

DARWIN'S EVOLVING LEGACY

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COMPENSATION AND CORRELATION OF THE ORGANS IN ÉTIENNE GEOFFROY SAINT-HILAIRE'S *TRANSMUTATIONISM*

GUSTAVO CAPONI*

INTRODUCTION

In his presentation of the thesis stated by Étienne Geoffroy Saint Hilaire (1833) in "Le degré d'influence du monde ambiant pour modifier les formes animales," Jean Rostand (1932: 90) explains the mechanism of the organic transformation proposed there by Geoffroy, appealing to a principle that he, Rostand, calls *the law of organic correlation*. With this label, Rostand seems to be referring to what we could portray as a *transformational* version of *the principle of correlation of parts* stated by Cuvier ([1812] 1992: 97). Nevertheless, if we pay attention to what was written by Geoffroy (1833: 83), we will find that, in his argument, the function that Rostand gives to that *law of organic correlation* is accomplished by *the principle of the compensation of the organs*.

Implicitly, Rostand seems to suppose that this last principle has a similarity or proximity to the principle stated by Cuvier, and this supposition settles a matter that transcends the comprehension of Geoffroy's transmutationism and involves his entire *Anatomical Philosophy*. The question is this: *Is it possible to consider the principle of compensation of the organs as if it were a transformational version of the principle of correlation of parts?* In the following pages I will try to support a negative answer to this question. I will say that even though Cuvier's *Law* could accept a transformational reformulation, *the principle of compensation of the organs* aimed to explain facts that were different from those that could be explained by resorting to that hypothetical *transformational Cuvierism* imagined by Rostand.

If that were not the case, Geoffroy's *Anatomical Philosophy* could not have been other than a risky speculative adventure to explain

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what Cuvier's *comparative anatomy* already allowed us to explain. But, far from being just that, the *Anatomical philosophy* intended to outline a strategy of research that not only would go further to the limits of Cuvierian *Comparative Anatomy* but also would explain some facts that the latter did not allow us to understand, and *the principle of compensation of organs* was a key resource to the accomplishment of that task.¹

THE TRANSMUTATIONIST THESIS OF GEOFFROY

Étienne Geoffroy Saint Hilaire never developed a complete and coherent system of transmutationist thesis like the one Lamarck (1802, 1809, 1815) developed in his later works. Nevertheless, Geoffroy's commitment with this type of thesis is shown, or it is implied, in several of his works (*cf.* Geoffroy Saint Hilaire, 1: 354, ff.; Appel, 1987: 130, ff.; Le Guyader, 1998: 110 ff.); and the nature of the explanation that he thought that could be given to the *origin of the new species*, or *new types*, was clearly shown in his already mentioned paper about "The level of influence of the environmental world in the modification of animal's forms."

In the paper, to reinforce his transmutationist convictions, Geoffroy (1833: 77 n. 1) quotes the observations of François Desiré Roulin and those of his own son, Isidore Geoffroy Saint Hilaire, about the influences of the environment on the profiles of animals. However, these observations, inspired by the idea of *acclimatization* (*cf.* Roulin, [1828]1835 and I. Geoffroy Saint-Hilaire, 1832) only refer to the differences that can be found among varieties and races of a single species submitted to different weather and food conditions. What Étienne Geoffroy Saint-Hilaire was looking for was a mechanism that could explain changes capable of transforming a reptile into a bird

¹ It may be important to point out that this work it is not about the famous debate before the Académie that Cuvier and Geoffroy held in 1830. This work is just an effort to understand Geoffroy's transmutationist ideas, putting then in the framework of his program of research. It's clear, anyway, that Cuvier's ideas were the main counterpoint of that program; and for this reason we won't be able to avoid references to Cuvier. We analyzed the Cuvier-Geoffroy debate in "El concepto de organización en la polémica de los análogos" (Caponi, 2006) and in the fourth chapter of *Georges Cuvier: Un fisiólogo de museo* (Caponi, 2008).

or a fish into a reptile. He knew that, in fact, it was not because of "an insensitive change that the lower types of oviparous animals have produced the higher grade of organization to which the birds belong," and he thought that the only way to explain that transformation was by appealing to a brutal reorganization of the organic economy, a reorganization analogous to those that produce monsters (*cf.* Geoffroy, 1833: 84-85), but with results functionally more harmonious than those that are usually studied by teratology.

