

Evolution and complexity: developmental constrains

by

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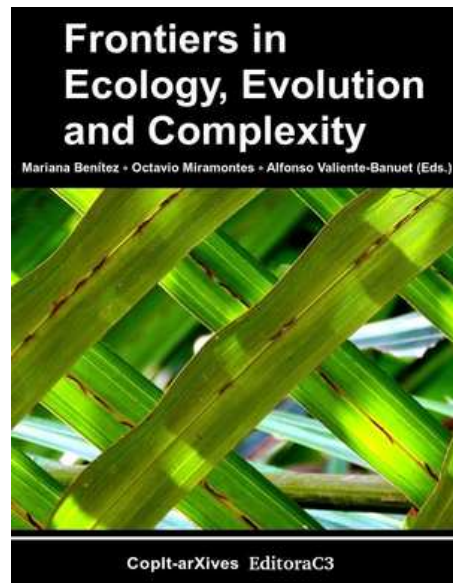
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Evolution and complexity: developmental constrains

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1 Abstract

In recent decades Complexity Sciences have added an important complement to the understanding of biological phenomena: the processes of self-organization that play an important role as a source of evolutionary novelty. In this view, the origin of the biological complexity is not due to natural selection alone but to a self-organized process. It is then when this new order will be modified in one direction or another by natural selection. Self-organization acts allowing the emergence of complex structures while natural selection operates on the existing ones.

2 Resumen

En décadas recientes, las Ciencias de la Complejidad han contribuido con novedosas ideas para complementar nuestro entendimiento de los fenómenos biológicos, particularmente con el concepto de auto-organización, el cual juega un papel muy importante como fuente de innovación evolutiva. Bajo esta visión, el origen de la complejidad biológica no se debe solamente a la selección natural sino a los procesos auto-organizados. Luego es que este nuevo orden será modificado en una u otra dirección por la selección natural. La auto-organización actúa permitiendo la emergencia de estructuras complejas mientras que la selección natural actúa sobre las ya existentes.

3 Introduction

It was the British naturalists Charles Robert Darwin and Alfred Russell Wallace who, independently of each other, advanced natural selection as the explaining mechanism for the evolution of species. In 1859 Darwin himself described and defended this mechanism in an encyclopedic way in his "The origin of species". Nowadays it can be described

as: (1) There exists an intrinsic variability in the different populations as a consequence of mutations and, specifically, of genetic recombination in sexual organisms. (2) New emerging features are transmitted to the offspring. (3) Some variations have higher fitness than others to survive. Individuals owing those features will have a higher mean rate of survival and/or reproduction. As a consequence, these new features will extend and standardize along the successive generations until fixation.

The theory of evolution is nowadays one of the soundest theories in science. As the geneticist Theodosius Dobzhansky (1900-1975) used to say [1]: “Nothing in Biology makes sense except in the light of evolution”. Its scientific success has reached far beyond Biology. Evolutionary Psychology and Evolutionary Medicine, Anthropology has gained insight on basic human emotions, innate language capacities, emergence of consciousness, biological basis of Moral and Ethics, Memetics, our knowledge about how the brain or the immune system works, genetic algorithms and evolutionary programming are just some examples of the large impact the Darwinian paradigm has reached out of its original field.

The idea on the book “Evolución y Complejidad” [2], by the authors of the present chapter, was to bring closer two perspectives of evolution which are usually introduced as confronted to each other. On one side, the vision which emphasizes contingency, frozen accidents and irreversibility and which determines an eminently historic science. On the other, a vision based on the comprehension of self-organized processes, analogous to physical systems far from thermodynamic equilibrium, which determines a structuralist science. This dialog between contingency and structuralism could well stand for the dialog between Biology and Physics the two authors represent. Multiple are the possible fronts: generality of the competition process, extinction of the less fit species, the concept of progress, the preeminent role of the gene in the evolutionary process, etc. We invite the reader to consult our book in order to gain further insight on these topics. Here, for reasons of space, we have decided to focus on a single topic: developmental constrains. The reason is twofold: the clarity of intellectual opposing positions and offer homage to the work of two great scholars of evolution as were Brian Carey Goodwin (1931-2009) and Pere Alberch (1954-1998).

Delimiting “the possible” in Nature

“Fauna secreta” [3] was an exhibition by Joan Fontcuberta and Pere Formiguera we were fortunate to enjoy in the late 90’s in Barcelona. It described the heterodox scientific work of the naturalist Peter Ameisenhaufen. It was an installation of old-style “cabinets of wonders” where you could see the collection of strange beings professor Ameisenhaufen had been able to collect and study throughout his life. The sample consisted of photographs, field drawings, films, videos, sound recordings, maps, laboratory instruments, correspondence, etc. that Fontcuberta and Formiguera had been recovering from oblivion in a casual and miraculous way.

