



## Richard Owen, Morphology and Evolution

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**Abstract.** Richard Owen has been condemned by Darwinians as an anti-evolutionist and an essentialist. In recent years he has been the object of a revisionist analysis intended to uncover evolutionary elements in his scientific enterprise. In this paper I will examine Owen's evolutionary hypothesis and its connections with von Baer's idea of divergent development. To give appropriate importance to Owen's evolutionism is the first condition to develop an up-to-date understanding of his scientific enterprise, that is to disentangle Owen's contribution to the modernization of typology and morphology. I will argue that Owen's Platonic essentialism is rhetorical and incongruous. On the contrary, an interpretation of the archetype based on Aristotle's biological works makes possible a new conception of type, based on a homeostatic mechanism of stability. The renewal of morphology hinges on homological correspondences and a homeostatic process is also the origin of serial and special homology. I will argue that special homology shows an evolutionary orientation insofar as it is a typically inter-specific character while serial homology is determined through an elementary usage of the categories of developmental morphology.

**Keywords:** Aristotle, divergent development, epigenesis, evolution, homology, morphology, Owen, typology, von Baer

### 1. Introduction

In his July 1860 review of *On The Origin of Species*, Asa Gray wrote: "Owen himself is apparently in travail with some transmutation theory of his own conceiving, which may yet see the light, although Darwin's came first to the birth."<sup>1</sup>

Gray was basically right. A few years later, Owen disclosed his own evolutionary "hypothesis." But in the meanwhile, his conflict with Huxley had blown up. In Owen's time, this conflict was the basis of most misunderstandings about his "anti-evolutionism" and recently, it has generated further

<sup>1</sup> Gray, 1963, pp. 84.

misunderstandings about his essentialism. After the publication of his 1860 malicious commentary on *The Origin of Species*, Owen was labelled the villain of the post-Darwinian debate.<sup>2</sup> Owen never approved of the basic points of Darwinian theory, natural selection and chance variation, and when evolutionism proved to be a more powerful theory than his “derivative” sketch of species change, his frustration resulted in a sort of rear guard reaction. He doggedly opposed Darwinian evolutionism and slid from a non-Darwinian into an anti-Darwinian stance.<sup>3</sup> As a result, Owen’s public image was ruined and his moderate conception of evolution was ignored. I believe the impact of this controversy on the history of evolutionary biology is much inferior to the peculiar acrimony of contenders. The controversy cannot be counted as an unconditional conflict between typology and evolution. First, Owen was not hostile to evolution and Darwin was not hostile to morphology, as I will show below. Historians of biology have started revising the common belief that Owen was a blanket anti-evolutionist and the existence of evolutionary ideas in his works has been revealed by Nicolaas Rupke. Second, Huxley himself, far from being hostile to typology, was actually a typologist.<sup>4</sup>

Richard Owen did not elaborate a grand biological theory of his own but covered the central subjects of nineteenth century biology. He was involved in the research program intended to build up a “natural system” out of the artificial taxonomies that had been popular in the eighteenth century. As a comparative anatomist, museum curator and paleontologist, he was in need of identifying a stable notion of “type” that could work as a basis for systematic classifications, museum collections and paleontological records. He was familiar with European research traditions and had a first-hand knowledge of the concepts of “form” and “function” that French and German biologists employed, under various elaborations, as unifying principles for taxonomic systems.<sup>5</sup> Therefore, morphology was the main framework of Owen’s research in taxonomy and ranked first before Cuvierian functionalism. Owen was also aware of the growing impact that embryology, developmental anatomy and even the uncertain emergence of evolutionary ideas was going to have on taxonomy and morphology, before 1859.

The challenge the present paper meets is first to show that Owen’s concept of evolution is not a belated reaction to Darwin’s achievement, but a coherent consequence of Owen’s acceptance of von Baer’s theory of divergent development. Second, I believe that Owen’s sophisticated conception of “type” is much more complex than the rough Platonic essentialism that has been

<sup>2</sup> See Desmond, 1982, 1989; Rupke, 1994.

<sup>3</sup> Ruse, 1979, p. 144.

<sup>4</sup> Lyons, 1999.

<sup>5</sup> Farber, 1976; Appel, 1987; Lenoir, 1981; Sloan, 1979.

attributed to him. Third, Owen contributed to the transformation of morphology by means of an evolution-oriented conception of special homology and a development-oriented conception of serial homology. I will argue that Owen's analysis of serial homology is the initial step of a complex research program in developmental morphology. This program had to pass through further stages before becoming operational and is still far away from completion. In this view, the nature of homologies can be fully grasped only today, in the light of the concept of "developmental constraints." Hence, a major problem in understanding Owen's place in the history of biology is to keep track of the dispersed time-slices where the conceptual shifts in which he was involved were performed.

The next section will be devoted to a clarification of the meaning of such concepts as "taxonomy," "typology," "morphology," "evolution," "essentialism," "development" and to the description of the historical modifications of this meaning. However, I will cover "evolution," "essentialism" and "development" only in part. I will detail the meanings of "evolution" in section three while the full meaning of "essentialism" and "development" will be clear only in section eight and nine.

## 2. Taxonomic Concepts

*Taxonomy* is the part of biology concerned with the systematic classification of biological taxa. The goal of taxonomy is achieved by attributing a name and a definition to each taxon and ordering all true definitions in a "natural" system.

*Typology* is that part of taxonomy which is concerned with the production of taxa definitions. A "type" is, therefore, a stable set of qualities or properties that are singularly necessary and jointly sufficient to define a taxon. Typology may achieve the goal of classification by means of essential definitions, or essences, fashioned after Aristotle's logical theory of definitions or Plato's theory of "forms."<sup>6</sup> If we assume that the definition of a type is unavoidably made up of essential qualities, then typology coincides with essentialism. If we assume that Aristotle's definition of biological species coincides with his logical definition of essence, then Aristotle is a typological essentialist. Both assumptions will be challenged in this paper.

Once the taxa have been defined, we need a unifying criterion or principle for assembling them in the "natural system" I mentioned above. For example, Cuvier held "function" as unifying principle of his classifications whereas evolutionary taxonomists utilize "phylogeny."

<sup>6</sup> Simpson, 1961; Hull, 1965; Mayr, 1969.

*Morphology* is the “science of organismal form” and broadly consists in tracing topological correspondences in organs that are therefore called “homologous.” Insofar as morphology is a descriptive discipline, its analytical devices or principles can serve as unifying principles in taxonomy. Owen’s archetype or Geoffroy’s unity of plan, as well as homologies, can be used as criteria for classification. Typology and morphology were two operational models in taxonomy, having the specific goal of introducing a systematic order into the manifold of life. Pre-Darwinian taxonomies were basically descriptive disciplines and did not include any causal explanation of the origin of taxa.<sup>7</sup> Owen’s work is a part of such a descriptive or “transcendental” morphology, also called “rational morphology” or “philosophical anatomy.” Its task was to compare anatomical parts, grasp their mutual connections and affinities and trace them back to archetypal models.

Yet, it is difficult to run a purely descriptive inquiry. Hence, morphology endured a lack of explanatory power. To make up for it, morphology had two possible options: it could either claim an explanatory power for the “forms” or combine with another biological discipline. The result of the first option was idealistic morphology and the result of the second was functional, evolutionary or developmental morphology. Charles Darwin, for example, implemented morphology in the *Origin of Species*. He ingeniously transformed Owen’s archetype in an evolutionary ancestor and led evolutionary taxonomists to use homology as a tool to recognize and set up phylogenetic relations.<sup>8</sup> Thus, “Darwin’s and his contemporaries’ conceptions of evolutionary change were given a distinctive shape by their morphological perspective.”<sup>9</sup> We will discover the remedy Owen adopted at the end of this section.

Indeed, from the middle of the nineteenth century to the present day, both typology and morphology have undergone numerous changes, many of them triggered by the Darwinian revolution. Some changes directly affected Richard Owen while others affected the attitude of philosophers and historians of biology toward Owen and thereby the way Owen is perceived today. So, I have to weed through this somewhat complicated process of transformation to assess the consequences related to Owen’s image. I will first consider typology, then morphology.

In the nineteenth century, the typological construction based on *essential* definitions remained untouched by the new ideas introduced in *The Origin of Species*. The conflict between Owen and Darwinism – as I will show later – consisted in the opposition between random selection and Owen’s

<sup>7</sup> Russell, 1916, p. 73; Ghiselin, 1980, p. 181; Mayr, 1982, p. 458.

<sup>8</sup> Coleman, 1976; Ridley, 1986, p. 113.

<sup>9</sup> Ospovat, 1981, pp. 146, 150.

preordained derivation. Owen's "essentialism" was not involved. As far as I know, no one even used the word "essentialism" at that point. No wonder that Thomas Henry Huxley was a typologist and an evolutionist at the same time. David Hull has explained that Darwin opposed "the ontological assertion that Forms exist [and] the methodological assertion that the task of taxonomy as a science is to discern the essences of species" but never challenged the *logical* assertion that a type must be defined by a set of *essential* properties, in the Aristotelian way. Darwin did not see that evolutionary species had to be defined as variable cluster concepts. In addition, the re-organization of taxonomies according to phylogenetic criteria, prompted by the Darwinian revolution, proved to be a long and painstaking business.<sup>10</sup>

The problem of essentialism and the incompatibility between typology and evolution surfaced much later, by the time of the "evolutionary synthesis." Mayr<sup>11</sup> maintained that there is an irreconcilable opposition between evolutionary (population) thinking and typological thinking. The "types" are Platonic or Aristotelian forms, unreal essences, whereas "populations" are real entities whose transformations have to be described in historical and statistical terms. Mayr argued that the philosophical method of classifying by means of *discrete* types and essences is not helpful in a science like biology, which deals with *continually* evolving organisms or species. He indicated that essentialism was a necessary property of typology and that biology should have eliminated any notion of "type." Obviously, such a position ended up representing a sort of proscription of Richard Owen from the community of true biologists.

A further step along this way was the individualistic conception of species introduced by Hull and Ghiselin.<sup>12</sup> They have persuasively argued that evolutionary species are not types but individuals, historical entities. Thus, if species lack a spatio-temporally unlimited existence, they cannot be the subjects of spatio-temporally unrestricted laws of nature. But is this argument sufficient to imply that types do not have any place in biology? This does not seem to be the case. As early as 1958, Marjorie Grene had disagreed with this expectation and had objected that flux alone cannot generate forms and organisms that physically persist in a discrete state.<sup>13</sup>

Recently, a number of philosophers of biology have started to reconsider the notions of natural kind and thereby of essentialism and type.<sup>14</sup> Relying strictly on inductive knowledge without implying any disclaimer of

<sup>10</sup> Hull, 1965, pp. 317 ff.; Mayr, 1969, p. 62; Hull, 1988, p. 97.

<sup>11</sup> Mayr, 1975, pp. 27–28.

<sup>12</sup> Hull, 1976; Ghiselin, 1974.

<sup>13</sup> Grene, 1958.

