



The wild type as concept and in experimental practice: A history of its role in classical genetics and evolutionary theory



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ABSTRACT

Wild types in genetics are specialised strains of laboratory experimental organism which principally serve as standards against which variation is measured. As selectively inbred lineages highly isolated from ancestral wild populations, there appears to be little wild or typical about them. I will nonetheless argue that they have historically been successfully used as stand-ins for nature, allowing knowledge produced in the laboratory to be extrapolated to the natural world. In this paper, I will explore the 19th century origins of the wild type concept, the theoretical and experimental innovations which allowed concepts and organisms to move from wild nature to laboratory domestication c. 1900 (resulting in the production of standardised lab strains), and the conflict among early geneticists between interactionist and atomist accounts of wild type, which would eventually lead to the conceptual disintegration of wild types and the triumph of genocentrism and population genetics. I conclude by discussing how the strategy of using wild type strains to represent nature in the lab has nonetheless survived the downfall of the wild type concept and continues to provide, significant limitations acknowledged, an epistemically productive means of investigating heredity and evolutionary variation.

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1. What are wild types?

The term ‘wild type’ is used in genetics to describe individual organisms or alleles deemed ‘normal’ or typical for their species. But more concretely wild type is what the standard lab strains of experimental organisms are commonly referred to as. These wild type strains operate as controls to measure variation in model organism systems. As the philosopher Rachel Ankeny observes (2007, pp. 49–50), without establishing a ‘wild type’ “it is not possible to have a ‘norm’ against which ‘abnormal’ (or more precisely, that which is variant) can be compared”. Selecting a wild type is therefore “the first step in the underlying strategy [of classical genetics]”. The importance of this first step was recognised early on. A 1921 ‘Report of the Committee on Genetic form and Nomenclature’ comments how “In most animals and plants it is convenient to settle on a standard type, preferably the wild type, when this is known. The effects of the various genetic factors are in general to be measured by the departure from type which they bring about” (Little, 1921, p. 176). The importance of the wild type’s role as a laboratory instrument for measuring variation has therefore been

acknowledged both by early 20th century geneticists and contemporary philosophers of science.

Lab wild types are however neither wild nor typical, but instead constitute a specialised class of domesticated organism, removed from wild spaces into controlled and artificially uniform indoor spaces. Isolated from their ancestral populations, they are forced to adapt to a manmade ecosystem of standardised nutriment, temperature and housing. Given these adaptive demands, plus research requirements such as easy availability, a familiar life history and known tolerance of captive conditions, it should not surprise that most model organisms in genetics have been selected from existing stocks of domesticated or commensal species (Ankeny & Leonelli, 2011), making them effectively doubly separated from ‘true’ wildness.

Despite these complications being widely known, claims that lab strains are representative of species in nature have been surprisingly enduring. One still widely used genetics textbook defines ‘wild type’ as “the type observed in the wild, in other words, in nature” (Griffiths, Gelbart, Miller, & Lewontin, 1999, p. 15). A later textbook (Guttman, Griffiths, Suzuki, & Cullis, 2011, p. 128) is admittedly more circumspect, asserting that “the term is useful only for certain experimental organisms: for ordinary human characteristics, such as eye color or blood type, no one allele can be considered the wild-type. And wild populations carry several

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alleles for many genes". The problem of utilising standard varieties to represent the species in the lab is here indicated, namely that they cannot properly represent the full extent of natural variation. This has led to some overt criticism of the very use of the term 'wild type'. Biologist Ken Weiss has for example blogged (2013) that 'wild type' is outdated terminology that only serves to confuse students, suggesting other terms such as 'reference', 'baseline' or 'control' be preferred.

My aim in writing this piece is not advocating terminological reform. Instead, I wish to place the wild type concept within its historical context and understand the reasons for its operational success in both past and present scientific research. I acknowledge that, literally interpreted, 'wild types' don't really exist. I want, however, to establish the reasons why past biologists thought they might exist, and why the concept has proven successful enough to become embedded within the language and strategy of genetics despite its inherent flaws. I will begin by, moreover, emphasising that some of the historical reasons for denigrating the wild type concept are overstated or based on a false picture of the history of biological thought. Much of the contemporary discomfort with the use of the term 'wild type' derives from the influential mid-twentieth century writings of certain evolutionary biologists involved in the 'Modern Synthesis' of Darwinism and genetics, in particular Theodosius Dobzhansky and Ernst Mayr. Dobzhansky – whose research on the genetics of natural populations did much to invalidate the naïve assumptions about variation in the wild held by lab-bound classical geneticists, e.g. his fellow 'Drosophilists' Alfred Sturtevant and Hermann J. Muller (see Kohler, 1994) – I will return to at the end of this paper. Mayr, though, I will deal with now.