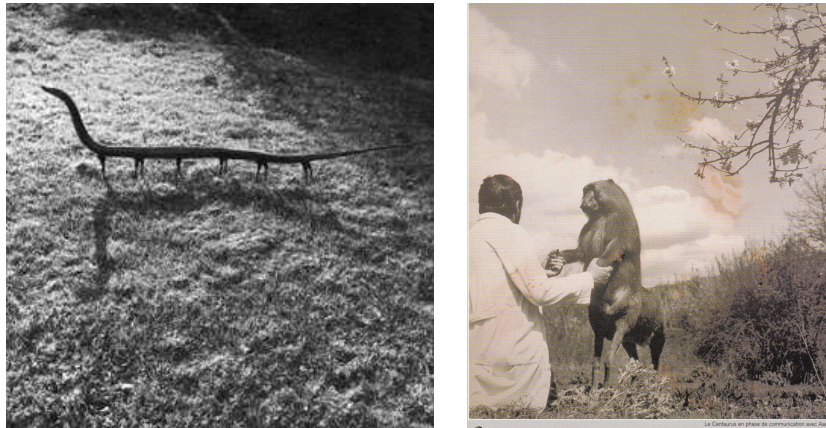


Figure 1: Left: *Solenoglypha polipodida* in attack position. In its behavior card we read: “Unlike the known reptiles, the *Solenoglypha* never rests after eating, on the contrary, it launches into a frantic race that stops only at the time of defecation”. Right: *Centaurus neandertalensis* in the throes of communication with Aaru-1. In the professor’s observations we read: “Every time I hear the recording of its voice calling my name (albeit with difficulty), I am possessed by a sense of unease”. Photographs from [3].

Upon entering, the public thought they were going to attend a scientific exhibition proper of a Science Museum. They ran into the typical avalanche of facts and details presented with the apparent rigor and the distinctive style in which scientific information usually is presented. The prestige of science has made that. Even when we do not understand something, we suppose that its discourse is true. The exhibition attacked the voluntary suspension of our critical sense by means of a parody of the scientific discourse which was taken to absurdity (Figure 1).

Formiguera describes how they liked to walk incognito by the exhibition and to listen to the comments of the public. He recounts the following conversation between an excited father and his child: “Son, do you realize the amount of natural wonders yet unknown?”. And the boy with the patience of a Buddhist said, “Dad, don’t you realize that everything is a lie?” Outraged, the parent snorted: “Don’t be silly, boy. Would it be exposed in a museum if it were a lie?”. The two pictures below are two examples of what we could find there.

Fontcuberta’s work [4] aims to stimulate our critical thinking and our imagination. Throughout his career, he has repeated similar formulas to “Fauna”, where photography seeks to undermine the authority of the techno-scientific discourse. Let us recall “Herbarium” [5], a criptobotanical parody described as a “visual vaccine” by its author or “Sirens”, devoted to the recently discovered fossil of an aquatic ancestor of hominids, the *Hydropithecus* (Figure 2).

“Fauna” was inspired by mythology and medieval bestiaries. But it was more than a



Figure 2: Left: Photography of a *Gilandria escoliforcía*, from the exhibition “Herbarium” [5], composed by “pseudoplants” made from detritus, plastics, animal bones or parts of various kinds. Right: Photography of a complete fossil of a *Hidropithecus tanaron*. This is an adult of 33 years and indeterminate sex, who was in good health but suffered food shortages, as evidenced by their dentition.

scientist bestiary, alternative worlds by Joan Fontcuberta invite us to reflect on why there are certain forms in nature and not others. The theory of evolution has shown us that the fauna today is only a subset of the possible (just remember Burgess Shale [6]). As Formiguera and Fontcuberta wrote: “We are pleased to work on zoology because it gives a very wide margin for uncertainty”. Are we able to define what it is possible in nature (and what is not)?

A textbook example of functionalism: the limbs of tetrapods

Evolutionary Biology has been traditionally focused on the study of the function of the various structures of a living being. In this context, we can consider it a predominantly functionalist science. Structures, such as a limb, a flower or an eye, appear throughout history and, if they provide some biological effectiveness to their possessors, they are fixed by natural selection. So, typically, you tend to search for a functional reason to each organic structure and attention to its origin is relegated to a fortuitous occurrence, then selected by the advantage that gives its possessor. Today, most evolutionary biologists would agree that functionalist explanations have been abused. As an example of functionalist description, we will focus on the work of natural selection operating on the adaptive radiation of animal limb of tetrapods (four-legged animals: birds, mammals, amphibians and reptiles). The functionalist arguments will seem loud and clear but we will see that they do not tell us the whole substance of the matter.