<sup>14</sup> See Wilson, 1999.

the Darwinian anti-essentialism or the individualistic conception of species, they have argued that it is possible to build up a definition of a type (or kind or species) that is not based on essential qualities. Such a definition can be based on “a family of properties that are contingently clustered in nature in the sense that they co-occur in an important number of cases. Their co-occurrence is, at least typically, the result of what may be . . . described as a sort of homeostasis.”<sup>15</sup> These correlations are therefore “projectable” (as stated by Nelson Goodman) that is we can assume they can be applied to future cases. This line of thought offers an alternative approach to the question of typology. Mayr’s theory of identity between typology and essentialism can be challenged.<sup>16</sup> This identity was not considered true in Owen’s and Darwin’s time and it is untrustworthy today. By the same token, typology and evolution can no longer be considered an ironclad antithesis. To be sure, theological or Platonic essentialism is a serious concern. It determined Owen’s rejection of natural selection, affected his typology and thereby spread over morphology. But the existence of evolutionary concepts in Owen’s work (section seven, below) implies that Owen’s image as a staunch essentialist is to be revised.

Let us return to morphology and to the possible remedies to its lack of explanatory power. In the first half of the nineteenth century, German *Naturphilosophen* had claimed that morphology had the power to explain the various characteristics of living beings. In the tradition of German speculative idealism, as championed by Oken or Schelling, the shape of reality is precisely determined by a dynamic power of ideas that materialize in physical entities of flesh and blood. Owen never approved of such misleading explanatory practices<sup>17</sup> but his acceptance of natural theology and his sporadic references to Plato’s ideas were also an attempt to bestow an explanatory power to forms. Ideas or forms are like blueprints that transfer divine plans into reality. Owen insisted that once divine plans are transposed onto nature they turn into a system of “secondary causes” that are the object of a scientific inquiry. But this tactic was particularly uncongenial to evolutionary biologists

<sup>15</sup> Boyd, 1999, p. 143. A homeostatic mechanism is broadly any self-regulating process by which a biological system maintains its functional stability while adjusting to external conditions by means of feedback circuits.

<sup>16</sup> Amundson, 1998.

<sup>17</sup> Criticism to German idealism and *Naturphilosophie* is scattered in all of Owen’s works. The following passage is one of the clearest: “All Oken’s writings are eminently deductive illustrations of a foregone and assumed principle, which, with other philosophers of the transcendental school, he deemed equal to the explanation of all the mysteries of nature. [. . .] By Oken, it [the vertebral theory of the skull] was applied chiefly in illustration of the mystical system of Schelling – the ‘all-in-all’ and the ‘all-in-every-part.’ [. . .] and Cuvier ably availed himself of the extravagances of these disciples of Schelling to cast ridicule on the whole inquiry” (Owen, 1884, p. 751).

and Asa Gray made fun of “Prof. Owen’s ‘axiom of the continuous operation of [secondary causes in] the ordained becoming of living things’.”<sup>18</sup> This is a crucial point because the problem of causal power of forms overlaps to that of typological essentialism. In fact, morphology could go nowhere if it was confined to theological hypotheses and to the bare analysis of anatomical similarities. Morphologists had to shift the causal focus of their inquiries from the notion of the divine plan to a source that could offer an alternative explanation of the origin and evolution of forms. This source turned out to be developmental biology, the discipline that studies the ontogenetic development of an individual from the embryonic to the adult stage.

It must be admitted that Owen’s thought does not have a thorough solution to these typological and morphological problems. However, I think a number of elements show that Owen – rather than confine himself to metaphysical conjectures – maneuvered the tools that were available to him in a way that made possible the transition to a new-fashioned morphology. He vindicated the consistence of his taxonomy by separating metaphysical from mechanical causes. Hence, his rhetorical essentialism can be reduced to an extra-theoretical option and we can discern a *realistic* concept of “type” behind it. Finally, Owen explained the formation of the spinal column in vertebrates by means of a developmental process, the serial reproduction of a basic unit (the vertebra). In other words, he extended the descriptive commitment of transcendental morphology toward the causal commitment of developmental morphology by means of the notion of serial homology.

Owen’s contribution did not receive much attention because – as I said above – no research program in developmental morphology was operational in the first half of the nineteenth century. Such a program needed external contributions (Darwinian evolution and evolutionary morphology, among others) before being able to build up a basic theoretical structure. In addition, following Darwin’s initial thrust, the process of interaction between morphology and evolution was very slow and fragmentary in England. Also Bateson’s more detailed study about segmentation and homeotic variation was nearly ignored, a few decades later.<sup>19</sup> Modern historiography has downgraded the impact of evolutionism on morphology and has acknowledged the relative autonomy of morphology.<sup>20</sup> Things went different in Germany. In the last decades of the nineteenth century a certain integration was achieved thanks to the work of Hæckel and Gegenbaur. Then, biologists started focusing on ontogeny as a clue to explain phylogeny and evolution. Thus, at the end of the nineteenth century, morphology accomplished its transforma-

<sup>18</sup> Gray, 1963, p. 73.

<sup>19</sup> Bowler, 1992.

<sup>20</sup> Bowler, 1996; Ruse 1996.

tion into a causal science that was called – following a suggestion of W. Roux – *Entwicklungsmechanik*.<sup>21</sup>

Later, the rise of Mendelian genetics paved the way for the “evolutionary synthesis” and crowded out both morphology and developmental biology. Morphology and developmental biology survived especially in the areas of paleontology, mainly confined to inquiries into the physical and geometrical processes of conservation of form that are epitomized by the work of D’Arcy Thompson. The “evolutionary synthesis” developed without any notable contribution from morphology.<sup>22</sup>

Today, attempts are being made “to facilitate” the thus far failed or unattended “integration of developmental and evolutionary biology.”<sup>23</sup> No contradiction is presumed to exist between random evolution and the *stability* of certain forms or processes that endure in the historical development of life. Biologists have stressed the stability of a species in the course of time (problem of “punctuated equilibria”) and now are focusing on the stability of an anatomical trait in the evolution of species, particularly the concepts of developmental constraints and homology. “Evolutionary conservatism”<sup>24</sup> is receiving more and more attention and the interactions between morphology and evolutionism are being appreciated again.

I will proceed as follows: in the next section I will outline the meanings of “evolution.” Subsequently, I will trace the progress of Owen’s evolutionary ideas and their explicit statement after the publication of *On the Origin of Species*. Then, I will argue that Owen’s concept of “evolution” puts his own essentialism in a critical position and makes it incongruous and contradictory. To be sure, essentialism cannot be ignored. But once its pressure has been counteracted, the bulk of Owen’s work in typology and classification will be appreciated. While taking up evolution and essentialism, I will also examine the slippery question of the philosophical background of Owen’s work. I will argue that Platonism will turn out to be no more than a rhetorical device for justifying Owen’s notion of archetype. On the contrary, we can discover hints of Kant’s influence within Owen’s ideas of causality and a large debt to Aristotle within Owen’s conception of classification and type. In the final part of the paper I will verify the possibility that Owen’s work on the homologies afford us a better comprehension of the relations between evolution and morphology as well as of the passage from transcendental to developmental morphology.

<sup>21</sup> Russell, 1916; Coleman, 1976.

<sup>22</sup> Bowler, 1988, pp. 105 and ff.; Ghiselin, 1980. However, Bowler (1996) argues that evolutionary morphology cannot be considered a “sideline” in the development of biology.

<sup>23</sup> Hull, in Hull and Ruse, 1998, p. 90.

<sup>24</sup> Shubin, 1994.

### 3. Owen and German Embryology

In the history of biology, the word “evolution” has two meanings.

In the eighteenth century, “evolution” first designated “the embryological development of a single individual” and we can conveniently embed it in the controversy between Preformation and Epigenesis. Preformationists, like Haller or Bonnet, believed that the divine force “encapsulates” in the embryo a miniature adult that subsequently unfolds or “evolves” during gestation by a mere “expansion of parts already present within the germ.” On the contrary, supporters of epigenesis argued that the “sequential formation of [the] various parts” of an organism does not unfold by means of a divine agency, but under the power of an essential force (C. F. Wolff), or a non-mechanical *Bildungstrieb* (Blumenbach) which ensures harmony between the mechanical forces and the “vegetative” and developmental processes of an organism.<sup>25</sup>

The second meaning of “evolution” is the Darwinian one, referring to the phylogenetic transformation of a species into another by means of a random selection. Both the ontogenetic and the phylogenetic process are joined through complicated biological links, whose nature has yet to be discovered. An example of this link may be the concept of recapitulation, according to which the stages of ontogenesis recapitulate the stages of phylogenesis.<sup>26</sup> Yet recapitulation is only the most acknowledged, not the most effective, relationship between ontogenesis and phylogenesis. I will examine below whether the concept of *divergence* is a better way to combine the ontogenetic concept of individual development with the phylogenetic problem of the evolution of species and to associate ontogeny and phylogeny in the realm of evolutionary biology.

I must now put Owen into this picture. He was a comparative anatomist, the curator of the Hunterian Museum with the job of illustrating the collections in an annual course of twenty-four lectures.<sup>27</sup> His core business was the search for morphological correspondences in adult animals, and homology was the tool specifically aimed at this objective. As I said above, comparative anatomy was a basically descriptive activity. Nevertheless, Owen was looking also for a causal explanation of both anatomical regularities and diversity. The reticence that prevented Owen from dealing with the question of origin of species before 1859 was probably an effect of such descriptive quality of transcendental morphology. In any event, embryology was, at the time, the domain where anatomical traits could be explained. Its explanatory model was grounded in the concept of development set out in Germany between the

<sup>25</sup> Bowler, 1973, 1975; R. Richards, 1992; Needham, 1959.

<sup>26</sup> Gould, 1977.

<sup>27</sup> See Rev. R. Owen, 1894, vol. I, p. 104.

end of the eighteenth and the beginning of the nineteenth century. Bowler has argued that such a “non-Darwinian” model of evolution (to be distinguished from the end-of-the-century “anti-Darwinism”) is based on embryological development and can be traced through all nineteenth century biological thought from Owen to Gegenbaur’s evolutionary morphology.<sup>28</sup> As a first step, Owen’s idea of evolution can be understood by means of this simple embryological model.

