William Johannsen and the Genotype Concept

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Recent secondary literature on the rise of modern genetics has begun to drag out of the shadows of historical neglect one of the major accomplishments in the history of biology. I refer to the conceptual distinction drawn between "phenotypes" and "genotypes," the use, if not the full meaning of which was fashioned in 1909 by Wilhelm Johannsen. Vorzimmer in his study of Darwin's later years has indicated how unaware Darwin and his contemporaries were of this distinction.[1] Both Allen and I have referred to the fundamental yet often misunderstood nature of this dichtomy,[2] and just recently in an essay review Mayr has described the failure to make this distinction as the basic confusion which was "by far the most damaging" to the progress of modern genetics.[3] Following these leads, I intend to explore the phenotype-genotype distinction in an effort to discover what it meant to geneticists at the time of its inception. First, however, it is of value to remind ourselves how we define this distinction for contemporary students, who must fully grasp it in order to understand modern genetics, ecology, psychology, the study of behavior, and above all modern evolution theory.

The definition given in J. D. Watson's *Molecular Biology of the Gene* is typical and has the advantage of conciseness. Watson writes: "We refer to the appearance (physical structure) of an individual as its *phenotype*, and to its genetic composition as its *genotype*."[4] Monroe Strickberger in a standard textbook, *Genetics*, is somewhat more elaborate. "In their broad definitions," he writes:

1. Peter J. Vorzimmer, *Charles Darwin: The Years of Controversy, The Origin of Species and Its Critics, 1859-1882* (Philadelphia: Temple University Press, 1970), pp. 19, 43-44.
2. Garland Allen, "Thomas Hunt Morgan and the Problem of Sex Determination, 1903-1910," *Proc. Am. Phil. Soc.*, *110* (1966), 53. Frederick B. Churchill, "Hertwig, Weismann, and the Meaning of Reduction Division circa 1890," *Isis*, *61* (1970), 446.
3. Ernst Mayr, "The Recent Historiography of Genetics," *J.. Hist. Biol.*, *6* (1973), 125-154; see particularly pp. 129-130.
4. J.D. Watson, *Molecular Biology of the Gene* (New York: W.A. Benjamin, 1970), p. 14.

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the *phenotype* refers to all the manifold biological appearances, including chemical, structural and behavioral attributes, that we can observe about an organism but excludes its genetic constitution. The *genotype* defines only the particular genetic material that an organism inherits from its parents. Therefore, although the phenotype changes with time as the appearance of the organism changes, the genotype remains relatively constant except for the rare genetic changes known as *mutations.*[5]

Note particularly that in both these definitions the author refers exclusively to the phenotype and genotype of individual organisms; note also that in Strickberger's definition the material of transmission is viewed as markedly stable in constitution.

Let us turn now to the creator of the expressions "genotype" and "phenotype," Wilhelm Johannsen. In doing so, we discover that scandalously little has been written about him outside of the Scandinavian tongues. In the most recent biographical sketch L. C. Dunn insisted, without overdoing it, that "Johannsen's place in the history of biology may come to be seen as a bridge over which nineteenth-century ideas of heredity and evolution passed to be incorporated, after critical purging, into modern genetics and evolutionary biology."[6] Dunn, however, could trace only five very brief secondary articles on Johannsen – a measure in itself of past historical neglect.

Johannsen was born in 1857, two years before the publication of the *Origin of Species.* To put it another way, his date of birth came nine years after de Vries's and nine years before Morgan's, an interesting antiquarian tidbit in light of Dunn's bridge metaphor. Johannsen's technical training was not in biology proper but as a pharmacist's apprentice, which initiated him into the studies of botany and chemistry. After occupying a minor position in pharmacy, Johannsen became an assistant in the chemical department of the Carlsberg Laboratories in Copenhagen. Considering his non-university training, there was no reason to suppose that he would climb onto, let alone climb up, the university ladder. Johannsen's work on winter dormancy of buds and his development of the technique of seed etherization, however, edged him somewhat closer to the centers of academic life; he was appointed first lecturer then professor at the Royal Veterinary and Agricultural

5. Monroe Strickberger, *Genetics* (New York: Macmillan Co., 1968), p. 102. The first emphasis is mine.

6. L.C. Dunn, "Johannsen, Wilhelm Ludwig," *Dictionary of Scientific Biography* (New York: Charles Scribner's Sons, 1970) *7,* 113-115. I have also consulted Fritz von Wettstein, "Wilhelm Ludwig Johannsen," *Die Naturwissenschaften, 20* (1928), 350-352; and Öjvind Winge, "Wilhelm Johannsen: The Creator of the Terms Gene, Genotype, Phenotype and Pure Line," *J. Hered., 49* (1958), 82-88.

College at Copenhagen. After the publication of his initial "pure line" studies on barley and the princess bean, Johannsen became professor of plant physiology at the University of Copenhagen – an extraordinary feat on the European scene for someone who did not have a university degree. He held this position for twenty-two years, until his death in 1927.

Johannsen's work on heredity forms a surprising unity. From his classic paper on pure lines of 1903[7] to the third and final revision of his basic text on genetics in 1926,[8] the historian will recognize many common threads which stretch tautly across the years. It is at once evident that Johannsen's work is highly experimental and committed to a mathematical analysis of the data. In both respects his writings contrast markedly with the descriptive and qualitative studies of heredity found commonly in the nineteenth century. Five of the first six chapters in Johannsen's *Elemente der exakten Erblichkeitslehre* drive the point home by laying out basic principles of the statistical analysis which was essential to render genetics an exact and qualitative science. These elementary lessons, he tells his biologist readers, were intended "to make the pain as slight as possible."[9] From the beginning to the end of his career, Johannsen openly conceded that Sir Francis Galton's studies were inspiration and guide to his own analyses. He dedicated his pure line research to Galton, and throughout the *Elemente* there are repeated references to Galton's law of regression and stirp model of heredity.[10] The imprint of Hugo de Vries's intracellular pangenesis and mutation theory is evident from the outset. And finally, Johannsen's own experimental contributions of the first decade, chiefly his pure line

7. Wilhelm Johannsen, *Ueber Erblichkeit in Populationen und in reinen Linien. Ein Beitrag zur Beleuchtung schwebender Selektionsfragen* (Jena: Gustav Fischer, 1903). I thank William Provine for pointing out the existence of a little known English translation: "Concerning Heredity in Populations and in Pure Lines," trans. Harold Gall and Elga Putschar, in *Selected Readings in Biology for Natural Sciences 3* (Chicago: University of Chicago Press, 1955), pp. 172-215. This is a lucid translation which includes the Introduction, Summary, and the first of three "Research Series" contained in the original.

8. Wilhelm Johannsen, *Elemente der exakten Erblichkeitslehre* (Jena: Gustav Fischer, 1909); 2nd ed., 1913; 3rd ed., 1926.

