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A geneticist named Theodosius
Says a colleague of his is atrocious:
To ascribe speciation
All to macromutation
Is surely dementia precocious.

Robert Glaser[1]

Introduction

Before the Nazis dismissed him from the Kaiser Wilhelm Institute in 1935, Richard Goldschmidt was one of Germany's most prominent geneticists.[2] By the time he retired from the University of California, Berkeley, in 1948, he had become the world's most visible iconoclast on matters of evolution. His reputation as an iconoclast has its roots in his 1940 book, *The Material Basis of Evolution*.[3] At a time when the increasingly accepted view was that

[1] Limerick with caricature, April 5, 1950, Curt Stern Papers, American Philosophical Society Library, Philadelphia, PA. Macromutations are heritable changes in the genetic material that produce a large effect. Goldschmidt associated these large changes with speciation. For a taxonomy of different interpretations of the term "macromutation," see Michael R. Dietrich, "Macromutation," in *Keywords in Evolutionary Biology*, ed. E. Keller and E. Lloyd (Cambridge, Mass.: Harvard University Press, 1992), pp. 194–201.

[2] Goldschmidt was a director at the prestigious Kaiser Wilhelm Institutes in Berlin-Dahlem, editor of a leading journal, author of widely used genetics textbooks, and a leading authority on issues of sex determination, geographic variation, general genetics, and zoology. Some young biologists trying to make it in Germany referred to him as the "Leiber Gott von Dahlem": Salome Gluecksohn-Schoenheimer in Scott Gilbert's, "Induction and the Origins of Developmental Genetics," in *A Conceptual History of Modern Embryology*, ed. Scott Gilbert (Baltimore, Md.: Johns Hopkins University Press, 1991), p. 184.

evolution below and evolution above the species level were linked by t same mechanism of gradual change, Goldschmidt argued that there wa: bridgeless gap separating micro- and macroevolution. According to him more radical mechanism of genetic change was required for evolution at t species level and higher.

Recently Stephen Jay Gould has revived interest the *The Material Basis Evolution* and has tried to make use of Goldschmidt's "heresies" in conte porary controversies in paleobiology.[4] From a historical perspective, wl Gould and other contemporary reviewers of *The Material Basis of Evoluti* have demonstrated is that Goldschmidt's reputation as a scientific here is currently well established, and has been so since the 1960s. The typi encounter of Gould and his generation with Goldschmidt's views is simi to the one Guy Bush describes as follows:

> My indoctrination into the follies of Goldschmidt's heretical ideas macroevolution and speciation began as a graduate student when I to part in a course on evolution offered jointly by Ernst Mayr and George Simpson. Although Goldschmidt was seldom mentioned, when his na did come up it was inevitably in the context of "hopeful monsters" and the accompaniment of subdued snickers and knowing nods. It didn't ta long to learn that Richard B. Goldschmidt was not to be taken seriou as an evolutionary biologist.[5]

Given this kind of indoctrination, it is not surprising that, in Gould's ju ment, Goldschmidt was fated to be both "ridiculed and unread."[6] Inde Alan Templeton has argued recently that *The Material Basis of Evolut* should remain unread and should be given its "long overdue internment These are, however, contemporary assessments that fail to put *The Mate Basis of Evolution* and Richard Goldschmidt into their historical c text.

Shortly after it was published, *The Material Basis of Evolution* was wid read and taken as a challenge worthy of serious consideration. Review and correspondents from Sewall Wright to Julian Huxley considered Go

[4] Stephen Jay Gould, "The Uses of Heresy: An Introduction to Richard Goldschmidt's *Material Basis of Evolution*," in Richard Goldschmidt, *The Materials Basis of Evolution*, (N Haven: Yale University Press, 1982), pp. xiii–xlii; Stephen Jay Gould, "The Hopeful Mon Revisited," in *The Panda's Thumb* (New York: W. W. Norton, 1980), pp. 186–193.

[5] Guy Bush, "Goldschmidt's Follies," *Paleobiology, 8* (1982), 463–469 (quotation pp. 463–464). Gould was also a graduate student under Simpson.

[6] [illegible]

schmidt's book "a challenge that must be met."[8] Theodosius Dobzhansky's review even ends with the following endorsement:

> Goldschmidt's keenly critical analysis has emphasized the weakness and deficiencies of the neo-Darwinian conception of evolution, which are numerous, as even partisans should have the courage to admit. It would seem that this fact alone obliges anyone interested in the modern evolutionary thought to read Goldschmidt's book.[9]

Such a comment from Goldschmidt's harshest critic and one of the most respected biologists of the time clearly indicates that Goldschmidt was taken quite seriously in the 1940s, even if he is not taken seriously today.

In this paper I will put Goldschmidt's evolutionary biology and his reputation in context by examining the challenges he raised and the various responses they elicited. His challenges, I will argue, set an agenda and provided a common target for a group of scientists interested in establishing evolutionary biology as an autonomous discipline capable of unifying previously diverse scientific groups and domains.[10] The architects of this new evolutionary synthesis, the neo-Darwinians, could all agree to disagree with Goldschmidt, although they held different ideas as to which parts of his program were most objectionable. The result was a closing of the ranks in the 1940s in opposition to his views, which accelerated the creation of an evolutionary orthodoxy. It is only in light of this neo-Darwinian orthodoxy that Goldschmidt can be easily brushed aside as a heretic on matters of evolution. Richard Goldschmidt played a significant role in the development of the evolutionary synthesis, but in doing so he helped to create the conditions for his own ostracism as a heretic.

[8] Julian Huxley to Richard Goldschmidt, June 25, 1940, Richard Goldschmidt Papers, Bancroft Library, University of California, Berkeley, Calif. See also Sewall Wright, "Review of *The Material Basis of Evolution*," *Sci. Monthly, 53* (1941), 165–170; Carl Hubbs, "Reviews and Comments: *The Material Basis of Evolution*," *Amer. Nat., 75* (1941), 272–277; Theodosius Dobzhansky, "Catastrophism versus Evolutionism," *Science, 97* (1940), 356–358; C. H. Waddington, "Evolution of Developmental Systems," *Nature, 47* (1941), 108–110.

[9] Dobzhansky, "Catstrophism versus Evolutionism" (above, n. 8), p. 358.

[10] See Vassiliki B. Smocovitis, "Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology," *J. Hist. Biol., 25* (1992), 1–65; idem. "Organizing Evolution: Founding the Society for the Study of Evolution (1939–1950)," *J. Hist. Biol., 27* (1994), 241–309; J. A. Cain, "Common Problems and Cooperative Solutions: Organizational Activity in Evolutionary Studies," *Isis, 84* (1993), 1–25; and Ernst Mayr and William Provine, eds., *The Evolutionary Synthesis* (Cambridge Mass.: Harvard University Press, 1980).

A "Mandarin" in America

When Goldschmidt moved to Berkeley in 1936, he was fifty-eight years old. His career in Germany had brought him to a level of eminence and authority unknown among his counterparts in the United States. From a middle-class upbringing in Frankfurt, he had worked his way through the German academic system to become the second director of the prestigious Kaiser Wilhelm Institute for Biology in Berlin.[11] He had become a paradigm of what Fritz Ringer has called the German Mandarin: he was a member of a social and cultural elite whose status owed more to education than to heredity.[12] Without question the elite status of the German professoriat helped shape Goldschmidt into a formidable personality. Described as authoritarian, autocratic, and often aloof by some, to Max Delbrück, he was "a clear victim of the German system of permitting the growth of "BONZEN" [bosses]."[13]

For a man such as Goldschmidt to be forced to leave his country and his position for a public university in the United States was deeply disturbing. Goldschmidt describes the time he spent searching for a new position as the bitterest time in his life. Obtaining a position at Berkeley was a great relief, but Berkeley failed to furnish him with a laboratory for his first year and saddled him with large introductory classes of noisy undergraduates. He had not had to teach for twenty-three years, and he was much more at home with heads of state than with brash American undergraduates; after his first year he turned over his introductory class to a junior colleague. This first year at Berkeley was a terrible shock for Goldschmidt and undoubtedly contributed to his later belief that he had been spoiled in Germany.[14]

Goldschmidt's scientific reputation prior to 1935 was based primarily on his contributions to two areas: the study of sex determination, and geographic variation. Sex determination had been a major issue at the turn of the century and served as a proving ground for the young science of genetics, as biologists

[11] Richard Goldschmidt, *In and Out of the Ivory Tower* (Seattle: University of Washington Press, 1960); Curt Stern, "Richard Benedict Goldschmidt (1878–1958): A Biographical Memoir," *Biog. Mem. Nat. Acad. Sci., 39* (1967), 141–192 (reprinted in *Richard Goldschmidt: Controversial Geneticist and Creative Biologist, Experientia, suppl. 35* [1980], 69–99.

[12] Fritz Ringer, *Decline of the German Mandarins: The German Academic Community, 1890–1933* (Cambridge, Mass.: Harvard University Press, 1969), p. 5. For a masterful analysis of the styles and institutional settings of German geneticists in the interwar period see Jonathan Harwood, *Styles of Scientific Thought* (Chicago: University of Chicago Press, 1993).

[13] Interview with Gerda Mathau, September 3, 1991 (Mathau was an undergraduate student of Goldschmidt's in 1941 and 1942); Max Delbrück to Curt Stern, March 26, 1968, Curt Stern Papers (above, n. 1), Delbrück's emphasis. Delbrück was responding to Stern's biographical sketch of Goldschmidt.