In 1837, “evolution” and embryology were used only in relation to the ontogenetic development of an individual. Owen wrote that “to obtain an insight into the laws of development, the signification or *Bedeutung* of the parts of an animal body, demands a patient examination of the successive stages of their development in every group of Animals.” He also mentioned Tiedemann, Purkinje, Baer, Rathke, Wagner, Valentin and Muller as the main representatives of German scholarship.<sup>29</sup> As a consequence, he treated the anatomy of generative organs and the development of the embryo in his 1840 *Hunterian Lectures* and in his 1843 lectures on *Invertebrates*. Owen’s interest in divergent development is witnessed by the priority disputes with Barry, Carpenter and Milne-Edwards in which he engaged from 1840 onward. He was also fully aware of the fact that embryology had developed in Germany earlier than in England.<sup>30</sup> His lifelong rival, T. H. Huxley, even held that embryology could replace comparative anatomy as the main source of evidence for investigations in systematics. Owen did not go that far but included embryology in his list of the seven “kinds” of anatomy, as the one that “takes a particular species in the course of individual development, from the impregnated ovum, tracing each organ step by step in its evolution up to the adult condition.”<sup>31</sup>

To understand how the idea of “evolution” migrated from the ontogenetic to the phylogenetic level, we first have to reappraise the outcome of the Preformationism-Epigeneticism controversy and then to take into account Karl Ernst von Baer’s theory of divergent development within a given type. I am going to do that in the two following sections. Before doing so, I want to point out that until the concept of “divergence within a type” is introduced, embryology will remain but a static appendix of comparative anatomy. In 1846,<sup>32</sup> drawing upon von Baer’s doctrine, Owen reworked his 1837 concept of embryological development into that of *phylogenetic* divergence from an

<sup>28</sup> Bowler, 1988; Di Gregorio, 1995.

<sup>29</sup> Owen, 1992, p. 191.

<sup>30</sup> E. Richards, 1987; Ridley, 1986.

<sup>31</sup> Owen, 1866–68, I, p. VII; Huxley, 1898.

<sup>32</sup> I refer to the *Report on the Archetype and the Homologies of the Vertebrate Skeleton* (BAAS Report, pp. 169–340) which Owen published in 1846. I will quote from the 1848 reprint, which is included in my References List.

archetype and this very process involved an idea of evolution. Once Owen's idea of evolution is made fully explicit (after 1859) it becomes possible for us to appreciate retrospectively the implicit potential of his 1846 outline of developmental morphology. We shall discuss that in due time.

#### 4. Epigenesis and Secondary Causes

According to Roe's excellent analysis,<sup>33</sup> the Preformation-Epigenesis controversy had no definite resolution. Preformationism fell into demise and was replaced by a variety of epigenetic theories but, over decades, none of them could provide a scientific explanation of embryonic development. The existence of a vital force was simply taken for granted and no justification of its origin and purposiveness was offered. Epigeneticists agreed with Preformationists in this respect and rejected a purely materialistic explanation of the organization of life. Yet, while they admitted the purposiveness of vital forces, they also accepted the seclusion of that implicit teleology in the realm of metaphysics.

This is the compromise solution retrieved by Kant in § 81 of the *Critique of Judgment*. The teleological nature of life is only a regulative idea, namely a *subjective* maxim of judgement. It cannot be an object of experience and science but calls for inductive investigations into mechanical causes and secondary laws that govern the history of life. The Kantian compromise fits in with traditional British empiricism and its conception of inductive causes as the only source of scientific explanation. The only condition is the acceptance of creation by law and the rejection of special creation. Newton, Lyell, Reid (like Descartes before them) had successfully adopted this tactic.<sup>34</sup> The origin of alleged teleological organization of life is a kind of divine architect, maybe God himself, but we cannot know him except from his works. Hence, as in Kant's *Critiques*, he has to be isolated in an untouchable metaphysical domain. God's action was henceforward set apart from the method and rules of induction. It could be even considered a sort of truism.<sup>35</sup>

As a consequence, empirical processes were considered to be dependent on "secondary causes" and these causes, in their turn, are subject to strictly inductive criteria of admission. Owen has maintained this stance in all his writings. Only divine agency is the true and efficient cause. But once this

<sup>33</sup> Roe, 1981, pp. 150 ff.

<sup>34</sup> Lenoir, 1982. If one had to consider this question in theological terms, one could say the substitution of preformationism by epigeneticism marks a considerable widening of the role of laws in the creation at the expense of the idea of special creation (Hull 1974, pp. 55–66; Bowler 1973, p. 276). For Descartes' procedure, see Clarke 1982, pp. 77 ff.

<sup>35</sup> Winsor, 1976, p. 175.

hypothesis has been assumed, there is no cognizance of the link between the first cause and secondary causes. There must be a gap between them. Therefore, it would be wrong to consider these doctrines as disguised theology. We have to recognize that so far as they are coherent with the limitations imposed by the compromise, they are science. Otherwise they are not even proper metaphysics but only logical confusion. The relevance of this issue will be clear when I make my point about Owen's purported Platonism.

Did Owen know Kant's work? Sloan correctly highlights that Joseph Henry Green, an influential predecessor of Owen's at the Hunterian Museum, used in his lectures the Kantian distinction between Physiography (description of facts concerning nature), Physiology (facts ordered under principles and laws) and Physiogony (historical presentation of natural events in different times and spaces).<sup>36</sup> Thanks to Green, Owen must have been aware of this distinction, which possibly allowed him not to overlook the historical implications of von Baer's idea of divergent development and to understand that divergence is an historical process. Nevertheless, there is nothing, to my knowledge of Owen's writings, that suggests his having read any work by Kant.<sup>37</sup>

In any case, Owen seems to come along precisely with the Kantian compromise. He makes this point precisely in connection with the problem of evolution: "As to the successive appearance of new species in the course of geological time, it is first requisite to avoid the common mistake of confounding the propositions, of species being the result of a continuously operating secondary cause, and of the mode of operation of [a] creative cause. Biologists must entertain the first, without, accepting any current hypothesis as to the second." [...] "The inductive demonstration of the nature and mode of operation of such secondary continuously operative species-producing force will henceforth be the great aim of the philosophical naturalist."<sup>38</sup>

With the above in mind, we can understand that Kant<sup>39</sup> was in favor of epigenesis "[because] with the least possible expenditure of the super-

<sup>36</sup> Sloan, 1992, pp. 24 and ff. Kant elaborated such distinction mainly in *Metaphysische Anfangsgründe der Naturwissenschaft* (1786) and *Über den Gebrauch Teologischer Principien in der Philosophie* (1788).

<sup>37</sup> Rupke (1994, p. 199) has the same opinion and Sloan (1992) has documented Green's influence on Owen but not Kant's.

<sup>38</sup> Owen, 1860, p. 403. I just want to note that Owen steadfastly applied these strictly empirical criteria to his own scientific activity and to criticize transmutation, (1992, p. 192) Darwinism (1974) and German transcendentalism. As a consequence of Owen's coherent empiricism, the idea that he was a supporter of German idealistic Naturphilosophie must be sized down.

<sup>39</sup> Kant, 1952, § 81.

natural it entrusts to nature the explanation of all steps subsequent to the original beginning.” Owen also seems to endorse the Kantian analysis: “It can no longer be doubted that the germ is not the mere miniature of the later organs, pre-existing already formed and mechanically expanded by the generative processes, as Bonnet and Haller believed; – but that the germ is amorphous matter, vivified by an organizing principle which [...] arranges and forms it into the organs by whose harmonious action, Life is afterwards to be maintained.”<sup>40</sup> Obviously, the option for epigenesis does not rule out the role of God. But this is now a God who – consistent with the separation of causes – governs by means of natural laws and not by singular erratic acts. God has originally put the formative power into the germ or into the “common organic prototype” of each species. Then He has stepped aside so that “All subsequent organisms henceforward result from properties imparted to the organic elements at the moment of their creation, pre-adapting them to the infinity of complications and their morphological results, which now try to the utmost the naturalist’s faculties to comprehend and classify.”<sup>41</sup>

The problem is that the very key-notion of the system, the idea of vital force, still lacks any empirical evidence whatsoever. It has remained an occult quality of matter. Its origin is unexplained, its mode of operation unknown. To become the object of a scientific inquiry it should be restated in empirical terms. In particular, the connection pointed out between the ontogenetic and the phylogenetic level of operation is a problem. The more it opens up new perspectives, relating embryology to natural history and to the question of the diversity of species, the more the tool available for dealing with these problems, the recapitulation theory, turns out to be insufficient.<sup>42</sup>

## 5. Owen, von Baer and Divergence

Owen described the notion of vital force by means of the concepts of divergence and archetype that came to him from von Baer.<sup>43</sup> In his most important work, von Baer had considered the process of organic differentiation that has to be traced back to the “grade of development” of an animal. This is the amount of “heterogeneity of its elementary parts” and the complexity of its apparatuses<sup>44</sup> and combines with the “type of organization.” This consists of “the mode in which [the] organs of the animal body are united together” and

<sup>40</sup> Owen, 1992, p. 220.

<sup>41</sup> Owen, 1859; 1974, p. 191.

<sup>42</sup> Owen, 1992, p. 192.

<sup>43</sup> Owen, 1853, pp. 54–55; 1868, III, p. 809.

<sup>44</sup> von Baer, 1853, p. 195.

can be recognized as a “modification of a certain archetype.”<sup>45</sup> Such archetypes represent the most fundamental forms of life in the animal kingdom and Von Baer – like Cuvier – believed that “four archetypes may be clearly demonstrated.” Thus, “the product of the grade of development with the type [of organization] yields those separate larger groups of animals which have been called classes.” Indeed, the history of life unfolds into the intersection of two processes: a process of typological variation, in classes, families and finally species and subspecies that affects the fundamental archetypes and a second process of individual development that affects straightforwardly the individual embryo and involves the rise of the most special from the most general forms.<sup>46</sup> Von Baer rejects both “the conception of uniserial development of the whole animal kingdom” and the idea that “the development of each animal follows the same laws as that of the whole animal series.” As a result “*Every embryo of a given animal form, instead of passing through the other forms, rather becomes separated from them.*”<sup>47</sup> Von Baer does not mention any modification of an archetype or type into another.

Owen follows von Baer’s in his dismissal of recapitulation: “Thus as we trace the development of the Molluscous animal, we find the application of the term unity of organization progressively narrowed as development advances; [...] every animal in the course of its development typifies or represents some of the permanent form of animals inferior to itself: but it does not represent all the inferior forms, nor acquire the organization of any of the forms which it transitorily represents. [...] There is only one animal form that is represented, permanently or transitorily, throughout the animal kingdom: it is that of infusorial Monad.”<sup>48</sup>

However, the modification of the concept of evolution we have thus far considered has altered the general framework of the species question (see the table below for an overview). Can the mechanism of epigenesis, along with von Baer’s concept of progressive development from-general-to-special, be helpful in explaining the multilinear process of development, which – according to von Baer – occurs in the domain of a given type? The idea of recapitulation and the law of parallelism, both laid aside by von Baer and Owen, were unsuccessful first attempts. Now von Baer’s concept of divergence from an unspecialized archetype, which Owen picked up as well, could

<sup>45</sup> Von Baer, 1853, p. 179. Von Baer uses the word “Haupt-typen,” whereas Owen used to talk about “archetypes” (Ospovat, 1976). Huxley translated “Haupt-typen” with “Archetypes” as well.

<sup>46</sup> Von Baer 1853, pp. 196–197, 208.

<sup>47</sup> Von Baer 1853, pp. 187, 209–214; (von Baer’s emphasis).

<sup>48</sup> Owen 1843, pp. 369–370.