9. Ibid. (1909), p. 1.

10. The dedication reads: "Dem hochverdienten Schöpfer der exakten Erblichkeitslehre *Francis Galton F.R.S.* in Ehrfurcht und Dankbarkeit Gewidmet vom Verfasser." Ruth Schwartz Cowan, "Francis Galton's Statistical Ideas: The Influence of Eugenics," *Isis, 63* (1972), 509-528; and William B. Provine, *The Origins of Theoretical Population Genetics* (Chicago: University of Chicago Press, 1971), pp. 14-24 and Appendix, are two recent studies which help untangle the complexities and changes in Galton's ideas.

studies of *Phaseolus*, form the basis of his orientation and theoretical discussions up until the time of his death. Across this variant warp, however, the historian will also recognize a changing woof which plays an important role in Johannsen's continuing discussions of phenotypes and genotypes. It is this change within the consistency which I wish to draw out, for it carries us some way toward a history of the phenotype-genotype distinction. To emphasize this change I will treat Johannsen's work in two blocks. The first covers the seven years from his pure line study in 1903 to the publication in 1909 of his *Elemente*; the second concentrates on the third edition of the *Elemente* of 1926. Between this somewhat artificial cleavage, I will place a short intermezzo, the propriety of which I hope will be obvious.

PURE LINE STUDIES, 1903–1909

In spite of his sincere reverence for and obvious debt to Francis Galton, Johannsen was a severe critic of Galton's legacy—the school of English biometricians led by W. F. R. Weldon and Karl Pearson.[11] The cause of irritation was certainly not the invocation of mathematics and a statistical method; rather, Johannsen was reacting against their goal of measurement and calculations. In their eagerness to examine the influences of selection on populations, to lay out variations in neat distribution curves, to correlate with mathematical precision one variation with another, and to calculate the contributions of distant ancestors to a given offspring, Johannsen felt that the biometricians were distorting the basic biological problem of inheritance. In short, he explained, "We must pursue the science of heredity *with* but not *as* mathematics."[12]

The point about biometricians measuring the wrong thing was repeatedly driven home by Johannsen in his pure line studies. His favorite demonstration was to show that several populations of biologically dif-

11. Sketches of the theoretical contributions of the biometricians to genetics may be found in L.C. Dunn, *A Short History of Genetics* (New York: McGraw-Hill, 1965), chap. 12, and Provine, *Origins*, chaps. 2 and 3. For a valuable study on the institutional development of biometry see Lyndsay Andrew Farrall, "The Origin and Growth of the English Eugenics Movement," unpub. diss., Indiana University, 1969.

12. Johannsen, *Elemente* (1909), p. 2. This is a consistent theme with Johannsen. For example, in commenting upon a critical outburst against Bateson by Weldon, he remarked: "These are clear words and they contain an unfortunately not unjustified attack on the occasionally inexact experimental methods of certain modern biologists. But statistical theory alone surely cannot clarify the fundamental problems of biology!": "Heredity ... Pure Lines" (1903), p. 178.

ferent types, each of which exhibited a nice binomial distribution of a particular measurable character, could be extracted from a combined population which also exhibited a regular binomial distribution of that same character. Both sets of populations could be described by means of their respective curves of variation; both the combined population and the subpopulations would rank from a statistical standpoint as legitimate natural types. The reverse was also true; two or more populations exhibiting overlapping binomial distributions of a given character could be mathematically combined to produce a single population exhibiting a nice binomial curve. In short, a type described by a binomial distribution of a quantifiable trait told nothing about its biological unity; it was merely a statistical concept.

Such conclusions were derived from Johannsen's own extensive experiments with self-fertilizing plants, particularly with a variety of *Phaseolus vulgaris* known as the princess bean. But Johannsen was also adept at demonstrating the same principle with Galton's own numerous statistics of heights in human populations. Let us follow him briefly through one of his first examples which challenged the biometrical or statistical type and led Johannsen to his pure line definition. [13]

In the fall of 1900 Johannsen collected 5,000 *Phaseolus* seeds taken randomly from a uniform stock (see Figure 1). The next spring he chose 100 seeds, the weight of each being as close as possible to the average weight of the 5,000; he planted them in numbered plots. He also planted the 25 smallest seeds (by weight) and the 25 largest seeds (by weight). [14] Upon collecting the fall harvest (F_1 beans) Johannsen found that the weights of the offspring, whether tabulated according to the three weight groupings of the parent beans (25 smallest, 100 average, and 25 largest) or whether tabulated collectively, fell into regular variation curves. The collective curve coincided with the distribution of weights of the parent beans; the three separate curves confirmed Galton's law of regression in that they indicated that the offspring of deviating parents deviated on the average less from the mean of the entire population than their parents. So far his investigation contained no surprises.

However, when Johannsen went back to his record of the parent seeds and reclassified the groupings of large and small beans not accord-

13. Abstracted from Johannsen, *Erblichkeit ... in reine Linien*, pp. 15-39, and "Heredity ... Pure Lines," pp. 183-206.

14. His figures also include the weight of the other seeds used for other experiments; so in total there were 287 parent seeds used in the research series.

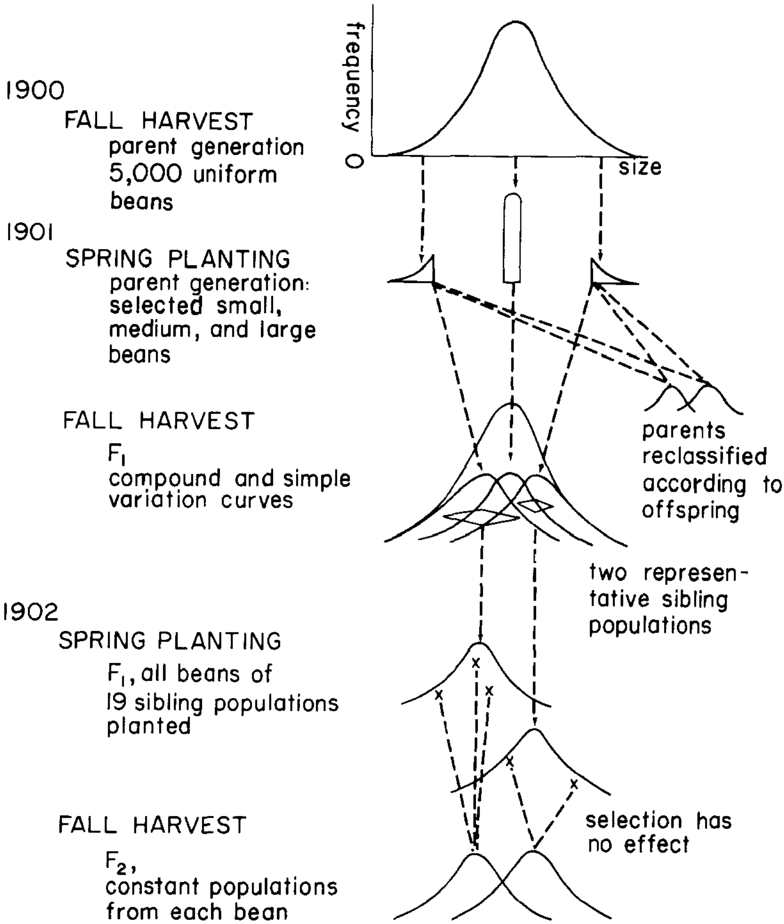

Fig. 1. Schematic outline of Johannsen's pure line experiments on *Phaseolus*, 1903.

ing to their own weight but according to the average weight of their own offspring, he found not a suggested binomial distribution but a bimodal curve. It seemed clear that very similar parent beans could produce very different offspring and could belong to different genetic classes despite the binomial distribution of their offspring tabulated collectively. The practicality and beauty of this demonstration of different genetic types lay in the fact that *Phaseolus* was a self-fertilizing plant and that Johannsen had isolated and measured genetically pure lines.

