

ON SOME MORPHOLOGICAL PRINCIPLES IN BOTANY ARISING FROM MATHEMATICAL CONSIDERATIONS

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RÉSUMÉ

On étudie dans cet article l'apparence morphologique des plantes à travers des modèles géométriques et statiques puis on examine quelques caractères-clés des processus de croissance à la lumière des propriétés de certains systèmes différentiels.

1. INTRODUCTION

In this introductory article, I intend, in the first section, to recall some data of natural philosophy, already presented in "*Topologie et Perception*" (Bruter, 1976).

The second section uses these data. It adapts an elementary mathematical model (Bruter, 1973, 1976) to the rudimentary study of some main features of vegetal morphology. These considerations, which concern the static aspect of morphology, contribute to reinforce the link between form and function. Then the formation of buds and flowers is considered from a topological point of view.

In the third section, grounded on some classical mathematical facts, I show how one can begin to understand the mechanism of ramification and the process of proper metamorphosis.

The author is not a botanist, but a mathematician who sometimes lets himself go to philosophy and to dream. It's without any kind of pretension that he gives the suggestions which follow, which sometimes are, he knows, quite candid.

2. SOME DATA FROM NATURAL PHILOSOPHY

From the corpus of primary and subsequent observations developed in (Bruter, 1976), the following can be of some interest in vegetal morphology.

One of the first is stated as the *criterion of extremality*. The extremality may take several forms such as simplicity, optimality, stability. In Bruter (1976), this criterion is

formulated in the following way: "Primary Observation (OPB): Every object is stable only if it obeys some property of extremality".

In his *Plants' Metamorphosis*, Goethe considers four fundamental types of dynamical processes involved in plants; development: "expansion", "contraction", "compression", "anastomosis". In Bruter (1976), which has a more general aim, it is also said that "Primary Observation (OP6): "The archetypal forces are forces of repulsion, capture, and annihilation".

I shall not use here what has been called since Antiquity the "principe des semblables", according to which similar objects, that is, objects of the same kind, have a tendency to join together. This principle is useful to understand the formation of colonies, groups and societies.

But I shall emphasize the morphological importance of the following data: "Primary Observation (OP23): Any stabilizing control of an object operates in a transversal manner to the object".

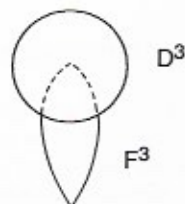
The last consideration which will be used here refers to the bond between stability and symmetry. Symmetry is viewed as a consequence of the process of stabilization. In a simple form, this fact is presented as follows: "Methodological Observation 2 (OM2): Nature tends to stabilize an unstable object by duplicating it, then binding the object with its replica through a regulator which is transverse to each object".

These data apply to any field of knowledge, and can be widely discussed. It is worthwhile to keep them in mind when reading the next sections.

3. MORPHOLOGICAL CONSIDERATIONS ARISING FROM STATIC MODELS

3.1. The morphological pair (D^3 , F^3) and its functional role

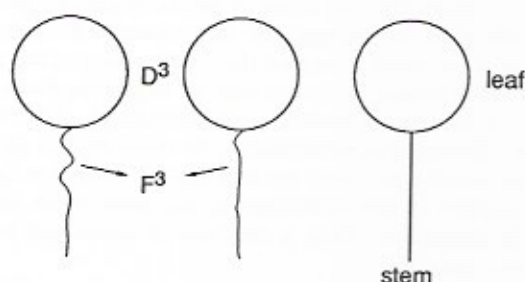
I wrote my thesis on a class of objects called matroïds. By the previous rule of extremality, it was appropriate to look at the minimal objects of this family, which, after all, are nothing else but n -simplices. So in dimension 3, if we adopt the topological point of view, the minimal matroïd corresponds to the 3-disk D^3 , an orange if you like. It happens that any matroïd has a dual; the two objects should never be dissociated in the mind. Thus any topological object has a dual, but it is very rare that mathematicians consider it. I called the dual of D^3 , F^3 , a *spindle*. The



Since D^3 may represent a physical object, there is no reason why F^3 should not also represent a physical object. Given the fact that F^3 is transverse to D^3 , and given the primary observation (OP23), I proposed that if D^3 represents the fundamental

morphology of an imbedded object in R^3 , F^3 represents the fundamental morphology of the regulatory system of the object which has to exist in order to ensure the persistence of the object in the ambient space R^3 (Bruter, 1973, 1976).

