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Normal development and experimental embryology: Edmund Beecher Wilson and *Amphioxus*

James W.E. Lowe*

Department of Sociology, Philosophy and Anthropology, and Egenis, The Centre for the Study of Life Sciences, University of Exeter, UK

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ABSTRACT

This paper concerns the concept of normal development, and how it is enacted in experimental procedures. To that end, I use an historical case study to assess the three ways in which normal development is and has been produced, used, and interpreted in the practice of experimental biology. I argue that each of these approaches involves different processes of abstraction, which manage biological variation differently. I then document the way in which Edmund Beecher Wilson, a key contributor to late-nineteenth century experimental embryology, approached the study of normal development and show that his work does not fit any of the three established categories in the taxonomy. On the basis of this new case study, I present a new interpretation of normal development as a methodological norm which operates as a technical condition in various experimental systems. I close by suggesting the questions, and ways of investigating developmental biology, that are opened up by this perspective.

1. Introduction

Since the advent of embryology as an academic discipline, practitioners have identified and/or used a 'normal development' as part of their investigations. Normal development has been instantiated in practice in a variety of different ways. Hopwood described the creation of normal stages and tables for comparative morphological work, which provided a standardised basis for comparison of samples within the same species (Hopwood, 2007). In these tables, and subsequently produced laboratory handbooks, the development of a particular organism is divided into particular stages. For some organisms, these stages are temporal, corresponding to a certain period of time post-fertilisation (e.g. a standard developmental time for zebrafish). For others, they are defined by the presence or absence of certain (usually morphological) characteristics (such as the classic normal staging of the chick by Hamburger & Hamilton, 1951). In experimental embryology and developmental biology, the normal development allows biologists to compare the effects of experimental manipulation to a non-manipulated 'control'. In modern biology, the normal development is a product of a particular community (such as a model organism community) and the resources available to scientists may include actual organisms bred for the purpose, with accompanying normal series. Scientists, through training and experience, will become familiar with the normal development for that organism.

I am interested in the way in which normal development is enacted in biological practice. This topic intersects with literature on the normal in biology and medicine (Boorse, 1977; Canguilhem, 2008 [1965]) normality and its relationship with attributions of function (Amundson, 2000; Wachbroit, 1993), and aspects of the practice of biology such as standardisation, representation, abstraction and the genesis and role of model organisms (Ankeny & Leonelli, 2011; Griesemer, 2007; Leonelli, 2008; Love, 2010; see also Logan, 2001; Meunier, 2012). I will examine the role of normal development in experimental embryology. Three different types of normal development used in embryology have been identified (by DiTeresi, 2010), essentialist, statistical and reference standard. The latter is emblematic of twentieth and twenty-first-century experimental work in embryology and developmental biology. The different types of normal development, what I call the taxonomy of norms, are different ways of conceptualising and managing variation. I assess the production and use of such norms in terms of abstraction and standardisation – how certain observed variation is omitted, and how the normal development functions as a standard. To do so, I examine a case of the production and use of normal development in an early example of experimental embryology, the 1892 experiment by Edmund Beecher Wilson using the marine invertebrate *Amphioxus*, now known as *Branchiostoma lanceolatum*, also known as a lancelet. This experiment was conducted before the establishment and entrenchment of various kinds of standards in

* Byrne House, St. German's Road, Exeter, Devon EX4 4PJ, UK.
E-mail address: j.w.e.lowe@exeter.ac.uk.

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experimental embryology; standardised normal tables, stages, or series, and standard(ised) organisms in particular. This therefore represents an era where the relationship of scientific communities to standards was quite different. In this paper I examine how one such standard – that of normal development – was formulated and put into practice. This was an individual standard (or proto-standard) used for particular experiments, rather than a community standard employed in a general experimental culture.

As we shall see, the characteristics of *Amphioxus* also made this creature valuable for conducting experiments to try to answer questions about the relative importance of different factors (i.e. internal and external) in the development of an organism. Towards the end of the nineteenth-century there was a move towards more experimental methods of investigating embryonic development. The aim for many of these experimenters was to establish mechanistic explanations of development, particularly the progressive differentiation of the organism from an undifferentiated, relatively homogeneous egg (cf. Driesch, 1974 [1892]; Roux, 1974 [1888]). Wilson rode this wave with his work on *Amphioxus*. Trained as a morphologist under William K. Brooks at Johns Hopkins University, in the early 1890s Wilson's career moved from a concern with comparative morphological problems to a greater interest in the processes of development themselves and their causes (Benson, 1985, p. 199; Maienschein, 1978, p. 139). In this paper I focus on one part, one paper, of a long and varied research career (which has been covered extensively by Jane Maienschein, see especially 1978, 1981, 1990, and also by Baxter, 1976, 1977). My analysis of Wilson's *Amphioxus* experiment is used to make philosophical points concerning the nature, production, and use of normal development in experimental embryology. It is not my intention to make any wider historical claims about Wilson's career and research, beyond the small part of his overall work that I am concerned with here.