Johannsen relentlessly pursued his research on pure lines into a second filial generation. In 1902 he planted all seeds (F_1) produced by 19 selected plants of the 1901 season. Since he chose these plants (the parent generation) on the basis of their successful production of a large number of seeds, a fair distribution by weight of the F_1 beans was assured. The strategy rendered 19 populations of beans in the 1902 harvest, the average weight of which could be determined and compared, the weight of whose immediate parent beans (F_1) had been determined, and the weight of whose grandparent bean was known. The outcome revealed that the F_1 beans, their weight notwithstanding, individually produced offspring whose average weight did not differ significantly from the average weight of the F_1 siblings calculated together. Johannsen, in effect, had set up 19 self-fertilizing lines; he could perform a mental or paper selection of F_1 beans and could measure the effects on the next generation of this selection. The experimental design and the results were also telling in his crusade against the biometricians – this time particularly Karl Pearson. Johannsen had shown that within established pure lines a constancy of type measured statistically was evident despite any selection in the F_1 generation. Moreover, it was clear that within these pure lines Galtonian regression had evidently reached completion; that is, pure line beans no matter how much they deviated from the average weight of their siblings produced offspring whose average weight not only approached but coincided with the average weight of the parent generation. As Johannsen explained it: "The personal character of the mother-bean has no influence, that of the grandmother, etc., also none; but the *type of the line* determines the average character of the offspring."[15]

It was just such analyses which forced Johannsen to tease apart the

15. Johannsen, "Heredity ... Pure Lines," p. 206. Provine includes a useful account of the criticism levied against Johannsen's pure line studies by the biometricans Pearson, Weldon, and Yule: *Origins*, pp. 96-100, and 105-108.

difference between a statistical and genetic description of type. In writing the text of his pure line studies, he emphasized the importance of this distinction: "The concept 'type' or 'typical value,"as statisticians mostly define it . . . does not have to agree with the concept 'type' of genetic theory."[16] In 1909 he designated this difference by coining the words "phenotype" and "genotype" terms which were introduced within the context of his by then customary demonstration of the absence of biological unity in a binomially distributed population. "Thus we recognize," wrote Johannsen,

> that the "type" in Quetelet's sense is only a phenomenon of superficial nature which can deceive: only further investigations will decide whether a single or several biologically different types are present. Therefore one might designate the statistically derived type as appearance type [*Erscheinungstype*] or more simply as "Phenotype."Such Phenotypes are in and for themselves measurable realities: exactly what can be observed as characteristic; thus in variation distributions the centers about which the variants group themselves. With the word phenotype the necessary reservation is made, that no further conclusion may be extracted from the appearance itself. A given phenotype may be an expression for a biological unity; but by no means does it need to be. Most of the cases of phenotypes found in nature by statistical investigation are not! [17]

In 1909 this was essentially the gist and extent of his definition of phenotype. But before discussing its implications let us see how he introduced the term "genotype."In the same chapter, after also coining the "hypothesis-free" word "gene,"[18] Johannsen referred to "genotypical difference." The associated noun was defined with even less precision than "phenotype."His mention of "genotype" at the outset of the next chapter came as close as anything in the book to an explicit definition:

> The manner in which the phenotypes manifest themselves . . . says from the outset absolutely nothing about the genes. Very obvious phenotypic differences can appear where no genotypic difference is present; and there are also cases where under genotypic differences the phenotypes will be similar. For this reason it is of the utmost importance to separate the concept Phenotype (or *Erscheinungstypus*) from the concept Genotype (or *Anlagetypus* one might say). It is true we cannot operate with the last concept – a genotype does not clearly appear in the phenomenon; the derived concept of genotypic difference, however, will be useful to us on many occasions.[19]

The content of both these definitions should surprise the modern biologist. Compared with the textbook definitions given at the outset of

16. Johannsen, "Heredity ... Pure Lines," p. 175, n.1.
17. Johannsen, *Elemente* (1909), p. 123; modified from L.C. Dunn's translation, *Short History*, pp. 91-92.
18. In German the singular is "Gen," the plural "Gene." *Elemente* (1909), p. 124.
19. Ibid., p. 130.

this paper, they raise real questions about Johannsen's objective. Let us examine the text for a moment and see what he intended as he fashioned the phenotype-genotype distinction.

As initially introduced, the concept "phenotype" obviously sprang directly from Quetelet's statistical notion of type. It was conceived of as the mean of a distribution of variations or, to repeat Johannsen's words, to "designate the statistically derived type as the 'Appearance type' or simply as 'Phenotype.' " The forms observed, the structures measured and counted, all the data collected by descriptive biology were indeed concerned with appearances, but in a statistical way. Johannsen's primary definition of a phenotype implied that a race described by a binomial curve had a phenotype; it implied that the pure lines of beans which he had extracted by self-fertilization each had its phenotype. What is more, Johannsen, in describing the mean, also could describe the entire binomially distributed population in question, and he implied that mixed populations (i.e., races, subspecies, and species) had their own phenotypes. This put a curious twist on the term which J. D. Watson had referred to as "the appearance (physical structure) of an individual"; the twist, however, is understandable given Johannsen's context of usage.

The import of the statistical nature of Johannsen's phenotype concept can best be illustrated by a few excerpts. He was, for example, constantly chiding the biometricians for displacing the phenotype when they applied selection to a mixed population.[20] In comparing genetically similar groups of organisms in different situations, he explained, "for each living condition [there is] a special phenotype."[21] And in discussing the continuity seen in organic nature he wrote: "Between individuals and also between phenotypes we find again and again continual transitions."[22] All three of these examples suggest that Johannsen had populations in mind. One can, too, find places in the text where the phenotype concept might be interpreted as the *Erscheinungstypus* of the individual,[23] but these are not common and they do not fit in with the general thrust of Johannsen's text.

20. E.g., "Der Phaenotypus vieler nach Selektion in einer Population gewonnenen Nachkommenserien erscheint in der Selektionsrichtung verschoben; und dies ist einfach eine Folge davon, dass die Population (der Bestand) in genotypischer Beziehung gemengt, also unrein war!" Ibid., p. 141.

21. Ibid., p. 215.

22. Ibid., p. 327.

23. For example, "Gerade hier, wo man nicht unmittelbar an jedem Individuum dessen Phaenotypus erkennen kann, sind die Schwierigkeiten fur die Forschung am grössten und die Fehlerquellen die ergiebigsten gewesen." Ibid., pp. 130-131.

When the historian turns to Johannsen's original expression, "genotype," he runs into additional puzzles. Recalling the pertinent passage reprinted above, he will note that Johannsen does not define the term in any explicit way except for equating it with the *Anlagetypus*. This characterization may seem nearly as satisfactory as Watson's or Strickberger's definitions, which mention "genetic composition" and "genetic material," but again in both these modern definitions there is the explicit reference to the genetic make-up of an *individual* which is absent from Johannsen's discussion. Furthermore, Johannsen went out of his way to admit that the genotype did not "appear in the phenomenon" and that the biologist would be unable to "operate" with the concept in its substantive form. It is not altogether clear at this juncture what Johannsen had in mind; at minimum he seems to have argued that the genotype was microscopically an unknown and perhaps an unknowable; it may be that he felt that the "genotype" was an abstraction. I think there is some of both connotations involved. Let us pursue this further.

