, despite the apparently discontinuous firing of neurons, continuous and differentiable models of a "metabolic" character may be applied to describe psychic activity. It is possible to apply all the ideas of chreods, catastrophies ... to the faculty of language; the meaning of a word, that is a *concept*, can be associated to a "figure of regulation" quite similar to the figure of regulation of living beings; a concept has in general a kind of animal-vegetative gradient, and a system of excited states which insure its stability. Such a viewpoint gives rise to a topological theory of meaning, to a geometric interpretation of semantics. In particular, the fundamental grammatical categories (like noun and verb) can be given a topological interpretation. But, for lack of space, we shall not say more on this subject [see [15]).

§5. CONCLUSION

Are these models amenable to experimental control? Because of their inherently qualitative character, the answer is no. Practically any morphology can be given such a dynamical interpretation, and the choice between possible models may be done, frequently, only by qualitative appreciation and a mathematical sense of elegance and economy. Here we do not deal with a scientific theory, but more precisely with a *method.* And this method does not lead to specific techniques, but, strictly speaking, to *an art of models.* What may be, in that case, the ultimate motivation to build such models? They satisfy, I believe, a very fundamental epistemological need. As long as scientific laws and mathematical formulae give us a very strong control on the phenomena (as in classical electromagnetism), there is no need to worry about possible models, and we may neglect for some time our irrepressible inclination to understand by images the basic nature of the natural processes. But, as soon as we run into difficulties, contradictions (like in Elementary Particle theory now), or when we feel overwhelmed by the mass of empirical data without a clear notion of the problems at hand (like in to-day Biology), then the need arises for some conceptual guidance in order to classify the data and to find out the most significant phenomena. If scientific progress is to be achieved by other means than pure chance and lucky guess, it relies necessarily on a *qualitative understanding* of the process studied. Our dynamical schemes—with the ideas of attractors, bifurcation, catastrophies, which remind us of the old Heraclitean ideas of fight and conflict—provide us with a very powerful tool to reconstruct the dynamical origin of any morphological process. They will help us, I hope, to a better understanding of the structure of many phenomena of animate and inanimate nature, and also I believe, of our own structure.

REFERENCES AND NOTES

1. See for instance the theory of " Mach's reflection " in Von Neumann's complete works, p. 300, Vol. VI, Pergamon Press, 1963.
2. The original Memoire of Henri Poincaré is: Sur les courbes définies par une équation différentielle. 1881 (Oeuvres complètes, Vol. 1, Gauthier-Villars, Paris).
   An historical survey of Qualitative Dynamics may be found in M. M. Peixoto: *Qualitative theory of Differential Equations and Structural Stability*, *Differential Equations and Dynamical Systems*, Academic Press, 1967.
3. Let us make this point more precise.
   An attractor A of the differential system (M, X) is a closed invariant set such that:
   i) There exists an open neighborhood U of A such that the trajectory through any point u in U admits A as ω-limit set.
   ii) If a trajectory g is such that A meets the set $\alpha(g)$, then g lies in A. (No trajectory leaves A).
   iii) A is *indecomposable*, that is almost any trajectory in A is everywhere dense in A.
   Then the conjecture is:
   If M is a compact differentiable manifold, then almost any vector field X on M admits only a finite number of attractors, each of which is topologically structurally stable.
   According to some unchecked reports, this conjecture would have been disproved during the Berkeley Summer Conference 1968. Even so, I do not think this fact would fundamentally invalidate our model: what is important here is not the topological type of an attractor A, but its thermodynamical type: an attractor may undergo some local topological variation (for instance a local " blowing up "), provided it does not move too far away from its original location under a small perturbation. This is certainly the case when the attractor A is defined as a connected component of the singular set of some local Liapunov function.
4. These considerations do not apply to the conservative Hamiltonian systems of classical Mechanics: because of the invariance of Liouville's measure, there are no attractors—strictly speaking—in these systems. Nevertheless, they admit some kinds of " vague attractor ", like a closed central trajectory and the associated system (studied by Kolmogoroff, Moser) of trajectories spiraling around it. These vague attractors probably are related to the " stationary states " of Quantum Mechanics.
5. *Tossing a dice* is a familiar case of such a situation.
6. See for instance, J. Mather: Stability of differentiable mappings, *Ann. Math.* (1967).
7. We use here a well-known theorem of Marston Morse: The calculus of variations in the large, *Am. Math. Soc. Colloquium Publications*, Vol. 18. 1934.
8. The function $V(x_i)$ admits the origin $x_i = 0$ as singularity of finite codimension, if, in the algebra of formal power series $C\,xi$ the ideal generated by the Taylor expansions of the first partial derivatives $\partial V/\partial x_i$ contains a power of the maximal ideal (x_i). For holomorphic functions, this is a necessary and sufficient condition.
9. The word "chreod" was introduced by C. H. Waddington: *The Strategy of the Genes*, p. 32, Allen & Unwin, 1957.
10. Let K be the discontinuity set —the "catastrophy set"—of a process taking place in a domain U of space time $t > 0$, for a system (s) of initial data given at $t = 0$. We say that K is described by a "chreod" of support U, if, for any system s' of initial data sufficiently near s ($|s - s'| < \eta$ in a conveniently chosen norm), the process following s' exhibits a set of discontinuities K' such that there exists an homeomorphism $h : U \rightarrow U$, with $|h(x) - x| < \varepsilon$ and $h(K) = K'$.
11. See C. H. Waddington: *Introduction to Modern Genetics*, Allen & Unwin, 1940.
    Max Delbruck: Unités biologiques douées de continuité génétique, *Colloque C.N.R.S.* Paris, 1945.
12. D'Arcy Thompson: *On Growth and Form*, Abridged Edition, Cambridge University Press, 1961.

13. C. Child: *Patterns and Problems of Development*, University of Chicago Press, 1941.
14. Let two dynamical systems (M, X), (M', X') be given, each provided with a system of "approximate" first integrals defined by the differential fibrations: $M \to P$, $M' \to P'$. The fibres are said to be "verticals" in M, resp. M'. On each point $p \in P$, define a vector Y as follows: let Z_p be the local dominating attractor of the dynamic in the fibre defined by the "vertical component of X; then Y is the averaged value of the horizontal component of X along Z_p. We get in that way vector fields Y, Y' in P, resp. P', with discontinuities along the catastrophy sets K, K' in P, P'. We say that the system (M', X') simulates the system (M, X) if there exists a homeomorphism $h: P \to P'$ which carries any trajectory of Y onto a trajectory of Y'.
15. These models are described in a book by the Author, to be published by Benjamin (New York) under the title: *Stabilité structurelle et Morphogénèse.*
16. For a description of the "epigenetic landscape", see C. H. Waddington: *The Strategy of the Genes*, Fig. 4, Allen & Unwin, 1957.
17. C. Zeeman: *Topology of the Brain. Mathematics and Computer Science in Biology and Medicine*, Medical Research Council, 1965.

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