With the recent mapping of the human genome, scientists have dramatically increased their ability to explain inheritance patterns. Yet, even so, developmental genetics remains relatively elusive. The discrepancy between these two approaches to genetics is not a new divide in the research community. Richard Goldschmidt is one scientist in the past who attempted to bridge this divide. As a German scientist (fed on the holistic notion of *Entwicklungsmechanik*, which emphasizes a physiological approach to embryology), he felt compelled to relate gene action to the problem of transmission. Consequently, he confronted scientists of his time with several controversial developmental theories. In his keynote speech at the 1951 Cold Spring Harbor Symposium, Goldschmidt upset many attendees by proposing that the chromosome constituted the unit of function and that there was no such thing as a gene. His suggestion has become a stock joke for historians. Nonetheless, the obscured significance of his work proves more interesting than the humor of his inaccuracies.

Many questions surrounding Goldschmidt’s career deserve the attention of history: Why did his *Drosophila* work of the 1930s and 1940s go widely unnoticed? (James Crow calls Goldschmidt’s article on chromosome maps in the fly “particularly foolish” and later refers to a genetic theory of sex determination proposed by Calvin Bridges—rather than the émigré German (Crow, 2000). Robert Kohler fails to properly crown Goldschmidt as a “Lord of the Fly” in his well-known book.) What made his experiments on *Lymantria* so controversial and later forgotten? To answer these questions we must understand Goldschmidt as a scientist geographically, ideologically and historically displaced. We are also obliged to take into account the material culture of his experimental practice, described by Kohler as “something more than single instruments, but less than the productive machinery of a laboratory or research field” (Kohler, 2001). Indeed, Goldschmidt’s choice of *Lymantria* as the organism for his studies on genic balance during the early twentieth century may have influenced the historical reception of his work.

Those who have sought to revive a discussion regarding his science, including C. Lynne Littlefield, Peter Bryant, Curt Stern and Stephen Gay Gould, emphasize the questions he raised as paramount to the conclusions he reached. In their eyes, he did the discipline of genetics a service by highlighting the shortcomings of the static genomic model. Goldschmidt’s rebellious attack of the conventional concept of the gene may have indeed induced a healthy debate among geneticists, but it undoubtedly cast a stub- born shadow over his authority with respect to the theory of genic balance.

**NO FOREIGNER TO SCIENCE**

Richard Goldschmidt was born on April 12, 1878, in Frankfurt-am-Main, Germany, into a well-respected family (Stern, 1980). This social and cultural elite to which he belonged owed their status more to education than heredity (Dietrich, 1995). Indeed, Goldschmidt himself demonstrated a passion for learning. By the age of seventeen, he could read French, English, Italian, Latin and Greek and attempted to educate himself about the works of difficult philosophers (Stern, 1980). He enrolled in the Heidelberg University as a medical student and left for Munich two years later, after passing his examinations. Abandoning his medical training, Goldschmidt became a student of Richard Hertwig, and by the age of 21, he had completed his first scientific paper. After returning to Heidelberg to write his thesis and giving a year of
his life to the compulsory training period in the German army, he joined Hertwig's staff in Munich, where he stayed through the early 1910s (Stern, 1980).

According to Scott Gilbert, Goldschmidt battled anti-Semitism throughout his scientific career. Because of his Jewish background, he encountered difficulties while researching under Hertwig. Gilbert writes, “Goldschmidt made the most of his reputation while working as Richard Hertwig's assistant, and he could never hope to get a tenured position in the university even though he essentially ran Hertwig's laboratory and taught Hertwig's courses” (Gilbert, 1988). Yet Goldschmidt triumphed over the anti-Semitic sentiment of his contemporaries when he became a division director of the Kaiser-Wilhelm Institute for Biology in 1913.

