What we could not discuss in 1995 was information transmission through small non-coding RNAs. This was not recognized until the late 1990s, when the discovery of gene regulation through RNA interference and the realization that it provided a powerful research tool gave epigenetics research an enormous boost. It soon became clear that the small RNAs that mediate gene silencing can not only be transmitted to daughter cells, but also move to more distant cells, including germ cells. Thus, another route through which epigenetic changes can affect future generations was revealed, one that might have significant effects in all species, including those with early segregation of the germ line. Weismann’s barrier was breached in a surprising way, one that was reminiscent of Darwin’s unaccepted idea that hereditary information is transmitted from body cells to the reproductive organs through small molecules called gemmules.10

Today, ‘epigenetic inheritance’ has become an umbrella term covering the many interacting ways through which variations that do not depend on DNA differences are transmitted in lineages of cells and organisms. In disciplines as diverse as animal behaviour, plant ecology and epidemiology, it is recognized that through epigenetic inheritance acquired variations can have an impact on later generations. Sadly for us, in our own field of evolutionary biology, with a few exceptions,11 either the significance of epigenetic inheritance is down-played or the subject is treated with hostility; many evolutionary biologists have not bothered to get acquainted with epigenetic research. We have continued to argue that epigenetic and other types of non-DNA variations must be included in evolutionary thinking. Our hope is that now that studies of heredity and development have moved away from the gene-centric approach that characterized the last half of the 20th century, the developmental system approach that is replacing it will lead to more interest in evolutionary epigenetic research and to a more widespread acceptance of the importance in evolution of the inheritance of acquired epigenetic variations.

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References

Commentary: A conceptual revolution limited by disciplinary division

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In the past decade or two we have witnessed a remarkable thaw in the long chilly relations between the biological and social sciences. For more than a century it seemed that there was only one basic way the two modes of enquiry...
could fit together: biology (or genetics or evolutionary forces) would be fundamental, the basis or bedrock upon which behaviour and society (or culture or social relations and structures) are formed. And the relationship would be basically deterministic, perhaps probabilistic, but certainly unidirectional. The question would be how biology shapes society. The social sciences’ best recourse was to assert their cognitive autonomy, declaring society as sui generis, and resist and criticize the incursion of biology. In this regime, biologists might one day aspire to colonially dominate their neighbors—E.O. Wilson’s ‘consilience’, but most would prefer to avoid that quagmire and do their work separately.

This conceptual framework and the relationships it presupposes are certainly not dead, but they are definitely on the decline and faced with a raft of competitors. Eva Jablonka and Marion J Lamb’s ‘The inheritance of acquired epigenetic variations’ was early in a series of publications that were as responsible as anything for breaking the hold of the prevailing framework. The article synthesized and codified an emerging research programme that established epigenetic inheritance as an important intergenerational and perhaps evolutionary force.

They present the striking image of the ‘gene’s phenotype’—no longer pure information, the gene has a body too. And that body makes the gene open to the environment. Not once does the article mention ‘society’ or the ‘social’ and, indeed, few social scientists have a particular interest in evolutionary theory. But the gene’s phenotype opens the door to social scientists by fracturing the old biology/society relationship. No longer hierarchical, or at least not only hierarchical, epigenetics flattens the relationship. For example, in Michael Meaney and Moshe Szyf’s famous mouse studies of the epigenetic transmission of maternal care and stress responses, factors such as stress experience, maternal licking behaviour, cortisol, the glucocorticoid receptor, methylation of the receptor promoter and DNA sequence all exist as necessary elements in a complex causal cascade. None has ontological priority as the ‘basic’ or ‘primary’ cause; the concept of environment has fractured and ramified, and distinctions like social vs biological are less important than location within the causal network.

Jablonka and Lamb were eager to establish epigenetics as a potentially important force in evolution. But the article’s influence, I think, is due less to its evolutionary argument than to the intergenerational logic that drives it. Everyone acknowledges that environment matters in that, say, nutritional deprivation during gestation may lead a body never to develop properly. But once the fetus’s eventual grandchildren or great-grandchildren might be affected, suddenly more seems to be at stake. Where before the environment, social forces, etc. might arguably still be seen as separable from an organism’s or population’s true (genetic) essence, intergenerational effects, especially those beyond the offspring, somehow demand different scientific respect and attention.