The expression "genotype" is obviously a compound, combining the notion of "type" with the newly improvised term "gene." It seems clear from his vehement reactions that Johannsen coined this latter word to bring about a moratorium on speculations about hereditary particles: the micellae, the pangenes, the Ids and the Idioblasts which flowed all too freely from the pens of his predecessors and contemporaries. Johannsen claimed as much; the designation "gene" was intended to be neutral and noncommittal. Listen to his entreaty as he introduced the noun:

> The word gene is completely free of any hypothesis; it expresses only the certain fact, that many characters of the organism are somehow or other stipulated by the special, separable, and consequently independent *conditions* [*Zustände*], *rudiments* [*Grundlagen*], or *Anlagen* which are present in the gametes – in short, by that which we now wish to designate as genes. [24]

Johannsen was right; it was time to wax less speculative about biological units which assimilated material, grew and self-replicated. [25] Poor child of science! He was wrong in believing he could avoid hypotheses

24. Ibid., p. 124.

25. In defending his own understanding of the gene, Johannsen at one point likened the hereditary organic particles to the famous horse in the locomotive: "Die Auffassung der Gene als Organoide, als Körperchen mit selbständigem Lebe u. dergl. ist aber nicht mehr von der Forschung zu berücksichtigen. Voraussetzungen, welche eine solche Auffassung nötig machen sollten, fehlen gänzlich. Ein Pferd in der Lokomotive steckend als Ursache der Bewegung – um Lange's klassischen Beispieles zu gedenken – ist eine ebenso 'wissenschaftliche' Hypothese als die Organoidlehre zur 'erklärung' der Erblichkeit." Ibid., p. 485. See also L.C. Dunn, *Short History*, pp. 131-132.

– in this case, I should add, avoid assumptions about the hereditary process. He had rejected one alternative: special, living particles or organic units. There is no reason to suppose for a moment that he had any inclination toward another alternative championed by his contemporary Hans Driesch – namely, an entelechy and vitalism. But there were several intermediate positions, and the pharmacist and chemist in him encouraged Johannsen to stand tentatively by one.

Here and there as he talked about mutations, the meaning of dominance, the determination of sex, or the correlation and coupling of genes, Johannsen dropped hints that he thought of organic "structural chemistry" as providing an analog for the hereditary stuff in the gametes.[26] The suggestions are slight, but the underlying assumption is no less real. In 1910, before an audience of American geneticists at Ithaca, New York, Johannsen was less guarded about his chemical model for the germinal material. An attempt to reconcile the discontinuities revealed by classical Mendelian experiments and Castle's work, which suggested an erosion in the segregation patterns, gave him the context for launching into a chemical anology:

> If we suggest an analogy between the radicals of chemistry and the genes, the (partial) genotype-formulas in Castle's manner may be able to demonstrate ramifications of the genes inserted upon the main group of the genotype-constitutents. Pausing a moment on this metaphor, it may be suggested that the "branch" or "branches" of a ramified gene may be more difficult to separate from its "trunk" than the whole gene from the totality of the genotype. I shall here only ask if such views may be of any use as working hypotheses.[27]

Like the wizard from Woolsthorpe who promised "to frame no hypotheses." Johannsen evidently did not take his own advice seriously.

More to the point, Johannsen commonly talked of a germinal *"Etwas."*[28] The expression was provisional, but Johannsen felt certain

26. For example, while discussing the implications of Mendelizing and non-Mendelizing traits, Johannsen resorted to a common chemical analogy: "Die 'konstanten,' nicht (oder jedenfalls nicht in allen Charakteren) spaltenden Bastarde sagen selbstverständlich gar nichts gegen die Annahme selbständiger Gene überhaupt. Sie geben sogar eher eine Andeutung über die Natur der Gene. Denn wie die Spaltungserscheinungen an Auskristallation erinnern – mit Möglichkeit oder gar höchster Wahrscheinlichkeit für gelegentliche unreine Trennung – so erinnert das Nichtspalten an nicht oder schwierig zu trennende körper, wie es z.B. viele Fettstoffe sind. Die Andeutungen über die Natur der Gene laufen immer mehr und mehr darauf hinaus, dass chemische Zustände massgebend sind." *Elemente* (1909), p. 426. Also ibid., pp. 482-484.

27. Wilhelm Johanssen, "The Genotype Conception of Heredity," *Amer. Nat.*, *45* (1911), 148. See also p. 158.

28. Johannsen, *Elemente* (1909), pp. 123-124.

that this *"Etwas"* would eventually be described in simple chemical terms. "From the further development of general physical chemistry," he commented with his customary reserve, "we can especially anticipate the points of view presented for theories about the operation of chemical hereditary factors." [29]

A prescience of future molecular biology? Perhaps, but in the context of the early twentieth century such"chemism"told more about the author's opposition to factorial genetics. His viewpoint also placed a telling imprint on the phenotype-genotype distinction as he had fashioned it. This can best be argued by first referring to the case of Ernst Haeckel, nineteenth-century materialist and reductionist, who championed a mixture of Darwinism and Lamarckianism, and who expounded profusely on questions of heredity. Haeckel described the hereditary process as an "overgrowth" or "a growth of the organism over and beyond the individual mass, one part of which is elevated to the whole." [30] Thus the processes of development and heredity for him were essentially the same and were to be identified in simple chemical terms. In short, Haeckel made no clear-cut distinction between the genetics of transmission and the genetics of development.

One does not have to go back into the nineteenth century, though, to find examples of chemical theories and their inherent tendency to confuse the hereditary and developmental processes. Telltale passages may be selected from T. H. Morgan, who in 1910 contrasted what he called the "physico-chemical reaction" school and the "particulate theory of development." Allen has described this moment in his life as the time when Morgan was going through the throes of a personal revolution in hereditary theories; it is not clear from Morgan's 1910 paper on "Chromosomes and Heredity" that he had completed the transition – a transition, in fact, from a physico-chemical theory to a third alternative, which will be discussed below. [31] Morgan's personal conviction, however, is not crucial for the general point I am making about chemical theories. The approach was a real option at the time, and Morgan's descriptions convince me that his physico-chemical position utterly confounded the difference between development and

29. Ibid., p. 485.

30. For a detailed treatment of Haeckel's attitude, see Frederick B. Churchill, "August Weismann and a Break from Tradition," *J. Hist. Biol., 1* (1968), 91-112. For the quotation in question, see p. 97.

31. Garland Allen, "Morgan and Sex Determination." Thomas Hunt Morgan, "Cromosomes and Heredity," *Amer. Nat., 14* (1910), 449-496.

heredity. Three excerpts, I hope, will make this point clear: (1) In discussing the meeting of homologous chromosomes during fertilization, Morgan stated that "this has been interpreted to mean that an actual fusion takes place as complete as when two drops of water unite into one."[32] (2) In describing the epigenetic development implied by the physical-chemical school, Morgan pictured "the germ-cells as consisting of one fundamental material, or at most of a few materials that change as development proceeds, until finally the end-product[s] of the changes are the kinds of materials that he know to differ in a number of ways."[33] And (3) in summarizing various explanations of Mendelian segregation, Morgan concluded – and I think with personal conviction – "that the essential process in the formation of the two kinds of gametes of hybrids in respect to each pair of contrasted characters is a reaction or response in the cells, and is not due to a material segregation of the two kinds of materials contributed by the germ cells of the two parents."[34]

In short, these three passages take up serially: the process of fertilization, the process of differentiation, and the process of gamete formation; collectively they represent a complete ontogenetic cycle. At no point in the circle did Morgan recognize a marked difference between the process of transmission and the process of development. Both included an unspecified "physico-chemical reaction," and there seemed to be a cyclical continuity from one to the next. Allen has commented on the ambiguities underlying Morgan's state of mind; his remark is pertinent to my theme. "Behind all of Morgan's objections to Mendelism in 1910 lies one fundamental problem. This is his confusion of the phenotype and genotype of an individual."[35]

To return to Johannsen, to insist that his chemical conception of the germinal *Etwas* merely reflected the primitive state of chromatin chemistry and his own cautious manner would be fair but would miss the point. The question remains, how did this primitive chemical view influence the phenotype-genotype distinction?

