Essay: The Cuvier-Geoffroy Debate [1]

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In 1830, a dispute erupted in the halls of l'Académie des Sciences in Paris between the two most prominent anatomists of the nineteenth century. Georges Cuvier [4] and Étienne Geoffroy Saint-Hilaire, [5] once friends and colleagues at the Paris Museum, became arch rivals after this historical episode. Like many important disputes in the history of science, this debate echoes several points of contrasts between the two thinkers. The two French naturalists not only disagreed about what sorts of comparisons between vertebrates were acceptable, but also about which principles ought to underlie a rational system of animal taxonomy and guide the study of animal anatomy. Digging deeper into their differences, their particular disagreements over specific issues within zoology and anatomy culminated in the articulation of two competing and divergent philosophical views on the aims and methods of the life sciences. The emergence of these two distinct positions has had a lasting impact in the development of evolutionary and developmental biology. This essay will provide an overview of the conceptual themes of the debate, its implications for the development of the life sciences, and its role in the history of embryology [6] and developmental biology.

1. The Debate: Conceptual Themes

Debates in the history of science that are still studied and discussed centuries after they have occurred tend to be rich in conceptual content and philosophical implications. The Cuvier-Geoffroy debate is a perfect example. Historical interpretations of the debate, including E.S. Russell's *Form and Function* [7] (1917), often stress the divergence between Cuvier's teleological or functional approach to comparative anatomy and Geoffroy's emphasis on morphology [8]. The "form vs. function" distinction played a critical role in the two thinkers' articulation of the rational principles underlying their systems of classification and guiding their comparative work. Second, their functionalist and structuralist approaches, respectively, represented the development of two distinct research programs in nineteenth-century natural history [9]: functional anatomy and philosophical (or transcendental) anatomy, which reflect some of the major themes in the intellectual currents of eighteenth-century and early nineteenth-century natural history [9]. Third, their commitment to distinct research programs in anatomy and zoology escalated into a larger dispute about the role of hypothesis in scientific thinking, a prevailing theme in nineteenth-century philosophy of science that affected theories in astronomy, chemistry, geology and biology. And lastly, the two Académeciens disagreed about the possibility of the transformation of species, i.e. evolution [10]. However, contrary to what is often assumed, the topic of evolution [10] did not occupy a central position in the debate; rather, Cuvier was dismissive of the issue as he tended to view it as merely another problematic corollary of Geoffroy's penchant for unbridled theorizing. The first section of this essay will delineate these four conceptual themes of the debate.

2. Function vs. Form: Rational Principles, Taxonomy, & Comparative Anatomy

In his essay, *The Titular Bishop of Titiopolis*, the late paleontologist and evolutionary biologist Stephen Jay Gould [11] remarked: "Historical changes in classification are the fossilized indicators of conceptual revolutions" (Gould 1983, 72). The Cuvier-Geoffroy debate represents an excellent exemplar of the stakes involved in deciding how to cut nature at its joints. During the late eighteenth and nineteenth century, systematizing natural history [9] meant properly classifying species of organisms according to rational principles. When Cuvier first arrived in Paris in 1795, he was charged with collecting, comparing and classifying animal specimens for the newly formed National Museum of Natural History in Paris. Cuvier pioneered a system of classification of animal anatomy based on a firm teleological view of life in which all distinct animal forms were explained in terms of *function*. Emphasis on teleology in the life sciences was not new; it had been a part of biological explanations since Aristotle [12]. However, Cuvier's strict functionalist approach led to a classification of the animal kingdom that diverged from the prevailing view in the eighteenth century of the *scala naturae*, or the great chain of being, in which there was thought to be a natural progression from the simplest life forms towards more complex animals, with humankind occupying the dominant position of the hierarchy. Cuvier proposed four separate categories, or *embranchements* [3] (branches), in the animal kingdom that he identified by means of his two main principles—the *conditions of existence* and the *correlation of parts*—and a corollary principle—the *subordination of parts*.

Cuvier's regulative principles of anatomy are found, most notably, in his 1817 work, *Le Règne Animal* (The Animal Kingdom), but they also appear in his collection, *Leçons d'anatomie comparée* (Lessons on Comparative Anatomy) (1800-1805). The principle of the *correlation of parts* underscored the functional relationships that exist between organs to produce a viable [13] organism. According to this principle, if one were to discover the fossil remains of sharp claws, one could rationally infer that they belonged to a carnivore, and further infer that it had teeth with the structure necessary to seize and tear up prey. The principle of the *conditions of existence* reinforced the idea of the functional integration between parts of animals by further requiring that these parts be in harmony with the animals' lifestyle according to its environment. In other words, there must be a relationship of adaptedness between organic form and environment. The additional principle of *the subordination of characters* (which had been introduced in botany before Cuvier) placed an emphasis on those parts of the organism that were essential for its mode of life, such as the nervous system, the circulatory system and respiratory system, over other subordinate characteristics. So, for example, birds [14] and mammals share certain respiratory characteristics and differ from fish [15] by having complex pulmonary circulation which provides the extra energy needed to sustain movement in non-aquatic environments (Appel 1987, 46). Cuvier argued that taxonomy should be based on these kinds of essential and functional characteristics.