The basic vegetal morphologies can be represented by this rudimentary geometrical model. All the objects of the vegetal kingdom, whether they have stiff or flexible "feet", flagelli, roots, stems or pseudo-podes or feet, can be viewed, in a first approximation,



Schizomyceta
Myxophyta

Eumycophyta
Spermatophyta

note that this pair
reproduces the whole tree

as pairs (D^3 , F^3), where F^3 denotes the regulatory organ whose function is mainly of a spatial nature, contributing to guarantee the spatial stability of the object in R^3 .

As a general rule, any part whose principal function is to regulate shows a spindled morphology. It may be shown externally - the case of lashes, hair, thorns which play a protecting role and are disposed orthogonally to the bodies they protect; or it may be internal - the case of canals, and of various pipes along which is worked out the circulation of the elements which are necessary to the interval homeostasis of the object.

The D^3 part of any object will be called the *reproductive-vegetative* part. At first, its role is more temporal than spatial. It is to guarantee the perennality of the being, either, in an immediate manner, by the transformation of the energy locally received or, in the longer term, by storing reserves, or by preparing the reproduction of the object.

The fundamental difference between the animal kingdom and the vegetal kingdom comes from the fact that the immediate vegetative function is performed in an active way in the animal whereas in the vegetal case, it is practically passive. Thus no kind of inventive or constructive support, namely the nervous system, which had no reason to expand in the vegetal, developed there in.

In other respects, Nature proceeds with an economy of means, trying to bring into play the greatest possible number of roles to the structures actually present. For instance, the structure D^3 may have two functions, that of regulation and that of reproduction. It happens of course that a local specialization or degeneration appears according to the local constraints. Parts of D^3 may have no immediate reproductive role. On the contrary in the case of mushrooms, for instance, since they only use the resources from their germinative cells and from the earth for their development, it follows that they are more ephemeral than the plants with leaves, and hence D^3 contains only the reproductive apparatus. But in the rhodophyta, pteridophyta or

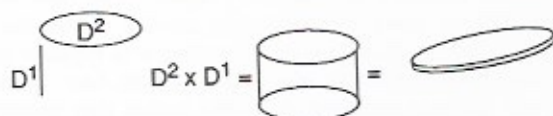
spermatophyta, the transportation of germs of the chlorophyllian function at the apex has allowed the unfolding of the foliar system.

3.2. The leaf as $D^2 \times D^1$ and its functional role

It is possible to consider several growth patterns of plants, for instance the following. For some plants, the first shoot of growth is due to the energy contained in the resources of the seed, by the transfer of substances through the roots. But this shoot has shown itself too weak to ensure the development of the reproductive system. The apical milieu has remained immature, and the vegetative tissue, instead of pursuing a kind of process of dessication leading to the formation of the reproductive system, has remained non-differentiated, accumulating its chlorophyllian elements until bursting into small branches which will spread out into leaves. Their first function is vegetative, allowing the introduction of new substances to the plant, which can repeat its process of growing until its exhaustion. Thus, a new row of leaves will be formed unless the apical cells suddenly mature.

Then, as Goethe had already thought, the foliar system develops to give birth to the whole flower which protects the etamines, then, by a new differentiation, to the fruit which protects and contains the seed.

According to these views, the leaf is a kind of sensori-vegetative placode, homeomorphic to a thickened disk $D^2 \times D^1$. (All the placodes seem to have the same



topology, cf. Bruter, 1976, 1985). Now, think of the skin, or of the peel of an orange, or of the shell of an egg: it is a thickened 2 sphere $S^2 \times D^1$, the 2-sphere S^2 being the envelope without the interior of the 3-disk D^3 . This shell can be broken into pieces which, like leaves, are homeomorphic to $D^2 \times D^1$. Since $S^2 \times D^1$ has an obvious protecting role, we must accept that the leaf, because of its morphology, has a *protective function*.