[14] Goldschmidt, *Ivory Tower* (above, n. 11), pp. 305–306; Richard Eakin, "Contributions to the Department of Zoology, University of California, Berkeley," in *Richard Goldschmidt* (above, n. 11), p. 64. Eakin was the recipient of Goldschmidt's Zoology 10 course.

from Carl Correns to Thomas Hunt Morgan tried to give it various Mendelian interpretations.[15] Goldschmidt's work stood apart from typical Mendelian accounts by providing a quantitative basis for sex determination. For him, sex was the result of a complex relation between quantities of different types of chromosomal material. The organismic system for his work was the gypsy moth, *Lymantria dispar*. *Lymantria* moths were usually sexually dimorphic: females were large with dark bands on white wings, while males were small with brown wings. When two hybrids of *Lymantria* were mated, however, the offspring were not dimorphic; instead, they produced a high proportion of intersexes, which showed intermediate sexual characteristics or a mixture of male and female ones. This sexual plasticity helped orient Goldschmidt toward a more complex model for sex determination capable of explaining these intersexes.[16]

The problem of understanding the genetic basis of sex determination in *Lymantria* is bound up with the study of their geographic variation – Goldschmidt's second area of expertise. His original cross of *Lymantria* in 1911 was between a European species, *L. dispar*, and an Asian species, *L. japonica*.[17] The idea that different geographic races would produce intersexes took Goldschmidt to Japan several times in order to collect *Lymantria* from different regions; his careful study of the moths' geographic variation across the Japanese archipelago was ground-breaking research that became widely cited in the evolutionary literature.[18]

Underlying Goldschmidt's work on sex determination from 1911 to 1934 was a theory of genetics that was both quantitative and physiological. Where American geneticists under the influence of Thomas H. Morgan emphasized gene transmission, Goldschmidt emphasized gene function or gene action. In other words, he thought that a vital aspect of genetics was the integration of the gene with *physiological* processes of development.[19] Before 1934, he was developing a view of the gene as an enzyme that controlled a specific

[15] A good account of the history of sex determination and Goldschmidt's work on this subject are given in Marsha Richard, "Richard Goldschmidt and Sex Determination: The Growth of German Genetics, 1900–1935," Ph.D. diss., Indiana University, 1986.

[16] An intersex has both male and female traits, but all of its cells are the same genetically.

[17] Richard Goldschmidt, "Über die Vererbung der sekundaeren Geschlechtscharaktere," *Sitz. Ges. Morph. Physiol. München*, *27* (1911), 115–118.

[18] Goldschmidt's work on *Lymantria* culminated in his monograph "Lymantria," *Bibliog. Genet.*, *11* (1934), 1–185. Of this work, Ernst Mayr wrote: "The present generation of evolutionists can hardly appreciate the enormous impact of the demonstration by Schmidt (1918) for the fish *Zoarces*, by Goldschmidt (1912–1932) for the gypsy moth (*Lymantria dispar*), and by Sumner (1915–1930) for the deermouse *Peromyscus* that the slight differences between geographic races have a genetic basis" (*Animal Species and Evolution* [Cambridge, Mass.: Harvard University Press, 1963], p. 298).

[19] For an exposition of differences between Goldschmidt and Morgan's *Drosophila* school see Garland Allen, "Opposition to the Mendelian-Chromosome Theory: The Physiological

reaction.[20] The chromosome was made up of a number of these enzymes that created a coordinated reaction system. The action of genes controlling development was, thus, explained in terms of genetic material controlling reactions with specific rates or velocities, which were in tune with other reactions. In this system, mutations were changes in the number of genes that in turn altered the reaction velocities underlying the differentiation of the character in question.[21]

In the early 1930s, however, Goldschmidt's views on the gene and the nature of mutation underwent a profound change. The catalyst for this change was a growing body of work on position effects. In its simplest form, there is a position effect when the position of a gene relative to other genes on the chromosome has an effect on that gene's action. Research on position effects, such as the "bar eye" case in *Drosophila*, convinced many geneticists that the independence of the units of heredity, the genes, was incomplete.[22] Detailed work on the action of X rays on *Drosophila* chromosomes lead H. J. Muller and his coworkers to argue that small rearrangements were capable of producing the same kind of effect as gene mutations (changes in the chemical constitution of the gene.)[23] Using this research on position effects, Goldschmidt argued against the idea that genes could be thought of as independent corpuscular molecules, or metaphorically as beads-on-a-string. But, where Muller suggested that position effects should be understood in terms of chemical interactions among gene products, Goldschmidt went further: he reinterpreted position effects and gene action exclusively in terms of chemical reactions, and eliminated genes from the picture entirely.[24]

In the place of genes, Goldschmidt offered the chromosome as the unit of heredity. If the chromosome is assumed to be a large chain molecule each of whose residues acts chemically in different reactions, then any deviation from the typical steric arrangement of the molecule chain would have an effect on the coordinated system of reactions it controls. There would be

and Developmental Genetics of Richard Goldschmidt," *J. Hist. Biol.*, *7* (1974), 49–92; and Richmond, "Richard Goldschmidt and Sex Determination" (above, n. 15).

[20] Richard Goldschmidt, "Genetic Factors and Enzyme Reaction," *Science*, *43* (1916), 98–100.

[21] See Richard Goldschmidt, *Die quantitative Grundlage von Vererbung und Artbildung* (Berlin: J. Springer, 1920); idem, "The Gene," *Quart. Rev. Biol.*, *3* (1928), 307–324.

[22] Theodosius Dobzhansky, "Position Effects on Genes," *Biol. Rev.*, *11* (1936), 364–384; Herman J. Muller and A. Prokofyeva, "The Individual Gene in Relation to the Chromosome and the Chromosome," *Proc. Nat. Acad. Sci.*, *21* (1935), 16–26; Richard Goldschmidt, *Physiological Genetics* (New York: McGraw-Hill, 1938), pp. 308–309.

[23] Herman J. Muller and A. Prokofyeva, "Continuity and Discontinuity of the Hereditary Material," *Com. Rend. Acad. Sci., USSR*, *4* (1934), 74–83; H. J. Muller, A. Prokofyeva, and D. Raffel, "Minute Intergenic Rearrangement as a Cause of Apparent Gene Mutation," *Nature*, *135* (1935), 253–255.

[24] Goldschmidt, *Physiological Genetics* (above, n. 22), pp. 310–311.

no point mutation or mutant gene, just a change in a chain (a deficiency or rearrangement) that would affect its chemical properties.[25] The first detailed treatment of these admittedly, "nonconformist views" of the gene was given in *Physiological Genetics*, although Goldschmidt had been presenting his views in public lectures prior to 1938.[26] Goldschmidt reports that the response to these ideas about the gene was that he had gone crazy.[27]

In Germany Goldschmidt had been no stranger to controversy, but in the United States his forceful denial of the existence of corpuscular genes seriously threatened his hard-earned reputation.[28] Undoubtedly his plunge into what would be a very hotly contested dispute was partly the result of his radical change in status.[29] It was clear to some readers of *The Material Basis of Evolution* that Goldschmidt was engaged in "A too-obvious striving for priority and credit, for a place in the scientific sun."[30] Controversy may have acted as a means for Goldschmidt to try to regain some of the prestige he had lost when he was forced to leave Germany. Or it may have been, as he says it was, a matter of "genetic makeup" that encouraged him to "run ahead of the facts with conclusions" and immediately assign new facts "their place within the whole." With characteristic faith in his eventual vindication, Goldschmidt concluded this bit of introspection by declaring:

> It makes me happy to have a complete picture of a field in which I am interested and I prefer being wrong to a terribly cautious agnostic. I work afterall because I love to do it and because I thoroughly enjoy galloping around the field of ideas. If others enjoy teaching my horse to draw a bus, let them have their fun. Time will tell who goes farther.[31]

[25] Ibid., pp. 311–313.

[26] See Richard Goldschmidt, "The Theory of the Gene," *Sci. Monthly, 46* (1938), 268–273 (the written version of a lecture given in 1937).

[27] Goldschmidt, *Ivory Tower* (above, n. 11), p. 323.

[28] See L. C. Dunn to Curt Stern, May 28, 1938; Stern to Dunn, June 6, 1938, Curt Stern Papers (above, n. 1). This exchange discusses how to get Goldschmidt to revise a paper submitted to *Genetics* in order to avoid damaging his reputation by making extravagant claims based on incomplete data (Dunn was then editor of *Genetics*).

[29] This dispute was made even worse by the fact that Goldschmidt's opposition to the gene was also a thinly veiled attack on Morgan's *Drosophila* group and their entire approach to genetics. To arrive in America, where virtually everyone followed the Drosophilists, and announce the death of the gene was not the most graceful possible entrance into the American genetics community, especially since relations between Goldschmidt and Morgan's group had been strained since the 1920s. A more detailed analysis of the impact of Goldschmidt's immigration upon his views of the gene is presented in Michael Dietrich, "On the Mutability of Genes and Geneticists: The Americanization of Richard Goldschmidt and Victor Jollos" (in preparation). See also Stern, "Richard Goldschmidt" (above, n. 11), p. 83.

[30] Hubbs, "Reviews and Comments" (above, n. 8), p. 273.

[31] Richard Goldschmidt to L. C. Dunn, May 27, 1940, L. C. Dunn Papers, American Philosophical Society Library, Philadelphia, PA.

In this same letter to his close friend and colleague L. C. Dunn, he warned that his upcoming Silliman Lectures, published as *The Material Basis of Evolution*, would soon appear and were "typical Goldschmidt with everything I like about him, and some others dislike." Although he knew he was going to take some punishment for his views on evolution, I do not think he knew how much.