Cuvier's theoretical principles led him to classify the animal kingdom into four main classes, or *embranchements* [3]. Before Cuvier, naturalists and anatomists divided the animal kingdom into two main groups: the vertebrates and invertebrates. Cuvier's divided the invertebrates into three additional branches: Articulata (arthropods and segmented worms [16]), Mollusca (which included all the bilaterally symmetrical invertebrates), and Radiata (cnidarians and echinoderms). Cuvier insisted that the four categories represented natural kinds in the animal kingdom, and that individuals in one category could never transform into another category over time. It would be contrary to all of his rational principles, he believed, to think that an organism could change one part of its structure without any repercussions to its functionally-integrated whole. If an organism's structure could evolve piecemeal and slowly transform into new forms, as suggested, it would not be able to sustain itself. It was evident, to Cuvier, that nature was purposeful in its designs.

Cuvier welcomed the comparison of his principles with the notion of Aristotelian final causes, as he understood his principles to be working together to ensure both an internal harmony of anatomical organization [17] and an external harmony with the animal's environment, both of which are necessary for the existence of self-organized and functionally-integrated living beings. Moreover, these principles provided regulative standards for the practice of comparative anatomy by allowing anatomists to infer structures from the functional requirements of an animal's internal organization [17] and its adaptive needs, and to explain the presence of these structures, at the same time.

Geoffroy, on the other hand, prioritized form over function, and argued that Cuvier's principles could not serve to elucidate the obvious structural affinities between species. He regarded the *structure* of an animal's anatomy as providing insight into the kinds of relations between taxa that could properly serve as the foundation for the study of anatomy. In his *Philosophie anatomique* (Philosophy of Anatomy or Anatomical Philosophy), published in 1818, Geoffroy challenged Cuvier's authority on animal classification, and proposed instead a system of classification and description of anatomy based on the *unity of plan* (also referred to as *the unity of organic composition*). Geoffroy's principle of unity was supported by his theory of *analogies* (now referred to as *homologies*). For Geoffroy, analogues (now *homologues*) between species depicted similarities in the structure of animals regardless of their function or purpose, or whether they differed in shape and other secondary details. His theory of analogies was influenced by the transcendental approach to comparative anatomy, current in Germany during the first two decades of the nineteenth century, which looked for similarities in structural organization [17] between different parts of the *same* animal. Geoffroy, alternatively, was more fascinated by the structural similarities in *different* animals. In 1843, the British anatomist, Richard Owen [18], clarified this distinction, describing Geoffroy's insight as *homologues* and naming the previous *analogues*. As a result, it is common to refer to Geoffroy's comparisons as depicting homologous parts, although the concept of homology underwent further change after Darwin's theory of common descent. Geoffroy's pre-Darwinian understanding of the similarities in the connection of anatomical features in different species did not assume common descent. Rather, he understood the structural similarities to indicate an ideal pattern, depicting his principle of unity of plan, and serving as a sort of universal law of nature that could explain away organic diversity.

Geoffroy's system of classification featured a morphological approach to comparative anatomy guided by his *principle of connections* and his *law of balance* or *compensation*. The principle of connections highlighted the relations between elements, such as bones, within anatomical structures that gave rise to similar characters, and it articulated the means by which morphologists could discover homologies between different species. He illustrated his principle as follows:

Nature, I have said above, tends to cause the same organs to reappear in the same number and in the same relations, and it varies to an infinite degree only in their form. According to this principle, in the determination [19] of the bones of the head of fishes, I will never have to decide according to considerations of their form, but only according to that of their connections (quoted in Appel 1987, 89; Panchen 2001, 42).

The secondary differences observed between homologues were then explained away by Geoffroy's law of compensation that presumed that when one feature becomes overdeveloped within an integrated structure, the other features would be reduced to compensate for the change in form. This law was a consequence of his belief that "*nature works constantly with the same materials. She is ingenious to vary only the forms. As if, in fact, she were restricted to the [same] primitive ideas, one sees her tend always to cause the same elements to reappear, in the same number, in the same circumstances, and with the same connections*" (quoted in Appel 1987, 89).