Table 1. Transition from embryological development to evolution of species

Theory	Type of Transformation	Transforming Entity	Transformation process
Epigeneticism	Embryological development	Embryos	from embryo to adult animal
Von Baer	Typological development	Types	from unspecialized type to specialized animal
Owen	Phylogenetic development	Archetypes	from archetype to species
Darwin	Selective evolution	All species	from ancestor species to descendant species

be a better candidate. But it has a substantial shortcoming: it is originated by a vital force that has not been explained at all, as yet. Such a force is still subject to the above mentioned Kantian compromise and cannot be treated but as an occult entity. We do not have presently any empirical cause that can explain the process of divergence. Neither Owen nor von Baer provides a scientific definition of this idea. We must wait for Darwin to reach one. Is that all? I think it is possible to dig further into the concept of divergence in order to make the most of its evolutionary potential.

Von Baer is a difficult character to assess. We can easily dismiss him as an antievolutionist if we take into account the radical criticism of Darwin he produced at the end of his life. Alternatively, he can be praised, in a vague way, as a “forerunner of Darwin.” Let me suggest a third view that consists in tracing his contribution to the establishment of the idea of evolution.

According to von Baer, there is a unique principle of divergence that separates all the different classes, families and species that have ever existed in historical time. It separates birds from mammals, apes from men, within the framework of a *branching* scheme. Paleontology must have taught both von Baer and Owen that this process occurs not only in space but also in time. Contrasting Lyell’s Uniformitarianism, Owen boldly stated that “there are traces in the old deposits of the earth of an organic progression among the successive forms of life.”<sup>49</sup> Both the biological process of divergent development and the historical sequence of paleontological records proceed in the same direction – towards an increase in complexity and specialization *in the course of time*. At this point “evolution” has taken another step

<sup>49</sup> Owen, 1851, p. 451. For further confirmation, see the tables of geological distribution of animals in Owen, 1860.

forward. Species can be ranged in a historical and temporal succession, according to the unfolding of a unique principle, the principle of divergence. Owen asserted that the development of a class consists in a “multilinear process with many lines diverging away [. . .] toward different adaptive modifications.”<sup>50</sup> The immediate further step should be the admission of the ancestor-descendant relation between species.

Von Baer could not take this step because he was the man of another epoch. Although he admittedly “furnished some material . . . concerning the development of organic forms,” he did not entertain any true doctrine of evolution but just “a general perspective of development embedded in [the] view of the increasing specialization and individualization of the embryo.” In any event, this “limited amount of evolution” can occur only within the boundaries of each type. At last, in his writings on Darwin, he explicitly rejected the possibility that one species might be derived from another species. In von Baer’s conception of development, the process of formation of each species follows a separate teleological pattern of its own rather than the logic of a competitive selection between several species and within a species itself. von Baer just applied the embryological view to the historic development of species, so that “evolution was goal-directed in the same way as embryogenesis.” His concept of *multilinear* development is quite an important achievement but does not bring forth a transition from the ontogenetic to phylogenetic level.<sup>51</sup>

## 6. Divergence and Evolution

Owen took the step von Baer had not been willing to take.

In this section, I will show how Owen incorporated a shift from ontogenetic to phylogenetic level into von Baer’s idea of divergent development. At last, he moved forward to a middle-of-the-road concept of evolution that was partly devised under the pressure of Darwin’s achievement.

Although von Baer was not ready to conceive of the idea that species are generated from one another, the evolutionary implications of his theory were not missed in England where the debate about transmutation was in progress. British naturalists were perhaps in need of a theory of species change that did not go as far as French transmutationists did. As a consequence, they made use (to a different extent) of von Baer’s doctrine of development and forcibly appended to it consequences and implications that later, at the end of his

<sup>50</sup> Bowler, 1976, p. 102; Ruse, 1979, p. 135.

<sup>51</sup> See Oppenheimer, 1959, p. 299; Churchill, 1991, p. 9; Russell, 1917, pp. 126 ff.; 229; Lenoir, 1982, pp. 85–86; Nyhart, 1995, pp. 118–119.

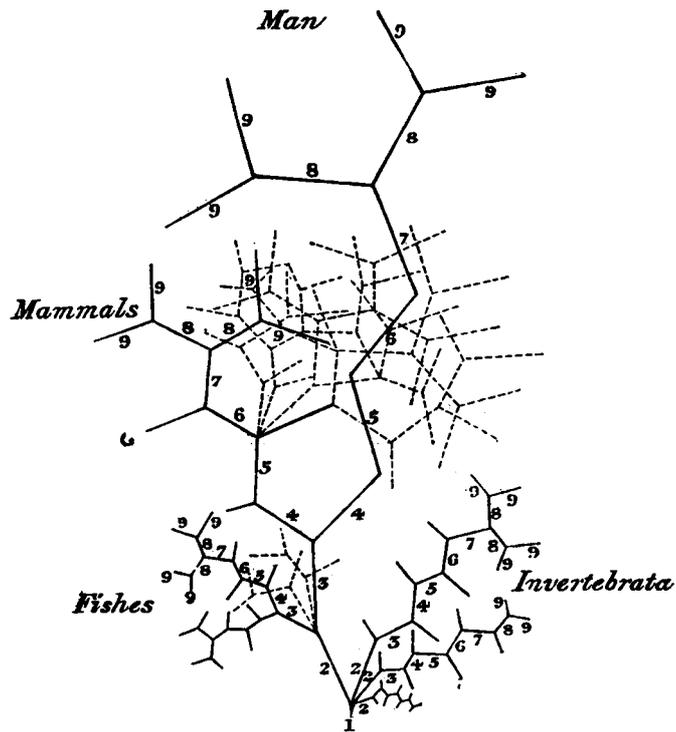


Figure 1. The Tree of animal development. (From Martin Barry, "Further Observations on the Unity of Structure in the Animal Kingdom" [*The Edinburgh New Philosophic Journal* 1836-37], p. 346.)

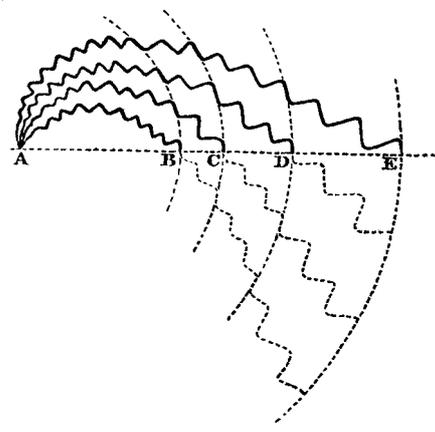


Figure 2. The fundamental unity and the causes of variety in structure. (From Martin Barry, "On the Unity of Structure in the Animal Kingdom." [*The Edinburgh New Philosophic Journal* 1836-37], p. 134.)

life, the author was to reject.<sup>52</sup> Barry,<sup>53</sup> Carpenter and Chambers conveyed through imaginative diagrams<sup>54</sup> the hint that there existed a kind of evolutionary – as Barry’s caption says – “tree of animal development; showing fundamental unity in structure and the causes of variety; the latter consisting in *direction* and *degree* of development.”

Owen wrote almost nothing about evolution before 1859. Historical reconstructions of his view are based on just a few letters and deductions drawn from his major works. In an 1848 letter to the publisher John Chapman, Owen writes that he had refrained from publishing on “secondary causes of species” because he still needed “additional observation and experimental testing.”<sup>55</sup> According to the majority of historians with the exception of N. Rupke, this reticence is due to the fact that Owen seemingly believed in a “naturalistic theory of organic change” but refrained from disclosing it for reasons of opportunism and allegiance to the conservative Anglican Oxbridge establishment.<sup>56</sup> In his fascinating works, Desmond has gone so far as to argue that Owen’s use of von Baer’s embryology was entirely “ideological” and was intended for cashing in an “antitransformist pay-off” and keeping at a distance the horrifying continuity between the ape and the man.<sup>57</sup> I think this conclusion is too drastic as it has been successfully shown by revisionist historiography. We should remember that Owen had discovered no *vera causa* for species change and therefore his cautious attitude was epistemically legitimate. Besides, he had appreciated the 1858 presentation of Darwin’s and Wallace’s evolutionary ideas.<sup>58</sup> Indeed, in 1859 Darwin finally published his grand theory of evolution and after some hesitation, in 1863, Owen fully disclosed his moderate evolutionary “hypothesis” in the *Monograph on the Aye-Aye*.<sup>59</sup> He first rules out natural selection as a possible cause of species change because it is too dependent on “external circumstances.” Subsequently, he describes his concept of “derivation”: “I deem an innate tendency to deviate from parental type, operating through periods of adequate

<sup>52</sup> Oppenheimer, 1959, pp. 316 ff.; Ospovat, 1976, 1981.

<sup>53</sup> Barry, 1836–37b, p. 346 and Figure 1.

<sup>54</sup> E. Richards, 1987, pp. 134 ff. Desmond (1989, p. 338) states that Owen “cannibalized” Barry’s articles in his lectures of 1837. But the articles were just a synthesis, though insightful, of German embryology and French transcendental anatomy, subjects which Owen was already familiar with. Moreover, in the lectures on Invertebrates, (1843, p. 24) Owen frankly acknowledges his debt to Barry. For a further illustration of the concept of divergence see Barry’s diagrams and comments on “causes of [...] variety in structure” in Barry, 1836–37a, pp. 134 ff.

<sup>55</sup> Rev. R. Owen, 1894, pp. 310–311; see also Desmond, 1982, p. 210.

<sup>56</sup> Rupke, 1994; E. Richards, 1987.

<sup>57</sup> Desmond, 1989, pp. 344–351; see also Wilson, 1996.

<sup>58</sup> Owen, 1858, p. 329.

<sup>59</sup> The 1863 monograph is the expanded version of an *Address* delivered to the British Association for the Advancement of Science, the year before.

duration, to be the most probable nature, or way of operation, of the secondary law, whereby species have been derived *one from another*.<sup>60</sup> This statement corresponds *partially* to the principle of divergence which Darwin had incorporated in his theory. Owen maintained that one archetype existed for each of the four main types of animals and that within each type there is a unity of organization that is progressively lost as the individual proceeds towards its specialized form. Thus, evolution is precisely this process of *increasing divergence* from the elementary archetype toward a single species and homology is intended, accordingly, to reveal a pattern (or the clues of unity of organization) in the diverging development. As a matter of fact, divergence implies an increasing and cumulative distance between the archetype and a given species. In the long run, “*the prevalence of unity of organization at early periods [...] is lost in the diversity of special forms as development proceeds*.”<sup>61</sup> Thus, the more the power of the archetype gets progressively lost the more the power of chance or, better, natural history grows. Owen’s stance in favor of divergence was the opposite of Lyell’s,<sup>62</sup> who framed “the formation of races” and the “deviation from an original type” in a uniformitarian process that turns out to be converging in the long run. Let us review the above quotations from *On the Anatomy of Vertebrates* more carefully. On page 807, Owen speaks of an “innate tendency to deviate from parental type,” not from the archetype. And he also speaks of “the secondary law, whereby species have been derived *one from another*.” (emphasis added) In both quotations he refers to an ancestor-descendant relationship, not to participation in an archetype. Although in the context of severe criticism, Asa Gray nevertheless conceded that Owen’s derivation included a genealogical relation between species.<sup>63</sup> Hence, divergent variations should result from the composition of: (1) less-and-less-archetypal (or “ancestral”) characters of a given organism, according to the internal and lawlike pattern of organic development; (2) external haphazard agencies which Owen before 1859 gathered under the rubric of “adaptive force” and after 1859 grudgingly connected to species change.<sup>64</sup> It must be admitted that these implications give strength to Owen’s evolutionary ideas and shorten the conceptual distance between Owen and Darwin.

