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LIVING FORMS IN BECOMING BETWEEN OLD CONSTRAINTS AND UNEXPECTED OPPORTUNITIES OF CHANGE

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1. Understanding forms

«We really understand a form when we know how it emerges from its principles». So Burdach,[1] in the pages of the first book where the word "morphology" (*Morphologie*) appears in the title. But what can be the principles of a form?

Decades of biology dominated by an evolutionary reading of the living world could lead us to focus on adaptation: form responds to a function and the forms of living beings change due to selection, i.e. depending on their fitness – the measure in which the different variants of a trait differently meet the demands of the environment.

This is certainly not the nature of the principles that Burdach called into question, but these are not unlike those that inspired Goethe, for example in his interpretation of the bodily organization of the plant and its parts, where everything is leaf (*Alles ist Blatt*) [Goethe 1790].

In the two centuries that separate us from the birth of morphology, the search for possible universals of form has sometimes turned towards the abstract aspects suggested by geometry (in particular, by topology), more often towards adventurous generalizations of the functional value of individual classes of shapes, an aspect we will not deal with in these pages.

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[1] «wir streben, den Sinn und Ursprung der Gestalt aus höhern Begriffen zu entwickeln» [Burdach 1817, 43].

In the instances where the universals of form are sought in terms of geometry, the connection between the different forms does not necessarily have an explicit biological basis. Such a foundation is lacking even in the famous geometric transformations of D'Arcy Wentworth Thompson [1917], based on a purely visual equivalence between the body shapes of different animals. A modern version of this comparative approach to organic forms based on geometric relationships is geometric morphometrics.[2]

Some approaches to the geometry of organic forms have taken a different, generative path, through the formulation of algorithms that reproduce families of regular organic forms, e.g. inflorescences [Prusinkiewicz *et al.* 2007] or mollusc shells [Meinhardt 1998], up to the 'superformula' of Gielis [2003], which intends to unify a great variety of forms, biological (e.g. leaves) and not as different solutions of a single equation of the maximum generality.

A separate chapter is represented by models that use fractal geometry to describe complex shapes in which the same unit form is repeated several times on different scale, such as on the surface of a cauliflower or in the repeated branches of many fern fronds [Minelli 2018]. It should be noted, however, that a close resemblance between natural forms and those generated by these models is not necessarily a proof that the former are produced in the same simple, mathematically 'elegant' way as the latter.

2. Living forms between development and evolution

In recent times, the never-abated dissatisfaction with a reading of living forms in purely functional terms has taken on new vigor, fueled by the spectacular progress that developmental biology has experienced over the last half century through an increasingly substantial contribution of molecular genetics. Natural selection can only act on those forms that have been actually built, that is to say on those that fall within the possible products of the developmental mechanisms actually operating

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[2] Useful introductory works to geometric morphometrics are Bookstein 1991; Rohlf & Marcus 1993.

in nature. Before comparatively evaluating the fitness of the various phenotypes in a given environmental context, it is therefore reasonable to deepen our knowledge of their actual possibility (and probability) of realization. A couple of examples will help explaining this statement.

In earthworms, the number of segments into which the body is divided varies, even considerably, within each species and each individual population. For example, if the most frequent value is 105 segments, there will also be individuals with 104, 103 etc. and with 106, 107 etc. segments. A similar continuity in the numerical variation is not found, however, in the chilopods or centipedes, that is in the scolopenders and in their closest relatives. In adult condition, these animals always have an odd number of leg pairs. This number is fixed in some groups, but can instead be variable, even considerably, although always avoiding even values. In geophilomorph centipedes the variation is quite evident: in a single population there can be for example individuals with 53, 55, 57, 59 or 61 pairs of legs, none however with 54, 56, 58 or 60. What are the reasons for the total absence of chilopods with an even number of pairs of legs? An explanation in functional terms is unthinkable: what disadvantage could derive, in fact, from having only one pair of legs in excess or in defect of 57 pairs? Moreover, it seems difficult to hypothesize a hereditary mechanism that completely excludes the production of individuals with an even number of pairs of legs by parents with any possible combination of odd numbers. It is far more reasonable to think that the absence of chilopods with an even number of leg pairs is due to the fact that these cannot be produced: in other words, there would be a constructive constraint, an intrinsic limit to the mechanism by which these animals produce the modular units (the segments, with a pair of legs each) of which their long trunk is formed.