The Material Basis of Evolution

In 1932, as he started his final consolidation of years of work on geographic variation in *Lymantria*, Goldschmidt broke with his previous opinion on evolution and began to cast doubts on the ability of a gradual accumulation of small variations to result in the creation of a new species.[32] The next year, at the meetings of the American Association for Advancement of Science in Chicago, he further articulated his position on evolution as a mixture of skepticism and optimism.

Goldschmidt was skeptical that geographic *Rassenkreis* could trigger speciation. A *Rassenkreis* was a series of subspecies or races whose characteristics varied over their geographic distribution. Immediate neighbors in such a "race-ring" may be very similar, but subspecies on either end of a *Rassenkreis* can be quite different, overlapping in distribution and behaving like full species. Goldschmidt objected to the idea that subspecies on the ends of a *Rassenkreis* could eventually become different enough, as they adapt to their local environments, to become separate species.[33] His extensive study of the geographic variation of *Lymantria* had convinced him that there was a geographic *Rassenkreis* for *Lymantria* across the Japanese archipelago, but the nature of the genetic differences between these subspecies was quantitative: it showed a "plus-minus character." According to Goldschmidt, adaptation to local conditions can explain why a subspecies in a warmer region has a longer dispause and a subspecies in a colder region has a shorter diapause – but these adaptations are quantitative shifts within the same character, length of diapause.[34] In contrast, he found that different species living in the same area addressed that area's environmental challenges in fundamentally different ways. For example, he examined three techniques for egg laying that

[32] Richard Goldschmidt, "Genetik der geographischen Variation," *Proc. Int. Congr. Genet.*, *6* (1932), 173–184. For Goldschmidt's previous position in evolution see Richard Goldschmidt, "A Preliminary Report on Some Genetic Experiments Concerning Evolution," *Amer. Nat.*, *52* (1918), 28–50; and Goldschmidt, *Die quantitative Grundlage von Vererbung und Artbildung* (above, n. 21).

[33] Richard Goldschmidt, "Some Aspects of Evolution," *Science*, *78* (1933), 540.

[34] Diapause is a period of dormancy, usually during hibernation.

would ensure the proper conditions for hibernation in three different species of *Lymantria*. Although these species shared the same environment, he found that their egg-laying techniques were not quantitative variants of one another, but were altogether different. For Goldschmidt, the differences he observed between species were of a different nature from those he observed between the subspecies of a *Rassenkreis*. In his words, "the changes necessary for the formation of a new species are so large that the relatively small differences of the subspecies as a starting point would hardly count."[35]

Goldschmidt's optimism about evolution concerned the potential of physiological systems to respond to genetic changes in such a way as to produce the large evolutionary changes needed for speciation. The developmental system he envisioned was a set of reactions in tune with each other and with definite, controlled velocities to create a coordinated reaction system.[36] Mutations in genes altered specific reactions and ran the risk of upsetting the entire reaction system. This is why most mutations are lethal. What sparked Goldschmidt's optimism was the possibility of mutations affecting the early stages of development. "Would such a change," he asked, "if possible at all without breaking up the whole system of the orderly sequence of development, not at once have the consequence of changing the whole organization and bridging with one step the gap between taxonomically widely different forms?"[37] Mutational shifts in the rate of development were known to occur, usually with disastrous results. The rare survivors of such a shift would be monstrosities – but, in Goldschmidt's eyes, today's monster was tomorrow's special adaptation. If the monster stands the test of selection and finds a niche for which it is preadapted, then it is possible that further mutations could improve it, and it could survive as a radically new phenotype.

Two features of this account are worth noting. First, Goldschmidt argued for the possibility of mutations affecting early development, leading to sudden speciation; but he had no concrete examples of the kinds of changes he was talking about in 1933. Second, this theory of sudden speciation could be entirely compatible with the classical theory of the gene as a bead-on-a-string. Goldschmidt's rejection of the gene in the mid-to-late 1930s, however, also had significant implications for his views on saltational evolution.

Goldschmidt reconciled his theory of genetics without genes and his saltationist view of speciation when he was asked to give the Silliman Lectures at Yale. Just after receiving this invitation, he became very ill and suffered a massive heart attack.[38] While recovering he wrote the manuscript for *The*

[35] Goldschmidt, "Some Aspects of Evolution" (above, n. 33), p. 542.
[36] Ibid., p. 543.
[37] Ibid., p. 544.
[38] Goldschmidt, *Ivory Tower* (above, n. 11), pp. 306–307.

Material Basis of Evolution in spiral notebooks as he sat in his garden. The series of eight lectures, given in December 1939, was excerpted from the already completed manuscript of *The Material Basis of Evolution*.[39]

Goldschmidt's theory of evolution in 1940 was built upon a foundation laid down in his *Physiological Genetics*, published in 1938. Where Muller's discussion of position effects had done much to change Goldschmidt's views on the nature of the gene in *Physiological Genetics*, it also provided a conservative contrast to Goldschmidt's views on evolution. Muller, Alexandra Prokofyeva, and Daniel Raffel called for a serious effort to distinguish rearrangements from genuine mutations, because they believed that "the range of possibilities of phenotypic change through intergenic rearrangements alone must be far from adequate for any indefinitely continued evolution."[40] This was the gauntlet that Goldschmidt took up. A lifetime of work on the potentialities of development in connection with the action of the genes gave him the resources to argue for the evolutionary power of genetic rearrangements; and where it did not, he was not slow to speculate.

The principle thesis of *The Material Basis of Evolution* is that microevolution and macroevolution are distinct phenomena, and the slow and gradual accumulation of micromutations characteristic of microevolution is not a sufficient mechanism to bridge the gaps between species in an evolving lineage. In order for these bridgeless gaps between species to be crossed, Goldschmidt argued, large-scale systemic mutations are needed. Systemic mutations are complete changes of the primary pattern of the chromosome (the reaction system of the chromosome) into a new, well-integrated pattern. According to Goldschmidt, a new pattern emerges in a series of consecutive steps, but these steps need not have an visible effect until a new stable pattern is created. The sudden appearance of a new phenotype after genetic rearrangement depends on what he called a "threshold concept."

In *Physiological Genetics*, Goldschmidt argued that normal development, or the normal expression of one's genetic material, depends on the production of a minimum amount of a particular decisive chemical substance. In other words, normal phenotypic expression depends on whether or not this decisive substance reaches a certain threshold.[41] Threshold values are influenced by genetic and environmental factors, and therefore some fluctuation in expression can be expected.Thus, with systemic mutations, partial rearrangement or repatterning of the chromosome may have no phenotypic effect because the products of these new reaction systems have not reached the proper threshold values. According to Goldschmidt, "only when by chance a pattern, viable

[39] "Silliman Lectures," Goldschmidt Papers (above, n. 8), carton 1.

[40] Muller, Prokofyeva, and Raffel, "Minute Intergenic Rearrangement" (above, n. 23), p. 255.

[41] Goldschmidt, *Ivory Tower* (above, n. 11), pp. 306–307.

in homozygous condition and above the threshold, has been reached; i.e., such as the patterns actually found when comparing species, does the new system of reaction suddenly emerge, though prepared by subliminal steps."[42] Systemic mutations are expressed as fundamental phenotypic changes when a stable reaction system is formed with thresholds that allow the expression of the recent genetic repatterning. Systemic mutations, then, can do what micromutations cannot: they can result in new species in what appear to be large and rather sudden steps.

Goldschmidt's rhetoric of sudden change and rapid speciation created some confusion about whether or not both genetic change and phenotypic change have to be sudden. I interpret Goldschmidt to be saying that phenotypic change is sudden, but that genotypic change can be more gradual and can remain unexpressed; systemic mutation will be quicker than the accumulation of small mutations, but it need not occur in a single step.[43] Sewall Wright interpreted him as holding that both had to be sudden. Goldschmidt's comments about a new genetic pattern being formed in a series of steps were problematic to Wright because they seemed to contradict Goldschmidt's denial of incipient species.[44] This denial of incipient species, however, was specific to expressed quantitative traits that Goldschmidt thought were responsible for variation within a species. His objection to incipient species was an objection to the idea that gradual genetic change with resulting gradual phenotypic change is a sufficient means for the formation of new species.

A crucial part of Goldschmidt's argument is that changes in intrachromosomal structure or pattern are the basis for species-level differences. In making this argument, he does not simply marshall his evidence; he instead focuses on the work of an influential neo-Darwinian, Theodosius Dobzhansky. The picture Goldschmidt paints of Dobzhansky is that of a man at a scientific impasse: he must decide whether species formation is a matter of genic differentiation or differentiation in chromosomal pattern.[45] According to Goldschmidt, Dobzhansky knew a decision had to be made when he wrote, in *Genetics and the Origin of Species*:

> To what extent the differences between such species as *Drosophila pseudoobscura* and *D. miranda* are due to position effects is also a matter of speculation; the greatly different gene arrangements in these species may be responsible for many alterations in the morphological and physiological properties of their carriers. In any event, position effects show

[42] Goldschmidt, *Material Basis* (above, n. 3), p. 246; see also p. 206.
[43] Ibid., pp. 206–207.
[44] Wright, "Review" (above, n. 8), p. 167.
[45] Goldschmidt, *Material Basis* (above, n. 3), p. 204.

> that gene mutations and chromosomal changes are not necessarily as fundamentally distinct phenomena as they at first appear.[46]

Dobzhansky's failure to take the next step and admit that chromosomal repatternings could be the decisive changes needed for speciation is, according to Goldschmidt, the result of "a dogmatic belief in the inflexibility of the classical theory of the gene."[47] Unfettered by the dogma of the gene, Goldschmidt could promote a theory of evolution that was compatible with the "facts" meaning Dobzhansky's and Muller's work on position effects and chromosomal differences. As we shall see, framing his position in this way issued a direct challenge to Dobzhansky and the neo-Darwinians: they had to come to terms with the possible evolutionary impact of chromosomal rearrangements.