Geoffroy's principle of unity entailed that anatomists ought to assume and look for morphological similarities in their comparative work and subordinate any considerations of the final causes of living beings. That is, any consideration of the animal's particular lifestyle and conditions of existence in a particular environment was rendered ancillary. Geoffroy was in fact basing his approach to the study of animal anatomy on a complete reversion of Cuvier's assumption of the causal order between form and function. Whereas Cuvier understood an animal's *function*, its mode of life, as governing the animal's structure, allowing the animal to fulfill its purpose; Geoffroy understood an animal's anatomical *structure* to determine, perhaps constrain, its ability to function and adapt to particular environments. The emphasis on form and structural similarities across species led Geoffroy to develop a research program focused on a new set of questions about animal anatomy, broadening the kinds of comparisons that anatomists could entertain. Consequently, these bold comparisons challenged Cuvier's established division of the animal kingdom into four distinct *embranchments*.

Because of the differences in the rational principles used to justify their systems of classification and methods of comparison, the dispute between Cuvier and Geoffroy that began in April 1830 at the Académie concerning the proper description of the anatomy of molluscs came as no big surprise. Although Cuvier seemed at first tolerant of Geoffroy's work at the Paris Museum, he became increasingly aggravated by Geoffroy's insistence on morphological considerations in comparative anatomy.

The dispute was instigated when Geoffroy presented a review of a paper by two naturalists, Meyranx and Laurencet, on the anatomical organization [17] of molluscs, insinuating that the factual descriptions in the paper suggested a way to bridge the gap between vertebrates and molluscs by emphasizing the similarities in the structure and organization [17] of organs in the body plans of cephalopods and vertebrates, and claiming that their paper supported his theoretical conclusions about the unity of organic composition. Geoffroy, knowing that Cuvier had produced perhaps the most extensive scientific work on mollusc anatomy in his *Mémoires pour servir à l'histoire et à l'anatomie des mollusques*(Memoires to serve as the history and anatomy of molluscs) published in 1817, intentionally baited Cuvier into the debate by claiming that while the author of that remarkable work on molluscs was commendable in his efforts to trace all the distinct anatomical properties of the cephalopod [20], this new work on molluscs indicated that comparative anatomy was now entering a new, more sophisticated stage in which the similarities between species would occupy a central role in an effort to gain "knowledge of the philosophical resemblances of beings" (Appel 1987, 146).

These remarks led to Cuvier's first response to Geoffroy in the 1830 debate. Cuvier decided to attack Geoffroy's morphological approach by bringing into question the very principle on which his approach was based: the unity of organic composition (Appel 1987, 148). Cuvier argued that Geoffroy's concept of the unity of composition could not serve as a regulative principle in comparative anatomy because it was too vague to be a useful heuristic. According to Cuvier, it would be absurd to think that Geoffroy's principle of unity signified a relation of *identity* between the actual structures of different species. That is, different animals, such as a bird and a fish [15], could not possibly be composed of the same organs arranged in exactly the same way, given their different lifestyles. Thus, Geoffroy's principle of unity could only signify vague *analogies* between the anatomical organizations of different species. But, if his principle could only point to vague analogies between different animals, then Geoffroy was not offering anything new to the study of zoology or anatomy because Aristotle [12] himself had described the possibility of certain resemblances between species. Besides, Cuvier argued, the discovery of resemblances between animals could only make sense in light of his own regulative principle – the principle of the conditions of existence – by which the possibility of resemblance could be derived, or explained, by appeal to a functional analysis of the internal integration of an animal's anatomy and the harmony, or fit, with its environmental conditions.

Having successfully drawn Cuvier into a debate, and acknowledging Cuvier's superior skill in analyzing mollusc anatomy, Geoffroy diverted the dispute concerning the legitimacy and fruitfulness of comparisons between mollusc and vertebrate anatomy towards a larger examination concerning the philosophical significance of prioritizing either form (morphology [8]) or function (teleology) in studying and systematizing knowledge in natural history [9].

3. Functional Anatomy vs. Philosophical Anatomy: Scientific Explanation in Comparative Anatomy

Instead of responding directly to Cuvier's challenge to his principle of unity, Geoffroy chose to defend his theory of analogies and argue that the search for similarity in structure provided a more practical and fruitful method for scientific progress in anatomy. In March 1830, Geoffroy presented a reply to Cuvier's criticism in "On the Theory of Analogues, to Establish Its Novelty as a Doctrine, and Its Practical Utility as an Instrument" (Appel 1987, 149). Geoffroy maintained that his morphological approach to anatomy provided a rigorous method for novel scientific discoveries. As an example, he offered the comparisons between the hyoid bones in human beings and cats (Appel 1987, 149-150). Under the teleological, or functionalist, view, the structures were believed to be similar only to the extent that they performed the same function in both human beings and cats; i.e. supporting movement of the tongue, the pharynx and the larynx. As a consequence, both structures were labeled as the hyoid bone. However, under the structuralist view supported by Geoffroy, the functional comparison grounding the homology was considered incomplete. As the hyoid was composed of nine pieces in the cat and only five small pieces in human beings, Geoffroy argued that it was necessary to align these pieces so that anatomists could first figure out which five pieces in the cat hyoid corresponded to the five pieces in the human hyoid, and then account for the four missing pieces in the human counterpart. Geoffroy believed that the missing pieces in the human hyoid were the result of humans' bipedal position, and that the other rudimentary pieces could be located in other parts of the human skull. To support his hypothesis, Geoffroy observed the development of these bone structures in the human fetus [21]. He then claimed that, because his method centered on form, he was able to make this novel scientific discovery in comparative anatomy. Therefore, he insisted, considerations of philosophical resemblances in anatomy were essential to develop the field. Functional anatomy, as practiced by Cuvier and his students, was becoming obsolete because it severely limited the kinds of questions that could be raised and answered in the study of comparative anatomy.