The conquest of the land environment by vertebrates marked an important milestone

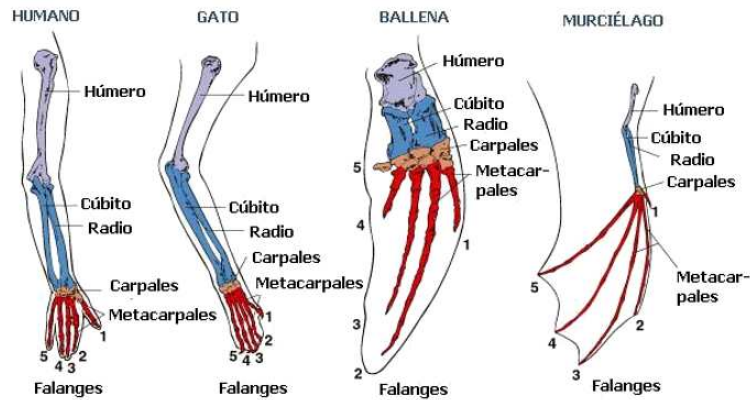


Figure 3: Scheme of the limbs of a human, a cat, a whale and a bat adapted form [7].

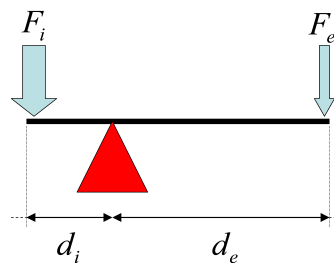


Figure 4: Schematic of a lever.

in the history of evolution. It imposed conspicuous morphological changes. Primarily, the development of four limbs on which supporting and moving the body. In parallel, changes occurred also in the structure of the spine, which was subjected to greater stresses, and the development of pelvic and pectoral girdles, which would serve to attach the limbs to the column.

The first limb derived from a primitive sarcopterygian fin, i.e., from a fin that had a central skeletal shaft coated with muscle, unlike the actinopterygian-type fin, characterized by having radius and be typical of the majority of fish. This primitive limb had the following structure: a first axial element, the stylopod, the closest to the trunk which in the front limb is called the humerus and in the rear limb is called femur. The zeugopod comes next: structure formed by two parallel bones (radius and ulna/tibia and fibula) and autopod finally, the structure corresponding to the hand or the foot (carpal/tarsal elements and metacarpal/metatarsal along with the fingers phalanges).

From this primitive pattern, we can see obvious changes driven by natural selection in order to achieve the adaptation to different forms of life as we see in Figure 3. In this

regard, the adaptive value of the extremities is unquestionable. From a physical point of view, a limb is just a lever with his proximal limb, distal limb and its fulcrum. Statics would says that, when a limb is at equilibrium, the torque is the same at both ends, that is, the following equality holds:

$$F_i \cdot d_i = F_e \cdot d_e \quad (1)$$

Where d_i and d_e represent, respectively, the distance of the proximal and distal limbs and F_i and F_e are the forces applied on the proximal and distal limbs (see Figure 4). Given the physical laws of a lever, we can predict the morphological changes that have been wrought in the molding of a tetrapod limb depending on their lifestyle. Consider a couple of examples.

A digging animal such as the mole needs to develop large strength at the end of the distal limb. His limbs are true shovels. In a lever, this distal force can be increased by reducing the distal distance (d_e) and elongating the proximal distance (d_i), as obtained from the expression:

$$F_e = F_i \cdot \frac{d_i}{d_e} \quad (2)$$

This is precisely the solution seen in digger animals such as the mole. In these animals we observe the presence of a short, flat and very strong humerus with many crests where the muscles can insert. The triceps muscle is highly built up. The surface of the hand is also very large, to act as an actual shovel. Even a carpal bone appears, mimicking the presence of six fingers, to maximize the digging surface. They also possess a very elongated olecranon (an evolution of the ulna giving rise to the elbow, the proximal limb).