In order to answer this, let us draw the unraveled skeins of our story together. We have found that Johannsen's pure line studies emphasized a population notion of phenotype. Through selective breeding he had

32. Morgan, "Chromosomes and Heredity," p. 463.
33. Ibid., p. 452.
34. Ibid., p. 479.
35. Allen, "Morgan and Sex Determination," p. 53. N.B. the author's last two words!

narrowed the phenotypic range; viz., he had segregated out several phenotypes from what had previously appeared to be a single statistical type. Once the population profile had achieved a stability through self-fertilization, it was a natural suggestion on his part, although it did get him into trouble with the biometricians, to say that the pure lines contained a constant and unfluctuating germinal base; viz., that the gametes were all alike and that the pure lines had a pure and stable genetic make-up. Johannsen was making a generalization principally about collectives on the *Erscheinung* level and extending it, keeping the emphasis on the collective, to the *Anlagen* level. A pure line on the first meant uniformity on the second. Recognizing the dangers of over-doing it, I want to claim that when he coined the expressions "pheno-type" and "genotype," Johannsen had performed a vertical rather than a horizontal analysis [see Appendix]. He had created and described very special populations – the narrowest and most precisely identified types. He was not making a cleavage which cut the individual organism figuratively in two, with the unchanging material of heredity at the base and with the ontogenetic processes rising out of it to give the *Erscheinungs-phenomena* of each generation. His chemical concept of the gene encouraged Johannsen to gloss over this critical divide between transmission and developmental genetics. [36]

One of the most fascinating features of the *Elemente* of 1909, which bears directly on this question of a horizontal cleavage of the individual, was Johannsen's skeptical stance toward cytology. This skepticism went beyond the contempt he displayed for the highly speculative germplasm theory which August Weismann had developed out of his own research on the cytology of reduction division. [37] Time and again Johannsen objected to the cytological efforts to bind Mendelian patterns of segregation to chromosomal phenomena. He thought the ideas of Strasburger and Boveri were "speculations moreover, which have never further affected experimental genetics." [38] The root of such skepticism lay in his concern that a fusion of Mendelian genetics and cytology would localize and materialize his conception of the gene, which for him must remain a dynamically chemical and physiological

36. Modern biology applies this cleavage not only to the individual but to populations when it speaks of a "gene pool." This conceptualization was only possible after the maturity of population genetics and the Morgan-Mendelian theory of the gene.

37. For particulars on this research see Churchill, "Reduction Division circa 1890."

38. Johannsen, *Elemente* (1909), p. 482. At the same time Johannsen did speak highly of Sutton's and Wilson's research.

notion: genes represented reactions. This opposition to cytology was at times very explicit: "Because a 'division' [Spaltung] of these small structures [chromomeres] is obvious in the processes of nuclear division," he warned his readers,

> this division will be arbitrarily conceived of as corresponding to Mendelian "segregation" [Spaltung]. Here we touch a conception of the gene as a material, morphologically characterized structure which is very dangerous for the smooth advance of genetics; a conception which we must urgently warn against here.[39]

Weismann's germplasm theory in particular, with assists from Nageli's ideoplasm theory and de Vries's intracellular pangenesis – all professedly cytological – had envisioned a spatial isolation of proto-gametic material from the events of ontogeny. The somatoplasm and germplasm, according to Weismann, were physically separated from each other in the organism. If ever there seemed to be a cytological model for the phenotype-genotype distinction, the germplasm theory would appear to be it. Johannsen would have none of it. "This conceptual separation," he asserted, "does not succeed [lässt sich nicht realisieren], the 'stirp,' the germplasm, thus the 'genes,' the 'hereditary unities' are not portrayable in their totality and purity."[40]

In 1909 transmission and developmental materials were regarded by Johannsen as one and the same; the individual organism according to his genotype-phenotype distinction was not to be cut horizontally in two.

ITHACA, 1910

For the promised intermezzo I take you to the Christmas 1910 meetings of the American Society of Naturalists at Ithaca, New York. A symposium on Johannsen's "Genotype Hypothesis" was one of the featured attractions – one year, it should be noted, after the coining of the term.

Johannsen came from Denmark to give the major address.[41] His views were essentially those elaborately detailed in his *Elemente* of the previous year. In a rambling way he criticized what he called "transmission conceptions" of heredity. By this he meant all theories which since time immemorial had endeavored to explain the transmission of personal qualities from parent to progeny. His attack was principally aimed at the biometricians, but he also assailed Darwin and the neo-

39. Ibid., pp. 375-376.
40. Ibid., p. 484.
41. Johannsen, "Genotype Conception of Heredity."

Lamarickians – they, too, had concentrated on the inheritance of appearances. He recognized Galton and Weismann as having made some effort to break away from the grip of "transmission heredity," and then he proceeded to review the literature on pure line breeding. These studies in combination with the Mendelian analysis of segregation, he argued, lead to the genotype concept.

During the course of the talk Johannsen described his chemical concept of the gene (excerpted above), and in a most revealing section he evaluated the contribution of microscopy to the genotype concept:

> Certainly the process of segregation must be a *cell-action* intimately connected with division. But all the innumerable detailed results of the refined cytological methods of to-day do not elucidate anything as to segregation. It seems to the unprejudiced observer that the much-discussed cytological phenomena of karyokinesis, synapsis, reduction and so on may be regarded rather as consequences or manifestations of the divisions, repartitions and segregations of genotypical constituents (and all other things in the cell) than as their causes. This view is applicable even in those cases where sex-determination can be diagnosticated cytologically.[42]

The message was clearly a repetition of his 1909 position. His genotype theory relied almost exclusively on the vertical analysis which arose out of his pure line studies and his continued low esteem for cytology.

There were seven other participants. Herbert S. Jennings, who had initiated the symposium, described his own pure line research with paramecia.[43] He concentrated on the implications which such studies had for the contemporary debate over evolution by natural selection (one of several points of attack on the biometricians). His definition of a genotype at the outset, however, is revealing. As he stated it, "the genotype is merely a race or strain differing hereditarily in some manner from other races."[44] There is nothing biologically wrong about such a characterization. With paramecium, which normally reproduces asexually, Jennings had achieved a pure line clone not possible for Johannsen with his *Phaseolus* studies. Today it would be fully appropriate to talk about the genotype of a clone, yet in those sixteen words Jennings revealed the vertical aspect of the phenotype-genotype distinction. George Shull[45] said many of the same things with relation to his experiments on maize while he understandably described some of the

42. Ibid., pp. 153-154.
43. Herbert S. Jennings, "Pure Lines in the Study of Genetics in Lower Organisms," *Amer. Nat., 45* (1911), 79-89.
44. Ibid., p. 80.
45. George Harrison Shull, "The Genotypes of Maize," *Amer. Nat., 45* (1911), 234-252.

applied aspects of pure line breeding. He equated genotypes with "petites espèces," "biotypes," and "elementary species." I read the same vertical implication into these comments, too.

