

**THE USES OF HERESY:  
AN INTRODUCTION TO RICHARD GOLDSCHMIDT'S  
*THE MATERIAL BASIS OF EVOLUTION***

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**I. BACKGROUND**

IN his autobiography, published posthumously in 1960, Richard Goldschmidt wrote of the work here reprinted, "I am confident that in 20 years my book, which is now ignored, will be given an honorable place in the history of evolutionary thought" (1960, p. 324). We are within the limits of statistical error on Goldschmidt's prediction and would have met it exactly had I honored an initial deadline. This reprint—since presses, even university presses, are not, at least by choice, eleemosynary institutions—commemorates the strong reawakening of interest in Goldschmidt's views among evolutionary biologists. If this attention be the harbinger of "an honorable place," then so be it—though I suspect that a self-assured, professional iconoclast like Goldschmidt would relish the renewed argument more than any potentially favorable outcome.

Richard Goldschmidt, one of the world's great geneticists, delivered the prestigious Silliman lectures at Yale in 1939 and published his remarks in 1940 as *The Material Basis of Evolution*. He wrote just as the Darwinian paradigm was coalescing into a confident general theory of evolution. The foundations of population genetics had been established and Dobzhansky (1937) had initiated the "modern synthesis" of traditional disciplines around this Darwinian core, with its central emphasis upon continuity in process and cause for all evolutionary events from the spread of alleles in local populations to major trends in the history of life. The observable and operational realm of microevolutionary change would become a model for all levels of evolution; speciation, as Darwin had argued, is a smooth extension of adaptive change in local populations. "Races, species, genera, and families are nothing more than different degrees of phylogenetic divergence" (Dob-

zhansky, 1951, p. 266). "Adaptation to local conditions and evolutionary change are two aspects of the same genetic phenomenon, the continuous adjustment of an integrated gene complex to a changing environment" (Mayr, 1963, p. 332).

Amidst this incipient chorus of consensus, so welcome after decades of strife and fruitless disagreement within evolutionary theory, Goldschmidt's views injected an especially disharmonious note. He seemed bent on undoing this unity and invoking the shade of de Vries to assert once again that macroevolution was a thing apart, abrupt in its occurrence, and unilluminated in principle by processes of microevolution that could be studied directly. He even invented an unforgettable and disturbing (if whimsical) name for his independent macroevolutionary agent—the "hopeful monster."

Of his reception by neo-Darwinians, Goldschmidt claimed (1960, p. 324) that he "certainly had struck a hornet's nest. The Neo-Darwinians reacted savagely. This time I was not only crazy but almost a criminal." Ernst Mayr recalls (1980, p. 420), "Even though personally I got along very well with Goldschmidt, I was thoroughly furious at his book, and much of the first draft of *Systematics and the Origin of Species* was written in angry reaction to Goldschmidt's total neglect of such overwhelming and convincing evidence."

The counterattack was successful, if not triumphant—though Goldschmidt (as I shall argue later) had largely himself to blame for burying his gems so deeply in unacceptable and overextended claims. Indeed, he suffered the worst fate of all: to be ridiculed *and* unread. Textbooks of the past forty years have generally included a polite and perfunctory paragraph of dismissal. The following is typical:

Some biologists have suggested that the origin of major groups of animals and plants, such as phyla, classes, or orders, may at times have come about through single mutations involving large and complex changes that happen to be successful. Such creatures, called by Richard Goldschmidt "hopeful monsters," seem with the advance of our knowledge, to be less and less necessary to explain the beginning of new adaptive advances. A monster is far more likely to be hopeless than hopeful. The gaps formerly present in our knowledge of many groups are being filled today by evidence of the usual, gradual transformation of characters under natural selection. [Eaton, 1970, p. 45]

