there is no evidence for this view. Certainly in such populations the “static” transitions between the genotypical differences manifesting themselves in several characters may be called continuous—but such a “continuity of museums,” as it might be called, is not at all identical with genetic continuity. Galton himself has emphasized the capital difference between the notions of continuity in collections and continuity in origin, and as yet the mutations really observed in nature have all shown themselves as considerable, discontinuous saltations. So in my own still unpublished experiments with pure lines. Natura facit saltus. The chemical analog to such mutations may be the formation of homologous alcohols, acids and so on. The greater mutations may be symbolized by more complicated molecular alterations. But such analogs are of very little value for the understanding of genetic evolution.

The genotype-conception supported by the great stock of experiments as to pure line work, Mendelism and mutations does not consider personal adaptation as a factor of any genetic importance. Phrases as “characters, won by adaptation and having successively been hereditarily fixed,” are without meaning from our point of view. Hence much talk of adaptive characters successively gained seems to us an idle matter. A closer study of desert organisms and the like may elucidate such things; here the suggestive researches of Lloyd as to stomates desert plants may be pointed out. And as to the old question of “mimicry,” this problem in the famous cases of butterflies has in a most convincing manner been put into Mendelian terms by the observations and experiments of Punnett, de Meijere and others. This stronghold of the united Lamarckism and selectionism has now been conquered for Mendelism, i.e., for the genotype-conception.

The genotype-conception here advocated does not pretend to give a true or full “explanation” of heredity, but may be regarded only as an implement for further critical research, an implement that in its turn may be proved to be insufficient, unilateral and even erroneous—as all working-hypotheses may some time show themselves to be. But as yet it seems to be the most prosperous leading idea in genetics.

Heredity may then be defined as the presence of identical genes in ancestors and descendants, or, as Morgan says in full accordance with this definition; “The word heredity stands for those properties of the germ-cells that find their expression in the developing and developed organism.”

And now it is time to end this communication, too long for its real contents, but too short for the importance and diversity of the great problem of heredity.

In concluding this address I must highly emphasize the eminent merits of Hugo de Vries. His famous book “Die Mutationstheorie,” rich as well in positive indications as in ingenious views, has been the mediator for the new and the old era in genetics. This monumental work is a landmark in the progress of our science. Like the head of Janus it looks at once forward and backward, trying to reconcile—at least partly—the antagonistic ideas of continuity and discontinuity in evolution and heredity; hence a great deal of the charm of De Vries’s work. But just these qualities have made the work of De Vries too eclectic for the stringent analytical tendencies of modern genetics—a tendency which has in recent years found a true home in American science.

Commentary: Genotype does not determine phenotype

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Wilhelm Johannsen’s ‘The Genotype Conception of Heredity’ introduced three fundamental terms into the lexicon of biology: ‘genotype’, ‘phenotype’ and ‘gene’; all seminal to the new emerging discipline of genetics. His paper was published 11 years after Hugo de Vries and Carl Correns ‘rediscovered’ what came to be called ‘Mendel’s laws of inheritance’. William Bateson introduced the term ‘genetics’ in 1905; he also added ‘zygote’ ‘homozygote’, ‘heterozygote’ and ‘allelomorph’ to the lexicon of genetics. Johannsen proposed his new terms in the context of heated debates over the modes of evolutionary change, the meaning of heredity, and hereditary factors. Their precise
definitions have changed over the past 100 years, but the arguments he made are as germane now as they were then.

Johannsen begins his discussion of the meaning of ‘heredity’ and ‘inheritance’ in biology and society. Those terms, he notes, are ‘ Borrowed from everyday language in which the meaning of these words is the “transmission” of money or things, rights or duties from one person to another: the “heirs” or “inheritors”. ‘The word ‘inheritance’ was confusing because in biology personal characteristics are not inherited. One had to distinguish the adult character from something else which is inherited and which somehow affects that character. Others had noted the same problem: the biological conception of heredity differed from the societal conception. Embryologist EG Conklin commented in 1908, ‘The comparison of heredity to the transmission of property from parent to children has produced confusion in the scientific as well as the popular mind’.2 Similarly, Thomas Hunt Morgan, who had left experimental embryology and founded the Drosophila school of genetics, wrote in 1910: ‘When we speak of the transmission of characters from parent to offspring, we are speaking metaphorically; for we now realize that it is not characters that are transmitted to the child from the body of the parent, but that the parent carries over the material common to both parent and offspring’.3

Johannsen’s articulation of the distinction between the social and the new biological meaning was derived from Mendelism and from his own famous selection experiments.1 The idea of an underlying ‘type’ for each species was the core behind his selection experiments with beans in 1903 (he had first introduced the term ‘genotype’ in a monograph written in German in 1909).4 The ‘genotype’, which he defined as the sum total of all the “genes” in a gamete or in a zygote, could only be discerned by experimentation.1 The ‘phenotype’, on the other hand, could be readily seen. ‘All “types” of organisms,’ Johannsen wrote, ‘Distinguished by direct inspection or only by finer methods of measuring or description, may be characterized as “phenotypes”’.1 He thus redefined ‘heredity’ ‘as the presence of identical genes in ancestors and descendants’.1

Naturalists and statisticians, whose views of heredity were based on direct inspection of organisms, were wholly mistaken because they assumed that an adult individual was a good representation of its genotype. Geneticists showed that an individual might have hidden recessive traits and therefore adult traits were not at all a fair representative of the genotype. Moreover, by observing phenotypes, one also could not distinguish between what was inherited and what was due to the environment.