As if to spoil a good story, Edward East and Raymond Pearl, both experimental breeders, edged toward an articulation of the horizontal cleavage of the individual. East, before describing his pure line experiments with maize, claimed the basis of the Johannsen genotype hypothesis was the difference between non-inherited variations in the "soma" and inherited variations that were germinal. "This being so," he added in a remark which could hardly have pleased his Scandinavian visitor, "it seems scarcely necessary for an elaborate proof of the proposition, for it is nothing but a corollary to that part of Weismannism which was already generally accepted." [46] Pearl, whose efforts to measure the inheritance of fertility in poultry presented a much more complex situation, also saw the distinction between somatic and germinal variations as being basic to the genotype hypothesis. [47]

There were two papers by men outside the pure line breeding fold. J. Arthur Harris, a biometrician, naturally enough took up the cudgel in defense. [48] After criticizing a number of specifics in the pure line data, particularly Pearl's, he concentrated on that portion of Johannsen's attack which concerned the biometricians the most, viz., the inefficacy of natural selection in pure lines. He claimed the genotype theory contained a circular argument, that by definition selection could not produce a change in a pure line and when change did occur that this was blithely attributed to a mutation, to an environmental influence, or as the circularity would have it to an impurity in the genotype. The argument had some merit, although Johannsen had first established his pure lines through self-fertilization, not selection. More to the point, such arguments suggested how completely Harris had focused on the vertical aspect of the phenotype-genotype distinction. Consider the following definition given by Harris at the outset of his paper: "A genotype or biotype is an organic unit, reproducing itself constantly except for the transitory, non-inheritable modifications due to environmental influence."[49] Here surely is a reference to the collective.

46. Edward M. East, "The Genotype Hypothesis and Hybridization," *Amer. Nat., 45* (1911), 160-174; quotation appears on p. 162.

47. Raymond Pearl, "Inheritance of Fecundity in the Domestic Fowl," *Amer. Nat., 45* (1911), 321-345; see esp. p. 322.

48. J. Arthur Harris, "The Biometric Proof of the Pure Line Theory," *Amer. Nat., 45* (1911), 346-363.

49. Ibid., p. 351.

The seventh contribution to the symposium was the most interesting of all. This was submitted by Morgan, who by this time had crossed the watershed of his personal revolution.[50] His paper dealt with sex determination, and in it Morgan presented several alternative formal schemes, all of which allowed for the 1 : 1 ratios involved but only one of which could account for secondary sexual characters and sex-limited traits. It is evident that by then he was seriously flirting with a chromosomal theory of inheritance and that his position involved an incorporation of the cytological accounts of accessory chromosomes. In other words, he was bringing to the bar the hypothesis that a suprafactorial structure carried the transmission material and remained stable, perhaps even unchanged, during development.

But what about the genotype theory and Johannsen – the subject supposedly of the symposium? Morgan freely used the term "gene" as though it were synonymous with "unit factor." Moreover, he concluded the paper with a repetition of the provisional suggestion made by de Vries that "the genes are contained in smaller bodies that can pass between homologous pairs of chromosomes."[51] The exact analog he had in mind is irrelevant; his cytological point of reference is absolutely clear. Morgan used the term "phenotype" once but in a very awkward context.[52] Despite the subject of the symposium he did not incorporate the term "genotype" into his text, and although he mentioned "pure lines" on occasion, not once in the printed text did he refer to Johannsen, who had come all the way from Copenhagen for the meetings. It is hard to consider the oversight unmeaningful when one notes that in his *Mechanism of Mendelian Heredity* of 1915, written jointly with Bridges, Sturtevant, and Muller, Morgan also failed to take full advantage of the expressions "phenotype" and "genotype."[53]

I have no intention of pointing an accusing finger at Morgan for a public slur or scholarly slight. To the contrary! My feeling is that Morgan of all the participants at the symposium on the genotype hypothesis was seriously concerned with matching Mendelian and pure line phenomena to the cytological events. To this extent he was the only one who clearly saw beyond the vertical analysis of populations empha-

50. Thomas Hunt Morgan, "The Application of the Conception of Pure Lines to Sex-limited Inheritance and to Sexual Dimorphism," *Amer. Nat., 45* (1911), 65-78.

51. Ibid., p. 78.

52. Ibid., p. 65.

53. T.H. Morgan, A.H. Sturtevant, H.J.Muller, and C.B. Bridges, *The Mechanism of Mendelian Heredity* (New York: Henry Holt, 1915).

sized by Johannsen to the horizontal cleavage of the individual organism stressed in the modern phenotype-genotype distinction. He alone would have subscribed at once and wholeheartedly to the definition of these terms by Watson and Strickberger given at the outset of this paper.

Allen has remarked that "it was, perhaps, his later ability to make a rigid distinction between genotype and phenotype (coming after his work with *Drosophila* began in 1910) which allowed Morgan to accept fully the Mendelian and chromosomal interpretation of inheritance." [54] I would like to change the order and modify the conclusion by saying that it was the chromosomal interpretation which allowed Morgan to make the phenotype-genotype distinction as we now commonly employ it. Since this arose so completely out of his cytological orientation, Morgan had no reason to employ Johannsen's expression, which after all did not describe the distinction as he himself saw it. How these terms eventually became incorporated into genetics in Morgan's fuller sense in another story, which cannot be explored here.

THE 'ELEMENTE' OF 1926

The sixteen years which separated the Ithaca symposium and the third and last edition of Johannsen's *Elemente* witnessed extraordinary achievements in *Drosophila* genetics. These have been described in brief by a number of recent historical sketches, and soon we will have full-length studies of at least two of the major participants. [55] There is no need to describe these activities here except to remark that the work on gene linkage, crossing-over and double crossing-over, nondisjunction of chromosomes, chromosomal maps, and interference contributed to the establishment of the chromosome theory of heredity and the "classical" theory of the gene. The general thrust of this work was to underline the existence of a stable, lineally arranged chromosomal architecture as the basic hereditary material.

In the light of this achievement it is instructive to turn to the third and last edition of Johannsen's textbook, the *Elemente* of 1926. Published the same year as Morgan's *Theory of the Gene* [56] and a year

54. Allen, "Morgan and Sex Determination," p. 53.

55. For example, Dunn, *Short History*; Elof Axel Carlson, *The Gene: A Critical History* (Philadelphia and London: W.B. Saunders, 1966); and A.H. Sturtevant, *A History of Genetics* (New York: Harper & Row, 1965). Garland Allen is completing a scientific biography of Morgan, Carlson a similar work on Muller.

56. Thomas Hunt Morgan, *The Theory of the Gene* (New Haven: Yale University Press, 1926).

before Johannsen's own death, the work with its changes and additions shows the author's efforts to adjust to the new genetics. Upon casual inspection it would be easy to claim that there had been few substantial changes. The chapters in the first two thirds of the text are easily correlated with their predecessors of 1909. Johannsen devoted the same six chapters to the problems of elementary statistics; he discussed pure line studies (with many new additions) in the same chapters; he introduced the terms "phenotype," "genotype," and "gene" in the same context; he expanded by a number of chapters his examination of the influence of selection on populations of various profiles. But all these additions did not represent a changed viewpoint. If the *Erscheinungstypen* can be deceptive, however, so too can tables of contents. Built into revisions of the text was, in fact, a substantial but cautious modification of Johannsen's phenotype-genotype distinction.