I have witnessed widespread dogma only three times in my career as an evolutionist, and nothing in science has disturbed me more than ignorant ridicule based only upon a desire or perceived necessity to follow fashion: the hooting dismissal of Wynne-Edwards and group selection in any form during the late 1960s and most of the 1970s, the belligerence of many cladists today, and the almost ritualistic ridicule of Goldschmidt by students (and teachers) who had not read him. I do not know how often it happened, and my memories have been pooh-poohed both by my older colleagues who knew and revered Goldschmidt and by younger colleagues trained in our present era of reawakening interest, but I know that I experienced it in classroom after classroom as a graduate student in the mid-1960s. My experiences are neither unique nor misremembered, for Frazzetta (1975, p. 85) reports from the same time and different place, "No one stopped to consider whether in all of Goldschmidt's assailable propositions, there existed anything worth thinking about. There was no time for such consideration as long as there was so much merry mayhem to be carried out. In my university classes, the name 'Goldschmidt' was always introduced as a kind of biological 'in' joke, and all we students laughed and snickered dutifully to prove that we were not guilty of either ignorance or heresy." An eminent senior colleague and former professor told me that he went to his library to consult *The Material Basis of Evolution* after reading an article that I had written in Goldschmidt's defense. He could not find it and was frustrated until he remembered—and then he was merely angry—that he had thrown it out several years ago as containing nothing of value. I do not think I exaggerated (Gould, 1977a) in comparing Goldschmidt with Goldstein, the object of daily "two minute hates" in Orwell's 1984.

Who then was this Goldschmidt whom so many reviled in ignorance? First of all—and this must be a general principle for objects of intense ridicule—he could not have been a minor or second-rate thinker, for such scientists are not worth the emotional energy devoted to Goldschmidt's intellectual persecution. No one likes to waste time on a nonentity. Goldschmidt was one of the premier geneticists of our century, a shoo-in on anybody's list of the top ten. He was born in Frankfurt in 1878, the son of a wealthy merchant and scion of an old, prosperous,

and intellectual Jewish family. He studied under the greatest teachers from the golden age of late nineteenth-century German biology: with Otto Bütschli and Karl Gegenbaur in Heidelberg and with Richard Hertwig in Munich. Along with T. H. Morgan and Th. Dobzhansky, he thus obtained the greatest gift and preadaptation that any future geneticist could receive for evolutionary studies: a rigorous training in classical morphology and embryology. He became Hertwig's assistant in 1903 (after defending a thesis on maturation, fertilization, and embryonic development in the trematode *Polystomum integerrimum*) and remained in Munich until 1913. When Theodor Boveri and Carl Correns organized the Kaiser Wilhelm Institute for Biology in Berlin, they invited Goldschmidt to become director of genetics, a post he held until 1935.

Goldschmidt was a professor in the stereotypical Germanic mode. He was arrogant and haughty, but invariably kind and even courtly. He wrote of a Nazi poster citing the genealogy of his family as a testimony to Jewish danger, "It could well be used as a chart demonstrating the effect of long selection of favorable hereditary traits upon the improvement of human families" (1960, p. 5). He enjoyed the prerogatives of office and expected the "deference due to a man of pedigree" (as Gilbert said of Pooh-Bah). Viktor Hamburger (personal conversation) recalls that his fellow students called Goldschmidt "the Pope," perhaps not so peculiar a title for an offspring of established German-speaking Jews who often surpassed many Prussians in their loyalty and assimilation (I can still hear the acid words of my Yiddish-speaking peasant grandmother, recalling the snubs of well-bred Viennese girls). He was erudite and enormously cultured, an expert on oriental art, and a man who never really accommodated to the incipient "California life-style" of prehippie Berkeley.

The two world wars affected Goldschmidt in the reverse order of Marx's famous statement that all events in history occur twice, the first time as tragedy, the second as farce. When the Great War broke out (so called until a greater occurred twenty-five years later), Goldschmidt was in Hawaii on a travelling fellowship. He went, virtually by necessity, to the American mainland and spent the war with us, first as a teacher, but finally, in the orgy of jingoism that engulfed us as we

entered the war in 1917, in an internment camp for enemy aliens. Repatriated to Germany after the war, he resumed his old post in Berlin, only to relinquish it by force in 1935 as Hitler destroyed German science by purging Jews and other racial and ideological “undesirables.” Goldschmidt again travelled to America, this time as a refugee, and became a professor at Berkeley in 1936, a post he held until he entered a continually active retirement. He died in 1958, his powers—and his faith in them—undiminished. The last words of his autobiography do not proffer cosmic advice, but merely state, “It is my greatest intellectual happiness that I can still work in my laboratory and even make interesting discoveries in the field of chemically induced phenocopies” (1960, p. 326).