By contrast, a runner animal is subjected to radically different selection pressures. What is needed here is high speed delivered at the end of the distal limb. It is easy to deduce the relationship between the speeds at the two ends of the lever, since the angular velocities must be identical. The angular velocity is equal to the linear speed divided by the length of the associated limb end. So that:

$$\frac{v_i}{d_i} = \frac{v_e}{d_e} \quad (3)$$

Where v_i and v_e stand for the speed of the proximal and distal limb respectively. If what is needed is a high speed for the distal limb (as in this case), we can derive the following expression by substitution in the former one:

$$v_e = v_i \cdot \frac{d_e}{d_i} \quad (4)$$

Therefore the speed of the distal limb will be higher when the length of the distal limb is increased or when the length of the proximal limb is decreased. What happens to runner animals like the horse? They have very long distal limbs. The bones have been elongated along evolution (humerus/femur and ulna-radius/tibia-fibula). But this is not all. To maximize the length of the limb, runner animals tend to stand, not on the hands and the feet as humans and bears do but on the fingers (like dogs and lions) and even on the nails (like horses or gazelles). In parallel, due to the frequent physical stresses that occur during a high speed race, that in turn may lead to dislocations and even breakups, it tends to be fusion between different skeletal elements, such as the fusion of the ulna with the radius and the tibia with the fibula.

4 Structuralism in Biology

There is no doubt on the remarkable differences between the limbs of a mole, a horse, a dolphin, a bat and a bird. The physical interpretation of these variations in terms of adaptation is elegant and clear. The divergence is often emphasized from a functionalist perspective. This theoretical framework, that of natural selection modifying a structure in a particular direction is, however, only part of the whole story. It provides no information about the origin of the structure, explanation which has only been postponed back in time along our historical description. How does a limb, or any other structure like an eye, a leaf or a flower, originate? In all these cases we have a lot of information like “this structure develops this function” but, what are the rational laws that allow us to understand the physical process by which these complex structures emerge? How does complexity appear and to which restrictions is it subjected?

It is clear that natural selection is the main source of biological complexity and the historical component is of most relevance to understand the evolutionary phenomenon. But let's not forget that natural selection is not almighty, it is subjected to physical and chemical laws.

In recent decades Complexity Sciences have added an important complement to the understanding of biological phenomena: the processes of self-organization that play an important role as a source of evolutionary novelty. In this view, the origin of the complexity is not due to natural selection itself but to a self-organized process. It is then when this new feature will be modified in one direction or another by natural selection. Self-organization acts allowing the emergence of complex structures and natural selection operates on the existing ones. The theoretical biologist Brian Goodwin, recently deceased, was one of the main drivers of this new way of thinking in Biology, which could be called structuralist [8, 9]. Structuralism attempts to find laws that account, in a simple and consistent way, for the emergence of organic structures. Its core idea lies in the belief that the structure precedes the function.

Let's return then to our question: we discussed the differences between different tetra-



Figure 5: Brian Carey Goodwin (1931-2009), the poet of evolution. Great scientist and excellent person. Goodwin was a pioneer in considering that self-organization play an important role as a source of evolutionary novelty. He wrote on the preface of his book *How the Leopard changed its spots* [8]: “Here we face another curious consequence of Darwin’s way of looking at life: despite the power of molecular genetics to reveal the hereditary essences of organisms, the large-scale aspects of evolution remain unexplained, including the origin of species. New types of organism simply appear on the evolutionary scene, persist for various periods of time, and then become extinct. So Darwin’s assumption that the tree of life is a consequence of the gradual accumulation of small hereditary differences appears to be without significant support. Clearly something is missing from biology. It appears that Darwin’s theory works for the small-scale aspects of evolution: it can explain the variations and the adaptations within species that produce fine-tuning of varieties to different habitats. The large-scale differences of form between types of organism that are the foundation of biological classification systems seem to require a principle other than natural selection operating on small variations, some process that gives rise to distinctly different forms of organism. This is the problem of emergent order in evolution, the origins of novel structures in organisms that has always been a primary interest in biology.”

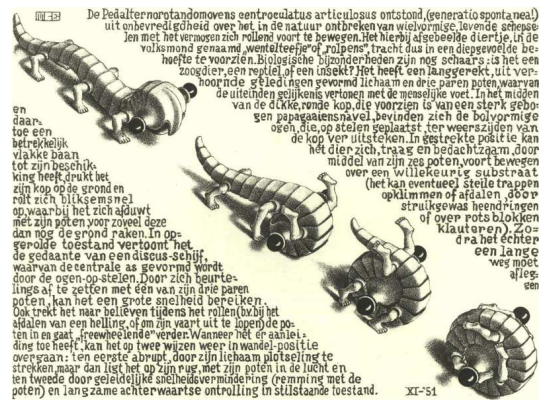


Figure 6: “Curl-up” by M. C. Escher. We all heard in school that nature had not invented the wheel, but it is not true. Howard Berg and colleagues found a wonderful example in the 60’s: the flagella of bacteria. An appendix driven by a rotary engine which can spin up to 17,000 revolutions per minute, although it usually reaches no further than 200 to 1000 revolutions per minute. Although the details of its operation are still unclear, this discovery turned the unresolved question from “why nature did not invent the wheel?” into “why this design has not been extended to higher scales?”.

pod limbs but, similarly, the presence of the same construction pattern becomes clear. There exist an invariance in the basic model that, although transformed over time, remains the same. What has made it possible for the above pattern to remain constant after millions of years of evolution?