Another instructive story of numbers is told by the giraffe's neck. Lamarck was the first author to use this animal to illustrate his evolutionary vision, according to which the morphological changes resulting from the repeated use of a body part end up being transmitted to the following generations. We can thus imagine that in ancient times giraffes had a neck much shorter than today but, being faced with the dry season, when in the savannah the only green leaves are found on the branches of the acacias at considerable height above the ground, they used to stretch it in the attempt to reach the food. The repeated effort would have produced a progressive lengthening of the neck, which would have been regularly transmitted to the offspring. Through a long series of generations, the giraffe's neck would thus have reached the proportions it has today.

Acacias and summer drought also play an important role in the Darwinian-style scenario in which a population of giraffes appears, somewhat different from one another in terms of neck length. We expect that, as a rule, those with the longest neck are those that most easily manage to survive and reproduce. To the extent that the length of the neck depends on hereditary factors, there will thus be, from generation to generation, a slow but progressive increase in the average length of the neck, until the current proportions are eventually obtained. This is a functional, adaptive explanation of the peculiar shape of the neck of this mammal. But it is a partial explanation at best: it does not tell us, in fact, how to make a giraffe's neck or at least its skeletal scaffolding.

We can imagine indeed that this is constituted by a high number of cervical vertebrae (more than the seven elements that support a human's head), or by a few, very elongated cervical vertebrae (perhaps just seven, as in our species). From a functional point of view, there might be some small difference between one vertebral composition and another, but the solution to our doubt must be sought in another direction. We realize this when we discover that the cervical vertebrae of the giraffe are just seven, a number virtually fixed in all mammals [Minelli 2009]. We have reason to think that there has never been giraffes with cervical vertebrae in number other than seven, although it is easy to imagine that, had nature been able to produce a more numerous set, this could have been advantageous over a lesser number of cervical vertebrae with similar average length.

Centipedes and giraffes therefore invite thinking of biological forms that, had they appeared, would have been successful, in terms of functional adaptation, but 'simply' never saw the light. There are also reciprocal examples: 'monstrous' individuals whose chances of survival are uncertain, while it is certain that they will not be able to reproduce and therefore to transmit their characters, and yet they often reach adulthood, demonstrating that existing developmental mechanisms are capable of constructing forms other than normal ones.

Developmental biology has long learned to use these abnormal individuals to improve our knowledge of morphogenetic processes; in addition to the 'monsters' occasionally found in nature, there are also those intentionally produced in suitable experimental conditions. Exemplary, from many points of view, are some *Drosophila* mutants, for example the so-called *Antennapedia*, in which a pair of legs replace the antennas. This anomaly can only be seen in the adult (in the previous stages, from embryo to larva to pupa, there are not antennae), so it is clear that the mutation does not hinder development, metamorphosis included. But an adult fly without antennas lacks chemical receptors that are indispensable for locating food and searching for partners: in other words, it is a total failure, from an adaptive point of view.

What can we learn from this perhaps unexpected counterpoint between flies without a future that can be produced nevertheless, and giraffes with twenty cervical vertebrates or scolopenders with twenty pairs of legs that cannot be built, although we can be sure that they would survive and reproduce? The lesson learned from these examples is that to understand living forms as these exist in nature we cannot be satisfied either with the functionalist logic of evolutionary biology, or with the explanations provided by developmental biology in terms of ontogenetic processes: separately taken, neither is sufficient to explain the biological forms we actually find in nature. However, we can attempt to integrate between the two approaches, following the recent program of evolutionary developmental biology (evo-devo).[3]

Evolutionary developmental biology began to take shape as an autonomous discipline only towards the end of the last century and is still searching for a precise identity [Arthur 2002; Müller 2008; Minelli 2015a]. It is often seen as a trading zone [Winther 2015] in which problems and methods of evolutionary biology confront those of developmental biology. Today, however, we are not only witnessing the overcoming (in itself a very important achievement) of the decades-long divergence between these two major branches of the life sciences [Amundson 2005], because in the context of evolutionary developmen-

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[3] See Hall 1992; Arthur 2002; Minelli 2003, 2009, 2018; Carroll *et al.* 2005.

tal biology an original program has now taken shape, mainly focusing on three points: the origin of evolutionary novelties, modularity and, most important, evolvability. It will be useful to start from the latter, before briefly reviewing a series of aspects of the evolution of living forms that variously express the modularity of these and of the developmental processes that generate them.