In pursuing this change, let us first examine Johannsen's increased interest in the development of cytology. He began the revised last third of his text with a discussion of the fertilization process, a process which involved "the union of the genotype of the egg with that of the sperm cell." [57] He recognized, furthermore, that the nuclei of both gametes were the bearers of the genotypic constitution. He went into a brief discussion of reduction division and borrowed an illustration from the recently published third edition of E. B. Wilson's *The Cell in Development and Heredity* to illustrate how different chromosomes might segregate into different gametes. [58] After commenting upon the threadlike structure of the chromosomes and their beadlike array of chromomeres, and after reviewing some of the arguments against regarding the chromosomes as primary structures, Johannsen confessed that "the behavior of the chromosomes, as we will see, shows in many cases such an astonishing parallel with certain hereditary phenomena after hybridization, that one is well persuaded to ascribe to them a wholly special significance."[59] Here Johannsen was expressing a reception of the discoveries of cytology entirely different from that accorded them in the 1909 *Elemente*.

57. Johannsen, *Elemente* (1926), p. 413.
58. Ibid., p. 415. The 3rd ed. of *The Cell* was published in 1925. Johannsen described Wilson's classic text as "wohl das bedeutendste Hauptwerk der Zytologie in bezug auf Vererbung." Ibid., p. 718. Herman J. Muller in an "Introduction" to a reprint of the first edition of this classic text has discussed in detail the influence Wilson had on genetics by bringing the cytological view to the fore. See Edmund B. Wilson, *The Cell in Development and Inheritance* (New York: Johnson Reprint Corp., 1966), pp. ix-xxxviii.
59. Johannsen, *Elemente* (1926), p. 418.

The emphasis on a parallel between nuclear events and hybridization results was further discussed, although not encouraged, when Johannsen turned to an explication of Mendel's own experiments of 1865. Johannsen saw Mendel's salient contributions as establishing (1) the independence of "genes," (2) segregation of "genes," and (3) the possibility of new combinations of "genes."[60] Such a summary was probably commonplace, but Johannsen went on to insist that Mendel had worked only with the phenotypic characters and had not analyzed the corresponding genotypes. The Mendelian symbols for traits, by the second decade of the twentieth century presented in the familiar form of upper-cases for dominance and lower-cases for recessiveness, were not to be identified with places or parts of the chromosomes, Johannsen warned. There existed, after all, a number of rival theories about what the allelomorphs actually were and what brought about dominant and recessive traits: perhaps opposing factors, perhaps the presence and absence of factors, perhaps the decay of factors. If this fundamental question could not be answered, he insisted, how could geneticists claim the Mendelian segregation patterns, based on patterns of dominance and recessiveness, demonstrated a correspondence between traits and places on chromosomes. Johannsen also pointed out that the Mendelian symbols were double-faced; they could specify on the one hand a trait or on the other some germinal material, but it should not be recklessly assumed that they denoted both at the same time. Hence, once again, the value of the noncommittal word "gene" seemed clear; Johannsen continued to maintain that it referred to chemical reactions in the ontogenetic processes.[61] Thus from this discussion of Mendel's work we seemed to have progressed no further than the stance in the *Elemente* of 1909 which held that the genes were part of an ill-defined chemical *"Etwas."* In broaching the issue of and giving partial sanction to the parallelism between cytology and Mendelism, Johannsen nevertheless had moved decidedly to the point of view that the organism might be cleaved into its phenotypic and genotypic components. This adjustment strikes the reader even more forcefully when he turns to Johannsen's treatment of the dramatic new developments in *Drosophila* genetics.

"We owe to Morgan and his collaborators, Bridges, Muller, Sturtevant, and others, the service of having achieved pioneering successes

60. Ibid., p. 423.
61. Ibid., pp. 423-438.

through extensive and simultaneous investigations of the cytology and hereditary relationships of the fruitfly."[62]

So began the twenty-seventh chapter of the *Elemente* of 1926. Johannsen had written these words with conviction; he went on to describe in textbook fashion the achievements of the Columbia school. Their work was impressive and presented in an experimental and statistically analyzable form which could not have failed to please him. The consequence of this work, Johannsen was quick to point out, was to localize the genes on the chromosomes, "just like pearls on a necklace or like soldiers on a skirmish line."[63]

Despite the clear indication of a relationship between his genes and Morgan's chromosomes, Johannsen could not commit himself to the chromosome theory. The sticking point again was what he considered to be the nature of the gene. The chromosomal studies to that date may have located some of the genes; "they say nothing, however, about the nature of these genes themselves."[64] Johannsen was hardly alone in arguing this view. Bateson's presence and absence theory was still supported, although not by Johannsen himself; Goldschmith's enzyme analogies forced important issues about gene action, which intrigued Johannsen; Morgan's studies appeared based almost exclusively on recessive abnormalities which *ipso facto* did not describe the organization of the normal genotype; the chromosomes themselves could not be considered stable unities simply because some abnormal genes could be located on them; cytology, in fact, told against considering the chromosomes inviolate structures. Finally, Johannsen insisted, even when all four-hundred-odd known mutations in the fruitfly were added together, a central core of the genotype remained unfathomable. Such a fruitfly, "nearly black, eye-less, split-legged, crumpled-winged, body deformed, etc., [is] still a *Drosophila melanogaster* – 'but don't ask how come!' – even such a fly has the core of a fruitfly genotype."[65]

62. Ibid., p. 528.

63. Ibid., p. 540. In a more general form, perhaps with a nod toward Hans Vaihinger, Johannsen wrote on the following page: "Die *Morgan*sche Lehre hat sich für diese Forschungsfrage als glänzende Arbeitshypothese gezeigt. Soweit wir jetzt die Tatsachen übersehen, dürfen wir sagen, dass die trennbaren bzw. verschiedentlich kombinierbaren Elemente des Genotypus – also unsere Gene – sich jedenfalls so verhalten, 'als ob' sie, wie *Morgan* denkt, in Chromosomen plaziert wären." Ibid., p. 541. Johannsen, however, certainly considered the chromosome theory a legitimate scientific theory rather than a convenient fiction, as implied by Vaihinger's philosophy of the "als ob."

64. Ibid., p. 641.

65. Ibid., p. 644. Johannsen's views on these questions are readily accessible in his article "Some Remarks about Units in Heredity," *Hereditas, 4* (1923),

Johannsen's understanding of the gene, to be sure, held him back from declaring a physical separation of transmission and developmental material, and in this respect he adamantly denounced the suggestion that Weismann's somatoplasm-germplasm dichotomy was an earlier expression of his own phenotype-genotype distinction.[66]

The virtues and vices of *Drosophila* genetics aside, the chromosome theory nevertheless had forced Johannsen to consider in greater detail the genetic composition of the individual organism. There is no better indicator that the horizontal cleavage had worked its way into Johannsen's thoughts than the redefinitions of "phenotype" and "genotype" that appear in the *Elemente* of 1926. In 1909 Johannsen had defined the phenotype as "the 'type' in Quetelet's sense."[67] In 1926 he felt called upon to add another paragraph to his definition:

> The word phenotype, however, finds its use not merely in statistically ascertained 'typical' averages but can simply be used as a designation of personal characters of any individual whatever. The phenotype of an individual is thus the embodiment of all of his expressed characters. The single organism, the individual plant, an animal, a man, – "What it is and what it does" – has its phenotype, i.e., it appears as a sum of traits which are determined by the interplay between "inherited *Anlagen*" and elements of the environment.[68]

Recall moreover that in 1909 Johannsen had scarcely bothered to define "genotype"; he had simply equated it with "*Anlagetypus*." In 1926 he defined the word at length and with the utmost care. A fragment of this definition further suggests his move toward Morgan's point of perspective.

