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12 The Decline of Soft Inheritance

Scott Gilbert

Soft inheritance sounds opposed to hard fact, a weak analogue kind of inheritance as opposed to the digital inheritance of the chromosomes. But there was, in fact, a “soft,” developmental version of inheritance during the early twentieth century, and evolution was understood by many leading biologists in terms of the rules of development. In 1893, the evolutionary champion Thomas Huxley wrote, “Evolution is not a speculation but a fact; and it takes place by epigenesis.” He didn’t say that it takes place by natural selection: he said that it takes place by epigenesis, by development. He was looking at a level different from the struggle of variations within a population. Rather, he was looking at the origin of variation.

Before World War I, the fields of genetics and development were united in the science of heredity (Coleman 1971; Gilbert, Opitz, and Raff 1996). There were many modes of inheritance, and one of the most popular and most researched was the mode called the morphogenetic field. One of the major research programs was *Gestaltungsgesetze*, the attempt to discover the laws by which ordered form was established at each generation.

A morphogenetic field was assumed to have definite boundaries, and to be made up from a collection of cells that were specified in a way that told them that they were members of the field. The interactions of these cells led to the formation of a particular organ, and at each generation, fields were established for the creation of body parts. The model organism in which the inheritance of morphogenetic fields was studied was the flatworm *Planaria*. The flatworm splits by binary fission—either transverse or lengthwise—and each part regenerates the other part. A head will regenerate a tail, and a tail will regenerate a head. In *Planaria*, the inherited information was embodied in the gradient that enabled the organism to form a head at one end and a tail at the other. Upon splitting, each half inherited the ability to make a whole and properly organized animal. This is reproduction, inheritance, and development all wrapped in one (see Child 1915, 1941). This notion of heredity was based on cells, not chromosomes, as the focal units of inheritance. Cells were seen as organizing into morphogenetic fields,

and the morphogenetic fields then formed organs (Gilbert, Opitz, and Raff 1996; Gilbert 2003).

The genetics program of biology was originally in direct opposition to the concept of morphogenetic fields, and the demise of the morphogenetic field approach in the United States was linked to the rise of genetics and to the research and writings of an eminent American embryologist-turned-geneticist, Thomas Hunt Morgan. At the turn of the last century, there were two main researchers studying morphogenetic fields in the United States: C.M. Childs at the University of Chicago and Thomas Hunt Morgan, then at Bryn Mawr College. At the beginning of his career, Morgan studied embryogenesis and regeneration, and he published several important articles and books on these subjects. However, in the early twentieth century Morgan abandoned the study of regeneration and lost belief in the ability of embryogenesis to serve as the scientific basis for the understanding of evolution. He started studying the genetics of *Drosophila*, where inheritance of variant traits (e.g., red versus white eye color) was shown to obey Mendel's laws and suggested the involvement of nuclear chromosomes. At first, he attempted to place his new mutations into a framework of development (see Falk and Schwartz 1993). Each of his mutant phenotypes was seen to represent a different developmental step on the way to the final phenotype. A mutation represented a frustrated developmental pathway. However, by 1913, Morgan realized that he, too, was frustrated in his attempts to make a unified genetics of transmission and development. In 1926 he claimed that genetics and the study of ontogeny have to be separated (Morgan 1926; Gilbert 1998). He then called the *Planaria* program unscientific and blocked the attempts of Child and his students to publish their findings. He considered such work old-fashioned and not good science (Mitman and Fausto-Sterling 1992). Indeed, Mitman and Fausto-Sterling sternly conclude that Morgan was so adamant in his ridiculing the field notion because, in the 1930s, the morphogenetic field was an alternative to the gene as the unit of ontogeny.

In order to see how the field notion and soft, developmentally constructed inheritance were removed from the evolutionary synthesis in the United States, we need to go to one of the founding narratives of genetics. "The Rise of Genetics" (Morgan 1932b) could have been subtitled "The Decline of Embryology," because in this article, as well as in *The Scientific Basis of Evolution* (Morgan 1932a), Morgan portrays embryology, and soft inheritance with it, as a failed research program. Genetics, he claims, is its victorious successor. Indeed, *The Scientific Basis of Evolution* was about what Morgan regarded as the *only* scientific basis for evolution—genetics. Everything else was the *unscientific* basis of evolution. Paleontology, morphology, and embryology were all considered to be "philosophical" old schools: "older speculative methods of treating evolution as a problem of history" (Morgan 1932a: 13). Genetics, however, "has brought that subject evolution an exact scientific method of procedure" (Morgan 1932b: 287).

Morgan tells a story, which would be amplified later by Dobzhansky and Mayr, about the rise of genetics and the fall of embryology and the developmental modes of inheritance. This story follows what philosophers of religion call the supersessionist paradigm, the narrative myth by which the early Christians claimed to have superseded the Jews, and the narrative by which Protestants later claimed to have evolved or developed past the Catholics. Morgan starts by redefining embryology as a science of gene expression (something that embryologists had not looked at), and having redefined it in such a way that it can't succeed, claims that genetics has superseded it. Moreover, all the things that embryology wanted to explain and had failed to do, genetics could do (Gilbert 1998).