<sup>60</sup> Owen, 1866–68, III, p. 807; emphasis added.

<sup>61</sup> Owen, 1843, p. 368. Notwithstanding his ambiguity on philosophical or theological matters, Owen was coherent about certain tenets of his scientific worldview like divergence, unity of type, adaptive force. Therefore, when dealing with such questions, I will make no distinction between works pre- and post-1859.

<sup>62</sup> Lyell, 1830–1833, II, pp. 37–39.

<sup>63</sup> Letters to Darwin, May 26, 1863 and July 21, 1863, in Burkhardt *et al.*, 1999, pp. 451, 547.

<sup>64</sup> Owen, 1848, p. 172; 1851, p. 429; 1863a, pp. 60, 66.

To sum up, Owen believed that new species, arranged in a phylogenetic tree according to the principle of divergence, are introduced on the earth throughout the course of natural history. He also believed that evolution's path is "foreknown" by God. Certainly, this is not Darwin's random evolution by natural selection. But there is an evolution of species after all, which is not a surrender to a new scientific fashion. I drew upon the history of developmental embryology to show that Owen took advantage of the transformations undergone by the concept of "evolution" through the second half of the eighteenth century, thereby putting together his doctrine of divergent development from an archetype. Furthermore, if we read in sequence von Baer, Owen and Darwin, we understand that the Darwinian concept of evolution was not born full-fledged merely from Darwin's own speculation. Rather, it is a result of the long historical accumulation on such concepts as development, generation, reproduction, a work that involved both Owen and Darwin, among others.<sup>65</sup> The evidence for evolution was already in place, but nobody save Darwin and Wallace was able to discern it.

Unfortunately, what before the *Origin* would have appeared too audacious after 1859 turned out to be hopelessly too timid.<sup>66</sup> Indeed, "derivation" is not a *vera causa* that may explain "the mystery of mysteries," the origin of species. It depends on a more fundamental causal process, the progressive differentiation of vital force, which has found so far no causal explanation. The Kantian compromise and the separation between secondary causes and primary cause should count as a justification for that shortcoming. Owen's extra-theoretical assumption is that God's Will is the *hypothetical* cause of derivation and variation. But after *The Origin* this scheme is no longer viable. Darwin has provided a *vera causa* for species change, an ultimate cause capable of contending with and replacing the Will of God.<sup>67</sup> The divine agency, if agreed upon as a hypothetical cause and segregated in the realm of metaphysics, cannot compete with natural selection. Therefore, the Kantian compromise is outdated by the rise of Darwinian theory.

What could Owen do to grapple with this problem? He insisted on downgrading both derivation and natural selection to the status of hypotheses,<sup>68</sup>

<sup>65</sup> Hodge, 1985; Bowler, 1988.

<sup>66</sup> E. Richards, 1987.

<sup>67</sup> Hodge, 2000. I am indebted to Jonathan Hodge both for having made clear to me the sense in which Darwinian natural selection is a *vera causa* theory and for letting me preview the manuscript of his paper before publication.

<sup>68</sup> See Owen 1863a: 62; 1866–68, I: XXXIV–XXXVI. It is well known that John Stuart Mill held the same position about Darwinian theory. Owen was however convinced that "derivation" was inductively more confirmed than natural selection (1863a: 65; 1866–68, I: 809). In a poisonous line of his anonymous review, he complained that "Belief is a state of mind, short of actual knowledge" (Owen 1974: 209). Darwin was appalled at this statement.

but this turned out to be no more than a rhetorical trick. Darwin's theory was taken seriously whereas the controversies in which Owen was involved dragged him down into the role of the loser. Neither helped Owen's own policy of patching together "oracular" syntheses of the positions of his opponents and the unchanging reaffirmation of his ideas.<sup>69</sup> On the one hand he conceded attention to the "battle of life" though only in determining the extinction, not the origin, of species. On the other hand, he claimed that a preordained plan regulates the divergence of generations. To sum up, Owen "found himself in the uncomfortable position of wanting to censure Darwin for enunciating his theory of evolution while simultaneously claiming priority for himself."<sup>70</sup> His frustration is candidly expressed in a 1863 letter written to the *Athenaeum* in the course of a dispute with Carpenter. While admitting that he "differ[s] from such a naturalist as Mr. Darwin with respect," Owen formulates in amazingly precise terms the contrast between evolution and morphology: "Neither [Darwinian theory] nor any better attempt to explain the transmutation of species, would entitle the guesser to appropriate to himself the application of the genetic relationship of species to a better comprehension of the cause of unity of plan, and of other established truths in the biological Science."<sup>71</sup> What seemingly offended Owen was "to arrogate for [the Darwinian] hypothesis" the power to explain precisely the morphological phenomena on which he had worked in his lifetime. And that was exactly what happened. Darwin appropriated the archetype under the form of an "ancestor." In addition, according to the unwritten rules of a controversy, Owen's opponents ruthlessly took advantage of his incoherence and we all know the end of the story: he was labelled an obscurantist and a backward essentialist, his evolutionary ideas were overshadowed and morphology fell into disrepute for decades thereafter. Historians have sanctioned the outcome of this process. They have portrayed Owen as a turncoat who first opposed Darwinian theory and then "proceeded to backtrack" and adapted himself to the victory of evolutionism.<sup>72</sup>

I prefer to stress that Richard Owen proposed a coherent evolutionary theory although a certainly less powerful one than Darwin's. In the next section, I will argue that an overall review of Owen's investigations, including his evolutionary account, will reveal the shortcomings of his own essentialism along with the possibility of determining a way out of the limits of such essentialism.

<sup>69</sup> Rupke, 1994, pp. 242 ff.

<sup>70</sup> Hull, 1974, p. 215.

<sup>71</sup> see Burkhardt et al., 1999, pp. 766–767.

<sup>72</sup> MacLeod, 1965, pp. 277 ff.; Ruse, 1979, p. 228. Subsequently Ruse (1996) has taken a more moderate stance.

## 7. Evolution and Essentialism

In 1848, the archetype was not only the first and simplest species in a divergent series but also “the fundamental or general type [...] on which a natural group of animals, the vertebrate for example, is constructed.”<sup>73</sup> Owen had conflated the two notions in such a way that the archetype was equivalent to an essence. It had been conceived by the “beneficent author of all” according to “a general law of conformity” answering to a “Platonic idea or specific organizing principle.”<sup>74</sup> This essence should work as the logical foundation of higher taxa – or “natural groups” as Owen terms them – and provide scientific criteria for their classification. After 1859, according to the derivative hypothesis, the essence should also work to explain the unity in the diversity of evolving species.<sup>75</sup> To this purpose, Owen utilizes Platonic metaphysics and its obscure notion of a participation of material entities in the perfection of ideal forms.

Scholars have repeatedly argued that Owen’s Platonism is confused and incoherent.<sup>76</sup> I think that precisely such an incoherence along with the little number of quotations that refer to Plato should lead us not to take seriously Owen’s Platonism. The largest part of Owen’s scientific research is not affected by Platonism. To start with, the crudity of Owen’s description of Platonic ideas speaks volumes about the reliability of his professed Platonism: “the ἰδέαι of Plato, deemed by that philosopher to be superadded to matter and mind, and which he defined as a sort of models, or moulds in which matter is cast, and which regularly produce the same number and diversity of species.”<sup>77</sup> In any event, the archetype, far from having the completeness and the perfection which is an essential character of Platonic ideas, is by definition the less developed and, as a consequence, the most imperfect specimen of a given type. Therefore, I do not see how the archetype can be counted as a Platonic form.<sup>78</sup> By making archetypes straightforward

<sup>73</sup> Owen, 1848, p. 6.

<sup>74</sup> Owen, 1848, pp. 102, 172.

<sup>75</sup> Owen, 1866–68, III, p. 808. MacLeod (1965, p. 276) carefully notes that “[f]rom at least 1862 onwards, Owen was putting the symbolic *Entwicklung* of the transcendentalists into a material form.”

<sup>76</sup> Rupke, 1994, pp. 196 ff.; Ruse, 1979, pp. 123 ff.; Ospovat, 1976; Amundson, 1998.

<sup>77</sup> Owen, 1848, p. 172.

<sup>78</sup> Platonism also turns out to be at odds with the very theological frame of Owenian morphology. Once the archetype has been created by God – as Owen claims –, what agency should operate development? God again? The Platonic demiurge? Nature? Why do the job twice? This is neither a coherent Platonism nor a coherent theology. Moreover, if one takes Owenian metaphysics as Platonic, that would imply the attribution of perfection to every single species, not only to supreme archetypes. In this way, the reality of development turns out to be denied and Owen should be dragged back to Special Creationism.

thoughts of God, purported Platonism renders unviable the crucial distinction between primary and secondary causes that supports the *inductive* character of Owen's comparative anatomy. Darwinians have emphasized a couple of Owen's misleading statements and have portrayed his notion of unity of type according to Platonic "participation." The aim of this tactic would be the exclusion of Owen from the advancement of evolutionary theory. But the price would be a misreading of the history of evolutionary biology. I rather believe that Rupke is right when he says that the Platonisation of the archetype was a sort of philosophical blanket imposed on Owen by his Cambridge patrons that had, however, no serious philosophical foundation. It was a seductive way of putting science in philosophical clothes, something good to tease clergymen of the time and historians of the future.

I must now proceed to an adequate assessment of the impact of philosophy on Owen's scientific activity. The above analysis of Owen's Platonism might corroborate the conclusion that philosophy for him was nothing but propaganda used only to please his most conservative patrons. Such an opportunistic attitude obstructed his capability to engage in a constructive interaction – like Asa Gray, for example, was able to do – between his own evolutionary hypothesis and Darwin's theory.<sup>79</sup> Certainly, philosophy can be used as propaganda and I am not going to question social-constructivist interpretations of its role. However, to have a full understanding of Owen's views on philosophy we have to consider other interactions regarding Kant and Aristotle that go beyond Owen's rhetorical use or abuse of Plato. While Owen does not address explicitly any part of their philosophical systems (he was a comparative anatomist and not a philosopher, after all) there is no doubt that Kant and Aristotle exerted a great influence on Owen's scientific determinations at certain crucial junctures. I have explained earlier the importance of the "Kantian compromise" before 1859.

An Aristotelian interpretation of the archetype has been flashed as an alternative to the bankruptcy of Owen's Platonism.<sup>80</sup> This proposal is worth careful examination because it gives us a clue for revising the essentialist conception of the archetype by considering it a *projectable* category. It is important to note that Owen does not address Aristotle as a philosopher but as a biologist<sup>81</sup> and that the Aristotelian philosophy of biology is the

<sup>79</sup> Rupke, 1994, p. 204.