However, that reorganization seemed absolutely possible to him. Geoffroy (1833: 80) believed, for instance, that if in the early stages of its development, the pulmonary sac of a reptile suffers a constriction, or a stress in the half that pushes all the blood vessels to the thorax, leaving the inferior part of that sac in the abdomen, that would be "a favourable circumstance to the development of an entire bird organization."² The key of that reorganization would be in breathing. With that new disposition of the pulmonary sac, this operation which, according to Geoffroy (1833: 75), regulates everything in living beings would be done with higher intensity and would produce a higher level of energy and that would lead to all the reconfigurations that would allow change from a reptilian to a bird type to occur. On the other hand for Geoffroy these types were just two very close variations of a *unique type*, this common plan of organization which all animals share (Geoffroy [1830] 1998: 141). It was because of this, in the end, that the jumps between types were possible.

However, if it is in the *unity of plan* that Geoffroy's transmutationism finds its condition of possibility, there is no doubt that, in his opinion, it is in the changes of the fluids that an animal respires that one can find the cause capable of triggering those large transformations that go beyond the slow and minor changes that according to

² Well, this was really a bizarre *mental* morphological experiment; quite similar to that proposed by Laurencet and Meyranx in 1830 for demonstrating the *unity of composition* of vertebrates and mollusks. Laurencet and Meyranx "attempted to show that if a vertebrate was bent backwards so that the nape of the neck was attached to the buttocks, then the internal organs would be arranged in a manner similar to that of mollusks" (Appel, 1987: 145); and what Geoffroy proposed three years later was that the strangulation of a reptile in the middle of his pulmonary sac would generate a redistribution of organs that could give us the same internal distribution of the organs that we find in birds.

The *memoire* where Laurencet and Meyranx proposed that idea deflagrated the Cuvier-Geoffroy debate.

Buffon (1766), and his more optimist followers, Isidore Geoffroy Saint-Hilaire (1832) and François Roulin ([1828]1835), could be produced by the weather, the diet and the habits. What happens is that, according to Geoffroy (1833: 79), the importance of respiration in the animal economy is so determinant that "it is not necessary that the respiratory fluids been modified very strongly and abruptly, to produce altered forms." Furthermore, as these changes in the respired fluids are accumulated with the passing of time, gradually or abruptly through the mediation of a cataclysm, the consequent changes in the animal form may be very striking. Gradually or abruptly, the modification of those fluids will produce alterations of the lung cells, and those alterations, "fortunate or unfortunate," will have an impact "on the other parts of the animal economy."

Geoffroy (1833: 82) said that one proof that these ideas were right could be found in the studies about the metamorphosis of the batrachians made by William Edwards.³ The change from the ichthyologic type, which we called tadpole, to the reptilian type that we call frog (Geoffroy, 1833: 82) was produced, according to Geoffroy (1833: 83), "by the combined action of light and oxygen" and this action explained why their metamorphosis was banned or delayed when they were kept under water, thereby avoiding contact with air and light. But Geoffroy (1833: 83-84) also supposed that what Edwards did on *a small scale* when he experimentally delayed or banned a complete metamorphosis of the frog, nature did on *a bigger scale* in the case of this inhabitant of underground waters which is the Proteus. "This reptile," said Geoffroy (1833: 84), "deprived of feeling the influence of light and of taking the energy from a free practice of aerial respiration, remains perpetually as a larva or as a tadpole; but, at the same time, it can transmit to his descendants those limited conditions of organization without any difficulty; conditions of its species that were maybe those of the first stage of existence of the reptiles when the Globe was completely submerged."

Nevertheless, in order to produce changes that affect the entire organism, the conditions that affect respiration need the mediation of what Geoffroy (1833: 83, 86) called *the principle of compensation of the organs*: "that law of living nature in virtue of which a normal or pathological organ never acquires an extraordinary prosperity, if another

³ He is Henri Milne-Edwards' brother (cf. Perrier, 1884: 109).

organ of the system or of its relations does not suffer in the same proportion" (Geoffroy: [1822]1998: 63; 1835: 59 n 1). The hypertrophy of an organ always produces the atrophy of another organ, because there is no unlimited supply of the required substance for the normal development of each structure (*cf.* Gil, 1986: 107), or as Edward Stuart Russell (1916: 73) explains when he discusses Geoffroy's thesis in *Form and function*: "The nutritive material available is limited for each species; if one part gets more than its share, the other parts get less—that is all the law means."