Between the first and second World Wars, Goldschmidt established himself at the forefront of science. His experiments on sex determination and differentiation in the gypsy moth *Lymantria dispar* led him to conclude that sex determination was controlled by interactions between specific male and female factors—and that the potency of these factors varied between races. Without the help of sex-linked mutations, he did his best to interpret the chromosomal constitution of the individuals during the course of his investigations (Littlefield, 1980). Based upon the results of his experiments, he produced the concept of genic balance, the time-law of intersexuality and theories about heterochromatin and sex determination. The first of these ideas proposes that competitive interactions between sex-determining factors on different chromosomes (rather than individual chromosomes alone) determine sex (Littlefield, 1980) Thus the theory of genic balance, with its emphasis on complex systems, provides a representative example of the holistic approach that grounded Goldschmidt's science. And though his theory's flaws were later revealed, the model was initially well received. Littlefield and Bryant state that, “The theory of genic balance as outlined by Goldschmidt met with general approval from other workers studying lepidopteran intersexes...” (Littlefield, 1980). His *Lymantria* research was not ignored by his contemporaries.

Gilbert states that Goldschmidt strove for a noble life and considered himself “a self-aware king in the scientific world of interbellum Germany” (Gilbert, 1988). The scientist's controversial character embodied the stereotypical German professor of his time. According to Gould, he was ‘arrogant, haughty, yet invariably kind and even courtly” (Gould, 1982). But Goldschmidt's life changed drastically in the half decade preceding World War II. In 1936, he was forced to flee Nazi Germany, leaving behind the Kaiser-Wilhelm Institute where he had been a director for 23 years (Dietrich, 1996). Goldschmidt suffered a blow to his authoritative position in Germany when he immigrated in the 1930s. While he had enjoyed a celebrated status as one of the most imposing figures of German intellectual life during the pre-Hitler days, he became “one of the large number of professors whose prestige was limited” when he came to the United States (Stern, 1980). According to Stern, Goldschmidt's status was questioned by many of his colleagues at this time. He writes in his biography of his mentor, “The attacks against their opinions, which he had waged for so long and their critical attitude to his own pronouncements did not provide a background for ready acceptance except where the person, not the scientist was involved” (Stern, 1980). Goldschmidt irritated researchers when he assaulted the theory of the gene in “Morgan's country.” During this time, he continued to reject the corpuscular picture of the gene and maintained that regions of specific function along the chromosome formed a single, long molecule (Caspari, 1980). Most geneticists, however, had accepted a model in which the location of specific genes on specific chromosomes. They pointed to studies of radiation-induced mutations as evidence to support the model of corpuscular genes.

In “An Evaluation of Goldschmidt's Work after Twenty Years,” Ernst Caspari reasons that because Goldschmidt's views ran counter to those of the majority, he found himself scientifically isolated and his work widely disregarded when he came to the United States (Caspari, 1980). Goldschmidt, who argued that “the whole
conception of the gene” was obsolete, found himself increasingly marginalized by the predominant idea of a static genome (Comfort, 2000). According to Gilbert,

By 1938, Goldschmidt had already alienated himself from the majority of geneticists with a series of increasingly serious breaks with the genetic “orthodoxy” of the Morgan School...[He] disagreed with the simple chromosomal genetics of sex determination espoused by Morgan, Bridges, and Sturtevant, preferring instead the physiological approach of the German school that he helped lead (Gilbert, 1988).

When Goldschmidt announced that “The theory of the gene is—dead!” (Stern, 1980) most geneticists actually believed that the concept was alive and well. His keynote speech at the 1951 Cold Spring Harbor Symposium struck a sour note with scientists studying heredity. Goldschmidt aggressively defended his own scientific views, but his intellectual independence cost him his popularity.

WHERE IS RICHARD GOLDSCHMIDT?

In his book, Lords of the Fly, Robert Kohler examines the network of scientists under Thomas Hunt Morgan who engineered the use of Drosophila as an essential laboratory instrument in genetic research. Kohler briefly mentions Goldschmidt’s work in several chapters of the text. He contrasts the German scientist’s holistic biological approach with the “narrowly reductionist perspective of genetics” produced by Morgan’s fly group (Kohler, 1994). More interestingly and perhaps more memorably, he uses Goldschmidt’s claim to intellectual priority on the topic of genic balance to illustrate the tolerance and generosity of Calvin Bridges, who, according to Kohler, “never held a grudge” (Kohler, 1994). In limiting his mention of Goldschmidt’s research, Kohler continues the tradition of ignoring the Drosophila work that the foreign scientist produced in the late 1930s and 1940s (Caspari, 1980).