Goldschmidt summarizes his case for macroevolution by systemic mutations as follows:

> Whether this model is good or bad, possible or impossible, the fact remains that an unbiased analysis of a large body of pertinent facts shows that macroevolution is linked to chromosomal repatterning and that the latter is a method of producing new organic reaction systems, a method which overcomes the great difficulties which the actual facts raise for the neo-Darwinian conception as applied to macroevolution.[48]

At this point, it seems that he could stop; but instead he continues with an additional 145 pages on evolution and the potentialities of development.

A key part of Goldschmidt's case for systemic mutations rests on the possibility of a quick change from one stable developmental system to another. In the last third of his book, he is concerned to demonstrate that a single genetic change can transform a functioning developmental reaction system into a fundamentally different, but still functional, developmental reaction system. Significantly, he takes pains to point out that this part of his argument does not depend on his view of genetic change. The genetic changes he considers in this last section could be understood as mutations in genes or as systemic mutations. Of course, he preferred that the genetic changes effecting developmental change be thought of as systemic mutations.[49]

It is important to note that the developmental macromutations discussed at the end of *The Material Basis of Evolution* were also the stuff of Goldschmidt's

[46] Theodosius Dobzhansky, *Genetics and the Origin of Species* (New York: Columbia University Press, 1937), p. 117; quoted in Goldschmidt, *Material Basis*, p. 204.

[47] Goldschmidt, *Material Basis*, p. 242.

[48] Ibid., p. 249 (this passage is italicized in the original).

[49] Ibid., pp. 251–252.

1933 paper on evolution. They captured the central idea of his thought on evolution; namely, that "a single mutational step affecting the right process at the right moment can accomplish everything, providing that it is able to set in motion the everpresent potentialities of embryonic regulation."[50] This idea garnered a significant amount of support among Goldschmidt's friends and enemies, but contrary to what he wished it did not draw many toward his theory of systemic macromutations.[51]

The Hornet's Nest

Reflecting on the response to *The Material Basis of Evolution* Goldschmidt commented that "the Neo-Darwinians reacted savagely." The fact that every reviewer treated *The Material Basis of Evolution* negatively – as a challenge that had to be answered – undoubtedly convinced him that he "had struck a hornet's nest."[52]

In order to understand how reactions to Goldschmidt's work affected the emerging neo-Darwinian synthesis, the nature of the synthesis must first be further clarified. It has been identified both with the emerging discipline of evolutionary biology and with consensus among such previously divergent fields as paleontology, zoology, botany, systematics, and genetics.[53] According to this interpretation, the synthesis refers to a time in the 1930s and 1940s when "barriers were removed" and various arguments were offered to show that these different fields were in fact consistent with each other. These developments did indeed help to spur on the emergence of evolutionary biology as a field of inquiry – as a new and centrally important discipline – but they do not demonstrate that a new synthetic theory of evolution was produced. As Will Provine and others have argued, there was no agreement about the mechanisms of evolution during the 1930s and 1940s.

Instead, what Provine suggests happened was not a synthesis, but an evolutionary constriction – "a vast cut-down of the variables considered important to the evolutionary process."[54] According to Provine,

> The term "evolutionary constriction" helps us understand that evolutionists after 1930 might disagree intensely with each other about effective population size, population structure, random genetic drift, levels of

[50] Ibid., p. 297.

[51] See Dietrich, "Macromutation" (above, n. 1), for different types of macromutation and their relative receptions.

[52] Goldschmidt, *Ivory Tower*, (above, n. 11), p. 324.

[53] Mayr and Provine, *Evolutionary Synthesis* (above, n. 10).

[54] William Provine, "Progress in Evolution and the Meaning of Life," in *Evolutionary Progress*, ed. M. Nitecki, (Chicago: University of Chicago Press, 1988), p. 61.

> heterozygosity, mutation rates, migration rates, etc., but all could agree that these variables were or could be important in evolution in nature, and that purposive forces played no role at all.[55]

While I agree with Provine's analysis of these features of the evolutionary constriction, I think that reactions to Goldschmidt force us to further refine the idea of an evolutionary constriction. Purposive elements were not the only things ruled out: Goldschmidt's systemic mutations and bridgeless gaps were also ruled out.

The "savage" reaction of the neo-Darwinians – such as Theodosius Dobzhansky, Ernst Mayr, George Simpson, Sewall Wright, and Carl Hubbs – is attributable primarily to two basic factors. First, Goldschmidt threatened the status of evolutionary biology as unified science. The formation of the synthesis was in part an attempt to bind together diverse biological specialties by demonstrating the central role of evolution in all of them. Evolutionary biology was to become the unifying element in biology that made it autonomous from chemistry and physics. The foundation for this evolutionary framework was laid by Dobzhansky's *Genetics and the Origins of Species* (1937) and was later reinforced by Mayr's *Systematics and the Origin of Species* (1942) and Simpson's *Tempo and Mode in Evolution* (1944). Goldschmidt's nonconformist views threatened the stability of the emerging neo-Darwinian view and its ability to unify and legitimate the biological sciences.[56] Second, his views challenged specific concepts and theories held dear by different individuals.

The responses of the neo-Darwinians addressed five major challenges presented by Goldschmidt. These challenges concerned (1) the validity of the theory of the gene; (2) the nature of mutation, and its role in evolution; (3) the origin of isolating mechanisms necessary for species formation; (4) the concept of species and incipient species, as well as what Ernst Mayr calls population thinking; and (5) the tempo of evolution. These issues were often interrelated, with individual critics varying their emphases, but these challenges set an agenda for the neo-Darwinians. Where they could, neo-Darwinians marshalled existing evidence, constructed new arguments, and clarified old ones in order to respond to Goldschmidt's claims, but in some cases they had to go back to the field. Nowhere was this more evident than with Theodosius Dobzhansky.

On April 29, 1940, Dobzhansky wrote Goldschmidt that he was impatiently waiting for his book. He had heard about the content of the Silliman Lectures

[55] Ibid.

[56] See Smocovitis, "Unifying Biology" (above, n. 10), in which this interpretation of the unifying role of the synthesis is advanced in much more detail.

and wanted to include a discussion of them in his revision of *Genetics and the Origin of Species*.[57] Dobzhansky's book was a cornerstone of the synthesis, and Goldschmidt's impact on the second edition was considerable: in the first edition, he received only nine references; in the second edition, he received thirty-four (only A. H. Sturtevant and Dobzhanksy himself received more). Of the new references, four were to new discussions of the validity of the gene theory, twelve were to substantial new sections on systemic mutations, and five were to discussions of incipient species and species differences.

Dobzhanksy was not about to give up genes in the face of Goldschmidt's attack, but neither was he willing to advocate the idea of genes as beads-on-a-string. He thought Goldschmidt had created a false dichotomy: "genes must either be separated by impregnable walls, or else they do not exist at all."[58] Goldschmidt had failed to consider the other alternatives. Dobzhansky defended his intermediate position by citing data showing that position effects were not widespread, and then rejecting the claim that all mutations were structural changes. The remaining claim that genes were not discrete entities Dobzhansky agreed with, although the extent of gene interaction was recognized to be an open question.

Some gene interaction may have been acceptable, but Goldschmidt's systemic mutations strained Dobzhansky's credulity. In a comment on Goldschmidt's style, he remarked that the role of mutations in evolution need not be settled by rhetoric since it was open to experimental attack. What was needed in order to resolve the question of the reduction of all mutations to chromosomal rearrangements, and the question of massive rearrangement leading to speciation, was an experimental program that could demonstrate "(1) that racial, specific, and other differences can be resolved completely into genic differences, (2) that these genic differences are of the same kind and magnitude as the observable mutations, and (3) that any kind of difference encountered between species may be present within the species as well."[59] These questions occupied Dobzhansky for a number of chapters, but in the end not all of these things could be demonstrated, given the research up to 1941.

What made Goldschmidt's challenges particularly vexing for Dobzhansky was that there were some species differences that he could not attribute to genes. Moreover, there was some cytological evidence of rearrangements – but whatever the nature of these undefined changes, he concluded, "they

[57] Theodosius Dobzhansky to Richard Goldschmidt, April 29, 1940, Goldschmidt Papers (above, n. 8).

[58] Theodosius Dobzhansky, *Genetics and the Origin of Species*, 2nd ed. (New York: Columbia University Press, 1941), p. 110.

[59] Ibid., p. 53.

certainly do not connote the attainment of the species level in evolution."[60] This of course does not completely resolve the issue of whether or not these remaining differences in any way resemble systemic mutations, and Dobzhansky knew it. Instead, Goldschmidt's challenge sparked the need for a program of experimental research to further justify fundamental claims of the neo-Darwinian view of evolution regarding mutation and variation.

Goldschmidt's theory of systemic mutations also raised concerns in Dobzhansky's mind about the origin of physiological isolating mechanisms. The difficulty of establishing isolation in a single step was thought by Dobzhansky to be fatal to Goldschmidt's systemic mutations – but systemic mutations provided a physiological account of isolation, which was lacking in accounts of geographic isolation. According to Dobzhansky, "geographical separation does not in itself guarantee the eventual advent of a reproductive one. This brings us face to face with a very difficult problem: what causes engender the development of physiological isolation between natural groups?"[61] He did not have a fully satisfactory answer to this question in 1941.