The following is what happens, according to Geoffroy (1833: 83), in the metamorphosis of the frog: the aerial respiration demands and produces new blood vessels that irrigate and cause the growth of parts of the body which before were smaller, and this makes other blood vessels contract, producing the atrophy of others parts by the lack of irrigation.

But, this also happens in the transformations that occur "through monstrosity." In both cases "an organ is submitted to a stoppage in its formation and the flow of the fluids that nourish it or that were meant to nourish it, is used by other organs [*sic*]." According to Geoffroy (1833: 86) this "law of compensation that regulates the opposite and reciprocal growth of the volumes clarifies that unusual march, in a way that all the different facts are coherent and are explained respectively, rarely denying the elucidation of its causality to the impassioned and well led inquiries." It is in that point where Rostand proposes his *Cuvieran* reading of Geoffroy.

COMPENSATION VS. CORRELATION

When discussing and explaining these passages of Geoffroy's *Memoire* that we are analyzing, Rostand (1932: 91), as mentioned above, does not refer to *the law of compensation of organs* but to *the law of organic correlation*, which, according to him, states that "all the parts of an organism act one over the other," in such way that "a variation initially limited, localized, generate, by its repercussion, a general and deep modification" of the entire organism. But it is not strange at all that Rostand uses the expression *the law of the organic correlation* to refer to Cuvier's *principle of correlation of parts*. Pierre Janet (1882: 351), for ex-

ample, had named it *The law of organic correlations*; the point that can be questionable is that he states it and formulates it as a law capable of explaining changes in the organic forms.

Cuvier's law, as Émile Boutroux ([1893] 1950: 92) and Ernst Cassirer (1944: 165) remarked, is not a *causal law* concerning the temporal succession of phenomena but a *law of coexistence* and that is why it can be said that its transmutation into a principle capable of regulating organic transformations is a transgression of its original meaning. Nevertheless, this transgression is possible; and it can be said that it is involuntarily implied in the formulation of Cuvier, who, against what the *legend* says, never quoted or used his principle as an *anti-transformist* argument (cf. Caponi, 2004: 247). When Cuvier ([1812] 1992: 97) says that no part of an organized being "can change without changing the other parts," the idea of a harmonious and functional transformation of living beings seems less denied than suggested.

Even though Cuvier was trying to say that if—in a given species—an organ has a certain structure and a special location, and in other species that organ shows a different structure or a different location, that difference will also be correlated with other differences, more or less pronounced in the configuration and position of the rest of the organs. It is rather easy to imagine a *causal* or *transformational* version of that principle. This principle could state that if, in a given species an organ changes, that modification will produce, more or less pronounced, correlative transformations in the others organs of the same species (cf. Caponi, 2004: 246). But, it is one thing to assume that a transformational interpretation of the *principle of organ correlations* is possible; and it is another thing to admit that the *principle of organ compensation* proposed by Geoffroy is, as Rostand seemed to suppose, the result of that interpretation.

If it were so, the functional coherence of the organic transformations that, according to Geoffroy (1833: 79), were triggered by the changes in the respiratory medium would be granted: those transformations would produce mutually correlated alterations that would always generate forms capable of satisfying the *principle of the conditions of existence* that Cuvier (1817: 6) stated in *The Animal Kingdom*. However that was not Geoffroy's idea (1833: 79), in his opinion, those transformations could be lethal—that is to say, they could generate forms without what Cuvier called *condition of existence*. "If those modi-

fications," Geoffroy said (1833: 79), "entail harmful effects, the animals that suffer them would disappear giving place to other animals with forms" also "slightly changed" but "changed in accord to the new circumstances." And this is so because that *compensation* of the organs was, according to Geoffroy, a mechanical process completely insensible to functional requirements.

The monsters would be a proof of that. If these show us how anatomical conformations can be modified with independence of functional demands, generating beings very often unviable (*cf.* Geoffroy, 1824: 53 ff.), this does not imply a denial of *the principle of correlation of parts*. Without functioning as a law capable of explaining the processes that lead the constitution of organic forms, that principle can still be considered as the postulation of organizational exigencies that inevitably will put limits to the blind changes that organic conformations can suffer. In fact, Geoffroy seems to suppose that of all the morphologies produced by the changes in the respiratory mediums, only those that, using Cuvier's words, have *condition of existence* remain (*cf.* Perrier, 1884: 110). But here it is important to recover the *Cuvierian* sense of the expression *condition of existence*: this must be considered especially in the sense of functional coherence and integration, of *correlation of organs* (Flourens, 1841: 139); and not in the Darwinian sense of adaptation to the contingencies of the *struggle for life* (*cf.* Russell, 1916: 239; Grene and Depew, 2004: 139; Caponi, 2005: 83).