The utility of monsters and the origins of order

We live in a world characterized by a great diversity of organic forms but, this is obvious, we can classify them because they are finite. However, structural plans different from the observed ones might exist, as evidenced by the artistic imagination of the next Escher lithograph (Figure 6). This ascertainment, discussed by the blighted theoretician of development and experimental embryologist Pere Alberch (Figure 7), can be the starting point to wonder about the source of order in the morphologies of nature. In other words, which factors make the existing configurations possible and, at the same time, prevent all other imaginary possibilities?

There are two major intellectual positions when answering this question. One is externalist, based on natural selection and the other is the structuralist or internalist. According to the first, natural selection is the main factor of generation of order, it avoids the unheard-of morphologies by removing them because of their dysfunctionality. The other position, the internalist, is to be developed in detail. In essence, it states that there are internal constraints, that the development process operates as a dynamical system and



Figure 7: Photograph of Pere Alberch (1954-1998) extracted from the poster of a Congress organized in his memory by the Cavanilles Institute of Biodiversity and Evolutionary Biology at the University of Valencia, Spain.

some solutions are more likely to occur than others.

The problem is how to distinguish between the two sources of order? Pere Alberch proposed a wildly imaginative approach. It is about understanding the “logic of monsters”, the study of teratologies, a fully developed during the nineteenth century discipline [10]. Such abnormalities are often deleterious and exhibit no biological efficacy. All of them are eliminated by natural selection. However, there is some order in the generation of such monsters. This order can be seen in the classification of teratologies by I. Geoffroy St. Hilaire in their book “Histoire générale et particulière des anomalies de l’homme et l’organisation chez les animaux”. Malformations are not only limited in number but can be classified hierarchically. Actually, from this type of classification we can conclude that not all teratologies are possible. So there is a source of order. Hence the advantage of studying the monsters: natural selection can not be the engine of that order, there is no point in talking about monsters better adapted than others, since they are all nonviable. It is clear that, at least in this case, the source of order is solely driven by internal factors.

In particular, it is interesting to note that the two-headed monsters are very common along the different animal groups. In contrast, as Alberch emphasizes, there are no more three-headed monsters than the ones the human imagination has produced (Figure 8). The reason must be sought in the dynamical mechanism of embryonic formation, a dynamical system for which some solutions are stable and others not. It is the dynamics of the generating system which introduces the asymmetry of the solutions, these constraints on the possible. Let us see then if we can narrow these claims.



Figure 8: Photograph of the Sisters Salon, a case of a woman with two heads. Interestingly there is no news of similar cases of three heads. Is there some kind of impediment? Is there a hidden order in teratologies?

Pattern formation in tetrapod limbs

One of the most fascinating current problems in biology is the understanding in physico-chemical terms of the embryonic development. The process leading from a fertilized egg (a zygote) to an adult individual is a paradigmatic example of self-organization, emergence of order and pattern formation. Until a few decades ago, it lacked a theoretical framework for understanding this self-organized system. Physics, specifically thermodynamics, was centered on the notion of equilibrium in isolated systems, there the Second Law of Thermodynamics unquestionably holds. Within this conceptual framework, life sciences seemed divorced from physical laws, surrounding with mystery the phenomenon of life. Nowadays, we know that biological systems do not violate the laws of thermodynamics, it is just that classical thermodynamics is not the appropriate framework for them. Biological systems are open systems and they must be addressed by modern nonlinear thermodynamics of irreversible processes, a discipline founded by the Nobel laureated Ilya Prigogine.

Dynamical processes involved in the pattern formation of a limb are highly stable spatial transformations for a wide range of initial conditions. And that is the main reason for its constancy along the evolutionary process. To support this claim, we will describe how the limb originates by summarizing the work, both experimental and theoretical, developed by P. Alberch, N. Shubin, G. Oster and J.D. Murray.