<sup>80</sup> Rupke, 1994, p. 197.

<sup>81</sup> Owen knew Aristotle's zoological treatises and the references indicate a first-hand acquaintance with the content. Most of Owen's quotations come from the more descriptive *Historia Animalium* rather than from the sophisticated treatments of biological causality displayed in *De Partibus Animalium* or *De Generatione Animalium* (see Sloan, 1992, pp. 132–133). In November 1837 he wrote a "Preface" for a collection of Hunter's papers that he would later edit. In this "Preface," he accurately examines Hunter's works in comparison

basis of Owen's work on typological classification. Systematic classification interested Owen since the beginning of his career. In the first two Hunterian Lectures of 1837, Aristotle is praised as the founder of comparative anatomy and Owen argues that although Aristotle did not take into due account the law of the subordination of characters in the groups of animals he exemplified, his "natural assemblages" can be recognized as "the basis of later systems" set up by Linnaeus, Cuvier and Hunter.<sup>82</sup> Furthermore Owen, far from using Aristotle's authority to support any form of typological essentialism, takes up Aristotelian empiricism: "[Aristotle] saw that the doctrine of innate Ideas as taught by Plato [...] however flattering for the pride of man [...] must ever keep him in ignorance [...] Aristotle therefore taught that man can acquire general Ideas only by abstraction; – that nothing occurs in the mind which has not first passed through the Senses; and hence that all knowledge necessarily takes its source in Observation and Experiment."<sup>83</sup> Owen's Aristotle seems, therefore, to confirm the methodological empiricism that in the tenets of Victorian Science usually coexisted with natural theology. As far as the theories of classification are concerned, such an empiricism was grounded on the rational belief that all animals were grouped in natural clusters according to hierarchical patterns of relationship. Systematists overlooked speculations on the origin of life<sup>84</sup> and therefore the type or the archetype were less thought of as an essence than as a category or model, effective on different taxonomic levels, under a functional or morphological perspective. Whewell, for example, described the natural "*Method of Type*" and contrasted it with the arbitrary "*Method of Definition*." He pointed out that the inductive arrangements of natural classes are adopted "according to the guidance which Nature herself offers; not prescribing beforehand the marks of each part, but distributing the facts according to the total resemblances." Therefore, definitions "are not absolute and permanent. [...] If we find a case [...] violating our definitions, we do not shut out the case, but alter our definitions."<sup>85</sup> Owen goes so far as to write that the vertebrate archetype is an "artifice" devised for the purpose of classification and morphological analysis. I will go back shortly to this crucial passage.

Such a confirmation of Owen's empiricism via Aristotle would be inconsequential if it did not lead us to dismiss Mayr's idea that Aristotle is the first advocate of typological essentialism. As to that, most systematists still line up

with the most eminent scholars of the time, namely Linnaeus and Cuvier, and quotes Aristotle a number of times as a reference for better understanding of the differences between Hunter and those great systematists.

<sup>82</sup> Owen, 1837; 1859, p. 3.

<sup>83</sup> Owen, 1992, pp. 90–91.

<sup>84</sup> Winsor, 1976.

<sup>85</sup> Whewell, 1847, II, pp. 422, 424.

behind Mayr.<sup>86</sup> But Aristotelian scholars have gone in the opposite direction (Lennox, 1987) arguing that the essence cannot express the whole nature or form of a living being precisely because a living being is a “composite.”<sup>87</sup> This seems enough to make a substantial difference between Aristotelian species and Platonic eternal forms. The issue here is the nature of species qua natural kinds as opposed to the nature of a single species qua individual. James Lennox maintains that Aristotle’s view is *not* that species are eternal in form, but rather that the *individual* partakes in such eternity precisely through the process of biological reproduction. Therefore, the definition of a species is stable not because its qualities can be assembled under one eternal form but because species reproduce according to a steady process of biological generation. Lennox hits a critical point because the process of reproduction is precisely a *homeostatic* mechanism.<sup>88</sup>

### 8. A New Concept of Type

Quite unexpectedly, the analysis of Aristotelian biology has provided grounds for revising our idea of natural kinds and for questioning our stereotypes of Owen and Aristotle as staunch essentialists. Now, let us focus on Owen by reviewing this explicit though isolated passage: “To demonstrate the evidence of the community of organization, I found that the artifice of an archetype vertebrate animal was as essential as that of the archetype plant had been to Goethe . . . and as the like reference to an ‘ideal type’ must be to all who undertake to make intelligible the ‘unity in variety’ pervading any group of organisms.”<sup>89</sup> Here the word “artifice” does not convey any longer the idea of arbitrariness or lawlessness but entails archetypes being taken just as scientific constructions or counterfactual models,<sup>90</sup> not essences. If we simply want to identify the “sameness” or establish a morphological correspondence of two organs we need an “ideal type,” a “Bauplan” that exhibits the common parts representing the sameness or the morphological correspondence.<sup>91</sup> Such constructions, far from being arbitrary or simply conventional

<sup>86</sup> Simpson, 1961; Panchen, 1992, p. 113; see a different opinion in Ridley, 1986, pp. 99 ff.

<sup>87</sup> Balme, 1987.

<sup>88</sup> Lennox, 1985; 2001, p. 128.

<sup>89</sup> Owen, 1866–68, III, p. 788.

<sup>90</sup> Owen (1866: 81–82; 1866–68, III: 789) has stressed the counterfactual nature of the archetype differentiating the “ideal type” from “types supposed to be exemplified by certain living species.” Huxley (1898: 571) accepted that there is no harm in considering the archetype as a “convenient diagram.” This conception of an “ideal type” also runs throughout German culture from Goethe to Max Weber. For another interpretation of the archetype as a law (not an idea) in the context of Coleridgian philosophy see Levere (1981: 98 ff.)

<sup>91</sup> Lankester, 1870; Woodger, 1945.

are justified by epistemically relevant patterns of research and verification. Indeed, nineteenth century systematists were interested in determining “natural” typologies that were not merely nominalistic. And not essentialistic either. Today, philosophers of biology have expanded on this issue. Boyd argues that types and natural kinds are “homeostatically sustained clusters of properties” whose explanatory reliability is based on the accommodation of definitions and relevant inferences to a “disciplinary matrix” of causal structures.<sup>92</sup> Griffiths takes this step further and stresses that a given homeostatic arrangement of properties stems from the homeostatic stability of a biological process or structure.<sup>93</sup>

As early as 1846, following von Baer’s, Goethe’s and Oken’s suggestions, Owen had provided the outline of a self-regulatory developmental process resulting in the formation of homological parts through the serial reproduction of a basic vertebra. Precisely this serial reproduction makes intelligible the “unity in variety” that is the base of a “realistic” typology: “General anatomical science reveals the unity which pervades the diversity, and demonstrates the whole skeleton of man to be the the harmonized sum of a series of essentially similar segments, although each segment differs from the other, and all vary from their archetype.” The recognition of similar elements “throughout the vertebrate series, but also throughout the vertebral segments of the same individual” is just “the determination of serial homologies.”<sup>94</sup> The above passages make credible a non-essentialistic interpretation of Owen typology. Thus, the essence of a natural kind is not necessarily a set of essential qualities. It is rather a causal homeostatic mechanism that is also the basis of the projectability of such a kind or type.

Examples of such a mechanism may be a micro structural constitution, a reproductive process or an ecological niche<sup>95</sup> and – I submit – a set of developmental constraints that produce a homological correspondence. A developmental constraint “is a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition or dynamics of the developmental system.”<sup>96</sup> This is the ideal cause for homologies. To be sure, Owen had no scientific theory for the concept of developmental constraints. But he provides a perceptive description of such a concept: “Specific characters are those that have been recognized in individuals of successive generations, propagating similar individuals as far back as observation has reached: [. . .] the derivative hypothesis

<sup>92</sup> Boyd, 1999, pp. 141, 147–149.

<sup>93</sup> Griffiths, 1999, p. 218.

<sup>94</sup> Owen, 1848, p. 164.

<sup>95</sup> Griffiths, 1997, p. 212.

<sup>96</sup> Maynard Smith et al., 1985.

[admits] their transmissibility and their maintenance for an unknown period through generative powers *obstructive of departure* from such characters.”<sup>97</sup>

## 9. The Archetype and the Homologies

In Owen’s time, homologies might have been subservient to an essentialist world-view and he seems to imply so when stating that “the divine mind which planned the archetype also foreknew all its modifications” or calling general homology “*Bedeutung*” and portraying it as the “essential nature” of an organ.<sup>98</sup> But when we investigate Owen’s anatomical works, the scattered references to the preordaining will of God appear harmlessly rhetorical in comparison with the analytical apparatus that he put together in his studies on the archetype and the homologies.

Owen considers three types of homologies – special, general and serial. Special homology consists in “the correspondence of a part or organ determined by its relative position and connections, with a part or organ in different animals”<sup>99</sup> and it is an operational tool that accommodates Owen’s fledgling approach to evolutionary biology. Indeed, the search for special homologies applies “to a particular organ instead of a particular species [...] by tracing such an organ or system throughout the animal kingdom [...] beyond the animals that *are* to those that *have been*.”<sup>100</sup> Furthermore, a homologue is “subject to modification, like the forms, proportions, functions and very substance of such parts, without their essential homological relationships being thereby obliterated.”<sup>101</sup> Thus a homologue is not an essential characteristic which belongs to every member of a species, but a part or an organ which, *under modification*, belongs to *many* species. As I argued above, this modification consists of an *historical* process of progressive specialization. Hence, special homology is essentially intertwined with evolution. In this view, homology, discernible as “correspondence of pattern,” has been paralleled with the evolutionary concept of replication, discernible as “continuity of pattern.”<sup>102</sup> Although the concepts of special and serial homology were originally formulated in the non-causal frame of typology and morphology, they accommodate an evolutionary analysis of variation and transformation of forms – with its causal commitment. I traced the evolu-

<sup>97</sup> Owen, 1863a, p. 63; my emphasis.

<sup>98</sup> Owen, 1849, pp. 86, 3.

<sup>99</sup> Owen, 1848, p. 7.

<sup>100</sup> Owen, 1866–68, I, p. VI.

<sup>101</sup> Owen, 1848, p. 6.

<sup>102</sup> Roth, 1994, pp. 313–319.

tionary elements in Owen's comparative anatomy precisely to unveil the transitional character of special and serial homology.

Yet, special homologies need a "re-investigation of what is truly constant" in the network of their characters<sup>103</sup> and general homology is indeed "a higher relation . . . in which a part or series of parts stands to the fundamental or general type."<sup>104</sup> Now we can discern the focus of Owen's interest. He does not confine himself to the systematic survey of hierarchical relations and anatomical transformations but seeks a causal explanation of "the unity of plan pervading the vertebrate structure." He explores three possibilities and immediately discards the idea that special homologies are matters of chance. That was obvious. Much less obvious is the rejection of Cuvierian functionalism due to the "inadequacy of the teleological hypotheses to account for the acknowledged concordances expressed . . . by the term special homology."<sup>105</sup> At this very juncture, the departure from Cuvier highlights Owen's passage from teleology to developmental morphology.