> The basis for the entire development of an individual is, however, – obviously – given by the constitution of the two gametes, by the union of which the organism arises. *This constitution we thus designate with the word genotype.*[69]

In both instances Johannsen had come around to associating the terms unambiguously with the individual organism. In so doing he introduced the viewpoint which permitted a horizontal cleavage of the organism

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133-141. E.S. Russell in *The Interpretation of Development and Heredity: A Study in Biological Method* (Oxford: Clarendon Press, 1930) summarizes many of the contemporary philosophical arguments against the chromosome theory.

66. "Die morphologische und begriffliche Sonderstellung der Keimbahnen mit der daraus abgeleiteten *Weismann*schen Antithesis 'Keimplasma-Soma' hat absolut nichts mit unserer Antithesis Genotypus-Phänotypus zu tun," Johannsen, *Elemente* (1926), p. 661.

67. See quotation cited in n. 17 above.

68. Ibid., p. 163, modified from translation in Dunn, *Short History*, p. 92. Dunn mistakenly attributed this passage to the first edition of the *Elemente*.

69. Johannsen, *Elemente* (1926), p. 166. The emphasis is mine.

(more figurative than literal in Johannsen's case) into transmission and developmental material. These two passages from the *Elemente* of 1926 could be interchanged without serious modifications with the definitions from Watson and Strickberger given at the outset of this paper.

To step back for a moment from the texts, it is worth asking what of more general interest arises from such a comparative analysis of Johannsen's phenotype-genotype distinction. It is at once obvious, should my interpretation be valid, that the mundane, often technically and visually obscure information dredged up by cytology at the turn of the century made a fundamentally important conceptual impact on genetics. The cytological view of the organism differs considerably from the physico-chemical view. Today we are so accustomed to seeing these differing stances as segments of a continuum which extends from macroscopic communities and organisms to the subatomic domains of nuclear physics that we often forget to search for the unique contributions each level must make for the advance of science. Johannsen was a chemist and statistician first. In his brilliant pure line studies he demonstrated his ability to move into an important area of the life sciences and to make one of the most fundamental distinctions in all of biology. Despite its biological relevance, however, the distinction as plied by him remained a chemical and statistical concept at heart. Only when the cytologically experienced investigators of the *Drosophila* school cut the "pie" in another direction did Johannsen's genotype concept gain the full dimension and the great importance that it has today.

APPENDIX

Horizontal and Vertical Analysis

The metaphor of a horizontal and vertical analysis of the phenotype-genotype distinction arises from Johannsen's own diagrams of variation curves viewed with their variable character (i.e., seed length, weight, etc.) on the base line and the frequency as the ordinate (see Figure 2). With this image in mind, I mean by a vertical analysis the study of the *Erscheinungsphenomena* represented by the area contained by a distribution curve with the conviction that under special circumstances (i.e., with pure lines or with segregating traits) one is able to make certain generalizations about the genetic composition "below" the *Erscheinung* level or metaphorically "under" the abscissa. The emphasis in such an analysis is to draw inferences "vertically" between what is seen and measured with whatever lies "under" the base line, or to change the metaphor, "below" the resolving power of the optical microscope. In such a vertical analysis there is no commitment made about the localization or spatial arrangement of the genetic input; it is even conceivable to envision this input in terms of forces and motions as well as or in

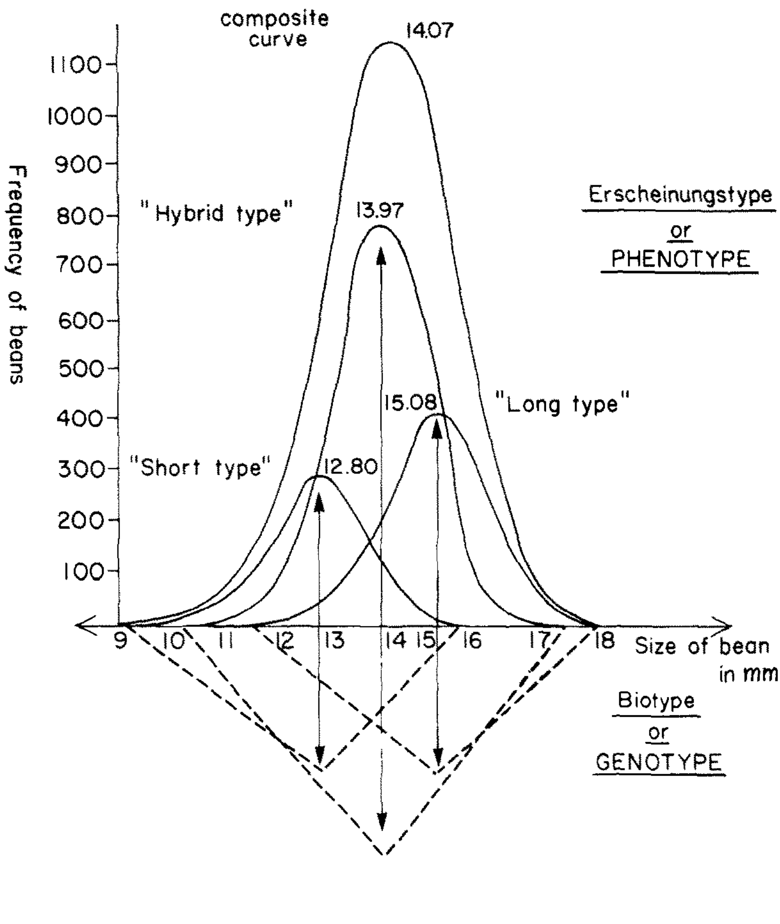

Fig. 2. Vertical and horizontal analysis of the phenotype-genotype distinction: The diagram presents a composite variation curve and three pure line variation curves taken from Johannsen's own data. All curves approximate a binomial distribution. For data in tabular form see *Elemente* (1909) p. 122.

place of material components. The vertical bond between the two levels remains the primary concern. Mendel's own paper on *Pisum* would be an example of such a vertical analysis. He statistically studied the *Erscheinungstype* and made predictions about different types of gametes; he tacitly implied a phenotype-genotype distinction on statistical, not anatomical grounds. It might be added, however, that in his concluding remarks he referred to the "material composition and *arrangement* [my emphasis] of the elements that attained a viable union in the cell." The suggestion hints at the possibility of a horizontal analysis as well.

By a horizontal analysis I mean an effort to examine directly the genetic composition sundered either conceptually or physically from the *Erscheinungsphenomena*. The emphasis is put on the material distinctness of this input from what is seen and measured for *Erscheinung* distributions. A complex molecular genetic make-up is generally, though not always, implied; the components of transmission tend to be distinguished from the components of development. Metaphorically such an analysis concentrates on whatever lies below the abscissa of Johannsen's variation curves, the horizontal coordinate having separated spatially the genetic composition from the *Erscheinungstype*. This analysis is most easily applied to individual organisms; it is the kind of analysis Weismann employed in describing the continuity of the germplasm.

The vertical and horizontal analyses are certainly not mutually exclusive; modern biology depends on both. The distinction has its value, however, when one examines the history of the phenotype and genotype concepts. Mendel and Weismann were among a number who tacitly made a phenotype-genotype distinction; Johannsen was the first of an army of investigators to explicitly employ the terms; yet as long as there is this double meaning to the phenotype-genotype concept, there is always room for misunderstandings among biologists and historians alike.

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