The limb of a tetrapod originates as an small expansion of the body in which there exists a uniform field of mesenchymal cells. These are surrounded by the extracellular

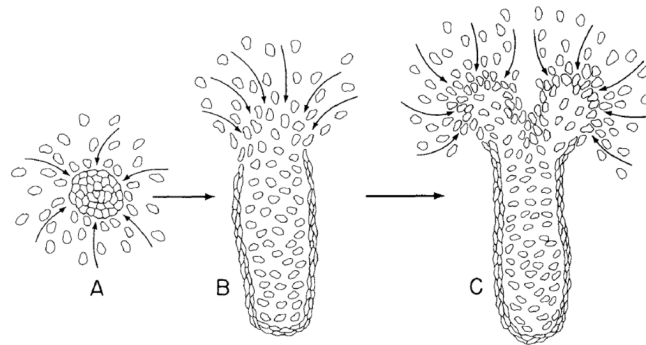


Figure 9: Diagram illustrating the formation and growth of cartilage by condensation (adapted from [11]).

matrix, consisting mainly of protein (Figure 9A). Although there are still many details of this process which remain unknown, we can form a picture clear enough for the present purposes (in [11] a more detailed discussion can be found). Once the first condensation has appeared, as the cartilaginous element develops the cells that form it begin to split into two groups (Figure 9B). The internal ones have a rounded morphology, while those that are located in the outer part are flattened. These latter ones differentiate giving rise to the perichondrium which encases the bone that is being developed. Its most direct action at this stage is to restrict the lateral growth of the cartilage which can only grow along its major axis because the subsequent recruitment of cells takes place exclusively in the distal end of the condensation. This causes its elongation.

In this pattern formation process, the size of the spatial domain is critical. Different foci of condensation compete for the cells. The size increases up to a threshold value for which a bifurcation occurs (Figure 9C). In this case, two different foci may appear, sufficiently distant from each other as to not interfere with one another. Thus, as the foci compete just for the neighboring cells, a completely heterogeneous distribution of them is formed, giving rise to zones between the foci which are substantially free of cells.

The model proposed by Oster et al. generates only three different patterns of condensation of cartilage, that is, three types of skeletal elements of the limb, shown in 10. The first is the focal condensation (Figure 10A), the second type corresponds to the branching of a pre-existing condensation (Figure 10B) and the third, called segmentation, is nothing but the fragmentation of a longitudinal element into two sub-segments (Figure 10C). These patterns have been experimentally confirmed and it should be noted that the whole process of formation of a limb, from its beginning to its final stages, is a process in which only those three patterns appear and always sequentially, never in parallel.

In the case of the tetrapod, the sequence would be as follows: the first focal condensation occurs and it elongates by recruitment of new cells at the distal extreme. The first

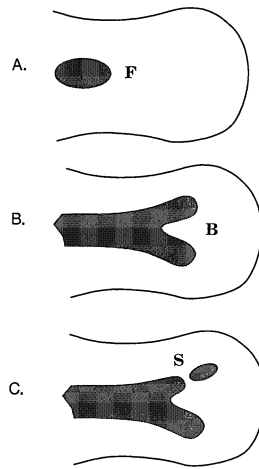


Figure 10: There are three types of cartilage by condensation: (A) focal condensation. (B) branching from a pre-existing condensation. (C) Segmentation, fragmentation of a longitudinal element S into two sub-segments (adapted from [11]).

element will lead to the humerus or femur, depending on whether we are considering an anterior limb or a posterior limb. When the length of this focus of aggregation exceeds a certain threshold, further growth by recruiting additional cells produces a branch, forming a Y-shaped pattern. Each of these branches will result in the following bone element: the pair ulna-radius in the forelimb and the pair tibia-fibula in the hind limb. In turn, these two bone elements begin to elongate and to repeat the branching process when reaching a certain size. For example, the ulna develop a new branch. The number of centers of condensation depends on the size of the limb bud, as different centers compete for a specific area of attraction. In this stage of development, this fact determines the next step in the process of sequential formation of the bone elements. The bifurcation of the ulna causes that one of the new branches is located very close to the radius. Due to the aforementioned inhibitory effect, the radius is prevented from branching itself. As a result of this competitive effect, the radius is forced to fragment longitudinally (this is the third type of cartilage condensation mentioned before). Such longitudinal fragmentation takes place when the length of the aggregate exceeds a certain critical value and the two ends become separate aggregation foci, dividing the segment in two parts. The process proceeds sequentially by repeating the three types of condensation described. The distal elongation progresses to the formation of carpal (or tarsal) proximal elements. At this stage, the development which, from the beginning, had taken place along the proximo-distal axis is interrupted and begins the sequential development along the anteroposterior axis. By means of the same processes of bifurcation and symmetry breaking, the phalanges of the fingers and the carpal (or tarsal) distal elements will be formed.