Cuvier initially responded by challenging some of Geoffroy's claims about the structure of the hyoid, pointing out that the hyoid structures in mammals, birds [14], and reptiles were all very different, while many animals had no hyoid bone at all (Appel 1987, 150). According to Cuvier, the abundance of differences gave good reason to dismiss Geoffroy's principle of unity and his theory of analogies because it was inapplicable in any general or principled way. Geoffroy did not respond by challenging Cuvier's anatomical claims about hyoid bones. His focus was now turned to the philosophical and methodological implications of their divergent views, declaring in his memoir: "It is a question of philosophy that divides us" (Appel 1987, 152).

Geoffroy intended to direct the dispute towards their conflicting views on the proper goals of anatomy andnatural history [9]. Geoffroy believed that his methodology of searching for resemblances within apparent dissimilarities could provide general scientific explanations for the observed diversity of structures in different classes of organisms. He preferred to steer clear of final causes, in favor of a reliance on structure, to define function. If anatomy was going to become a fruitful scientific research program in the nineteenth century, then a new explanatory agenda prioritizing morphology [8] was needed to replace the old research of anatomy based on teleological principles of function. Geoffroy's anatomical philosophy led him to adopt several theoretical commitments that, once drawn out and made explicit, served to widen the gulf between himself and Cuvier even further.

Geoffroy's research program delineated new epistemic goals that would require the explanatory tools of experimental embryology [6]. Although Geoffroy performed many of his own experiments inembryology [6], he was also to a great extent influenced by the theory of *arrests of development*, advocated by his friend, Étienne Reynaud Augustin Serres. Serres aspired to discover the morphological laws of animal development; what he called "transcendental anatomy." Geoffroy believed that Serres' research could help support his theory of analogies, and his focus on finding homologies across different animal taxa, by providing even more empirical evidence of similarities in embryonic forms leading to apparent dissimilarities in adult forms. Serres had been influenced by the theoretical developments in German biology, most notably by early versions of the recapitulation theory [22] proposed by Carl Friedrich Kielmeyer in 1793 and Johann Friedrich Meckel's theory of arrests of development in 1811. Like Meckel, Serres believed that it was necessary to study the transitional forms of embryos to understand the permanent adult forms of vertebrates. Doing so, he assumed, would reveal that the developed forms of the lower classes of animals – invertebrates, for example –mimicked the intermediate embryonic forms of higher vertebrates. This idea of development was expressed in the Meckel-Serres Law [23], and distinguished from the later evolutionary accounts of the recapitulation theory [22] proposed by Ernst Haeckel [24]. Serres' idea of arrests of development, and Geoffroy's understanding of it, was transcendental rather than evolutionary. For transcendental anatomists like Serres and Geoffroy, the semblances discovered in embryonic stages reflected a particular metaphysical view of life and a philosophy of anatomy exemplified by Geoffroy's principle of the unity of composition. The similarities inferred by these kinds of embryological studies did not necessarily represent the similarities of structure between vertebrates and invertebrates as an actual empirical fact of transformation from one species to another (i.e. an evolutionary account), but rather they represented the abstraction of an ideal type required by anatomists to form general laws of development and morphology [8] in biology (i.e. a transcendental account). In other words, the principle of unity, the theory of analogies, the theory of arrests of development and the search for homologies were all regulative principles that served as conditions for the possibility of scientific discoveries in the field of anatomy.

The kind of theorizing exemplified in Geoffroy's philosophical anatomy went beyond the collection of anatomical observations and the comparison of functional similarities that Cuvier espoused in his view of functional anatomy. General morphological laws weren't required in Cuvier's worldview of anatomy because the function of anatomical structures, given an animal's conditions of existence, sufficed to explain their presence in nature. Cuvier insisted that the teleological explanations of functional anatomy relied on nothing more than the empirical facts of anatomy. Moreover, according to Cuvier, Geoffroy's principles of unity of plan placed unnecessary restrictions on God's omnipotence in that it seemed to presuppose that the Creator was constrained to modifying the same material from a preordained type. To think this was to place serious limits on God's abilities. For these reasons, Cuvier believed that the teleological explanations of functional anatomy provided a better model to pursue scientific research in anatomy and proved consistent with a certain theological understanding of God's designs. Ironically, Geoffroy turned this line of argument against Cuvier by claiming that metaphysical speculations about God's intentions had no place in scientific arguments, while Cuvier, in turn, chastised Geoffroy for what he perceived to be an unsophisticated materialism [25] reminiscent of Lamarck and other eighteenth-century thinkers.