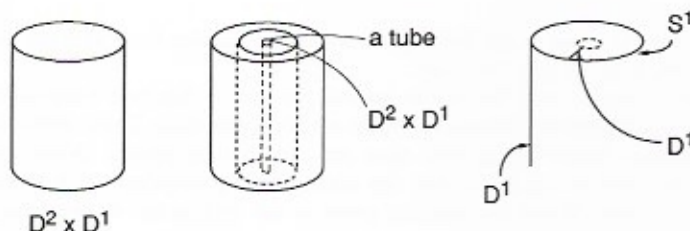
If we look at a tree, the foliar system can be viewed, according to the topological terminology, as an *atlas* of *charts* (each chart is a leaf) equivalent to the "shell" $S^2 \times D^1$ of the 3-disk D^3 . Then these leaves have a double function: the vegetative one which is *intraverty*, and the protective one which is *extraverty*. In the present case, the vegetative role seems to be predominant.

We may now look at what is called the flower: a set of leaves surrounding the reproductive apparatus. This set has a protective role. As we get closer to the reproductive apparatus, the protective function of the leaves increases either smoothly or in a catastrophic way at the expense of the vegetative role. The transition from the green sepals to the multicoloured petals is undoubtedly progressive. The vegetative function ranks first in the sepals and in the calyx. But, the carpelar leaves which constitute the ovary have mainly a protective role. The process describing the change

in appearance and in the function of the leaves is of a dynamical nature, and has to be described through bifurcation theory.

3.3. The topological formation of buds and flowers: preliminary considerations

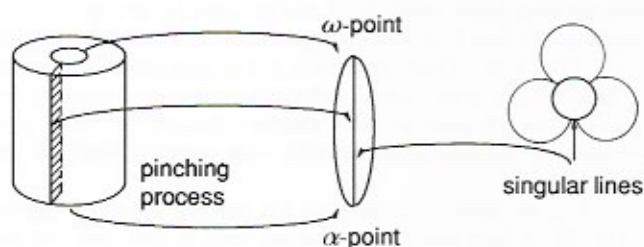
Let us first consider a part of the stem. It is a full cylinder $D^2 \times D^1$ divided into tubes $S^1 \times D^1 \times D^1$; together with a singular one, the central parenchymatic canal, again $D^2 \times D^1$.



The section of a generic tube is invariant under a group of symmetries $\mathbb{Z}/n\mathbb{Z}$, where n is the number of fascicles in the tube.

Let us suppose that we gather into a point the base and the top of such a portion of stem. The reduced bottom (respectively the reduced top) becomes a point which may be called the α -point (respectively the ω -point) of the pinched stem or bud. These points are *singular points*. The previous tubes are now *pinched tubes*.

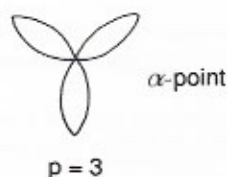
Now let us suppose that we reduce into a *singular line* a section of a pinched tube of such a bud by a *splitting plane* containing the singular points, and that, in fact,



there be $p \leq n$ such lines in a pinched tube, so that this tube is invariant under the group of symmetries $\mathbb{Z}/p\mathbb{Z}$.

Finally let us suppose that the ω -point is blown up or *exfoliated* into p points and that each singular line is also exfoliated into 2 lines. Then each pinched tube gives birth

to p leaves, branched at the α -point. Then we get the calyx and the corolla (thus the perianthe).



If the central canal is not developed, while the singular lines and the ω -point are not exfoliated, then we get the *ovary*.

We may imagine that the whole growth process of this bud from the α -point is mathematically defined by differential forms evolving with time. These differential forms have singularities whose traces with time are the splitting planes. When the splitting plane is orthogonal to the tube, then the corresponding singular line is exfoliated into 2 borders of leaves. When the splitting plane is not orthogonal to the tube, then two singular lines appear.