The understanding of the relationships between genotype and phenotype has undergone a radical change with the lucid analysis of Pere Alberch [1991], which focused on the fundamental role of development and the constraints it poses to the opportunities for phenotype change. A problem therefore arose: what are the most likely, less likely and perhaps also impossible scenarios of change? In other words, the central question became one of evolvability [Hendrikse *et al.* 2007; Minelli 2017], that is the evolutionary path of living beings in what we can call the labyrinth of forms: phenotypic distances that are apparently easy to bridge may actually require difficult or unlikely changes at the genetic level while, on the contrary, seemingly large distances between two different phenotypes are sometimes bridged at the price of minor genetic changes.

Important news, for example, can be the consequence of a ‘simple’ iteration of a developmental process already at work in the same organism, with results depending on the number of iterations and the polarity of the axes along which these are realized. There is evidence, for example, of evolutionary leaps in the number of segments of the body as a consequence of a probable overall duplication of the entire series of segments of which the trunk of the animal is composed. This may be the origin of *Scolopendropsis duplicata*, a centipede that has approximately twice the number of leg pairs compared to all the other scolopenders [Chagas *et al.* 2008; Minelli *et al.* 2009], and of the millipedes of the genus *Dobrodesmus*, similarly ‘duplicated’ with respect to their closest relatives [Shear *et al.* 2016]. Of major consequence can however be a duplication that gives rise to a new body axis, according to the principle of paramorphism that expresses the correlations between construction and regionalization of the main body axis and the corresponding processes in the axes of the appendages of the same animal [Minelli 2000].

3. Systemic changes and modular changes

Provided that we retain a critical attitude with regard to a somewhat simplified taxonomy, it is useful to distinguish, in the context of the changes of living forms in development and evolution, between modular changes that concern exclusively (or almost exclusively) individual parts of the body, and systemic changes in which the entire body organization is deeply modified [Minelli 2015b]. Let's start with the latter.

1) Systemic changes

A striking example of living forms resulting from a systemic change on an evolutionary scale is offered by the duckweeds, a small tribe of plants floating on the surface of freshwater ponds and ditches. In the most known and common representatives of this group, those belonging to the genus *Lemna*, there are neither branches nor leaves: the whole plant is just a small floating disk a few millimeters in diameter; its almost invisible flowers are reduced to a tiny ovary (female flowers) or a rudimentary stamen (male flowers). But there are also more simplified forms, overwhelmed by a systemic simplification that in the case of *Wolffia arrhiza* reduces the plant to a grain of green matter of just one mm in diameter, or even less. These simplified forms appear even more extreme when compared to the calla lilies, an example of the typical (not simplified) morphology of the plants of the arum family, to which the duckweeds also belong.

2) Modular changes

The independence enjoyed by the different parts of the body, from the point of view of the developmental processes from which they are generated, is clearly visible in the regeneration of lost parts, as in the case of the lizard's tail. However, to a greater or lesser extent, this also occurs during the normal development of the organism, which can therefore be described as a system of local modules dominated by distinct and specific developmental dynamics: «Modules are assemblages of parts that are tightly integrated internally by relatively many and strong interactions but relatively independent of one another because there are only relatively few or weak interactions between modules» [Klingenberg 2005, 6].

Developmental modularity is the condition that allows a whole series of important evolutionary changes (developmental reprogramming [Arthur 2000, 2002]), for which variations of ontogenetic processes, even of modest size, may be sufficient. Three main types are recognized – heterometry, heterotopy, heterochrony – which involve, in the order, changes in quantitative (metric or meristic, positional and temporal) aspects of the production of individual parts of the body during development.

Heterometry is a significant variation of the size relationship between two parts of the body. An extreme example is offered by the nematode *Sphaerularia bombi*. In this tiny parasitic worm, the reproductive system of the mature female hypertrophies up to become much larger than the animal itself and, following prolapse from the genital opening, it continues to grow outside the body of the worm, while the latter ends up representing only a small appendage of its reproductive organs [Poinar & van der Laan 1972].