Cuvier's functional anatomy and Geoffroy's philosophical anatomy represented divergent research programs in comparative anatomy and natural history [9]. The discordance in their theoretical commitments is apparent in the tensions between function vs. form, teleological explanations vs. transcendental explanations, and observation vs. abstraction. This last struggle implied a profound disagreement over the very nature of the scientific method, and represented perhaps the highest stakes for the future of the life science.

4. Observation vs. Hypothesis: The Role of Induction in 19th Century Science

While Cuvier insisted that young anatomists refrain from conjecturing grand theories and confine themselves to amassing positive facts, Geoffroy demanded that young anatomists go beyond Cuvier's stringent empiricism. Geoffroy believed that a productive research program leading to novel discoveries in anatomy required the use of one's faculty of judgment, in addition to providing accurate descriptions of facts. Their disagreements over the role of hypothesis and theory construction in science and about the limits of empiricism were common themes throughout nineteenth century philosophy of science.

As mentioned in the previous section, Geoffroy's principle of unity was based on a transcendental argument for the possibility of scientific knowledge in natural history [9]. This view of scientific knowledge originated in Immanuel Kant's Copernican revolution in metaphysics. In his *Critique of Pure Reason*, first published in 1781, Kant established a philosophical system in which he reconciled Hume's radical skepticism about induction [26] with Newton's discoveries of the physical laws of nature, by synthesizing aspects of rationalism – the view that the source of our knowledge is innate and originates in our ideas – and empiricism – the view that our minds are *tabulae rasae*, or blank slates, and all of our knowledge about the world comes from our experiences of it. Kant argued that the natural world cannot be entirely independent of our minds; rather, the world is in part constituted by the very structure of our understanding. Kant thought that natural philosophy—what we now call science—is not merely a collection of facts. Scientific knowledge requires metaphysical principles that cannot be justified by inference from experience alone, as these principles themselves are part of the conditions that make our experience of the natural world possible (McGrew *et al.* 2009, 188).

Kant's legacy to natural philosophy and history was a new argumentative form: the transcendental argument. Nineteenth-century philosopher of science, William Whewell, embraced this view of science, and its implications for scientific methodology. Whewell's philosophy of science serves well to illustrate the emphasis Geoffroy placed on the role of hypothesis in scientific methodology, and more importantly, on the process of induction [26] in forming generalities, or laws of nature, about collections of observations. Like Kant, Whewell sought a middle way between pure rationalism and strict empiricism. The production of scientific knowledge required what Whewell called *fundamental ideas*, which are independent of experience and provide the structure for our scientific concepts. According to Whewell, all of our observations are necessarily idea- or theory-laden. His fundamental ideas were not, like Kant, conditions for our experience, but rather conditions for gaining scientific knowledge. Fundamental ideas emerged in the course of the development or maturation of a scientific field and provided objective knowledge of the world.

Whewell's fundamental ideas allowed for a broader role for the process ofinduction [26] than that of the empiricist's use of induction [26]. The latter viewed the process ofinduction [26] as merely the act of reasoning from an observed uniformity to unobserved or future cases. Whewell understood induction [26] as a process which adds a new element by combining the enumeration of instances from the observed uniformity in a particular way. He called this process of induction [26] *colligation* and maintained that it can be used to discover the universal laws underlying the observed uniformity in nature by super-imposing the appropriate organizing concept on the collection of particular empirical facts (Snyder 2009). For example, in the 16th century, Tycho Brahe had already observed the points of the Martian orbit, but it was Johannes Kepler who *colligated* those points by using the conception [27] of an elliptical curve to discover the shape of planetary orbits. Whewell argued that true scientific discoveries where not only the result of collecting new observable facts, but the result of forming and applying the appropriate conception [27], or fundamental idea, to those empirical facts. Thus, Whewell believed that making inductive inference to unobservable properties or entities was an indispensable aspect of the scientific process.