4. MORPHOLOGICAL CONSIDERATIONS ARISING FROM DYNAMICAL MODELS

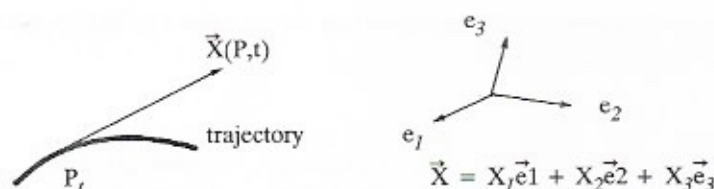
4.1. Two kinds of mathematical models

Let us consider a milieu, first characterized by the spatial domain U_t it occupies at time t in the usual ambient space \mathbb{R}^3 . Two main approaches can be used to describe the evolution of this milieu.

Either of these approaches is local. When the milieu is homogeneous, the solutions of the local model are also global. When the milieu is not homogeneous, it has to be divided into homogeneous parts where local models may be set up.

The first approach is based on local physical considerations, allowing the set up of energetic balances of the transformations arising in the local milieu. In the general case, we get systems of equations with partial differential operators together with integro-differential operators, taking into account memory factors. In usual physics, when memory is not-existent or infinite, equations with only partial differential operators are mainly considered.

In some cases (e.g. in classical mechanics), the physical approach meets the second approach, the cinemathical approach, in an obvious way. In that case, we pay attention to the evolution of each point (P, t) of the milieu U_t . This point describes a trajectory in \mathbb{R}^3 . The speed of evolution at (P, t) is represented by a vector $X(P, t)$ tangent at (P, t) to the trajectory of this point. The cinemathical approach lies in the properties of these speed vectors.



In the best cases, $X(P,t)$ is analytically defined. For instance the values of its components $X_i(P,t) = \frac{dx_i}{dt} = f_i(x_1, x_2, x_3, t)$ $i = 1, 2, 3$.

It is very easy to imagine other models of the same kind. For example, we may think that what characterizes a point of an organic milieu is the set $\{c_1, \dots, c_k\}$ of the concentrations c_i of products i at P , together with their speed of evolution $c_i' = \frac{dc_i}{dt}$. In that case putting

$$c_i = y_i \quad c_i' = y_{k+i} \quad y = (y_1, \dots, y_{2k}) = (c_1, \dots, c_k, c_1', \dots, c_k')$$

the speed of evolution of y is a vector defined by its components

$$\frac{dy_j}{dt} = f_j(y, t) \quad j = 1, 2, \dots, 2k.$$

In what follows, models of the form

$$\frac{dx_i}{dt} = f_i(x, t, p_1, \dots, p_n) \quad i = 1, 2, 3.$$

will be considered, where the x_i 's define P in \mathbb{R}^3 , and where the p_j 's ($j = 1, 2, \dots, n$) are parameters: external - for example temperature, light, water, food, components of the earth; or internal - for example biochemical products, coefficients of the tensor of internal mechanical constraints.

4.2. On growth

Let us consider the point P at time t , and its evolute P' at time t' . If t' is very close to t , an approximation of the equation of evolution $\frac{dx}{dt} = f(x, t, p)$ can be used to evaluate $x'(P', t')$. Let us suppose that, as happens frequently, this approximation is linear, i.e. defined by the linear part of the Taylor's development of f :

$$\frac{dx}{dt} = M(p)x$$

where M is a matrix whose coefficients depend on the parameter p . $M(p)$ is equivalent to a matrix of the following forms:

$$\begin{bmatrix} \lambda_1(p) & 0 & 0 \\ 0 & \lambda_2(p) & 0 \\ 0 & 0 & \lambda_3(p) \end{bmatrix} \quad (L) \quad \begin{bmatrix} \lambda(p) & 0 & 0 \\ 0 & r(p)\cos\theta(p) & -r(p)\sin\theta(p) \\ 0 & r(p)\sin\theta(p) & r(p)\cos\theta(p) \end{bmatrix} \quad (R)$$

According to the theory, the evolution is locally exponential, contracting along the i -direction when $\lambda_i(p)$ or $r(p)$ is negative, expanding along the j -direction when λ_j or $r(p)$ is positive (the usual mathematical terminology is the same as Goethe's). When the matrix of the R -type, there is besides a local rotation of angle $\theta(p)$ in the plane corresponding to the sub-matrix

$$\begin{bmatrix} r\cos\theta & -r\sin\theta \\ r\sin\theta & r\cos\theta \end{bmatrix}$$

Thus, this mathematical form characterizes a local phyllotactic development.