These possibilities are leading researchers across the range of post-genomic life sciences to think of epigenetics as ‘where environment, society and genetics meet’. Epigenetics has offered new ways to take society seriously as more than extraneous context but less than genetically determined. It offers a set of mechanisms and frameworks to talk about gene/environment interaction in ways that are more than statistical. And thus biological scientists have begun studying social forces and recognizing the necessity of an interdisciplinary approach to epigenetically mediated health conditions such as stress, anxiety and depression.

But here is the thing: biological scientists are talking about society and social forces without interacting with social scientists. It is incredibly rare for a social scientist to be listed as a co-author on an epigenetics article—even those articles ostensibly targeting effects of the ‘social’. With all due respect to the public health researchers who play the social science role in this research, potentially crucial social scientific expertise is largely excluded. At the same time sociologists, political scientists and economists who have become emboldened to take biology and genetics seriously, have overwhelmingly done so using quantitative genetic family studies or candidate gene association studies to partition genetic and environmental contributions to population variance for socially relevant traits. They have walked through the door opened by Jablonka and Lamb only to reproduce the old conceit that genes and environment are distinct and independently measurable causes.

Though Jablonka and Lamb’s work on epigenetics has helped tear down some of the conceptual walls separating the biological and social sciences, it has done less to reconfigure disciplinary habits of work. One practical legacy of the historical chill between the fields is that they have not yet figured out how to work together. Surely there are many more stunning advances that will emerge from the current configuration of epigenetics research. But I would like to suggest that the next level of advances will depend as much on changes to science organization and policy as on conceptual advances. That is, once we figure out how to incentivize and assemble truly multidisciplinary research teams in ways that overcome disciplinary divisions of labour (biologists in the laboratory, social scientists measuring the environment), then the truly transdisciplinary potential of an epigenetic approach to biosocial problems can be realized.

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A deeply staining substance known as chromatin (Flemming), is the nuclear substance par excellence, for in many cases it appears to be the only element of the nucleus that is directly handed on by division from cell to cell, and it seems to have the power to produce all the other elements.

In the 1870s, intensive microscopical work to analyse the dynamics of cell division produced a new entity for the cell: chromatin, so named by Walter Flemming because it readily took up histological dyes. The word means coloured substance. Thus it is a rather arbitrary word, more to do with the technique of visualization than a descriptor of the thing. Nonetheless, before the ascendance of the gene concept, the powers of heredity were ascribed to chromatin. As EB Wilson put it in 1900, chromatin ‘seems to have the power to produce all the other elements’ of the nucleus. With the rise of the gene in the 20th century, chromosomes were seen as gene-carriers; with the identification of DNA as the hereditary material, the importance of ‘chromatin as the physical basis of inheritance’—as it was frequently described in the first half of the 20th century—receded still further. This conceptual separation between DNA as the locus of information and its transmission, and chromatin as a mere scaffold was as arbitrary as the initial naming of chromatin: after all, chromatin is, by definition, the complex of DNA and proteins constituting the contents of the nucleus (and one wonders today if the definition of chromatin should not include RNA).

A key point of Jablonka and Lamb’s now classic ‘The inheritance of acquired epigenetic variations’ is to insist that DNA never comes alone: chromatin structure and conformation are redescribed as ‘the gene’s phenotype’. Italicized in the original to draw attention to the importance and perhaps anti-intuitive nature of the phrase, chromatin is highlighted here as the animate body of the gene. For this reader, it is a description that evokes both ideas of chromatin before DNA—such as De Vries’ notion of chromatin as a living colony of invisible biophores—as well as the future that would come after 1989, a renaissance in chromatin biology. Today, the complex architecture and topography of chromatin, as well as its temporal dynamism, is at the centre of research in gene regulation and epigenetics. Chromatin has become an ‘integration and storage platform’ for signals coming into the cell, the ‘physiological template of all eukaryotic genetic information’, the nuclear ‘landscape’ of pluripotency and senescence and ‘the physiological form of our genome’. Indeed, if the 20th century was the century of the gene, as historian Evelyn Fox Keller puts it, the 21st may well turn out to be the century of chromatin.

It is instructive, therefore, to return to the role of chromatin in this seminal theorization of epigenetic inheritance. Chromatin structure and conformation were proposed as the gene’s phenotype, that which ‘determines its functional state’. Evidence was offered from studies with nuclease enzymes, which were useful because they could only cut the DNA strand if the enzyme could get at it, implying an open conformation of chromatin. More important than the experimental evidence brought to bear on the question of chromatin conformation is the rhetorical construction of chromatin as an impressionable physical material. It was pliable enough to take the imprint of an environmental or developmental event, but stable enough to then hold that...