Kant and Whewell, and most other natural philosophers of the eighteenth and nineteenth centuries, embraced Newton's work as the epitome of scientific success and attempted to develop their philosophical systems in such a way as to demonstrate the normative reasoning involved in attaining this standard. Newton too had reflected on his work and provided his own philosophical reflections on how science should proceed. Newton advocated that theorizing in science should be held to a minimum. Newton's highest achievement in the *Principia* was his law of universal gravitation. However, Newton declined to "feign hypotheses" regarding the cause of gravitation, explaining that it was sufficient to establish that the force existed and that its effects can be treated through mathematical representation (McGrew *et al.* 2009, 105). The publication of Newton's *magnum opus* had a great deal of influence on the development of science in Europe for subsequent centuries. Specifically, the search for causes was subordinated to the task of giving an accurate description of natural phenomena. Likewise, in France, Antoine Lavoisier's success in chemistry in the late eighteenth century reflected quite similar normative rules guiding scientific method to those articulated across *la Manche* by Newton in the previous century. Lavoisier believed that scientific inquiry should be governed by the following maxims (McGrew *et al.* 2009, 239): First, scientists ought to proceed from known facts to what is unknown. Second, the search for truth ought to be guided only be experiment and observation. And third, scientists should never accept a conclusion that is not the immediate consequence of observation and experiment. All of these guidelines represented the Newtonian attitude of limiting the role of creative conjectures in scientific inquiry.

The debate between Geoffroy and Cuvier during the first half of the nineteenth century is an apt illustration of these different philosophical views on scientific method being developed and discussed at the time. In one of his last contributions to the debate, Geoffroy made known his belief that the future of anatomy required moving past the idea that it was the science of particular empirical facts. He argued that natural history [9], like Newtonian physics, should aim for the discovery of universal laws of nature, and that Cuvier's insistence on not moving beyond the description of observables threatened France's progress in the sciences. In his response, Cuvier linked Geoffroy's theories to others he opposed, such as Lamarck's idea of the transmutation of species and the doctrine of the great chain of being, insisting that such theorizing would lead young anatomists down the wrong path towards false theories. Cuvier insisted that natural history [9] and comparative anatomy must be restricted to a science of facts, and ridiculed speculative traditions such as the *Naturphilosophen* in Germany for being overly poetic to the point of obscurity. He also worried that an alternative philosophy of natural history [9] and anatomy in France could potentially encourage anti-religious and revolutionary tendencies. Nonetheless, Geoffroy insisted that it was time for natural history [9] and anatomy to become less descriptive and more philosophical. Geoffroy believed that Cuvier's insistence on a positivist methodology was too conservative and overly cautious.

Of course, Cuvier and Geoffroy's thoughts on the role of hypothetical conjectures in science were not merely a reflection of who might have influenced their scientific education, but they were also a sign of their political sympathies and position in society during the Napoleonic époque of nineteenth-century France. For most spectators of the Cuvier-Geoffroy debate, Geoffroy echoed the liberal-minded revolutionary, whereas Cuvier displayed the more sober conservative. As Goethe reported in his comments on the dispute, the gulf between the thinkers became part of a much larger philosophical, political and social division (Appel 1987). These differences included disagreement about the relative roles of analysis and synthesis in science, about whether facts or ideas were the building blocks of scientific knowledge, about who should control scientific ideas and what the academy's place should be in French society, and about the political power of scientific elites.

Because of the chasm between their philosophical commitments on which they intended to build the foundations for the life sciences, Cuvier and Geoffroy diverged on almost every issue in natural history [9] and comparative anatomy. Cuvier held firmly to the belief that function determined structure, and that inquiry in anatomy meant the search for teleological explanations. To expect more than this was to challenge God's freedom and ability to create life. Geoffroy was intent on discovering the similarities in diverse animal structures independent of functional considerations. To do so meant to discover God's general laws of nature that governed life. And, finally, Cuvier's commitment to the four *embranchements* [3] and his reliance on final causes to form explanations in anatomy precluded the possibility of species transmutationism. In contrast, Geoffroy's search for homologies in anatomy and embryology [6] and his commitment to the principle of unity and transcendental explanations of form across animal taxa led him to be somewhat more receptive to the possibility of evolution [10].

5. Limited Variation (within *embranchements* [3]) vs. Teratological Evolution

It was as early as 1825 that Geoffroy began considering whether his regulative principles, especially his principle of the unity of composition, implied a theory of common descent. During this time, before his debate with Cuvier, Geoffroy wasn't preoccupied with proving evolution [10] to be an irrefutable fact; rather, he preferred to invoke it as an idea that seemed consistent with his theoretical views on anatomy. The idea of evolution [10] was also consistent with his embryological experiments. Geoffroy hypothesized that physical and chemical agents in the environment could produce significant transformative effects on embryos during development. These external agents could perhaps be drastic enough to explain species creation and transformation. For Geoffroy, then, the evolutionary mechanism driving change was to be found in the environmental influences on development. Historian Toby Appel described Geoffroy's evolutionary views as a teratological theory of evolution [10] (Appel 1987, 131).

To test this theory, Geoffroy designed embryological experiments to investigate the external conditions that could interfere with embryological development at different stages, and to record instances of abnormal development. For instance, in a series of experiments on chicken [28] eggs, Geoffroy agitated, prodded and injected different substances into the eggs to see whether specific events or chemical agents could affect normal development. The logic of Geoffroy's experiments served as support for epigenesis [29], the theory that embryological development emerges gradually rather than the idea that organic form is predetermined in the fertilized egg [30]. The latter theory, preformationism, was held by many anatomists at the time, including Cuvier.