Instead of attributing the idea of genic balance to Goldschmidt, Lords of the Fly gives credit to Bridges. “When Richard Goldschmidt laid claim to his theory of sex determination,” writes Kohler, “Bridges refused to argue.” The word “his” in this sentence offers problematic readings. I understand “his” to be synonymous to “Bridges’s” because of its context within the paragraph (the previous seven sentences discuss the scholarship student at Columbia rather than the German outsider). In elevating the significance of Bridges’s work, Kohler creates a self-serving presentation of the theory of genic balance of sex determination. (He did, after all, write a book about Drosophila and not Lymantria.) Ascribing genic balance to American researchers, he aggrandizes the importance of Morgan’s fly group at the expense of historical accuracy.

Kohler is not alone in his historical treatment (or, rather, mistreatment) of Goldschmidt’s research on genic balance. In his essay celebrating the diamond anniversary of the publication Genetics, James Crow applauds Bridges for his article on genic balance and leaves out any mention of Goldschmidt’s claim to the concept. The frequency, phenotype and synopsis and segregation patterns of nondisjunctive types “led Bridges to his genic balance theory of sex determination” (Crow, 2000). Like Kohler, Crow idealizes Bridges’s persona. The small-town orphan turned bad-boy scientist died unexpectedly in 1938 at age 49—making him appear in many texts as the James Dean of genetics. His magnanimous and seemingly humble character, as presented by the two aforementioned authors, contrasts sharply with the haughty comportment of the scientific “Bosses” who reigned in the laboratories during the early twentieth century. Furthermore, Crow highlights the reconciliatory letter Bridges wrote to Muller and remarks that the founder of the Drosophila Information Service was underpaid throughout his life. When Crow does speak of Goldschmidt’s articles, he uses them merely to stress that earlier works in Genetics were not always in English (implicitly inviting the reader to exclaim, “Look how far we’ve come!”). He ridicules the German scien-
tist’s second paper in the publication, which argued against chromosome maps in *Drosophila* (Crow, 2000). Crow omits Goldschmidt from the scientific narrative behind genic balance while casting a glowing spotlight on Bridges, a Drosophilist like himself.

There is, of course, evidence of important contributions made by Calvin Bridges to the theory of genic balance. In 1921, using the genetic manipulations made possible with *Drosophila*, Bridges analyzed the effect of obtained triploid (2X3A) intersexes by crossing triploid (3X3A) females to diploid (XY2A) males (Littlefield & Bryant, 1980). The relatively advanced analyses in the fly labs enabled him to find that sex was determined by a quantitative relationship between the number of X chromosomes and the number of sets of autosomes. Reluctant to accept Goldschmidt’s idea that the alleles of just one or two genes controlled sex, Bridges concluded that there were many sex-modifying genes in the genome. In this fly model, he outlined that female modifiers dominated the X chromosome while male modifiers governed autosomes. Each organism’s sex was determined by the ratio between these two types of modifiers; intersexes arose as a result of abnormal ratios between female and male sex-modifying genes. According to Littleton and Bryant,

Bridges pointed out that although Goldschmidt had occasionally found with Lymantria that the strength of male factors became altered and had attributed it to a mutational event, recombination between several closely linked sex-modifying genes could have given the same result (Littlefield & Bryant, 1980).

Bridges’s research expanded and challenged that of Goldschmidt. Furthermore, the organism he chose for his study had a wide appeal in the American scientific community. Although historians such as Kohler and Crow have good reason to sing the praises of Bridges’s studies, they nevertheless deceive their readers by playing down Goldschmidt’s own contributions to the theory of genic balance.

Both Dunn and Caspari address the tangled story of authorship looming behind genic balance. Dunn initially states, “[T]he most spectacular application of the genic balance theory...was attained in Bridges’ (1922) interpretation of sex types in *Drosophila*” (Dunn, 1965). He then proceeds to acknowledge that the ideas involved in this theory had been previously proposed by Goldschmidt. Dunn reasons that Goldschmidt failed to garner recognition to the same extent as Drosophilists working on the problem because he produced gypsy moth intersexes within the normal diploid genome and did not identify or associate genes leading in the male or female direction with specific chromosomes (and was therefore unable to directly measure the relative strengths of his factors). Dunn writes,

Thus, although Goldschmidt was undoubtedly the originator of the balance theory of sex, the convincing nature of the proofs provided by Bridges and others working on *Drosophila* prevailed in giving that work greater influence upon the subsequent development of the genic balance theory (Dunn, 1965).

