Etienne Geoffroy Saint-Hilaire (1772-1844) [1]

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Étienne Geoffroy Saint-Hilaire, commonly known as Geoffroy, studied animals, their anatomy and their embryos, and teratogens at the National Museum of Natural History in Paris, France in the eighteenth and nineteenth centuries. Geoffroy also helped develop several specialized fields in the life sciences, including experimental embryology [6]. In his efforts to experimentally demonstrate the theory of recapitulation, Geoffroy developed techniques to intervene in the growth of embryos to see whether they would develop into different kinds of organisms. Moreover, Geoffroy emphasized the concept of *l'unité de composition* (the unity of plan). Geoffroy disputed in 1830 with Georges Cuvier [7] over whether form or function matters most for the study of anatomy and whether the transformation of organic forms can occur over time. Geoffroy's conceptual contributions, as well as his experimental research, influenced embryological research on animal morphology [8] and teratogens, and later the field of evolutionary paleontology.

Geoffroy was born 15 April 1772 in Étampes, France, a town south of Paris. Geoffroy was the seventh of fourteen children. His father, Jean-Géérard Geoffroy, a barrister elected to the court of Étampes, urged his son to enter the priesthood, but the young Geoffroy was more interested in the sciences. He attended the Collège de Navarre in Paris in 1788 on scholarship, where he received a broad education. At Navarre, Geoffroy took a course on experimental physics with the ornithologist Mathurin Jacques Brisson that solidified his interest in the sciences. After graduation in 1790 with a bachelor's degree in law, he pleaded with his father for permission to stay in Paris to attend courses at the Jardin des Plantes, later named the National Museum of Natural History. His father agreed, but only on condition that Geoffroy attend the Collège du Cardinal Lemoine in Paris to prepare for a career in medicine. When the French Revolution began, the medical college shut down, and Geoffroy did not complete his medical degree.

Geoffroy's connections with many scientists in France at the time aided him during the French Revolution. Despite the radical changes in French society at the end of the eighteenth century, Geoffroy secured employment at the Jardin des Plantes due to his connections with the mineralogist Abbé René Just Haüy and Haüy's student Louis-Jean-Marie Daubenton, who Geoffroy had met while attending the Collège du Cardinal Lemoine. In 1792, Geoffroy attended courses at the Jardin des Plantes and joined meetings with Antoine Lavoisier and Joseph-Louis Lagrange. When the Jardin des Plantes became the National Museum of Natural History (the Paris Museum) in 1793, Geoffroy became a professor of zoology at the age of twenty-one.

While working with the collections of mammals andbirds [9] at the Paris Museum, Geoffroy developed a system of classification for anatomy based on the unity of plan. Although Geoffroy first mentioned the idea of the unity of plan in the preface of his taxonomic work on lemurs in 1795, he more fully articulated this concept in the first volume of his *Philosophie anatomique* (Anatomical Philosophy) published in 1818. The unity of plan states that distinct forms in the animal kingdom are organized according to one common plan, and that naturalists could use that plan to classify animal taxa and to understand the taxonomic relations between distinct groups. Geoffroy argued that the unity of plan should serve as the basis for research in zoology and anatomy. He argued that anatomists should focus on tracing the similarities in the body plans of all vertebrates and look for universal unifying principles.

Geoffroy strived to study anatomy beyond mere description and classification, and to determine similarities between the structures of different species. For example, Geoffroy drew the first sketch of the skeletal similarities in the forearms of different vertebrates, comparing the structures of the forearm and hand of a human being, the claw of a cat, and the wing of a bat. These comparisons influenced later studies of homology, the resemblances or similarities between the parts of different animals, including the work of Richard Owen [10] in Great Britain in 1843. Geoffroy's research program, called philosophical or transcendental anatomy, reflected some of Geoffroy's intellectual influences, such as the Comte de Buffon's speculative doctrines on the animal kingdom.

In 1818, Geoffroy published *Philosophie anatomique*, which drew from his fieldwork conducted in Egypt as part of Napolean's campaign from 1798 to 1801. After his trip to Egypt, Geoffroy continued to develop a rational system of classification based on the unity of plan, all the while researching comparative anatomy at the Paris Museum. He spent 1802 to 1806 describing and classifying organisms.

Geoffroy's theories initially caused little controversy, but his essays written between 1818 and 1820 provoked discussion. When Geoffroy attempted to demonstrate the similarities between the body plans of arthropods and vertebrates, Georges Cuvier [7], who worked at the Paris Museum, attacked Geoffroy's comparisons as irrational and unsupported by empirical evidence. Their disagreement about structural similarities, and about the study of anatomy, led to the Cuvier-Geoffroy debate in 1830 that culminated in an intellectual, political and personal split between the two naturalists that lasted until their deaths. Geoffroy defended his views in his *Principes de philosophie zoologique* (Principles of Zoological Philosophy) in 1830. Geoffroy's arguments for the similarities between the body plans of arthropods and verterbrates were partly vindicated by embryological

studies conducted in the mid-1990s on dorsal-ventral inversions in developing embryos.