Certainly, medical and biological statisticians have in modern times been able to make elaborate statements of great interest for insurance purposes, for the ‘eugenics-movement’ and so on. But no profound insight into the biological problem of heredity can be gained on this basis.1

Thus Johannsen addressed two conceptions of evolution, which failed to distinguish between phenotype and genotype. These were the ‘Lamarckian’ view of the inheritance of acquired characteristics, and biometricians’s views of heredity based on ‘the law of ancestral inheritance’ of Francis Galton, Darwin’s cousin who had coined the term eugenics in 1883.

Conceptions of evolutionary change based on ‘Lamarckian’ principles of environmentally directed adaptive hereditary change suffered from the erroneous assumption that adult qualities of the individual are transmitted.1 External conditions may mould an individual’s phenotype in an adaptive manner, but there was no evidence that they could induce adaptive changes in the genotype. Genotypes affected the personal qualities of the parents, not vice versa. Biometricians’ views were equally faulty. Galton noted that in populations there was a statistical regression toward the mean in such traits as tallness of men. He attributed that to an ancestral heredity, which would he halved in every generation. It was a common-sense perspective, and one whose underlying mechanism was based on blending inheritance. Mendelian genetics showed, however, that although phenotypes blended, genotypes did not. That homozygous recessives could result from heterozygous parents was completely inexplicable by Galton’s law, and indeed refuted it. Thus Johannsen dismissed the ‘laws of ancestral influence’ as mere superstition.

Ancestral influence! As to heredity, it is a mystical expression for a fiction. The ancestral influences are the ‘ghosts’ in genetics, but generally the belief in ghosts is still powerful.1

Biometricians were Darwinians, who maintained that natural selection acting on gradual changes in populations was the basis of evolutionary change. In the early 20th century they were embroiled in a feud with the Mendelians who advocated a saltationist view, more common then than now, that new species may arise rather suddenly in discrete steps. As Johannsen commented, ‘As yet the mutations really observed in nature, have all shown themselves as considerable, discontinuous saltations’.1 It was later shown, in the 1920s, that most Mendelian gene mutations were actually rather small, not saltational.

Johannsen’s introduction of the term ‘gene’ also occurred in the midst of controversy over determinist views of hereditary factors. Postulations of biological determinants, endowed with the properties of reproduction, assimilation and growth, had been pervasive in the 19th
century: the ‘gemmules’ of Darwin, ‘physiological units’ of Herbert Spencer, ‘pangenes’ of de Vries and ‘bioblasts’ of Richard Altmann had been widely considered. The most elaborate 19th century theory of heredity and development was that of August Weismann who postulated the existence of a hierarchy of determinants, organized in chromosomes, which would segregate out of the cell nucleus in the course of development and determine cell types. Weismann’s theory was refuted in the 1890s when experimental embryologists showed that the fate of a cell during ontogeny was regulated at least in part through its relations with others.

Johannsen’s aim in introducing the term ‘gene’ was to dissociate Mendelian genetics from all such discredited, speculative conceptions of self-reproducing vital entities. ‘Of all the Weismannian army of notions and categories’, he said, ‘Mendelism may use nothing’. The nature of the gene was of course not known, but the idea that the Mendelian factors were ‘discrete particles of the chromosomes’ was not a corollary of his genotype conception. Johannsen’s ‘gene’ did not have the power to reproduce itself, to grow and to assimilate; it did not possess an independent life of its own. ‘The gene’, he said, ‘Was nothing but a very applicable little word’. As he later put it, ‘The Mendelian units as such, taken per se are powerless’.

Indeed, it behoves us to take note that Johannsen’s genotype conception of heredity is a version distinct from two erroneous views, which are heard too often to this day, that ‘genotype determines phenotype’ and that the ‘gene’/DNA is self replicating.

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References


Commentary: A century of Mendelism: on Johannsen’s genotype conception

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Inundated by so many recent exciting developments in genomics, we missed the 100-years anniversary of the re-introduction of Mendelism and especially the foundation of the genotype concept following the publication of the paper that changed the face of modern genetics, namely Johannsen’s 1911 ‘The genotype conception of heredity’.1

Wilhelm Johannsen (1857–1927), a pharmacologist by training, served, without any formal university degree, as assistant in the Chemical Department of the newly founded Carlsberg Laboratorium in Copenhagen. In 1892 he was appointed lecturer and later professor of plant physiology at the Royal Veterinary and Agricultural College of Copenhagen. Finally, in 1905 Johannsen was appointed Professor Ordinarius in plant physiology at the University of Copenhagen, and in 1917 he became rector of the university.2

The notes of the class in heredity which Johannsen taught, first published in 1905 in Danish, were extended in 1909 into a German volume of 25 lectures regarding the Elements of the Exact Theory of Inheritance (Elemente der exakten Erblichkeitslehre).3 Updated second and third versions were published in 1913 and in 1926, respectively. Already in the first edition, Johannsen rebelled against the notions of heredity of early Mendelian colleagues,