In this paper I detail the way in which Wilson formulated and used normal development and relate this to the other ways of understanding normal development, as essentialist, statistical or a reference standard. While Wilson was informed by previous accounts of the development of *Amphioxus*, his own normal development was based on the observation and assessment of the samples at his disposal. I discuss the role of normal development in key experiments and papers by Wilhelm Roux (1974 [1888]) and Hans Driesch (1974 [1892]) to provide a counterpoint to Wilson's own approach, which allows me to demonstrate more clearly the nature of Wilson's production and use of normal development. While Driesch and Roux are recognised today more for their theoretical and programmatic contributions, the experiments that they conducted generated significant results, and helped to inspire Wilson's own experiment with *Amphioxus*, which in part aimed to resolve the seeming contradictions between the results of Roux and Driesch's experiments, and which borrowed key elements of Driesch's method of experimental intervention.

Following a discussion of the results obtained by the *Amphioxus* experiments, I demonstrate that Wilson's normal development was produced by different processes of abstraction, the removal from consideration of some features and parameters of organisms, compared to the three main ways in which normal development can be characterised. One difference was Wilson's standard's individualised rather than collective nature. Furthermore, the organisms used possessed a different epistemic status in the sense of its role in relation to individual scientists and networks and communities of scientists, not being standardised model organisms. Examining the role of abstraction, and its relation to the management of variation and standardisation, I explicitly make connections between the different practices of abstraction and the types of normal manifested in biological science. In doing so, I analyse the various features of normal development, which towards the end I propose to be a methodological norm functioning as a technical condition within experimental systems concerned with various aspects of organismal development.

In closing, I have made suggestions as to normal development's significance for broader issues of historical and philosophical interest, such as the development of model organism systems in the twentieth-century. Returning to the present day, I suggest possible developments which presage a further transformation in the way in which 'normal development' will be produced.

2. The 'normal' and strategies of abstraction

Georges Canguilhem noted two linked meanings of normal, observing that "[s]ometimes it designates a fact that can be described through statistical sampling; … And yet it also sometimes designates an ideal, a positive principle of evaluation, in the sense of a prototype or a perfect form" (Canguilhem, 2008 [1965], p. 122). He observed that these senses are often linked, a point subsequently developed by others (Amundson, 2000; Dupré, 1998). Canguilhem was primarily concerned with the normal in relation to health. This is the original source of the term normal, traced by Ian Hacking to the 1820s in that context, though he also pinpoints other "nonmedical routes to the normal" which centre on the growing importance of standardisation in an industrialising world (Hacking, 1990, pp. 164–165). This link between the establishment and use of the normal and the development of standards is central to this paper.

Once this notion of the normal had been established in medicine, "it moved into the sphere of – almost everything" (Hacking, 1990, p. 160). It did not have to travel far to make it to physiology, and then to experimental embryology, which had adopted many of the methodological prescriptions of physiology. These included causal analysis, control of conditions and the use of controls (Churchill, 1973). In experimental embryology, normal development became a control, functioning as a comparator against which the effects of experimental manipulations could be observed, measured, and interpreted.

The more normative sense of normal imported from medicine via physiology would rest alongside a more descriptive sense of the term used in the work of the pioneering embryologist Karl Ernst von Baer (Hopwood, 2005). In the early days of comparative embryology the establishment of series of stages was not standardised. Each series was produced for particular local problems, organisms, and materials (Hopwood, 2005, p. 247, 2007, pp. 2–3). Normal development was standardised in tables of normal stages at the end of the nineteenth-century in comparative embryology (Hopwood, 2005, 2007). Most notably, in the 1890s embryologists Albert Oppel and Franz Keibel produced normal plates and tables to provide a basis for comparative investigation into the relationship between ontogeny and phylogeny, with the aim of testing theories such as the biogenetic law (Hopwood, 2007, pp. 7–8).

In experimental embryology, however, it was not until the 1920s that standardised normal stages began to be produced for circulation. Ross Harrison, in collaboration with the artist Lisbeth Krause, produced a series of drawings depicting the normal development of the salamander species *Amblystoma punctatum* (Hopwood, 2005, p. 275).[1] Harrison circulated these normal stages amongst his graduate students to ensure they had a common basis of comparison for their experimental work (Maienschein, 2014, p. 59). The stages then circulated with the graduate students to new jobs, and were also distributed by Harrison himself to other laboratories (Hopwood, 2005, p. 275).

[1] This species is now known as *Ambystoma punctatum* (Maienschein, 2014, p. 60).