When Morgan claimed in 1926 that heredity had to be split into genetics and embryology, he redefined both areas in terms of genes. Genetics was the science of gene transmission, and embryology was the science of gene expression. Then he claimed that the embryologists could not bridge the gap between the genes and the trait, which, in fact, *was not* what embryologists wanted to do. Embryologists were dealing with morphogenetic fields and cells, not with genes. (Indeed, many embryologists were distinctly anti-genetic and felt that the cytoplasm, not the genes, directed development.) Embryology, Morgan (1932a) said, ran a while after false gods and landed in a maze of ontological subtleties. Where embryology went into metaphysical subtleties, genetics went into concrete chemistry and math. It is noteworthy, however, that in the 1930s the gene was not any more "material" than the field. Neither "field" nor "gene" had been directly observed. Both were postulated on the basis of results of experimental data, and both sought to explain inheritance.

Mendelian genetics was very successful in explaining the inheritance of many traits, but there were hereditary phenomena that did not fit into its framework. It is fitting to recall that this year (2009) is the centenary of Wolterek's paper on phenotypic plasticity and the notion that what is inherited are potentials for development, and those potentials can be impacted by the environment. The example studied by Wolterek was the water flea *Daphnia* (Wolterek 1909). It develops in different ways in different environments: when the individual lives in a safe environment, it has a normal round head, but in an environment inhabited by predators it grows a protective helmet. And this developmental response is passed on to the next generation. It is not easy to explain this mode of inheritance within the classical framework of chromosomal inheritance. But these kinds of findings can be conveniently ignored if they do not fit into one's theoretical scheme. And they were often ignored. As Benkemoun and Saupe (2006) commented when discussing past work on the genetics of fungi, "exceptions" were routinely autoclaved. We do not treasure our exceptions, as William Bateson urged us to do. We autoclave them.

The Cold War and the rise of Lysenkoism in the Soviet Union provided much of the context in which genetics flourished and in which "soft inheritance" was mar-

ginalized or discredited (see Gilbert and Epel 2009). Due to the possible mutational aspects of radiation, the Atomic Energy Commission was responsible for funding many projects of population genetics in the United States, and in 1959 the American Genetics Society hired a public relations team to spread the good news of genetics: not to bad-mouth Lysenkoism, because the American geneticists feared that their colleagues in Russia would be hurt that way, but to tell that Mendel plus Darwin gives you evolution (Wolfe 2002; Gormley 2007.) Clearly, to stop a competing research program, you need not kill the scientists; killing their research funding will do.

And, of course, one can also write a historical narrative into which the competing data do not fit. This, as we saw, was one of the strategies of Morgan, soon followed by Dobzhansky and Mayr (Sapp 1987). Dobzhansky (1937) wrote a history of evolutionary biology, largely the history of experimental population genetics, saying that evolution is studied by looking at changes in gene frequency, and concluded by 1951 that “evolution is a change in the genetic composition of a population. The study of the mechanisms of evolution falls within the province of population genetics” (Dobzhansky 1951: 16). So we have a proper subset. Evolution is a proper subset of the mathematics of population genetics.

While Morgan and Dobzhansky wrote developmental mechanisms out of the history of evolution, Ernst Mayr wrote embryology and soft inheritance out of the philosophy of evolution (Mayr 1966, 1982). Embryology was seen to be mired—pardon the pun—in typological thinking rather than population thinking. It was, Mayr claimed, essentialist. But, as Polly Winsor (2006) has shown, in order to keep evolutionary biology focused on intrapopulation processes, Mayr invented a dichotomy that had actually been resolved well before the time of Darwin. Although Mayr did not think that evolution was merely a matter of changes in gene frequencies, his analysis led him to focus only on evolutionary/genetic changes within species. He maintained that evolution could be studied without paying any attention to the mechanisms by which genotypes generate phenotypes (Mayr 1982). And since evolution had no need for a theory of body construction, it had no need for the possibilities of soft inheritance.

We now can observe that inheritance can be affected by several means. DNA methylation can inactivate a gene as well as mutation, and gene methylation differences (epialleles) can be inherited from one generation to the next. Moreover, symbionts provide a parallel system of inheritance, and in many cases the symbionts can alter gene expression in their hosts or provide various proteins to their cells (see Jablonka and Raz 2009; Gilbert and Epel 2009; chapter 27 this volume). Here, variation can be provided by “soft inheritance.” This analysis could not have been accomplished without restriction enzyme analysis, polymerase chain reaction, and high-throughput RNA analysis. It is therefore ironic that the most reductionist, the

most analytical, molecular tools have actually ended up showing the necessity, and indeed the reality, of the soft inheritance that had been excluded from the study of evolution.

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