If in Geoffroy there exists something that we could describe as a *selectionist thought*, this *selectionist thought* certainly has little to do with the idea of a competition in the *struggle for existence*. This *struggle* always supposes that the alternatives, or parts, in competition have a minimum of viability, otherwise there will not be place for any competition. In fact, Geoffroy, as Maupertuis ([1746] 1985: 107) and Diderot ([1774] 1875: 253)⁴ had already, was just thinking of the simple elimination of what was absolutely unviable in itself.

Nevertheless, there is still a similarity between Geoffroy and Darwin in what concerns the relative disconnection between structure and function that both accepted and pretended to explain (Russell,

⁴ See also Rostand, 1932: 30, 37; Roger, 1993: 470-471; Papavero, Pujol-Luz, and Llorente-Bousquets, 2001: 105-144 with regards to this thesis of Maupertuis and Diderot. With regards to Maupertuis in particular see also: Carbalho Ramos, 2003: 57-58; and about Diderot: De Sousa, 2002: 78-79.

1916: 305; Piveteau, 1950: 363). For both Geoffroy and Darwin, the morphology of living beings is a document of a history that Cuvier never considered, and many of their structures or special features can only be understood as the remains of the processes involved in the constitution of these beings. This is why Darwin (1859: 455) and Geoffroy (1833: 73) were interested in the rudimental or vestigial organs (*cf.* Gould, 1983: 29; Gil, 1986: 107; Le Guyader, 1998: 37; Caponi, 2006: 40).

As Russell's well-known quotation (1916: 78) says, "the contrast between the teleological attitude, with its insistence upon the priority of function to structure, and the morphological attitude, with its conviction of the priority of structure to function, is one of the most fundamental in biology." Furthermore, if Geoffroy and Cuvier are considered as the two paradigmatic exponents of the alternative solutions that can be given to this dilemma, it can also be possible to agree with Russell (1916: 78) in that "theories such as Darwin's, which assume a random variation which is not primarily a response to environmental changes, answer the problem in Geoffroy's sense." That is to say, the structures change first, fortuitously and blindly, and then the environmental conditions, or the functional requirements, will say if those changes will be held or rejected. But even if they are held, the features that are built by this kind of processes, always keep certain *fault of origin*: a kind of *inadequacy*, a little *foolishness*. These features can hardly be digested by a severe functional analysis. That is the reason that Geoffroy had for not considering his *law of compensation* as a transformational substitute of the *Law of Cuvier*.

CONCLUSION

If Geoffroy had done so, as I said at the beginning, his *Anatomical Philosophy* could have only resulted in a simple speculative adventure whose empirical content would have never been ahead of the more cautious but productive *Comparative Anatomy* of Cuvier. One transmutationist formulation of *the principle of correlation of parts in the organized beings* would only allow us to understand those facts that were already included and explained in Cuvier's program, but this *transformational Cuvierianism* would do it without solving the difficulties of the *actual*

existent Cuvierianism: it would do it without being able to explain all those facts that were not intelligible from a functional perspective. In this way, besides assuming the *cost* implied by the defence of a transmutationist thesis, always difficult to justify, *Transformational Cuvierianism* would remain, one could say, sub-determined by the empirical evidence.

On the other hand, Geoffroy wanted an *Anatomical Philosophy* which, integrating the Cuvierian comparative anatomy and its achievements within a more comprehensive theoretical framework, could also explain phenomena, such as the different dental systems of birds (Geoffroy, 1824), that were very hard to understand from Cuvier's point of view; and it was his effort to understand such facts that led Geoffroy to a new agenda of topics. Topics that clearly he would have never needed to deal with from the Cuvierian perspective. The first of those topics was the analysis of the processes which presided the development of each living being (*cf.* Geoffroy, 1824: 21-22; Perrier, 1884: 133-134; Le Guyader: 37-38; Caponi, 2006: 48-49); and it was how Geoffroy arrived to the transmutationist themes that we have analyzed here (*cf.* Panchen, 2001: 44). Going beyond the functional analysis, Geoffroy arrived at the problem of development; and this topic opened his eyes to the idea of transmutation.

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