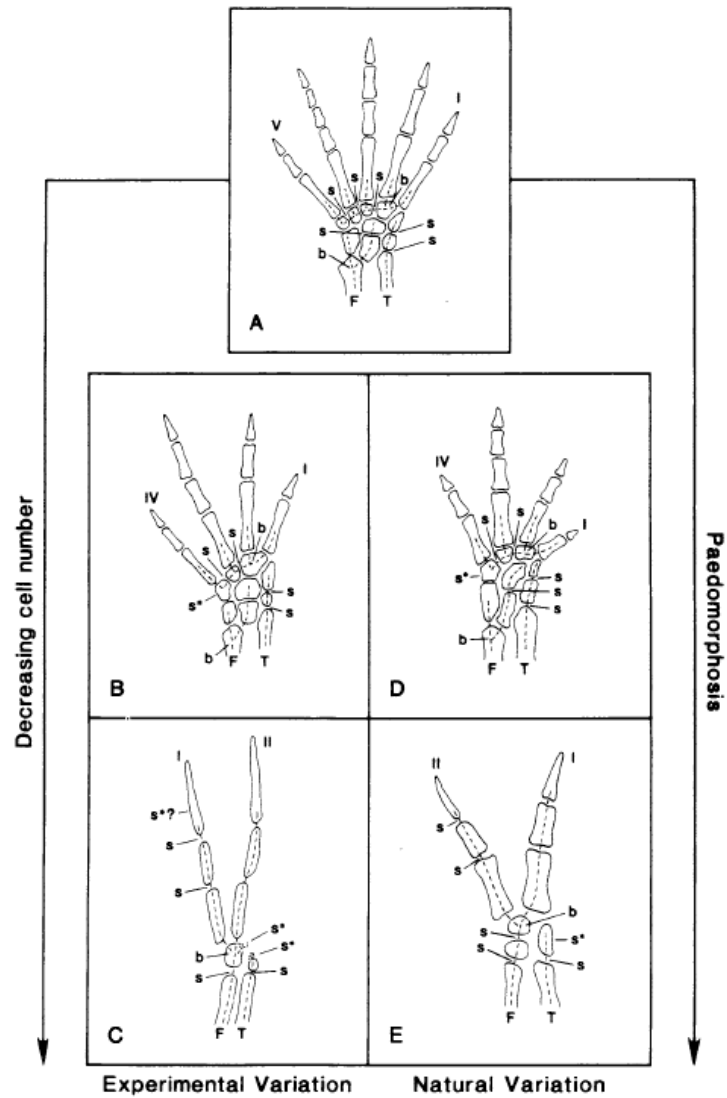


Figure 11: At the top: natural morphology of the hand of the salamander *Ambystoma mexicanum*. Series on the left (Figures B and C): two teratological forms of 4 and 2 fingers respectively, obtained experimentally. Each of these morphologies perfectly corresponds to a form observed in nature: to the species *Hemidactylum scutatum* and to the species *Proteus anguinus* respectively (adapted from [11]).

From a dynamics point of view, the three possible patterns represent robust attractors of the evolution in the embryonic field. This explains why the limbs of all tetrapods share such a well-defined and conserved pattern. As Oster et al. pointed out, other morphogenetic processes, even when they might take place, are extremely unlikely because they correspond to unstable physicochemical solutions. An example of this would be a trifurcation pattern, i.e., a three-branch condensation, as we had already mentioned when talking about teratologies or monstrosities.

Some cases of modification of the typical pattern of the limb corroborate the effect of the space in this cascade of bifurcations. Alberch and Gale [12–14] made a detailed study of the influence of the process of limb development in the genesis of an evolutionary trend developed in some amphibian species: the reduction in the number of fingers. This work is particularly illustrative of how evolution works restricting itself to the type of morphological variation compatible with the self-organizing process of forming a limb. And this is evidenced by comparison of the natural morphologies with those experimental patterns obtained by manipulation of some development parameters. Let us look at this in more detail.

The set of sequential rules described above for the formation of the skeletal elements that constitute the limb of a tetrapod establishes what may be called a development program. Minor variations will be obtained, not by changing the whole development program but through specific modifications of it. Because the size of the spatial domain has been so important for the development of this cascade of bifurcations, Alberch and Gale [12–14] tried experimentally to reduce the spatial domain of the developing limb and observed the type of change that was produced. To this aim, they made use of a mitotic inhibitor called colchicine which causes the cells not to divide for a certain period of time, therefore, at the end of the development period there should be a smaller amount of cells than usual, implying a smaller size of the spacial domain. Thus, depending on the model, one would expect that some of the branches did not show up because, due to their proximity, two centers of aggregation would interfere with each other and one of them would be absorbed by the other. Thus the number of skeletal elements should be reduced with the amount of colchicine provided. Once the embryo is developed, it will have experienced the loss of various phalanges, even of complete fingers. This is indeed the case in the experiments.

