Nils Roll-Hansen, University of Oslo: *"Whatever Happened to Wilhelm Johannsen's Genotype?"*

ABSTRACT: Apparently there is a revolution going on in fundamental theories of biology. New concepts and ideas are radically changing our understanding of heredity and development, of the evolution of species and the development of the individual, the relationship between phylogeny and ontogeny - as they used to be called. The gene is dissolving into the biochemical machinery of the cell, and the genotype is being displaced by the genome. Is the biological discipline of genetics simply collapsing into biochemistry?

In this situation it may be helpful to have a look at the origins of genetics about a century ago. Developments in cytology, plant and animal breeding and evolutionary studies during the final decades of the 19th century had prepared the ground for this new fundamental subdiscipline of biology. It was appropriately born in the year 1900 with the so-called rediscovery of Mendel's laws, and baptised as "genetics" a few years later by William Bateson. By 1915 T.H. Morgan and his collaborators had published a paradigm for the new discipline, *The Mechanism of Mendelian heredity*. The intervening period saw intense discussion to clarify the theoretical basis.

The ability to clearly distinguish hereditary from non-hereditary variations - theoretically as well as experimentally - was essential to the new discipline. The terms "genotype" and "phenotype" were introduced in 1909 by the Danish plant physiologist Wilhelm Johannsen, and his bean selection experiment (first published in 1903) became a classic demonstration of genotype stability and how to distinguish genotype from phenotype. Johannsen also coined the term "gene" for the hereditary factors that had been demonstrated so impressively by Mendelian hybridization experiments.

Johannsen, however, was deeply critical of the version of the chromosome theory that continued to dominate genetic thinking - the popular as well as the scientific - through the 20th century. According to Johannsen the fundamental biological entity was the genotype, not the gene. He insisted on a holistic interpretation of the

genotype, characterized his own view as “physiological” in contrast to the widespread “morphological” view of heredity, and drew historical lines back to Antiquity. Aristotle represented the physiological view and Hippocrates the morphological. According to Johannsen the segregating genes were only indentifiable as changing elements of a genotype that reacted as a whole to impulses from the environment. The “most comprehensive and most decisive part of the genotype does not seem to be able to segregate into units,” he explained. Johannsen saw Weismann as his arch-opponent, but he found similar tendencies, e.g., in de Vries and Bateson. They were not able to quite let go of the idea that phenotypic characters are transmitted from one generation to the next. A spirited explanation and defence of his genotype as fundamentally different from any morphological interpretation is found in Johannsen’s brief 1923 paper, “Some remarks about units in heredity” (Hereditas 4: 133-141). Here he also admitted that even he had struggled to grasp a clear concept of genotype: “ … originally I was somewhat possessed with the antiquated morphological spirit in GALTON’S, WEISMANN’S and MENDEL’S viewpoints.”

At a time when the genotype is being identified with DNA structures and the gene is dissolving, it may be useful to take a closer look at the ideas and arguments of the individual scientist who introduced the genotype- phenotype distinction. For instance, one might ask: Is there not a logically troublesome consequence of current descriptions of genotype and phenotype in biochemical terms? The genotype appears to be simply a part of the phenotype. The phenotype has swallowed the genotype. Is one result that the difference between heritable and non-heritable variations - which is essential to our understanding of the evolution of species - is slipping?