Moreover, Geoffroy's paleontological work also contributed to the development of the theory of transmutationism–the theory that preceded Darwin's theory of evolution [10] by natural selection–in eighteenth and nineteenth century France. In 1824, Cuvier published a study on the fossil remains of what he believed to be a crocodile near the city of Caen in the Normandy region of France. In 1825, Geoffroy took an interest in Cuvier's work on the discovery of these fossils in Normandy. Having studied living crocodiles during a research trip to Egypt, Geoffroy argued against Cuvier, insisting that the fossil remains were not from crocodiles. The remains represented, for Geoffroy, an intermediate form between reptiles and mammals, which he named *Teleosaurus*. It was this study that spurred Geoffroy to reconsider some of Lamarck's ideas aboutevolution [10]. He argued, during the debate with Cuvier, that although Lamarck was misguided in thinking that there was some sort of internal mechanism that pushed species to evolve in a certain direction, the idea that species were genealogically related was a defensible consideration.

Even though Geoffroy did not necessarily emphasizeevolution [10] during the debate in 1830, his speculations about this topic in his embryological and paleontological work published in the years preceding the debate contributed to another point of disagreement between the two men. Cuvier associated Geoffroy's philosophical anatomy with other speculative traditions, such as the evolutionary theories of the eighteenth century, and dismissed it on that account. Cuvier favored the view that only limited variation was possible within the four basic plans of organization [17]. Any transformation or transitions between *embranchements* [3] had to be impossible because it was *prima facie* inconsistent with his principle of the conditions of existence. Cuvier also objected to speculation about evolution [10] or common descent for metaphysical reasons. He argued thatevolution [10] severely limited God's ability to intervene in the natural world by limiting him to modify existing forms. In contrast, Cuvier stressed, functional anatomy was consistent with the theological idea of God's omnipotence because it allowed him to create new functionally-integrated structures at will.

6. After the Debate: Reinterpretations in the 20th and 21st Centuries

Immediately after the debate in 1830, many in the scientific community elected Cuvier as the victor because he had presented the most convincing arguments, supported by meticulous knowledge of anatomical details and logically sound, persuasive reasoning (Appel 1987, 170-171). Over the course of the second half of the nineteenth century, several natural historians in Britain and France attempted to reconcile the views of Cuvier and Geoffroy, as many began to see the benefits of the morphological approach to comparative anatomy advocated by Geoffroy.

Whewell's interpretation of the debate in his 1837 *History of the Inductive Sciences* was responsible for introducing the philosophical issues in French biology to British society (Appel 1987, 223). Although Whewell's philosophy of science captures well the essence of Geoffroy's transcendental anatomy, Whewell initially favored Cuvier's arguments when he first read about the debate between the two French thinkers. Sympathetic to Cuvier's functional anatomy, Whewell believed that scientific research in the life sciences could not proceed without the guidance of a principle of final cause. Teleological thinking was absolutely necessary for comparative anatomy and consistent with the current theological doctrine in Britain. However, with the growing influence of anatomist Richard Owen's work on homology in Britain, Whewell eventually changed his convictions about the morphological approach of philosophical anatomy and proposed a particular reconciliation between the two positions. Owen had showed that there were many structural similarities in apparent functional dissimilarities, as Geoffroy had insisted. These structural homologies often had no immediate utility or adaptive function for the animal. So, reliance on function alone would omit these interesting similarities in form in the study of comparative anatomy. To accommodate Owen's discoveries, Whewell made a transcendental move to connect morphology [8] with the teleological approach that was consistent with his natural theology: Whewell argued that nature displayed many different purposes, or final causes, in addition to adaptive utility, such as universality, symmetry and similarity. He argued: "If the general Plan be discovered after the contrivance has been noticed, the discovery may at first seem to obscure our perception of Purpose: but it will soon be found that it merely transfers us to a higher point of view. The adaptation of the Means to the End remains, though the means are part of a more general scheme than we were aware of" (Whewell 1857; quoted in Appel 1987, 224).

It was also through the influence of Owen's work on homologies that Darwin reconciled form and function in his theory of evolution [10] by natural selection [31]. After Darwin's publication, the debate's significance was interpreted largely through the lens of the issue of the evolution [10] of species. Later, in the early twentieth century, when evolution [10] was generally accepted, but the mechanism by which species evolved was still under discussion, the issue of evolution [10] took the backburner in the debate, and the issue of form versus function re-emerged as the crux of disagreement. This issue regained center stage when British zoologist, Edward Stuart Russell [32], published *Form and Function* [7] in 1916. As a Lamarckian, Russell argued that, despite the importance of the discoveries of homologies, teleological explanations in biology remained necessary. Any transcendental or pure morphological approach in anatomy had been neutralized by evolutionary theory and the focus on form had been re-oriented towards historical accounts of species.