Basically, the endoskeletal archetype is viewed as the result of a *developmental* process, originated through the steady reproduction of a fundamental component, the vertebra, by the action of a specific "polarizing force," operating under a "law of vegetative or irrelative repetition."<sup>106</sup> The "vertebrae" are precisely the primary segments of the skeleton and the forms of diverse bones result from variations that are explained by the "adaptive" force and – as I argued above – by evolutionary processes. However, evolution is not the point in question. We are now holding a developmental inquiry based on the following items: a secondary cause, the polarizing force, an elementary unit, the vertebra, and finally a morphological relation between the unit and the whole, the serial homology. The structure of a vertebra or bone is constituted around a few foci or "centers of ossification," the position and the number of which is the basis for homological correspondences.<sup>107</sup> It is remarkable that, with the obvious exception of a genetic organization, they retain certain features that are typical of the "developmental modules" used in contemporary morphology, such as hierarchical organization, connectivity to other modules, temporal transformations.<sup>108</sup> Rather amazingly, serial homology is turning out to be the key-factor of this inquiry. It consists of relations of similarity that can be traced throughout a series of repeating segments in

<sup>103</sup> Owen, 1848, p. 72.

<sup>104</sup> Owen, 1848, p. 7.

<sup>105</sup> Owen, 1848, p. 73. See also Rupke, 1994, p. 166. As a consequence, Owen's frequent mentions of the function of an organ are not to be taken as a rationale for defining correspondences and classifications. Rather, they are used to account for adaptive modifications.

<sup>106</sup> Owen, 1848, p. 172.

<sup>107</sup> Owen, 1848, pp. 28, 73 and passim.

<sup>108</sup> See Raff, 1996, pp. 326–327.

an individual body.<sup>109</sup> To sum up, the vertebrate endo-skeleton results from the interplay of repetitions and divergent or adaptive variations bearing on the vertebra.<sup>110</sup> Therefore, the structure of the archetype, being the result of the serial homology of the vertebra, is due to the action of polarizing force not to the power of Platonic ideas! The following passage sounds like a confirmation: “Now besides the *ιδέαι*, organizing principle, vital property or force which produces the diversity of form belonging to living bodies of the same materials, there appears also to be in counter-operation during the building up of such bodies the polarizing force pervading all space, and to the operation of which force, or mode of force, the similarity of forms, the repetition of parts, the signs of the unity of organization may be mainly ascribed. The Platonic *ιδέαι* or specific organizing principle or force would seem to be *in antagonism* with the general polarizing force.”<sup>111</sup> Thus, essentialism and the Divine Will are only useful in explaining the metaphysical fact, the existence of bio-diversity. The stability and the evolution of forms are to be explained by means of the antagonistic “polarizing force.” Some fluctuation notwithstanding,<sup>112</sup> this pattern will re-emerge in Owen’s evolutionary hypothesis.<sup>113</sup>

As a result of the above situation, Owen comes to be in need of a more formal definition of “vertebra,” one that is more ample than the functional definition and one that fits the multiple forces developmental morphology is requires to treat. Hence, the vertebra becomes the “ideal” vertebra and is no longer defined as a part or an organ “specially adapted for rotatory motion” but a segment of a series, “*one of those segments of endo-skeleton which constitute the axis of the body, and the protecting canals of the nervous and vascular trunk: such a segment may also support diverging appendages.*”<sup>114</sup> And if we also consider the extreme variations that the final vertebrae undergo to shift into the cranial bones according to the vertebral theory of the skull<sup>115</sup> we can understand why Owen ends up harbouring an ideal-typical image of the vertebra and extending it to the archetype. And if we consider that two organs may need to be compared in not perfectly corresponding time-slices of their development or may have different symmetries (radial and bilateral) and different morphological relations or may have undergone extreme transformations,<sup>116</sup> we must admit that the construction of a matrix of correspondences

<sup>109</sup> Owen, 1848, pp. 7, 164.

<sup>110</sup> Owen, 1848, pp. 117, 132.

<sup>111</sup> Owen, 1848, p. 172; emphasis added.

<sup>112</sup> Owen, 1849; see also Amundson, 1998.

<sup>113</sup> Owen, 1866–68, III, p. 789.

<sup>114</sup> Owen, 1848, p. 81, Owen’s emphasis.

<sup>115</sup> Owen, 1848, p. 8.

<sup>116</sup> Woodger, 1945.

(ideal type) is a much more complex business than the outline of an easily memorizable scheme.<sup>117</sup>

## 10. Conclusion

Owen's speculations about the vertebra may represent an effort to exceed the limit of a purely anatomical analysis of the skeletal structure via a developmental morphology. But this way was obstructed both by his limited knowledge of embryology and cytology and by his timid adherence to evolutionism. Again, the analysis of segmentation reveals the *transitional* character of Owen's transcendental morphology. On the one hand, *transcendental* morphology (adult anatomy) was too narrow a domain for *developmental* morphology to unfold its potential; on the other, the study of serial homology calls for a causal mechanism that can be provided only by means of a *developmental* theory of morphogenesis. But such a theory was not available to Owen in 1846. More than this, as we can learn from Bateson's case, developmental morphology took a back seat to the ascent of genetics and molecular biology. Nowadays, evolutionary biologists have downgraded homologies to a simple instrument for systematics<sup>118</sup> and have complained that Owen did not resolve the conflict between polarizing force and Platonic essentialism.<sup>119</sup> They have also pointed out that Darwin underestimated Owen because he had no scientific explanation (in terms of a *vera causa*) of both the stability and the transformation of forms.

But things are changing since persistence of forms and homologies have possibly found a material explanation in terms of developmental constraints.<sup>120</sup> Embryology and developmentalism are enjoying great attention. As far as modification of forms is concerned, Owen's developmental analysis of the archetype's formation by means of serially homologous parts is an example of a meristic process "in which organ arises from organ" according to specific laws.<sup>121</sup> Such laws are intended to make up a theory of morphogenesis dealing with the constraints imposed on genetic material and possible variations that organism can pass through. In this context, the notion of "morphogenetic field," which was so popular among German embryologists in the first half of the twentieth century has been rediscovered. The morphogenetic field should possibly serve as an intermediary concept

<sup>117</sup> See Camardi, forthcoming.

<sup>118</sup> Patterson, 1982; Nelson, 1994.

<sup>119</sup> Hull, 1989, p. 70.

<sup>120</sup> Amundson, 1994; Kaufmann, 1983; Wagner, 1994.

<sup>121</sup> Bateson, 1894, p. 30.

between the genetic and cytological levels or, in other words, it should translate genetic information into spatial entities.<sup>122</sup> However, enduring difficulties are due to the so-called “variability of developmental pathways,” namely to the fact that there is no pattern of correspondence between anatomical, embryological and genetic levels of organization and that a complete theory of development (or of morphogenesis) does not exist yet. In like manner, a morphological theory of organisms is still missing.<sup>123</sup>

Recent scholarship has argued that typology and the problem of morphogenesis were a major concern not only for Owen but also for Huxley, his archenemy.<sup>124</sup> Thus, both historical and theoretical data seem to endorse the basic idea of this paper: once we have shown that a coherent evolutionary sketch exists in Owen’s writings, then Owen’s morphology can unexpectedly disclose its modernity.

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<sup>122</sup> Webster and Goodwin, 1996, p. 129; Gilbert et al., 1996.

<sup>123</sup> Wagner, 1989, p. 1163; Arthur, 1997, pp. 93 ff.; Kaufmann, 1993, p. 538.

<sup>124</sup> Lyons, 1999.

### References

- Amundson, Ron. 1994. “Two Concepts of Constraints: Adaptationism and the Challenge from Developmental Biology.” *Philosophy of Science* 61: 556–578.
- 1998. “Typology Reconsidered: Two Doctrines on the History of Evolutionary Biology.” *Biology and Philosophy* 13: 153–177.
- Appel, Toby. 1987. *The Cuvier-Geoffroy Debate*. Oxford University Press.
- Arthur, Wallace. 1997. *The Origin of Animal Body Plans*. Cambridge University Press.
- Baer, Karl Ernst von. 1853. “Fragments Relating to Philosophical Zoology.” In: Thomas H. Huxley and A. Henfrey (eds.), *Scientific Memoirs, Selected from the Transactions of Foreign Academies of Science*. London: Taylor & Francis; part. engl. transl. of *Beiträge*

- zur Kenntnis der niedern Thiere (1826) and Ueber Entwicklungsgeschichte der Thiere (1828).
- Balme, David. 1987. "Aristotle's Biology Was not Essentialist." In: A. Gotthelf and J.G. Lennox (eds.), *Philosophical Issues in Aristotle's Biology*. Cambridge University Press.
- Barry, Martin. 1836–37a. "On the Unity of Structure in the Animal Kingdom." *The Edinburgh New Philosophic Journal* 22: 116–141.
- 1836–37b. "Further Observations on the Unity of Structure in the Animal Kingdom, and on Congenital Anomalies." *The Edinburgh New Philosophic Journal* 22: 345–364.
- Bateson, William. 1894. *Materials for the Study of Variation*. London: Macmillan. Reprinted 1992, Baltimore: Johns Hopkins University Press.
- Bowler, P. 1973. "Bonnet and Buffon: Theories of Generation and the Problem of Species." *Journal of the History of Biology* 6: 259–281.
- 1975. "The Changing Meaning of Evolution." *Journal of the History of Ideas* 36: 95–115.
- 1976. *Fossils and Progress*. New York: Science History Publications.
- 1988. *The Non-Darwinian Revolution*. Baltimore: Johns Hopkins University Press.
- 1992. "Foreword" to Bateson, William. 1894. *Materials for the Study of Variation*.
- 1996. *Life's Splendid Drama*. University of Chicago Press.
- Boyd, Richard. 1999. "Homeostasis, Species and Higher Taxa." In: Wilson, Robert. 1999. Camardi, G. (Forthcoming). "Ideal Types and Scientific Theories." *Poznan Studies in the Philosophy of Science and the Humanities*.
- Churchill, Frederick B. 1991. "The Rise of Classical Descriptive Embryology." In: Scott F. Gilbert (ed.), *A Conceptual History of Modern Embryology*. New York: Plenum Press.
- Clarke, D.M. 1982. *Descartes' Philosophy of Science*. Manchester University Press.
- Coleman, William. 1976. "Morphology between Type Concept and Descent Theory." *Journal of the History of Medicine* 31: 149–175.
- Desmond, Adrian. 1982. *Archetypes and Ancestors*. University of Chicago Press.
- 1989. *The Politics of Evolution*. University of Chicago Press.
- Di Gregorio, Mario. 1995. "A Wolf in Sheep's Clothing: Carl Gegenbaur, Ernst Haeckel, the Vertebral Theory of the Skull and the Survival of Richard Owen." *Journal of the History of Biology* 28: 247–280.
- Farber, Paul. 1976. "The Type-Concept in Zoology during the First Half of the Nineteenth Century." *Journal of the History of Biology* 9: 93–119.
- Gilbert, Scott, Opitz, J.M. and Raff, R.A. 1996. "Resynthesizing Evolutionary and Developmental Biology." *Developmental Biology* 173: 357–372.
- Ghiselin, Michael. 1974. "A Radical Solution to the Species Problem." *Systematic Zoology* 23: 536–544.
- 1980. "The Failure of Morphology to Assimilate Darwinism." In: Ernst Mayr and W. Provine (eds.), *The Evolutionary Synthesis*, pp. 180–192.
- 1997. *Metaphysics and the Origin of Species*. Albany: State University of New York Press.
- Gould, Steven. 1977. *Ontogeny and Phylogeny*. Cambridge: Harvard University Press.
- Gray, Asa. 1963. *Darwiniana*. Cambridge: Harvard University Press.
- Grene, Marjorie. 1958. "Two Evolutionary Theories." *The British Journal for the Philosophy of Science* 9: 110–127, 185–193.
- Griffiths, Paul. 1997. *What Emotions Really are*. University of Chicago Press.
- 1999. "Squaring the Circle: Natural Kinds with Historical Essences." In: Wilson, Robert. 1999.
- Hall, Brian (ed.). 1994. *Homology. The Hierarchical Basis of Comparative Biology*. San Diego: Academic Press.