Goldschmidt's attack on the genetic basis of species differences highlighted the need for further experimental research on this problem by Dobzhansky and other neo-Darwinians. Bruce Wallace, who was one of Dobzhansky's students during the 1940s, reports that Goldschmidt was constantly on Dobzhansky's mind in the field, in the laboratory, and in the classroom during his work on *Drosophila* in 1940s and 1950s. According to Wallace, Dobzhansky intensified his work on chromosomal inversions, translocations, and position effects, especially comparative work on a number of different *Drosophila* species, in response to Goldschmidt's objections.[62]

More specifically, Dobzhansky surveyed all of his current work on chromosomal differences in *Drosophila* to answer Goldschmidt, but even then he found that some translocations and inversions "may become not only established in natural population but may play an important role in speciation."[63] Translocations and inversions in some circumstances were presented as exceptions to the rule that "all the types of chromosomal changes which are known to differentiate species are met with in races as well."[64] This rule became the neo-Darwinian law as Dobzhansky vigorously pursued

[60] Ibid., p. 149.

[61] Ibid., p. 284.

[62] Bruce Wallace, "Reflections on the Still Hopeful Monster," *Quart. Rev. Biol.*, *60* (1985), 38. Inversions and translocations are specific types of chromosomal rearrangement.

[63] Theodosius Dobzhansky, "Chromosomal Differences between Races and Species of *Drosophila*," in *Cytology, Genetics and Evolution* (Philadelphia: University of Pennsylvania Press, 1941), p. 55.

[64] Ibid., p. 56.

the genetics of natural populations and explained away the exceptions that allowed Goldschmidt to argue for a bridgeless gap between evolution above and below the species level. A landmark study in this regard was Dobzhansky's and Carl Epling's *Contributions to the Genetics, Taxonomy, and Ecology of Drosophila pseudoobscura and Its Relatives*.[65] This monograph was widely heralded as a magnificent example of the new neo-Darwinian approach to evolution.[66] Dobzhansky's one-hundred-page chapter on the chromosomal races of *Drosophila* was in itself a tour de force for the neo-Darwinian rule against gaps based on chromosomal differences.[67]

Although Goldschmidt was not mentioned by name in Dobzhansky and Epling's monograph, he understood its import for his views and hotly contested its worth in correspondence with Curt Stern. As he had in *The Material Basis of Evolution*, he argued that Dobzhansky and Epling had not studied characteristics essential to species-level variation and had failed to address the production of position effects by inversions.[68] Dobzhansky undoubtedly thought he was dealing with evolutionarily significant characteristics and, as the neo-Darwinian rule implies, would have made no distinction between characteristics important to variation within a species and those important for variation between species.

Dobzhansky had not let the issue of position effects and inversions pass him by, as Goldschmidt thought he had in 1945. As a part of his Genetics of Natural Populations (GNP) series, Dobzhansky addressed the issue of position effects in GNP IX (1943), GNP XIII (1946), and finally in GNP XVIII (1948).[69] Although Goldschmidt is not mentioned by name, the position effect hypothesis raised in these papers, giving inversions a large evolutionary

[65] Theodosius Dobzhansky and Carl Epling, *Contributions to the Genetics, Taxonomy, and Ecology of Drosophila pseudoobscura and Its Relatives* (Washington, D. C.: Carnegie Institution of Washington Publication 544, 1944).

[66] Ernst Mayr, "Chromosomes and Phylogeny," *Science, 100* (1944), 11–12; Curt Stern, "A Study of Race," *J. Hered., 35* (1944), 314–316.

[67] Dobzhansky and Epling, *Contributions* (above, n. 65). The neo-Darwinian rule is emphasized in the conclusion and as the last point of the summary. (pp. 137 and 142, respectively).

[68] Richard Goldschmidt to Curt Stern, May 22, 1945, Curt Stern Papers (above, n. 1).

[69] Theodosius Dobzhansky, "Genetics of Natural Populations, IX. Temporal Changes in the Composition of Populations of *Drosophila pseudoobscura*," *Genetics, 28* (1943), 162–186; idem, "Genetics of Natural Populations. XIII. Recombination and Variability in Populations of *Drosophila pseudoobscura*," *Genetics, 31* (1946), 269–290; idem, "Genetics of Natural Populations. XVIII. Experiments on Chromosomes of *Drosophila pseudoobscura* from Different Geographic Regions," *Genetics, 33* (1948), 588–602. For more on the GNP series see William Provine, "Origins of the Genetics of Natural Populations Series," and Richard Lewontin, "The Scientific Work of Th. Dobzhansky," in *Dobzhanksy's Genetics of Natural Populations I–XLIII*, ed. R. Lewontin, J. Moore, W. Provine, and B. Wallace (New York: Columbia University Press, 1981), pp. 1–76 and 93–115, respectively.

impact because of their production of physiological position effects, had been associated with Goldschmidt's views by Dobzhansky earlier.[70]

This set of three GNP papers concerns differences found in the third chromosome of *Drosophila psuedoobscura* collected from different locations on Mount San Jacinto in California. Dobzhansky was interested in why the adaptive value of different gene arrangements varied with location. To explain the observed differences, he offered two hypotheses: gene arrangements could "exert their effects on the physiology of their carriers because of differences in the alignment of the genes (position effect)"; or, gene arrangements exert the effect they do as a result of "chance association of mutant genes with now one and now another gene arrangement."[71] He thought the position effect hypothesis was very improbable because one would expect that all of the different populations of flies with the same gene arrangement would show the same physiological effect, yet he had observed that the adaptive value of a specific gene arrangement did not show a consistent pattern of change in relation to population density and season from location to location. In GNP XIII, Dobzhansky updated his position with arguments in favor of polygene complexes over position effects.[72] In GNP XVIII, based on the results of new experiments with the flies from Mount San Jacinto in laboratory population cages, he claimed to have conclusively shown that "the adaptive properties of a chromosome are ... determined not by the gene arrangement but by the quality of the genes it contains"; although this did not preclude the possibility that inversions could produce position effects, he was convinced that it did demonstrate that "the adaptive values of chromosomes are not determined by position effects alone."[73] The only person to hold such an extreme view on the power of position effects in evolution was Richard Goldschmidt.

Ernst Mayr's *Systematics and the Origin of Species* was modeled on Dobzhansky's *Genetics and the Origin of Species*, but it was also written in response to Goldschmidt. Mayr writes that "even though personally I got along very well with Goldschmidt, I was thoroughly furious at his book, and much of my first draft of *Systematics and the Origin of Species* was written in angry reaction of Goldschmidt's total neglect of such overwhelming and con-

[70] Dobzhansky, "Chromosomal Differences" (above, n. 63), pp. 47–48. Dobzhansky's comments on position effects and inversions also fit into his general research plan on *Drosophila* and his growing advocacy of Sewall Wright's shifting balance theory of evolution. In the first edition of *Genetics and the Origin of Species* (above, n. 46), for instance, Dobzhansky spent quite a bit of time arguing for genic sterility over chromosomal sterility – that is, sterility caused by genes versus sterility caused by inversions, translocations, or ploidy (see pp. 259–295).

[71] Dobzhansky, "GNP IX" (above, n. 69), p. 177.

[72] Dobzhanksy, "GNP XIII" (above, n. 69), pp. 287–288.

[73] Dobzhansky, "GNP XVIII" (above, n. 69), p. 601.

vincing evidence [for the concept of geographic speciation]."[74] Mayr toned down the anger and disapproval in his comments concerning Goldschmidt for the final draft of his book.[75] In retrospect, he claims that Goldschmidt posed the right problem concerning isolation and speciation but came up with the wrong solution – this wrong solution, however, led Mayr to the correct one.[76]

Mayr had attended Goldschmidt's Silliman lectures and made a set of written comments on the manuscript of *The Material Basis of Evolution.* In correspondence with Goldschmidt, he made it plain that they held opposite views on the rate of evolution and the role of geographic isolation in speciation. Despite these differences he applauded Goldschmidt for having "the courage to contradict those who claim that all evolutionary problems have been settled with the discovery of gene mutations." He also acknowledged that Goldschmidt had picked out the vulnerable spots in the geneticists' arguments – namely, the issue of species crosses. According to Mayr, he and Goldschmidt agreed that "there is some other evolutionary process in addition to the ordinary gene mutations"; as to what that other evolutionary process was, they would never agree.[77]

Mayr's opposition to Goldschmidt was spurred on by Dobzhansky. In 1940, Mayr was preparing a presentation of his views on *The Material Basis of Evolution* to be given at Cold Spring Harbor. He circulated an early draft of his presentation to Dobzhansky, who responded that his only criticism was that Mayr had conceded too much, or had appeared to concede too much – he was "not severe enough."[78] Mayr's revised paper was more critical and formed the basis for his published critique in his 1942 book.

In *Systematics and the Origin of Species* Mayr's emphasis is on Goldschmit's challenge regarding mechanisms of isolation. He thought that Goldschmidt had been intellectually dishonest in his treatment of the data on geographic isolation – the charge is that he ignored data contrary to his position. More specifically, Goldschmidt had ignored Mayr's data, giving them only a passing reference in *The Material Basis of Evolution.*[79] Mayr thought that Goldschmidt had based his case almost exclusively on data concerning *Lymantria*. The taxonomy of *Lymantria*, however, in Mayr's opinion,

[74] Ernst Mayr, "How I Became a Darwinian," in Mayr and Provine, *Evolutionary Synthesis* (above, n. 10), p. 421.

[75] Ernst Mayr, pers. comm., March 13, 1991.