Caspari offers a more recent and celebratory perspective on Goldschmidt’s claim to this theory. He presents a broad narrative of Goldschmidt’s place in the history of genetics, emphasizing that the reception of the scientist’s work changed with the evolution in the scope of the discipline between the 1930s and 1940s (including “the rise of biochemical genetics, microbial genetics and finally molecular genetics”). His essay reveals that during the 1950s, when new complexities challenged earlier models of the gene, geneticists once again turned to Goldschmidt’s research and ideas (Caspari, 1980).

Caspari portrays a positive turn in the popularity of Goldschmidt’s science; however, recent texts (such as those of Kohler and Crow) continue the tradition of mocking and neglecting the German émigré. Surveying the table of contents and indexes of these books, a careful reader begins to wonder, “Where is Richard Goldschmidt?” When authors attribute the theory of genic balance to Bridges alone, they demon-
strate their bias in favor of American scientists working under Morgan as well as their prejudice against a foreign geneticist who went so far as to attack the classical concept of the gene.

**THE MATERIAL BASIS FOR FAME**

If anti-Semitism, American patriotism and “Drosophile” forces have marginalized Goldschmidt’s science, his choice of *Lymantria* as the organism for his studies also detracted from the permanence of his fame. While he conducted his experiments, collecting samples from around the world, the Fly Group managed to develop revolutionary analytical technologies and give researchers, such as Bridges, a scientific edge. Littlefield and Bryant assert that Goldschmidt had chosen an organism that “is by no means ideal for genetic manipulations…” (Littlefield & Bryant, 1980). In contrast, Bridges had a wealth of new techniques to examine his *Drosophila*. Moreover, his use of flies in his investigations concerning genic balance came with a built-in audience that only grew with time. This audience existed because Morgan had institutionalized a system of etiquette that enabled the Drosophilists to “make such progress in genetics that by 1920 they dominated the field” (Dietrich, 1996). The prevalent use of *Drosophila* in genetics today remains as evidence of the organism’s popularity as a scientific tool.

In selecting *Lymantria* for his research, Goldschmidt adopted what Robert Kohler would call a non-standard “system of production.” Kohler urges historians to consider organisms used in the laboratory, specifically those that were altered for the purposes of the experiment, as constructed artifacts (Kohler, 2001).

“Standard” animals, produced by generations of inbreeding are unambiguous examples of engineered instruments…Organisms and instruments come to embody libraries of knowledge and routine practices. That, by definition, is how they become systems of production (Kohler, 2001).

The practice of using *Lymantria* was not popularized to anywhere near the extent as the use of flies in genetic research. In fact, *Lords of the Fly* specifically focuses on the dramatic success of Morgan’s researchers in using *Drosophila* in a revolutionary system of genetic exploration. The new mutants and new genetic knowledge fueled more of the same in an autocatalytic process. In Kohler’s words, “*Drosophila* became, in effect, a biological breeder reactor, creating more material for new breeding experiments than was consumed in the process” (Kohler, 1994). Morgan’s network of labs became a “hegemonic” establishment and many bright minds were eager to join the fly bandwagon. Goldschmidt’s preferred organism for his sex-determination research (*Lymantria*) therefore placed him on a path that diverged from the overwhelmingly dominant Fly Group.