- Hodge, Jonathan. 1985. "Darwin as a Lifelong Generation Theorist." In: David Kohn (ed.), *The Darwinian Heritage*. Princeton University Press.
- 2000. "Knowing about Life: Darwin and His Theory of Natural Selection." In: R. Creath and J. Maienschein (eds.), *Biology and Epistemology*. Cambridge University Press.
- Hull, David. 1965. "The Effect of Essentialism on Taxonomy: Two Thousand years of Stasis." *The British Journal for the Philosophy of Science* 15: 314–326; 16: 1–18.
- 1974. *Darwin and His Critics*. University of Chicago Press.
- 1976. "Are Species Really Individuals?" *Systematic Zoology* 25: 174–191.
- 1988. *Science as a Process*. University of Chicago Press.
- 1989. "Darwin and the Nature of Science" (1983); reprinted in Hull, David. *The Metaphysics of Evolution*. Albany: State University of New York Press.
- Hull, David and M. Ruse (eds.). 1998. *The Philosophy of Biology*. Oxford University Press.
- Huxley, Thomas H. 1898. "On the Theory of the Vertebrate Skull" (1858). In: M. Foster and E.R. Lankester (eds.), *Scientific Memoirs of T. H. Huxley*, vol. I. London: Mac Millan, pp. 539–581.
- Kant, Immanuel. 1952. *Critique of Judgement*, engl. transl. J. C. Meredith. Oxford: Clarendon Press.
- Kauffman, Stuart. 1983. "Developmental Constraints: Internal Factors in Evolution." Brian Goodwin, N. Holder and C. Wylie (eds.), *Development and Evolution*. Cambridge University Press.
- 1993. *The Origins of Order*. Oxford University Press.
- Lankester, E. Ray. 1870. "On the Use of the Term Homology in Modern Zoology, and the Distinction between Homogenetic and Homoplastic Agreements." *Annals and Magazine of Natural History*, 4th series, VI: 34–43.
- Lennox, James G. 1985. "Are Aristotelian Species Eternal?" In: A. Gotthelf (ed.), *Aristotle on Nature and Living Things: Philosophical and Historical Studies*. Pittsburgh: Mathesis Publications.
- 1987. "Kinds, Form of Kinds and the More and the Less in Aristotle's Biology." In: A. Gotthelf and J.G. Lennox (eds.), *Philosophical Issues in Aristotle's Biology*. Cambridge University Press.
- 2001. *Aristotle's Philosophy of Biology*. Cambridge University Press.
- Lenoir, Timothy. 1981. "The Göttingen School and the Development of Transcendental Naturphilosophie in the Romantic Era." *Studies in the History of Biology*, vol. 5. Baltimore: The John Hopkins Press.
- 1982. *The Strategy of Life. Teleology and Mechanism in Nineteenth-Century German Biology*. University of Chicago Press.
- Levere, Trevor. 1981. *Poetry Realized in Nature. S. T. Coleridge and early 19th Century Science*. Cambridge University Press.
- Lyell Charles. 1830–1833. *Principles of Geology*, 3 vols. London: Murray. Reprinted 1990, University of Chicago Press.
- Lyons, Sherrie. 1999. *Thomas Henry Huxley. The Evolution of a Scientist*. Amherst: Prometheus Books.
- MacLeod, Roy M. 1965. "Evolutionism and Richard Owen, 1830–1868: An Episode in Darwin's Century." *Isis* 56: 259–280.
- Maynard Smith, John et al. 1985. "Developmental Constraints and Evolution." *Quarterly Review of Biology* 60: 265–287.
- Mayr, Ernst. 1969. *Principles of Systematic Zoology*. New York: McGraw-Hill.
- 1975. *Evolution and the Diversity of Life*. Cambridge Mass.: Harvard University press.

- Mayr, Ernst and W. Provine 1980. *The Evolutionary Synthesis*. Cambridge Mass.: Harvard University Press.
- Needham, John. 1959. *A History of Embryology*. New York: Schuman.
- Nelson, G. 1994. "Homology and Systematics." In: Hall, Brian. 1994.
- Nyhart, Lynn. 1995. *Biology takes Form*. University of Chicago Press.
- Oppenheimer, Jane. 1959. "An Embryological enigma in *The Origin of Species*." In: B. Glass, O. Temkin and W.L. Straus (eds.), *Forerunners of Darwin*. Baltimore: The John Hopkins Press.
- Ospovat, Dov. 1976. "The Influence of Karl Ernst von Baer Embryology, 1828–1859." *Journal of the History of Biology* 9: 1–28.
- 1981. *The Development of Darwin's Theory*. Cambridge University Press.
- Owen, Richard. 1837. "Preface" and Notes to Hunter, John. 1840. *Observations on Certain Parts of Animal Economy*. Philadelphia: Haswell, Barrington and Haswell.
- 1843. *Lectures on the Comparative Anatomy and Physiology of Invertebrates Animals*. London: Longmans Green.
- 1848. *On the Archetype and Homologies of the Vertebrate Skeleton*. London: Van Voorst.
- 1849. *On the Nature of the Limb*. London: Van Voorst.
- 1851. "Lyell – on Life and its Successive Development." *Quarterly Review* 87: 412–451.
- 1853. "Generalizations of Comparative Anatomy." *Quarterly Review* 93: 46–83.
- 1859. *On the Classification and Geographical Distribution of the Mammalia*. London: Parker.
- 1860. *Paleontology*. Edinburgh: Black.
- 1863a. *Monograph on the Aye-Aye*. London: Taylor and Francis.
- 1863b. "Origin of Species." *Athenæum*, 2 May: 586–587.
- 1866. "On the Osteology of the Dodo." *Transaction of the Zoological Society* VI: 49–83.
- 1866–68. *On the Anatomy of Vertebrates*, 3 Vols. London: Longmans Green.
- 1884. "Oken, Lorenz." *Encyclopaedia Britannica*, IX ed., vol. XVII: 749–752.
- 1970. "Presidential Address to B.A.A.S." Leeds, 1858. Repr. in G. Basalla, W. Coleman and R. H. Kargon (eds.), *Victorian Science*. Garden City: Doubleday & C.
- 1974. "Darwin on the Origin of Species." *Edinburgh Review*. 1860. 11: 487–532. Repr. in Hull. 1974: 175–213.
- 1992. *The Hunterian Lectures in Comparative Anatomy* (1837). University of Chicago Press.
- Owen, Rev. Richard. 1894. *The Life of Richard Owen*. London: Murray.
- Panchen, Alec L. 1992. *Classification, Evolution and the Nature of Biology*. Cambridge University Press.
- Patterson C. 1982, "Morphological Characters and Homology." In: K. Joysey and A. Friday (eds.), *Problems of Phylogenetic Reconstruction*. London: Academic Press.
- Raff, Rudolf. 1996. *The Shape of Life. Genes, Development and the Evolution of Animal Form*. University of Chicago Press.
- Richards, Evelleen. 1987. "A Question of Property Rights: Richard Owen's Evolutionism Reassessed." *The British Journal for the History of Science* 20: 129–171.
- Richards, Robert. 1992. *The Meaning of Evolution*. University of Chicago Press.
- Ridley, Mark. 1986a. *Evolution and Classification*. New York: Longman.
- 1986b. "Embryology and Classical Zoology in Great Britain." In: T. Horder, J. Witkowski and C. Wylie (eds.), *A History of Embryology*. Cambridge University Press.
- Roe, Shirley. 1981. *Matter, Life and Generation. 18th Century Embriology and the Haller-Wolff Debate*. Cambridge University press.

- Roth, Louise. 1994. "Within and between Organism: Replicators, Lineages and Homologues." In: Hall, Brian. 1994.
- Rupke, Nicolaas. 1994. *Richard Owen Victorian Naturalist*. New Haven: Yale University Press.
- Ruse, Michael. 1979. *The Darwinian Revolution*. University of Chicago Press.
- . 1996. *Monad to Man. The Concept of Progress in Evolutionary Biology*. Cambridge: Harvard University Press.
- Russell, E.S. 1917. *Form and Function*. New York: Dutton & C.
- Shubin, Neil. 1994. "History, Ontogeny and evolution of the Archetype." In: Hall, Brian. 1994.
- Simpson, George G. 1961. *Principles of Animal Taxonomy*. New York: Columbia University Press.
- Sloan, Philip. 1979. "Buffon, German Biology and the Historical Interpretation of Biological Species." *The British Journal for the History of Science* 12: 109–153.
- . 1992. "On the Edge of Evolution." Introductory Essay to Owen, Richard. 1992.
- Wagner, Günther. 1989. "The Origin of Morphological Characters and the Biological Basis of Homology." *Evolution* 43: 1157–1171.
- . 1994. "Homology and the Mechanism of Development." In: Hall, Brian. 1994.
- Webster, Gerry and Brian Goodwin. 1996. *Form and Transformation: Generative and Relational Principles in Biology*. Cambridge University Press.
- Whewell, William. 1847. *Philosophy of Inductive Sciences*, 2 vols. London: Parker; Reprint 1967. New York: Johnson Repr.
- Wilson, Leonard. 1996. "The Gorilla and the Question of Human Origins: The Brain Controversy." *Journal of the History of Medicine* 51: 184–207.
- Wilson, Robert A. 1999. *Species. New Interdisciplinary Essays*. Cambridge, Mass.: MIT Press.
- Winsor, Mary. 1976. *Starfish, Jellyfish and the Order of Life*. New Haven: Yale University Press.
- Woodger, J. H. 1945. "On Biological Transformations." In: W. Le Gros Clark and P. Medawar (eds.), *Essays on Growth and Form Presented to D'Arcy W. Thompson*. Oxford: Clarendon Press.