[76] Ernst Mayr, *The Growth of Biological Thought* (Cambridge, Mass.: Harvard University Press, 1982), p. 381. As Mayr puts it, Lyell was to Darwin as Goldschmidt was to him.

[77] Ernst Mayr to Richard Goldschmidt, December 13, 1939, Ernst Mayr Papers, Harvard University Archives, Cambridge, Mass.

[78] Theodosius Dobzhansky to Ernst Mayr, February 2, 1940, Ernst Mayr Papers.

[79] Ernst Mayr, pers. comm., March 13, 1991.

was completely disorganized, being based on uncritical compilations.[80] Inferences about species and subspecies in *Lymantria* were, thus, good only as suggestions of probable relations – more study was needed of the relation between the Palearctic species Goldschmidt studied and the more widespread tropical superspecies of *Lymantria*. The better-studied tropical birds that Mayr had worked on presented a stronger case for geographic variation and speciation.

In his lengthiest treatment of Goldschmidt's claims, Mayr devoted an entire section to proving that "geographic isolation is in most groups of animals a necessary condition for speciation."[81] In this section, he brought together his extensive discussion of the lack of differences between the characters of species and subspecies with a detailed discussion of difficult borderline cases where populations are not easily recognized as species as opposed to subspecies.[82] Goldschmidt's denial of geographic isolation as a means of speciation clearly spurred Mayr to consolidate the available evidence and address the borderline cases in a way that he had not done before. For Mayr, geographic speciation left no open questions.[83]

Mayr's confidence in geographic speciation, however, did not extend to other issues disputed by Goldschmidt, such as the genetic basis of species formation. "The fact," Mayr wrote, "that an eminent contemporary geneticist (Goldschmidt) can come to conclusions which are diametrically opposed to those of most other geneticists is striking evidence of the extent of our ignorance."[84] He agreed with Goldschmidt's emphasis on gene action and on the integration of genic effects in a reaction system. According to Mayr, "It is dangerous, if not completely incorrect, in view of the interrelationship of genes, to think of species merely as numerical aggregates of genes. Such a view underrates the important role which is played in speciation by the

[80] Ernst Mayr, *Systematics and the Origin of Species* (New York: Columbia University Press, 1942), p. 137.

[81] Ibid., pp. 162–185 (quotation on p. 162).

[82] For Mayr's discussion of which characters are subject to geographic variation see ibid., pp. 36–59.

[83] What was often overlooked in the 1950s and 1960s, even by Mayr, was that Goldschmidt at least partly capitulated to Mayr in 1948. Goldschmidt admitted that geographic speciation did legitimately result in the production of new species by neo-Darwinian means; his own position was then realigned to concern cases above the level of ecospecies – where ecospecies are defined as animal types that have a large range of distribution and occupy areas that are clearly geographically isolated. For Goldschmidt, ecospecies showed little difference from each other and were just glorified subspecies. He retained his interest in real species – species that differed from each other "not in small quantitative features but in important parts of their organization, ecology and physiology and which actually do occur or might occur in the same area without interbreeding" (Richard Goldschmidt, "Ecotype, Ecospecies, and Macroevolution," *Experientia, 4* [1948], 145).

[84] Mayr, *Systematics* (above, n. 80), p. 65.

various integration of gene effects. *Speciation will not be fully understood until we have more information about the nature of this integration.*"[85] The key to understanding this kind of integration was a careful examination of the "genetic elements" responsible for differences between species and subspecies. This is exactly the kind of research that Dobzhansky had called for to address Goldschmidt's challenge that chromosomal repatternings were the stuff of speciation. Mayr raised this problem not only because of its recognized importance, but because it was one of "the reasons why taxonomists have been reluctant to accept all of the conclusions drawn by geneticists."[86] Although he was quick to add that these reservations did not form a barrier between taxonomists and geneticists, and he referred to them as minor points and controversial problems, his discussion of the problem made clear that this was an issue raised by Goldschmidt that geneticists needed to resolve. Mayr's attitude toward the genetic basis of species formation carried over to the working groups and societies forming to discuss evolution and consolidate the neo-Darwinian synthesis in the early 1940s.

An important part of the evolutionary synthesis was the organization of scientists into working groups, such as the members of both the American Society of Ichthyologists and Herpetologists and the American Society of Mammalogists who met jointly at the American Museum of Natural History in New York in 1942 to discuss species criteria, as well as the New York group of the Committee on Common Problems in Genetics and Paleontology, which met from 1943 to 1945 when the Society for the Study of Evolution was founded.[87] While the history of these groups is multifaceted, it is significant that opposition to Goldschmidt's views was a prominent feature of both groups.

In 1942, the American Museum of Natural History hosted a meeting of specialists in ichthyology, herpetology, mammalogy, and ornithology to discuss their criteria for subspecies, species, and genera.[88] Although the proceedings of this meeting contain no long refutation of Goldschmidt's concepts of subspecies and species, it is significant that an ichthyologist (Carl L. Hubbs), a paleontologist (George Simpson), and a herpetologist (W. Frank Blair) all presented their views as directly opposing Goldschmidt's.[89] Interestingly, Ernst Mayr's contribution does not mention Goldschmidt at all. A more detailed and more significant treatment of Goldschmidt's view was

[85] Ibid., p. 69 (my emphasis).

[86] Ibid.

[87] Smocovitis, "Organizing Evolution" (above, n. 10); Cain, "Common Problems" (above, n. 10).

[88] The proceedings of these meetings are published as "Criteria for Vertebrate Subspecies, Species, and Genera," *Ann. N. Y. Acad. Sci., 46*: 2 (1943), 105–188.

[89] Ibid., pp. 121, 157, and 179–180, respectively.

provided at the 1943 meeting of the New York group of the Committee on Common Problems in Paleontology and Genetics.

The Committee on Common Problems began to take shape in 1942, when, after some encouragement from the National Research Council, Simpson and Dobzhanksy submitted lists of common problems for the Council's consideration.[90] Among the topics suggested for discussion were the following:

Geographic Variation
 Genetics: gene gradients, gene flow
 Paleontology: faunal migrations, range changes, dispersal facilities
Discontinuity
 Genetics: genetic basic for race and species concepts
 Paleontology: local populations, subspecies, "mutations," evolutionary steps
Evolutionary Trends
 Genetics: possible genetic backgrounds and possible causation
 Paleontology: paleontological evidence for "orthogenesis" and related phenomena[91]

This list was to organize the discussions of two groups of scientists: a West Coast Group that met in Berkeley, and an East Coast Group that met in New York.

In addition to Dobzhansky, Mayr, Simpson, and others, the New York group included Curt Stern. Stern had been a privatdozent in Goldschmidt's department at the Kaiser Wilhelm Institute from 1926 to 1932 and had relocated to the University of Rochester after Hitler's rise to power.[92] Although Stern was greatly influenced by Goldschmidt, he did not share his opposition to the gene or to neo-Darwinism. On April 2, 1943, Ernst Mayr wrote to Stern asking for assistance with the topic of discontinuity for the group's upcoming meetings at the American Museum of Natural History. Dobzhansky, who was supposed to be organizing the geneticists, had left for Brazil to collect *Drosophila*, and Mayr needed help in preparing the discussion of the genetic basis of discontinuity. He wrote:

> I would like to get from you some information on the following subjects: [(That is, I suggest you prepare a discussion which roughly covers the following points.)]

[90] Cain, "Common Problems" (above, n. 10), p. 10.

[91] From revised Appendix N in "Report of the Committee on Common Problems in Genetics and Paleontology," June 1, 1943, p. 9, folder: "1943: Committee on Common Problems of Genetics and Paleontology," National Academy of Sciences Archives, Washington, D. C.; quoted in Cain, "Common Problems," p. 11.

[92] For more on Stern see James Neel, "Curt Stern," *Biog. Mem. Nat. Acad. Sci., 56* (1987), 442–473.

1. Number of genic and chromosomal differences between natural populations and between good species – minimum figures; probability estimates; including some reference to botanic literature.

2. The number of possible [genetic] differences between individuals of the same interbreeding population.

3. The relative unimportance for origin of discontinuities of single mutations. [with specific exceptions]

The improbability of systemic mutations (sensu Goldschmidt)

4. The genetic effect of geographic isolation.[93]

The list went on, creating what Mayr knew was a tall order to fill. The purpose of the discussion, however, was not to provide answers, but, in his words, "to formulate concrete questions and to crystallize the real problems of our respective fields."[94] Stern's presentation to the New York group of the Committee on Common Problems has not survived, but the abstract of the presentation does end with systemic mutations.[95] Without question Goldschmidt's systemic mutations had become a common problem for genetics and paleontology.[96]

Stern returned to Goldschmdit's views in his comments at the Committee's 1947 conference at Princeton, in which he reviewed the interrelations between gene and character and their consequences for evolution. The relation between gene and character is the domain of physiological genetics and the study of gene action. It is not surprising, then, that Stern's discussion turns to Goldschmidt's views. He does not embrace Goldschmidt's bridgeless gaps or systemic mutations; instead, he takes up and defends Goldschmidt's work on the potentialities of development. Arguing against those who would reduce everything to the gradual accumulation of small mutations, he asks: "May not a mutational change of a gene become amplified beyond expectation in its developmental effect and thus make a cataclysmic origin of strikingly new characters be compatible with typical gene mutations?"[97] Stern does not provide a definitive "yes" as an answer, but his discussion of the ability of

[93] Ernst Mayr to Curt Stern, April 2, 1943, Curt Stern Papers (above, n. 1). Material in square brackets was handwritten; everything else was typed.

[94] Ibid.