After the Modern Synthesis of the 1930s, many historians, philosophers and biologists accepted some sort of middle ground between Cuvier's functionalism [33] and Geoffroy's emphasis on morphology [8]. Most scientists recognized that the views were in fact complementary and equally necessary to investigate the many research questions in modern biology. Nonetheless, it was the functional considerations of adaptation that dominated mainstream evolutionary biology during much of the 20th century. However, as new homologies were being discovered in development genetics during the last decades of the century, some of Geoffroy's speculative ideas, ridiculed by many of his peers during his time, were later vindicated and this generated renewed interest in the study of morphology [8] and morphogenesis.

Cuvier's main objection to Geoffroy's methodology in comparative anatomy involved Geoffroy's efforts to demonstrate that analogies existed between Cuvier's four *embranchements* [3]. In the 1820s, Geoffroy suggested that vertebrates and articulates shared a common body plan, with the exception of a 180° rotation in the dorsal-ventral axis (Travis 1995). More specifically, Geoffroy remarked that the nerve cord in articulates is found in the ventral area and its analogue, the spinal cord, in vertebrates is found in the dorsal region. He thus suggested that the body plan of a vertebrate is just like an arthropod flipped over on its back. This similarity, he claimed, supported his principle of the unity of composition. Cuvier responded to such claims by listing off in detail all the anatomically uncommon parts between two species from those two *embranchements* [3] and deriding Geoffroy's hypothesis in the process.

But, in 1994, developmental geneticists Detlev Arendt and Katharina Nübler-Jung of the Alber Ludwigs University of Freiburg [34], argued that it was highly likely that proto-vertebrates diverged from arthropods on the evolutionary tree as a result of an inversion of the dorsal-ventral axis in early embryonic development (Travis 1995; Panchen 2001). As support for this hypothesis, they pointed to the similar components of the genetic elements and mechanisms responsible for the intercellular signaling which leads to the dorsal-ventral orientations in frogs (*Xenopus*) and flies (*Drosophila* [35]). In fly embryos, the *dpp* gene synthesizes a protein which directs a specific population of embryonic cells to activate other genes [36] which guide the formation of dorsal structures. Researchers believe that *dpp*'s proteins also suppress the formation of the nervous system in the dorsal region of fly embryos. Another gene called *sog,* subsequently discovered, synthesizes a protein which suppresses the activity of *dpp*'s proteins in the ventral sections of the embryos to allow for neurogenesis in that area. In a strikingly similar fashion in frog [37] embryos, a gene called *bmp*-4 synthesizes a protein which functions like the *dpp* gene, suppressing the formation of the spinal cord and other neural structures, but functions in the ventral part of the embryo contrary to *dpp* in fruit flies which function in the dorsal region. Moreover, the *sog* gene found in fruit flies also has a counterpart in vertebrate embryos called the *chordin* [38] gene, discovered by Edward M. De Robertis and colleagues during the 1990s. This gene's protein is found in the dorsal part of the embryo where neurogenesis occurs in frogs. In a series of experiments substituting the Sog protein in the fly embryo with the Chordin protein from the frog [37] embryo, researchers showed that the two gene products, although composed of slightly different amino acid sequences, did in fact possess the same function in inducing and suppressing dorsal and ventral structures in the developing embryo.

These recent discoveries in developmental genetics and the discovery of the *Hox* genes [36] in animal morphogenesis have resurrected some of Geoffroy's optimism with regard to discovering a unity of plan in the animal kingdom through homologies. Current research in evolutionary developmental biology [39] of the twenty-first century is once again focused on form in that it aims to discover the developmental basis of the generation of morphological structures and their evolution [10].

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In 1830, a dispute erupted in the halls of lÕAcad mie des Sciences in Paris between the two most prominent anatomists of the nineteenth century. Georges Cuvier and tienne Geoffroy Saint-Hilaire, once friends and colleagues at the Paris Museum, became arch rivals after this historical episode. Like many important disputes in the history of science, this debate echoes several points of contrasts between the two thinkers. The two French Ânaturalists not only disagreed about what sorts of comparisons between vertebrates were acceptable, but also about which principles ought to underlie a rational system of animal taxonomy and guide the study of animal anatomy. Digging deeper into their differences, their particular disagreements over specific issues within zoology and anatomy culminated in the articulation of two competing and divergent philosophical views on the aims and methods of the life sciences. The emergence of these two distinct positions has had a lasting impact in the development of evolutionary and developmental biology. This essay will provide an overview of the conceptual themes of the debate, its implications for the development of the life sciences, and its role in the history of embryology and developmental biology.

Subject

Animals--Classification [55] Cuvier, Georges, baron, 1769-1832 [56] Geoffroy Saint-Hilaire, H. [57] Anatomy [58] Biological Evolution [59]

Topic

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