2. Mayr, wild types and 'typological thinking'

In many ways the principal ideologue of the Modern Synthesis, Mayr sought to demarcate the new evolutionary biology from its predecessors and competitors whilst also maintaining a clear link to Darwin's original thought. One means by which he did so was by invoking a dichotomy between 'typological' and 'population thinking' (Mayr, 1959). 'Typological thinking' (also conflated by Mayr with the broader 'essentialism'), is the assumption that species are defined by an underlying and static 'type' or 'essence', and was claimed by Mayr to characterise both pre-Darwinian and anti-Darwinian thought (including the wild type concept employed by classical geneticists). 'Population thinking', the belief that species are nothing but interbreeding populations in a state of constant flux, is attributed by Mayr to Darwin, the revolutionary hero of this narrative, but the revolution is presented as incomplete and endangered until its victory is secured by the Modern Synthesis (Witteveen, 2015; 2016). Mayr's dichotomy proved rhetorically useful but came under fire from historians of science (example quote: "This polemic usage does violence to the historical record and confuses contemporary debates rather than clarifies them" [Farber, 1978]). Philosophers of science also defended the historical use of typological strategies in the life sciences as based on best contemporary knowledge and practice, and not as grounded in mere dogmatism (e.g. Sober, 1980). Further analysis over the years has helped deflate Mayr's claim that 'essentialism' characterised pre-Darwinian natural philosophy (Müller-Wille, 2011; Winsor, 2006), as well as pointing to the benefits of typological methods in biological investigations (Di Teresi, 2010).

When pressured, Mayr admitted the typological-population dichotomy was a "temporary oversimplification" (Witteveen, 2015). Nevertheless, he had few qualms with using this distinction to anachronistically dismiss swathes of historical research as products of typological delusions. This strategy of presenting the

progress of biology as stalled by ideologically imposed 'epistemological obstacles', whilst appealing as narrative, acts to obscure the proximate causes of historical disputes, which would otherwise complicate Mayr's story.¹ For an example salient to the history of the wild type concept, we see Mayr dispute Provine's claim that "The conflict between the Mendelians and biometricians ... drove a wedge between Mendel's theory of heredity and Darwin's theory of continuous evolution" by stating that "It was not this conflict that delayed the synthesis but simply the typological thinking of the Mendelians and their inability to understand the population nature of species" (Mayr, 1973, p. 346). This rhetorical dismissal of early Mendelian thought disregards the fact that what was precisely in dispute was the compositional and evolutionary nature of populations and that the neo-Darwinian concepts of population that emerged in the aftermath of the synthesis were not the same as the 'palaeo-Darwinian' concepts of population maintained by the biometricians. What was needed was precisely the reconciliation of the particulate, discontinuous and biochemically stable nature of Mendelian factors with the Darwinian theory of evolutionary change through the selective accumulation of infinitesimally small 'individual differences', i.e. the synthesis' claimed great achievement. This admirable achievement, however, required half a century of painstaking research and theory in order to reconcile the genuine differences between Darwinism and genetics. It was therefore not simply the case that a synthetic Darwinian theory of the genetics of natural populations could have been arrived at earlier in the 20th century if not for the retarding force of 'typological thinking'.

Understanding the above, I suggest that we take the wild type concept as a serious theory of the composition of natural populations that in its own time was reasonably defensible based on the then available evidence. The attempt to align laboratory standard organisms with some kind of natural standard (see the aforementioned comments of the 1921 Committee on Genetic Form and Nomenclature) was motivated by a genuine belief in the real existence of typical or 'normal' forms in nature, and many researchers in early genetics believed that inbred domesticated strains were a means of studying these normal forms of the species under tractable circumstances. Despite well-known divergences between nature and lab, classical geneticists generally believed themselves justified in extrapolating to nature knowledge produced in the lab. This belief can only be understood by placing early genetics in the context of late 19th and early 20th century evolutionary theory. From this we discern that 'wild type' had a prior life before entering the laboratory, being part of a longer history of domestic organisms standing in for the wild in scientific theory and experiment (see Shapin, 2010, pp. 22–3 for more details on 'standing-for' relations). Interrogating this history helps us understand how lab wild types came to play the role they did in classical genetics and what presumptions about the relationship between domestic and wild, artificial and natural, this research strategy depended on for epistemic legitimacy. I shall show this by first investigating the early 19th century origins of the wild type concept, then tracing the theoretical changes that allowed it to move from a concept applied to organisms in wild nature to one

¹ See Sloan's comments in his review of *The Growth of Biological Thought*: "Mayr's history is, consequently, normative rather than descriptive; it proceeds by a selection of problems and individuals either relevant to the solution of these problems or to their confusion and lack of clarity"; "[In spite of committing to avoid doing so] In practice, however, he often does use history judgmentally"; "[T]he sharply drawn party labels [of essentialism and antiessentialism] tend in the end not to be helpful. They lead Mayr to miss some insights, and to some extent they perpetuate certain confusions that might have been avoided if he had been willing to view history in a more flexible framework" (Sloan, 1985, p. 147).

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