Note that we may pass continuously -Goethe also claimed for continuity- from a matrix of any type to a matrix of another type. The singular values of (x,p) for which new kinds of behaviour appear are called *bifurcation values*. These values play a key role in ramification and metamorphosis processes.

Other (less) singular values are those for which the components of the speed are zero in the local "horizontal" planes. We may suppose that this phenomena occurs along the central line of the parenchymatic canal. Such abstract liens where X is different from 0 only along the "vertical" direction will form what can be called the (abstract) *skeleton* of the plant.

4.3. On ramification

Let us introduce the *spatial acceleration* $A = f_x(x,p)$ where f_x is the derivative of f with respect to x .

When both X and A are null, mathematically and thus physically, some local degeneration or better, destructuring, occurs, allowing then the possibilities of new structures. We may think that such events characterize the steps instantly preceding a ramified development.

It is intuitive for instance that the growth of plants slows down and even stops (with zero acceleration) before the formation of a new sprout. I am indebted to Miss Ming Antony who gave me references of works confirming this feeling (cf. Marsequell-Meyer (1973), Brossard (1973), M. Antony: "It will be observed that the early inhibition of the growth of marginal cells is the first morphogenetic manifestation of the sprouting" (1980)).

Let us say that a function $L_t(x)$ is more symmetric at t than at t' if L is Z_p , invariant at t , Z_p invariant at t' , with $p' < p$. L is a kind of energy function (from which f can be derived) which degenerates at branching points in the sense that it loses some

symmetry. In plants' growth, the components of the speed X are invariant in the horizontal plane under the action of the Z_n symmetric group. But when one reaches the apex, it might be very hard to preserve all the symmetries (all the processes cannot be achieved in the same time at the same position): a breaking of symmetry may locally occur. Such a phenomena occurs in the neighbourhood of a branching point, since after a stop of growth, the push of elements can disturb the previous symmetry.

According to the mathematical theory (see for instance Golubitski & Schaeffer, 1985), the equations $X = 0$, $A = 0$, via the Liapunov-Schmidt reduction, reduce to an equation $g(x,p) = 0$. Among parameters p , it is convenient to distinguish subvector p_1 of unperturbed parameters and the subvector p_2 of the parameters which can be perturbed: $g(x,p) = g(x,p_1,p_2) = 0$. $G(x,p_1,p_2)$ will denote the general form of the standard mapping representing the class of those which are p_1 equivalent (in some precise sense) to g (G is called the universal unfolding of g). Then the perturbation of p_2 which occurs at the branching point gives rise to several branches of (x,p_1) : they are the (x,p_1) subsets for which $G(x,p_1,p_2) = 0$.

Along these branches, the horizontal components of the speed of evolution X are zero: they define the skeleton of the plant.

4.4. What is metamorphosis?

There may be several levels of metamorphosis. My feeling is that the lower levels of metamorphosis occur when at least one bifurcation occurs, without any change in the structure of the object under consideration. These kinds of metamorphosis may be called trivial (example: the transformation of leaves into corollae and petals).

A real metamorphosis appears when evolutions and bifurcations generate an object with an unstable structure which collapses into a stable structure.

Such metamorphoses are classically encountered for instance in embryology among the batracians, or in many insects. The homology between some insects and plants can be viewed as the result of an homology between the dynamics which guide the evolution of some respective cellular clones. The fact that insects go to the flowers having a similar appearance might rather be interpreted as a kind of self-recognition of the insect.

4.5. A query

The dynamical experimental models which have been used here could be numerically tested if...: would it be possible to study the speed and the acceleration of growth via functions of significant parameters p ?

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