However, as Alberch and Gale emphasized, experimentally generated variations are not produced randomly, but there is a certain sequential order in which the bone elements disappear. Stated differently, some of these elements are more susceptible than others of disappearing. This ordering is a consequence of the fact that the limb does not originate synchronously but sequential. The most important thing is that a clear and manifest parallelism between the experimental variation and natural one can be observed as it is dramatically reflected in Figure 11. At the top (Figure 11A), the morphology of the hand of the salamander *Ambystoma mexicanum*, an example of a primitive hand, can be seen untransformed. In the series of the left (Figure 11B and Figure 11C), two experimentally

obtained teratological forms with a progressive reduction in the number of fingers (they have 4 and 2 fingers respectively) can be observed. Each of these two morphologies perfectly correspond to those observed in nature. Thus, we find the stage of four fingers in the species *Hemidactylium scutatum* and the stage of two fingers is represented by the species *Proteus anguinus*. The qualitative similarity between the experimental and the natural series suggests that the mechanism by which the reduction in the number of fingers has occurred along the evolutionary line has been by reducing the spatial domain over which the process of self-organization operates. The order in the loss of fingers does not correspond to the order in the loss of phalanges in the fingers. The first sequence occurs along the anterior-posterior axis, while the second one occurs along the proximo-distal axis.

5 Towards a structuralist biology

We have seen an example of self-organization process where the interaction between the dynamics and the changing morphology (boundary conditions) can be stabilized in a finite number of structures. Other *a priori* valid solutions do not materialize because they are unstable against perturbations or because they are attractors with a very reduced basin of attraction. It is in this generative order, rather than in the historical inertia and natural selection, where we must seek the reason for the invariance of the structure of a limb. The structure can also be understood as the result of a self-organizing process, something that is eliminated from the classical evolutionary point of view. It is not a question of weighing both approaches, but of noting their complementarity, because natural selection is always at the end of the road.

The main lesson to be drawn from the studies of developmental constraints is that the structure cannot be separated from the process. In the words of Pere Alberch: "It is not enough to describe the form as a static entity, defined by the arrangement of its components in space, we must understand the dynamical process that controls its genesis". When we build machines, function precedes and determines the shape of the artifact. In Biology, the shape is generated by internal processes that do not strictly depend on the function. So the form and the function engage in a dialectic in biological evolution.

Regarding the role played in this process by the genes, it is clear that these are necessary but not sufficient in understanding the formation of such structures. In addition, under this structuralist perspective, the relationship between genetic and morphological change is richer. A reduction in the final number of skeletal elements occurred when the size of the spatial domain was reduced. This can be achieved by various genetic mechanisms such as reducing the rate of cell replication or by modifying the diffusion properties of mesodermal cells that migrate into the limb in formation. Changes in many genes that determine different parameters of development can lead to the same morphological change. Moreover, as Pere Alberch *et al.* proposed, there is a nonlinear relationship be-

tween genetic and phenotypic change, where a small genetic change can cause a huge morphological change.

The ideas developed in this chapter are an example of the substantial increase in our understanding of the process of generation of morphological order along evolution. The structuralist approach represents a paradigm shift as opposed to the reductionist program. Under the influence of the latter, the gene was the fundamental unit and the origin of all complexity. The underlying principle can be summarized roughly as follows: a good knowledge of the genes will give us a good understanding of the resulting organism and its organizational characteristics. But in the example described herein, a reductionist approach is insufficient, many properties are emergent, i.e., can not be explained by the behavior of its individual parts.

Reductionism operates through a unidirectional, bottom-up causality, from the parts to the whole. Structuralism, by contrast, emphasizes the existence of a loop, a bidirectional causality between different levels: the genes generate a morphological structure that, in turn, modifies the boundary conditions on which these genes operate. The parts generate the whole which, in turn, modifies the behavior of the parts. In this sense, the limb of the tetrapods is formed from a cylindrical expansion. This morphology conditioned the orientation in which the system began to bifurcate as a result of the subsequent dynamical process. The first condensation will form a single bone element that will elongate in anteroposterior direction as a result of the cylindrical morphology upon which is acting. But the first bifurcations are also conditioning the resulting morphology as well which, in turn, will cause the symmetry breaking to be more probable in certain directions than in others.

Genes continue to have a great importance because they determine factors such as diffusion rates of certain morphogens or the size of the embryo from which the cascade of bifurcations will take place. And based on these values different morphologies can emerge. But genes –or they regulatory networks– alone do not explain fully the process by which morphological order originates. The work of Pere Alberch on teratologies is an exceptional example of this fact. Genes tell us nothing about why two-headed monsters exist but abnormalities with three heads never show up. Simply put, the greater stability of a bifurcation versus a trifurcation introduces a bias in the range of possibilities *a priori*.

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