Heterotopy is the term used to describe a change in shape that occurs during the development of the individual or in the evolutionary history of a group of organisms, affecting the spatial relationships of a single module in respect to the remaining of the body architecture. This is the case, for example, of flatfish. These, at the beginning of the development, have a normal bilateral symmetry, but in the following phases one of the eyes migrates towards the opposite side of the head.

Heterochrony is an evolutionary change in the rates or timing of developmental processes. There are several types of heterochrony, characterized by different forms of temporal change: the time of onset of an ontogenetic process (for example, the first visible evidence of the forming brain) can be anticipated or postponed; in turn, the moment at which it ends can be anticipated or delayed; and the speed with which the process takes place can also vary.

The traditional approach to heterochrony [de Beer 1930, 1940; Gould 1977; McNamara 1986; McKinney & McNamara 1991] took into account almost exclusively the variations in the temporal course of somatic growth with respect to reaching sexual maturity. Thus two main forms of heterochrony were recognized: paedomorphosis and peramorphosis. In the first case the animal reaches maturity while maintaining juvenile or larval characteristics in the somatic features, in the second the growth period is prolonged and maturation is delayed. The most recent research on heterochrony is based, instead, on the recognition of a more extended modularity of the developmental processes, thus allowing an analysis of the variations in the order in which the different events occur within the ontogenetic sequence (sequence heterochrony [Velhagen 1997; Smith 2001, 2002; Jeffery *et al.* 2002a, 2002b, 2005]). An example of sequence heterochrony is provided by the order in which the anterior and posterior limbs first appear in the embryo or the larva of different groups of terrestrial vertebrates: in the newt, in the hedgehog and in the mole, for example, the forelimbs appear first, in some anuran amphibians the opposite occurs, while in birds and in many mammals the two pairs of limbs appear simultaneously [Bininda-Emonds *et al.* 2007].

Classic examples of heterochrony are those of animals that reach sexual maturity while preserving a larval aspect, such as the olm (*Proteus anguinus*), the blind cave amphibian of the karstic regions between the Isonzo River and the South of Bosnia-Herzegowina, that maintains gill breathing throughout life, typical of the larvae of its relatives (newts, etc.) which instead metamorphose into adults that breath atmospheric oxygen.

4. Genotype and phenotype

The clamorous success of molecular biology and the explosive development of studies on the genetic control of developmental processes in recent decades could suggest that a thorough knowledge of the genotype of an animal or plant is sufficient to predict its structure. The possibility of "computing" an embryo has been discussed.[4] But this would be a

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[4] «Will the egg be computable? That is, given a total description of the fertilized egg – the total DNA sequence and the location of all proteins and RNA – could one predict how the embryo will develop? This is a formidable task […]. It may, however, be feasible if a level of complexity of description of cell behavior can be chosen that

hasty conclusion. In fact, the path from the genotype to the phenotype is anything but simple [Alberch 1991; Draghi & Wagner 2008; Pigliucci 2001; West-Eberhard 2003]. It is rare that the expression of a gene corresponds precisely and unambiguously to the production of a given phenotypic trait. Generally speaking, the expression of one gene will be involved in many traits (pleiotropy), while identical or almost identical traits can be achieved even in the presence of differences in the genes or in the gene networks involved in their control (convergence or redundancy). Moreover, the phenotype that actually shows up depends, to a greater or lesser extent, also on influences from the environment in which development takes place.

1) Not everything from genes

Phenotypic plasticity[5] is the ability to produce different phenotypes in the absence of genetic differences between individuals: which phenotype is actually obtained depends instead on the environmental conditions to which the animal was exposed in a (generally early) critical phase of its development [Pigliucci *et al.* 2006]. The best known example of phenotypic plasticity is probably the development of a female bee into either a fertile queen or a sterile worker: in this case, the factor responsible for the production of one or the other phenotype is the food (with or without royal jelly) that the insect received during the larval stage.[6] In the alligator and in other reptiles, under environmental control is the determination of sex, which depends on the temperature at which the egg is incubated [Janzen & Phillips 2006].