Goldschmidt did more than just hold off on becoming a Drosophilist; he maintained a holistic approach to the study of heredity that ran contrary to the pragmatic style of American geneticist (Dietrich, 1996). According to Gilbert, Goldschmidt sought “to place American genetics into the German type of developmental physiology” (Gilbert, 1988). This challenge presented great difficulty at the time. Employing Wilhelm Johanssen’s distinction between genotype and phenotype, “Morgan had separated the transmission of hereditary traits (genetics) from the expression of those traits (embryology)” (Gilbert, 1988). Using *Drosophila* to churn out dazzling discoveries, the Fly Group made this question of gene transmission more exciting than that of gene action. The *Entwicklungsmechanik* perspective Goldschmidt maintained cost him the esteem of scientists in America for many years. Although he came to the United States and devoted himself to analyzing the spontaneous mutations in *Drosophila* from 1939 to 1945 (Dietrich, 1996), Goldschmidt refused to surrender his complex view of heredity. Thus, even though he adopted the material of Morgan’s labs, he remained at odds with many geneticists of his time and failed to break into the limelight in history books.
THE REBEL’S REDEMPTION

Those who seek to resurrect discourse about Goldschmidt’s work bring attention to the cruel treatment he has received. In the introduction to Goldschmidt’s book, *The Material Basis of Evolution*, Gould writes that the scientist “suffered the worst fate of all: to be ridiculed and unread” (Gould, 1982). In science courses, students laugh at Goldschmidt’s ideas dutifully to prove that they are not guilty of either ignorance or heresy (Gould, 1982). His heretical denial of the conventional gene, however, provides historians with more than comedy. It presents one possible explanation for the neglect of his theories. In the revisionists’ story, most geneticists were not ready to confront the challenging models he championed. Goldschmidt’s own audacity cast a shadow over his insight. Just as Kohler and Crow depict Bridges as a social rebel censured for his promiscuous behavior, Allen and Dietrich portray Goldschmidt as a scientific rebel outcast for his rejection of the classical concept of the gene. Seen in the context of his time, Goldschmidt acquires a new allure of someone who possessed the courage to stand apart from the crowd to promote what he believed.

Building upon this interpretation of Goldschmidt as an intellectual rebel, Allen and Comfort suggest that he should be remembered for the *kinds of questions that he posed* if not for his actual research. His contrarian views—including his struggle against the notion of a static genome—pushed the discipline of genetics forward. According to Comfort, “By playing the devil’s advocate, Goldschmidt forced geneticists to reconsider their assumptions. For all his crotchetsiness, Goldschmidt was and is an important figure in genetics” (Comfort, 2000). Similarly, Allen writes, “Goldschmidt may often have been wrong, but his ideas had imagination and fire” (Allen, 1980). He adds that, “Our understanding of, and approach to, genetic processes today bears the mark of the kinds of questions which Goldschmidt persisted in asking, often irreverently, throughout his entire career” (Allen, 1980). Stern likens Goldschmidt’s thinking to the scaffolding of a building on which other scientists were able to reach the spaces where they could “fit their parts into the yet imaginary structure” (Stern, 1980). The German Boss was, in Stern’s opinion, a designer of frameworks of the future (Stern, 1980).

Additionally, Goldschmidt’s holistic perspective has gained newfound appreciation among historians. Littlefield and Bryant conclude that his proposal that genes control rates of reaction “shed one of the first rays of light into the still-very-dark black box that connects the genotype with the phenotype” (Littlefield & Bryant, 1980). These commemorative statements give Goldschmidt the applause that the majority of “Drosophile” historians do not offer in their texts.

THE EVOLUTION OF CELEBRITY

If we evaluate Goldschmidt’s refutation of the classical concept of the gene out of context, it becomes easy to ridicule. This presentist tendency to find humor in his mistaken models serves no constructive purpose. Instead, it merely diverts our attention from his authority on ideas such as genic balance. Kohler and Crow both err in de-emphasizing Goldschmidt’s theoretical contributions. We cannot write him into the story of the Fly Group, but we must not carelessly disregard him either.

It would incorrect to conclude that historians have reached a definitive agreement over the importance of Goldschmidt’s role in genetics. One need only compare Kohler’s discrediting presentation of Goldschmidt’s relationship to the theory of genic balance with the earlier essay by Littlefield and Bryant to see that the debate continues. Dietrich has recently written on the exceptional significance of the German scientist’s work. He writes, “Goldschmidt’s work stood apart from typical Mendelian accounts by providing a quantitative interpretations of sex determination” (Dietrich, 1996). Thus, our views on Goldschmidt’s importance continuously evolve. His place in history is by no means static.