Motivated by the anatomical similarities he found among different vertebrates, Geoffroy used embryology [6] to test what some considered the universal laws of development. Geoffroy relied on early versions of the recapitulation theory [11], proposed by Carl Friedrich Kielmeyer in Stuttgart, Germany, in 1793, and discussed by Geoffroy's friend Étienne Serres in Paris in the 1820s. Ernst Haeckel [12] in Jena, Germany, further developed recapitulation theory [11] in the late nineteenth century. Proponents of early versions of the theory suggested that the stages of the development of an embryo recapitulates, or mimics, the evolution [13] of simple species to more complex species over time. To test this theory, Geoffroy experimented on chicken [14] eggs and other embryos to confirm whether organisms that he considered simple, such as fish [15], represent the earlier embryonic stages of vertebrates that he considered as more complex, such as chickens. In a series of experiments, Geoffroy hypothesized that if he could intervene in the development of chicken [14] embryos at the right stage, then these embryos would develop into some sort of simpler organism, such as fish [15]. His experiments failed, but Geoffroy's experimental efforts helped start the field of experimental embryology [6].

Geoffroy's embryological experiments led him to question what external conditions could interfere with embryological development at different stages. Throughout the 1820s, Geoffroy once again conducted a series of experiments on chicken [14] eggs. He shook, prodded and injected different substances into the eggs to see whether those manipulations affected development, and he recorded the abnormalities. Geoffroy's experiments supported epigenesis [16], a theory that an organism's form emerges gradually in development, and that it isn't preformed or predetermined in the zygote [17] or fertilized egg [18]. As a result of this work, Geoffroy created the scientific field of teratology [19], the study of abnormalities in development. Abnormalities and malformations, then called monstrosities, became seen less as signs of demonic intervention, and more as cases of malfunction due to external interference in the causal mechanisms of developmental processes.

Geoffroy devoted much of his later career to the study of teratogens. Most of Geoffroy's manuscripts about malformation appear in the second volume of his *Philosophie anatomique* (Anatomical Philosophy), published in 1822, and *Considérations générales sur la monstruosité, et description d'un genre nouveau observe dans l'espéce humaine, et nommé aspalasome* (General Considerations on Monstrosities, and a Description of a New Type Observed in the Human Species, Named Aspalasome) in 1825. Geoffroy's son Isidore Geoffroy Saint-Hilaire continued his father's work and produced a three-volume work, *Traité de tératologie* (Treatise on Teratology), from 1832 to 1836, which promoted and systematized the science of teratology [19].

Geoffroy's studies of fossils contributed to the development of the theory of transformism, sometimes referred to as transmutationism. These ideas preceded Darwin's theory of evolution [13] by natural selection [20]. In 1824, Cuvier published his study on the fossil remains of what he believed to be crocodile fossils, found near the city of Caen in the Normandy region of France. Geoffroy in 1825 took an interest in Cuvier's work on the discovery of these fossils in Normandy. Having studied living crocodiles during his trip to Egypt, Geoffroy argued against Cuvier, insisting that these fossil remains were not from crocodiles. To Geoffroy, the remains represented an intermediate form between reptiles and mammals, which he named Teleosaurus. He published his work in his *Recherches sur de grands Sauriens* (Studies on the Great Saurians) in 1831. Historians often mark Geoffroy's studies on these fossils as the beginning of evolutionary paleontology.

During the 1830s and 1840s, Geoffroy's work, increasingly theoretical and somewhat poetic, delineated a grand theory that aimed to unify the rules of the universe and of life with human thought. Throughout his intellectual life, Geoffroy was influenced by Immanuel Kant's metaphysics and Isaac Newton's system for physical science. Geoffroy aimed to produce similar universal laws and regulative principles for the life sciences that would mirror the achievements of these philosophical and scientific paradigms. In 1842, the French novelist, Honoré de Balzac, in Paris at the time, dedicated his novel, *Le Père Goriot*, to Geoffroy in admiration of his contributions to the life sciences. As a result, Geoffroy became a symbol for a liberal-minded progressive vision of scientific knowledge in French society, in contrast to the depiction of Cuvier as a conservative defender of rigorous analytical science. In July 1840, a cataract caused Geoffroy to go blind, and by 1842, his mental health had begun deteriorating. He died on 19 June 1844.

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