[95] "Report of the Committee on Common Problems in Paleontology and Genetics, October 1943," Committee on Common Problems in Paleontology and Genetics, 1943–1944, H. J. Muller Papers, Lilly Library, Indiana University, Bloomington. Ind.

[96] Goldschmidt's *Material Basis of Evolution* is also one of seven books on a recommended reading list in genetics circulated among members of the Committee on Common Problems: "Reading List in Genetics," Committee on Common Problems in Paleontology and Genetics, 1946–48, H. J. Muller Papers.

[97] Curt Stern, "Gene and Character," in *Genetics, Paleontology, and Evolution*, ed. G. Jepsen, E. Mayr, and G. Simpson (Princeton: Princeton University Press, 1949), p. 17.

small genetic changes to produce considerable phenotypic effect demonstrates that he thought that developmental macromutations were possible, if not plausible.[98]

Interestingly, Stern's position is very similar to that presented by George G. Simpson in *Tempo and Mode in Evolution*.[99] Simpson's book brought paleontology into the evolutionary synthesis, and in a long section in the second chapter he discussed "the most disputed evolutionary question, in genetics and in paleontology, today" – the nature of mutations.[100] He was not convinced that Goldschmidt's discussion of systemic mutations argued for anything more than the manifold effects of single genes, which was widely accepted. The best case for saltational evolution, he thought, lay with Goldschmidt's discussion of the potentialities of development, and with the phenomenon of homeosis in particular. Simpson described homeosis as the phenomenon of a single mutant producing the "phenotypic characters typical of other families (or still higher groups) than that in which the mutant appears."[101] In contrast, Goldschmidt described homeosis as the "appearance of a homologous appendage in a segment to which it does not belong."[102] Dobzhansky also described homeosis as "a very interesting class of mutations [which] causes transformation of some organs into others, revealing the homology between the two."[103] The differences in definition are significant. Simpson's definition of homeosis and his arguments against its significance focus on one part of Goldschmidt's argument where he tries to trace the implications of homeosis for taxonomy and comparisons between different species.[104] This aspects of Goldschmidt's interpretation had been amplified in a review article on homeosis by Claude Villee, who had been a Ph.D. student of Goldschmidt's at Berkeley.[105]

Simpson presented two arguments against Goldschmidt's and Villee's interpretation of the role of homeosis in evolution. First, he argued that homeosis did not create new reaction systems. The difference between homeotic mutants and most other mutants was merely a matter of the degree of their

[98] D. Dwight Davis shared Stern's position in his paper in the same volume: "Comparative Anatomy and the Evolution of Vertebrates," in ibid., pp. 64–89.

[99] George G. Simpson, *Tempo and Mode in Evolution* (New York: Columbia University Press, 1944), pp. 48–62.

[100] Ibid., p. 48.

[101] Ibid., p. 52.

[102] Goldschmidt, *Material Basis* (above, n. 3), p. 326.

[103] Dobzhansky, *Genetics and the Origin of Species*, 1st ed. (above, n. 46), p. 18.

[104] This difference is probably the source of W. Dwight Davis's claim that Simpson had contributed to the misunderstanding of homeosis: see Davis, "Comparative Anatomy" p. 70. Simpson expressed his puzzlement over this charge in George G. Simpson, *Major Features of Evolution* (New York: Columbia University Press, 1953), p. 85 n. 2.

[105] Claude A. Villee, "The Phenomenon of Homeosis," *Amer. Nat.*, *76* (1942), 494–506.

phenotypic effect. The accumulation of a large number of homeotic mutants would still be required for speciation. Second, Simpson argued that "the appearance of a mutant individual is not evolution."[106] In order to present a viable evolutionary theory, Goldschmidt had to explain how these mutations affected populations, and in order to do this he had to appeal to neo-Darwinian factors. According to Simpson, even if homeosis "could not substantiated as real, it would supplement, not supplant, the population theories that involve selection acting on unit deviations of variable but usually small degree."[107] Goldschmidt did adopt parts of neo-Darwinian population dynamics requiring small isolated populations, but his emphasis was on the dynamics of genetic expression, not population change.

Simpson's comments were singled out by Goldschmidt for response: he wrote "An Empirical Evolutionary Generalization Viewed from the Standpoint of Phenogenetics" as a response to Simpson's attack on homeosis and the dangers of "forgetting that evolution is to a large extent also a problem of development."[108] Goldschmidt was particularly concerned with Simpson's claim that the high variability of some traits is to be accounted for by the selection of small variants. Large variants, such as homeotic mutants, according to Goldschmidt, also show high variability, which does not have to be interpreted in terms of additional small modifying mutants. Using his theory of physiological genetics, he argued that a single mutant could express all of the variability described by Simpson.[109]

Goldschmidt wanted to explain the low penetrance, high variability, and asymmetry of actual homeotic mutants, such as podoptera, using basic concepts from phenogenetics (the study of the action of mutations upon development).[110] The scheme he proposed was presented graphically (see Fig. 1). The ordinate represented the quantity of active substance determining the action of the mutant, and the abscissa represented time. A threshold was designated as the concentration of the active substance needed for the reaction to be effective and expressed. A maturation zone was specified as the length of time during development when the determination of the trait can be affected. Different chains of reactions producing the active substance of the

[106] Simpson, *Tempo and Mode* (above, n. 99), p. 53.

[107] Ibid. This objection was also made by Sewall Wright in his "Review of the *Material Basis of Evolution*" (above, n. 8), p. 166.

[108] Richard Goldschmidt, "An Empirical Evolutionary Generalization Viewed from the Standpoint of Phenogenetics," *Amer. Nat.*, *80* (1946), 305. In a letter to Mayr, Goldschmidt admits that Simpson's book encouraged him in his "impossible ideas," since it presented more material in favor of his views than in favor of neo-Darwinian views, "thus forcing the author to make all kinds of summersaults in order to come out on the right side" (Richard Goldschmidt to Ernst Mayr, September 20, 1945, Ernst Mayr Papers (above, n. 77).

[109] Goldschmidt, " 'Empirical Evolutionary Generalization' " (above, n. 108), p. 312.

[110] Goldschmidt, *Physiological Genetics* (above, n. 22), p. 23.

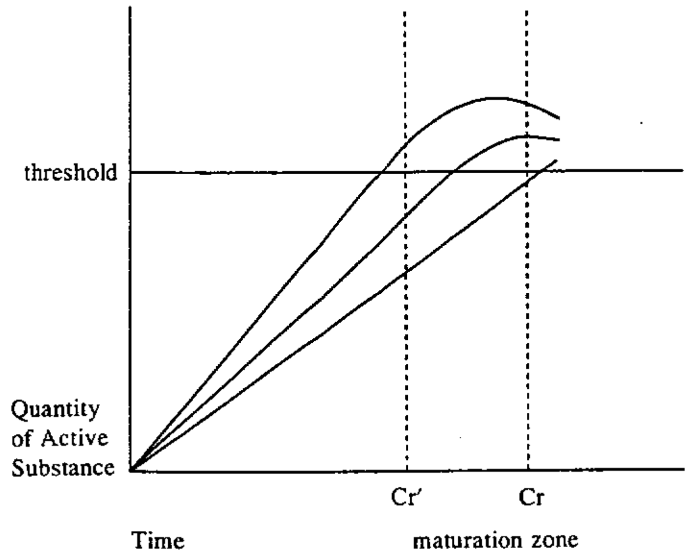

Figure 1. Phenogenetic explanation of homeotic mutants. If the threshold of action is reached before *cr′*, then a perfect homeotic mutant is produced. The later the threshold of action is reached in the maturation zone, the more normal the homeotic mutant appears. If the threshold is reached after *cr*, then a normal organ is produced. (After Fig. 1 in Richard Goldschmidt, "'An Empirical Evolutionary Generalization' Viewed from the Standpoint of Phenogenetics," *Amer. Nat.*, *80* [1946], 309.)

mutant are represented as curves indicating the change in quantity over time. Where these curves cross the threshold is crucial: If the threshold of action is crossed before the maturation zone, a perfect homeotic mutant is produced. The later the threshold of action is crossed within the maturation zone, the more normal the homeotic mutant appears. If the threshold is reached after the maturation zone, then a normal mutant appears.[111] Variability in expression and penetrance, according to this scheme, were the result of normal variations in the chain of reactions and in the position of the action threshold and the maturation zone.

Most importantly for Goldschmidt, with this phenogenetic scheme he could account for the variability observed by appealing to only a single genetic mutation. He saw this as a great advantage over the complicated scheme offered by Simpson where a mutation may produce a new tendency in a developmental field, but the expression of that trait requires the action of numerous modifying genes. Appealing to Simpson's two examples used against him, Goldschmidt asked: "Must we now conclude that the evolution from the fluctuating crest (or incipient united metaloph, in another example) to the large crochet (or united metaloph) is the product of selection of many small

[111] Goldschmidt, "'Empirical Evolutionary Generalization'" (above, n. 108), p. 310.

mutants?" His answer was not a resounding "no"; instead, he wrote: "This can be the case; but it is also possible that the first mutant already had the potency for the maximum effect and therefore represented one large step which became, however, phenotypically visible only when another mutation in the developmental system changed the variables to a different timing."[112] What Goldschmidt was striving to demonstrate was that there was more than just the neo-Darwinian strategy for explaining the facts concerning these mutants and their expression. To his mind, the neo-Darwinians had once again been too quick to generalize and overlook the importance of development for evolution.

