Francis Maitland Balfour (1851-1882) [1]

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During the 1870s and early 1880s, the British morphologist Francis Maitland Balfour contributed in important ways to the budding field of evolutionary embryology [4], especially through his comparative embryological approach to uncovering ancestral relationships between groups. As developmental biologist and historian Brian Hall [5] has observed, the field of evolutionary embryology [4] in the nineteenth century was the historical ancestor of modern-day evolutionary developmental biology [6]. Balfour's work was notably inspired by Charles Darwin's theory of evolution [7] and Ernst Haeckel's account of the relationships between embryology [4] and evolution [7]. Only a decade after Balfour's program of research began, an alpine climbing accident robbed Britain of its most promising embryologist.

The fifth of eight children, Balfour was born to Lady Blanche Gascoyne-Cecil and James Maitland Balfour on 10 November 1851 in Edinburgh, Scotland. His father was a wealthy landowner and MP; his mother was the Second Marchioness of Salisbury. Francis—or "Frank" as he was known throughout his life—showed an early aptitude for natural history [8]. Raised in Scotland, Balfour attended preparatory school at Hodesdon, Hertfordshire, and then Harrow. Balfour's first academic work, published years later with one of his brothers, was an essay on the geology of East Lothian, Scotland, that brought him to the attention of Thomas Henry Huxley [9]. He entered Trinity College, Cambridge, in 1870, and a year later secured the Natural Science Scholarship at Trinity upon examination by Huxley. As an undergraduate, Balfour worked with the Praelector in Physiology Michael Foster [10], who became Balfour's mentor and life-long friend. Foster encouraged Balfour to study chick [11] embryos. This work came quickly to fruition, and in an 1873 paper Balfour demonstrated that the primitive streak [12] in the early chick [11] embryo and the blastopore [13] of the amphibian embryo are homologous. Many of Balfour's subsequent publications used this same approach: determining evolutionary relationships based on homologies supported by evidence from comparative embryology [4]. As Hall notes, for several decades after Darwin's *Origin of Species*, many naturalists considered embryology [4] to be the single best method of determining ancestral relationships between groups.

From the early 1870s on, Balfour's work and reputation were well known throughout Britain and beyond. He published papers in embryology [4] that were considered by numerous scientists like Darwin and Huxley to be important contributions to the understanding of evolutionary relationships. Also, as an undergraduate, Balfour co-authored a textbook, *The Elements of Embryology* [14], with Foster. In December of 1873 he passed his Natural Sciences Tripos'.

While at Cambridge, and encouraged by Darwin, Huxley, and Foster, Balfour provided financial aid to Anton Dohrn's fledgling *Stazione Zoologica* [15] in Naples. Balfour's family wealth and enthusiasm for the sciences led him to be a financial advocate of several developing research organizations like the *Stazione*. These philanthropic efforts were aided by the social standing of Balfour's politically minded family—especially his brother Arthur James Balfour, a philosopher and politician who later became Prime Minister of England. Balfour went to Naples for the first time in February of 1874 to begin studies of the comparative embryology [4] of sharks and dogfish. Working alongside Ambrosius Arnold Wilhelm Hubrecht, Edwin Ray Lankester [16], and Albert George Dew-Smith, Balfour studied these elasmobranch embryos with the ultimate goal of uncovering a better understanding of the evolutionary origin of the vertebrates. His work also revealed that the mesoderm [17] forms independently from the ectoderm [18] and endoderm [19] in normal vertebrate development. Balfour's studies of embryos in Naples led to publication of the four-volume work *A Monograph on the Development of Elasmobranch Fishes* [20] published in 1878. This inductive and descriptive study began with a full description of the development of both egg [21] and embryo before making phyletic (evolutionary) inferences. The book enhanced his reputation as one of Britain's leading evolutionary biologists, and earned him election as a fellow to the Royal Society in 1878 at the age of twenty-seven.

Upon returning from Naples, Balfour set up a laboratory at Trinity College, called the Cambridge Morphology Laboratory [22] (CML). Under the guidance of Balfour, the CML saw a period of productivity and drew students from near and far, many of whom went on to distinguished careers in the natural sciences. The most historically noteworthy of these students were Adam Sedgwick [23], William Bateson [24], D'Arcy Wentworth Thompson, Walter Weldon, and Arthur Haddon. The American contingent included Henry Fairfield Osborn [25] and William Berryman Scott, who later incorporated a strong embryological component into their studies of vertebrate paleontology. The eventual success of these students was fostered by two aspects of working at the CML: Balfour provided them with a conceptual framework by which to meaningfully interpret their comparative studies along with the techniques required for using the latest technological advancements, such as the first rotary microtome [26] and newest Zeiss [27] microscopes.

While the students in the CML handled the daily research, Balfour organized and supervised their projects and through the final years of the 1870s. He incorporated much of this laboratory work into his two-volume *Treatise on Comparative Embryology* [28], published in 1880 and 1881, a book that was well received. For example, in his review of the first volume in the journal *Science*, Osborn called it an important, broad-reaching, and descriptive analysis of the state of comparative embryology [4]. Within the biologist and historian Edward Stuart Russell's *Form and Function* [29], Balfour's work (and especially *Treatise*) is central to the period of evolutionary embryology [4] (or "evolutionary morphology [30]," in Russell's terminology) that was prevalent in the second half of the nineteenth century.

From a theoretical perspective, Balfour advocated Darwinian natural selection [31] as the causal mechanism of evolutionary change. He also accepted the biogenetic law [32] of recapitulation, whereby embryological change (typically) follows the evolutionary transformation of the species. In some respects Balfour's recapitulationism was similar to that of Carl Gegenbauer's in that they both distinguished between primary and secondary evolutionary characters. Contrary to many evolutionists at this time, Balfour was one of the first to argue that natural selection [31] could occur during embryonic stages of growth. As such, he was one of the first embryologists to seriously consider the evolution [7] of development itself.

Balfour's *Treatise* brought him even more academic acclaim than his earlier work. His sterling reputation can be seen in the fact that both the University of Edinburgh [33] and Oxford University offered him prestigious professorships; positions that he refused in favor of the Cambridge Professorship of Animal Morphology. Unfortunately, Balfour's promising future was cut-short on 18 July 1882, when, despite objections from family and friends, Balfour died while attempting to scale the *Aiguille Blanche de Peuteret*, one of the most difficult peaks in the Alps. As a memorial to Balfour's death, Cambridge established the Balfour Library and the Balfour Studentship, which remind modern Cambridge biologists of the productive, albeit brief, career of one of Britain's most influential Victorian embryologists.

Sources

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[3] https://embryo.asu.edu/keywords/evolution
[4] https://embryo.asu.edu/search?text=embryology
[5] https://embryo.asu.edu/search?text=Brian%20Hall
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