Recent studies have shown how easily alternative phenotypes controlled by the environment can sooner or later fall under genetic control [Brisson 2010]. In the pea aphid (*Acyrthosiphon pisum*) individuals of either sex can be winged or wingless, but this difference has different

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is adequate to account for development but that does not require each cell's detailed behavior to be taken into account» [Wolpert 1994, 571-572].

[5] See Fusco & Minelli 2010; Pigliucci 2001; Schlichting & Pigliucci 1998; West-Eberhard 2003, 2005.

[6] In the case of ants, mechanisms underlying cast determination are more complex [Abouheif, Wray 2002].

causes in the male, where it is the expression of a genetic polymorphism, and in the female, where the presence or the absence of wings is instead a case of polyphenism, i.e. it represents the response to different environmental signals. However, the difference between the two conditions is subtle, since the gene responsible for the development of the wings in the male also plays a role in the response of the female to the environmental signals [Braendle *et al.* 2005a, 2005b].

2) Whose genes?

In many animals, including humans, normal life depends on a functional association between cells of different genetic identity: only a part of these derives from the zygote, the others are bacteria of many different species. Collectively, these bacterial cells form a microbiome that accompanies the animal throughout its life and strongly influences its vital processes. We can therefore state that the biological system that we usually call an individual is actually a consortium of functionally integrated animal and microbial cells [Gilbert *et al.* 2012; Gilbert & Epel 2015].

The best known multigenomic biological systems are the lichens, each of which is the product of a symbiotic relationship between a fungus and an alga. In many cases, the individual species of lichens (or rather, as we prefer to say today, the individual species of lichenized fungi) have precise and recognizable forms, expressions of processes of growth and development that depend jointly on the genomes of the fungus and the alga. Even more specific and predictable are the shapes of plant galls, especially of those that are induced by the puncture of plant tissues by the different species of cynipid wasps. From the point of view of comparative morphology and morphogenesis, lichens and galls would indeed deserve much closer attention than they have got up to now [Minelli 2017].

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Keywords

Development; Evolution; Evolutionary Developmental Biology; Evolvability; Fractals; Genotype-Phenotype Relationship; Heterochrony; Heterometry; Heterotopy; Modularity; Morphology; Multigenomic System; Paramorphism; Systemic Change

Abstract

What does it mean to understand a biological form? Traditional approaches have tried to generate families of form through generative algorithms, often mathematically elegant (e.g., fractals) but very far from biological reality, or to explain it in terms of adaptation. In recent times, a different reading of living forms has been fueled by progress in developmental biology. The key point is that natural selection can only act on the products of the development mechanisms actually operating in nature. There are biological forms that, had they appeared, would have been successful, but simply never saw the light. There are also reciprocal examples of 'monstrous' individuals whose chances of survival are uncertain and are not able to reproduce, yet they often reach adulthood, demonstrating that existing developmental mechanisms are capable of constructing forms other than normal ones. Thus, to understand living forms as these exist in nature we cannot be satisfied either with

the functionalist logic of evolutionary biology, or with the explanations provided by developmental biology in terms of ontogenetic processes: separately taken, neither is sufficient to explain the biological forms we find in nature. However, we can attempt to integrate between the two approaches, following the recent program of evolutionary developmental biology (evo-devo). Within this discipline, an original program has taken shape, focusing on evolvability, modularity and the origin of evolutionary novelties. Evolutionary and developmental changes of living forms can be modular or systemic. Modularity allows different kinds of development reprogramming: heterochrony, heterotopy, heterometry, which involve, in the order, changes in temporal, positional and quantitative aspects of the production of individual body parts during development. Despite the explosive development of studies on the genetic control of developmental processes, a thorough knowledge of the genotype of an animal or plant is not sufficient to predict its structure. The expression of one gene is generally involved in many traits (pleiotropy), while identical or almost identical traits can be achieved even in the presence of differences in the genes or in the gene networks involved in their control (convergence or redundancy). Moreover, the phenotype that actually shows up depends also on influences from the environment in which the development takes place (phenotypic plasticity), and on often standing and specific interactions with other organisms, as in the fungus-alga symbiosis of lichens and the interactions of multicellulars – humans included – with their microbiome.

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