Goldschmidt's admonitions did not always fall on deaf ears. The potential to produce massive phenotypic change from a mutation affecting early developmental processes was the one element of *The Material Basis of Evolution* to gain acceptance among neo-Darwinians. The proceedings of the 1947 Princeton conference of the Committee on Common Problems in Paleontology and Genetics, published in 1949, contain Stern's defense of this idea (as discussed above), as well as supporting arguments by W. Dwight Davis and Sewall Wright.

W. Dwight Davis was curator of the Division of Vertebrate Anatomy at the Chicago Natural History Museum. His contribution to the 1947 conference is remarkable for its extended discussion of the relation of embryology to comparative anatomy in which he considers Goldschmidt's views of development in relation to evolution and contrasts them to the older tradition of descriptive embryology. While he is clearly in favor of Goldschmidt's "causal analytic" account of developmental mechanisms and the very important role of ontogeny in phenotypic expression, he is not willing to advocate Goldschmidt's profound and abrupt changes.[113] As a fan of Goldschmidt's view of development in terms of reaction velocities, Davis strongly advocated the idea that alterations in ontogenetic rates could produce changes in morphological pattern. This is nowhere more evident than in his comments on Simpson's *Tempo and Mode*. Davis wrote:

> Simpson's list of the various means by which saltation might occur (p. 52) does not include the most likely of all, mutations affecting developmental velocities, and there is no evidence that he has considered it. This is one of the weakest points on his whole argument. Origin of the "raw materials" for the higher categories via this means is the core of the theories of

[112] Ibid., p. 36.
[113] Davis, "Comparative Anatomy" (above, n. 98), pp. 71–2.

> Schindewolf, Goldschmidt, and most recent embryologists. It certainly deserves more attention than it has been given by geneticists.[114]

Sewall Wright, as one of America's foremost physiological geneticists, would have been in a position to consider the effects of mutation on developmental rates, and he did discuss this aspect of Goldschmidt's work in his review of *The Material Basis of Evolution*. By the time of the Princeton conference, however, he considered Goldschmidt's views in terms of what they claimed about speciation, not mutation and development. Wright's contribution was a sometimes technical essay on adaptation and selection. As he set out the details of his shifting balance view of evolution, he came to the topic of speciation:

> The multiplication of species relatively rarely leads to generic differences and still more rarely to families and higher categories by a gradual cumulative process. There seems to be a large measure of truth in the contention of J. C. Willis and Goldschmidt that evolution works down from the higher categories to the lower rather than the reverse. Nevertheless the critical event in the appearance of a higher category seems to be a major environmental opportunity rather than any sort of mutation.[115]

Goldschmidt had always emphasized the need for the right kind of environmental opportunity for his new mutants and had followed Wright's account of evolution in this regard. Wright's rejection of Goldschmidt's account of mutation, however, is a sign of the growing attitude of geneticists, undoubtedly influenced by Dobzhansky (Wright and Dobzhansky were collaborators during the 1940s).

Similarly, Dobzhansky's third edition of *Genetics and the Origin of Species* freely allowed that mutations affecting early development can have massive phenotypic effects.[116] Mutations affecting development were incorporated into the variety of genetic changes possible. They were not treated as the only mechanism for species formation, but as one of many mechanisms for producing genetic and phenotypic change, which can then form the basis for evolution by natural selection. Goldschmidt's changing status relative to the evolutionary synthesis is also reflected by the amount of time devoted to his views: in Dobzhansky's second edition, they had required an extended discussion; by the third edition, they were mentioned as opposed views that had been taken care of, as challenges that had been met.

[114] Ibid., p. 75, n. 4.

[115] Sewall Wright, "Adaptation and Selection," in Jepsen, Mayr, and Simpson, *Genetics* (above, n. 97), p. 387.

[116] Theodosius Dobzhansky, *Genetics and the Origin of Species*, 3rd ed. (New York: Columbia University Press, 1951).

This same attitude was also expressed in the last extended treatment of Goldschmidt's evolutionary claims: George G. Simpson's *Major Features of Evolution*, published in 1953. Simpson made it clear that by 1953 the neo-Darwinians had fully responded to some aspects of Goldschmidt's program. In the case of systemic mutations, for instance, Simpson commented: "The rejection of this view by the consensus of geneticists in the twelve years since it was most fully expressed makes it unnecessary to belabor the point now as much as when I first discussed it (a critique written in 1941–42 and published in Simpson, 1944a)"; the consensus among geneticists was explained in a footnote as follows: "An early reaction of a competent geneticist was that of Wright (1941), which seems fairly typical of the consensus of Goldschmidt's peers: profound respect and admiration for his genetical work but disagreement with his hypothesis on the origin of species and higher categories."[117] Moreover, Simpson argued that without systemic mutations, the disagreement between Goldschmidt and the neo-Darwinians was much less profound than it first appeared. He even agreed with Goldschmidt's proposal concerning phenogenetics and the variable expression of homeotic mutants. Goldschmidt's scheme appeared to Simpson to be "at least a possible physiological mechanism for the production of the observed variations."[118] What Simpson denied was the evolutionary significance of Goldschmidt's proposed physiological mechanism. There may be homeotic mutants, they may have the kind of phenogenetics described by Goldschmidt, but they do not produce new species.

Goldschmidt's work highlighted a number of serious problems in the neo-Darwinian approach to evolution. Where his challenges were not met with a detailed presentation of the available evidence, organized often for the first time just for this purpose (as with Mayr and geographic speciation), they accentuated the need for new experimental work to fill in important gaps (as with Dobzhanksy and the genetics of species formation). Goldschmidt's most serious challenge was the one issued to Dobzhansky over the possibility of systemic mutations and their ability to lead to the sudden appearance of new species.

Conclusion

In his review of *The Material Basis of Evolution* for the *American Naturalist*, Carl Hubbs summarized Goldschmidt's claims in tabular form (see Table 1). The explicit contrast between "The Old, Neo-Darwinian Concepts, To be

[117] Simpson, *Major Features of Evolution* (above, n. 104), p. 85.
[118] Ibid., p. 76.

Table 1. Excerpts from Carl Hubbs's tabular summary of *The Material Basis of Evolution.* (From Carl Hubbs, "Reviews and Comments: *The Material Basis of Evolution,*" *Amer. Nat.,* 75 [1941], 273.)

The old, neo-Darwinian concepts, to be rejected	The new, Goldschmidtian concepts, to be accepted
Evolution proceeds through the accumulation of small changes.	True evolution results from large single-step mutations.
Subspecies grade into species, and are incipient species.	Subspecies do not grade into species, and are not incipient species; there are not incipient species.
Evolution is gradual; missing links will be found.	Evolution is by large steps; "missing links" never existed.
There is a common, unified type of evolution: a gradually expanding system.	Evolution is of two distinct sorts: microevolution (within species) and macroevolution (between species and all higher groups).
Genes are the basis of heredity, and the gradual accumulation of small gene mutations is the basis of evolution, at all systematic levels. Genes are essentially independent in their action, though interdependence in effects may arise through genic balance.	Genes, if they exist at all (which is doubted), can only be involved in microevolution. Through single-step systematic mutations, chromosomal rearrangements (translocation, inversions, multiplication) produce the reaction systems that comprise macroevolution. Whole chromosomes or even the entire genomes may act as a unit.
[These concepts are frequently contrasted with the "classical" or neo-Darwinian genetics, though the distinctions are not always made clear, except in the comparison of "genic balance" with Goldschmidt's "reaction systems," and of "pattern effect" with "systemic mutation."]	Evolutionary changes as well as modifications result from the operation of various factors at different, critical periods of development. The changes have a physiological basis in the quantity and quality of catalysts and hormones, and in the time and rate of their action. Different reaction systems, based on systematic mutations, are involved.

Rejected" and "The New, Goldschmidtian Concepts, To Be Accepted" articulated diametrically opposed positions. In Carl Hubbs's eyes, Goldschmidt had approached evolution through a "series of all-or-nothing contrasts."[119] Presenting the neo-Darwinian and Goldschmidtian positions in this way placed all of the emphasis on the differences between them and heightened the sense of controversy. But it also allowed Hubbs and the neo-Darwinians an easy victory, if they could repel Goldschmidt's "Don Quixotic" attacks. They expended considerable effort to address Goldschmidt's challenges, but

[119] Hubbs, "Reviews and Comments" (above, n. 8), p. 273.

declaring them the victors in an all-or-nothing contest obscures the dynamics of the dispute and Goldschmidt's influence on the neo-Darwinians.

Similarly, declaring Goldschmidt's views heresies sets them into an all-or-nothing relationship with "the orthodoxy."[120] These binary categories fail to capture the diversity present as the synthesis was forming, just as they erase the varying mutual influence that these diverse viewpoints had. That there was an eventual constriction in the later 1940s and afterward may be taken as evidence for the emergence of a neo-Darwinian orthodoxy. But if this is the case, then I hope that I have shown that Goldschmidt's views helped define the neo-Darwinian orthodoxy and in doing so created the conditions for his own exclusion. I am not claiming that there was not an emerging orthodoxy before Goldschmidt, but that he accelerated this process and redirected it in important ways. Contemporary biologists are free to make what they will of Goldschmidt's "heresies," but the fact that Goldschmidt's theory of evolution was a significant factor in the formation of the evolutionary synthesis cannot be denied.

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[120] This label was actually used by Goldschmidt in his autobiography published in 1960. Mayr uses the label "heterodox," but Gould has brought "heresy" back into fashion – so much so, that when *The Material Basis of Evolution* was reissued in 1982 and reviewed, Allan Templeton actually provided a ranking of Goldschmidt's heresies ("Why Read Goldschmidt?" [above, n. 7]). The Grand Heresy is the decoupling of micro- and macroevolution.