Goldschmidt’s scientific writings spanned a range often included in several university departments. (Goldschmidt’s autobiography, 1960, contains a complete list of his publications. A short summary of his life and works, and a list of primary and secondary sources can be found in the entry by A. Téry in the *Dictionary of Scientific Biography*, vol. 5, pp. 453–55.) He spent most of the first decade of his career working in classical morphology. He helped to establish and explicate the fascinating phenomenon of cell constancy in nematodes and made many important contributions to the histology and embryology of protochordates. From this phase of his life, though written late in 1921, comes Goldschmidt’s most charming work, a classic that spread his name to thousands who would never encounter the rancor of his professional opposition: *Ascaris*, a popular book ostensibly about a “lowly” nematode, but extending outward (as its parasitic subject must) into all areas of zoology. Still read and admired in Europe, its English translation (1938) never attained the popularity that Goldschmidt had anticipated.

When Goldschmidt moved into genetics, he chose the gypsy moth, *Lymantria dispar*, as his primary subject. (I write this essay in May 1981, as caterpillars of the gypsy moth swarm, locustlike, over New England.) This work led him in two major directions. First, he studied several problems in microevolution from a Darwinian standpoint. He travelled throughout the world and performed one of the most inclusive and elegant of early studies on geographic variation in phenotypes with

known genetic bases. He also elucidated the genetics of industrial melanism and proposed scenarios that sought the adaptive value of dark color not directly in crypsis against visual predators, but indirectly as the by-product of a metabolic change that permitted the caterpillars to feed upon plants loaded with industrial chemicals.

Secondly, Goldschmidt studied the genetics of sex determination and recognized that normal sexuality is a quantitative phenomenon produced by a balance of male and female sex determiners. He developed a series of graded intersexes by altering these balances experimentally. During this decade between 1910 and 1920, most geneticists devoted their attention to the principles of transmission. Goldschmidt, on the other hand, maintained a primary interest in gene function, and his work on intersexes in *Lymantria* led to his most important insight and to the profession that he called physiological genetics. He recognized that genes work by controlling the rates of chemical processes. Normal development requires a proper balance and definite timing of substances; evolutionary change occurs when the timing of development alters. If genes affect timing, then experimental manipulations of temperature and chemical surroundings might induce changes identical to those found in mutants, thus confirming the rate hypothesis. Goldschmidt produced these mutant phenotypes without mutations and christened them phenocopies. We see, in this work, the germs of Goldschmidt's later apostasy on macroevolution, for he recognized that a small genetic change, operating early enough in ontogeny, might engender a cascade of effects producing a large phenotypic "jump" in a single genetic step. In Berkeley, Goldschmidt turned his attention to the physiological genetics of *Drosophila*.

In the midst of this experimental effort, Goldschmidt developed his radical views about macroevolution by a gradual personal ontogeny. He began, he often stated with pride and irony, as a convinced neo-Darwinian before the neo-Darwinian school arose. Why else devote so much time to the study of geographic variation in *Lymantria*?

As a convinced Darwinian I believed geographic races to be incipient species. I hoped to prove by such an analysis the correctness of this idea. I was completely acquainted with what twenty years later was rediscovered as "the new system-

atics," and my convictions, as expressed in 1920 and 1923, were practically the same as those of present-day Neo-Darwinians. [1960, p. 318]

In Goldschmidt's first step to heterodoxy, as mentioned above, he employed "rate genes" from his physiological genetics to explain the rapid origin of discontinuities that could not be bridged by smooth geographic variation:

Such conclusions forced me to think of what addition to Darwinism was needed in order to account for the macroevolutionary processes. The solution was the existence of macromutations, which, in rare cases, could affect early embryonic processes so that through the features of embryonic regulation and integration at once a major step in evolution could be accomplished and fixed under certain conditions. I spoke half jokingly of the hopeful monster in my first publication on the subject, a lecture read by invitation in 1933 at the World's Fair in Chicago. [1960, p. 318]

Had Goldschmidt stopped here, his heresy would have been mild indeed. Darwinians, with their traditional preferences for gradualism and continuity, might not shout hosannas for large phenotypic shifts induced rapidly by small genetic changes that affect early development; but nothing in Darwinian theory precludes such events, for the underlying continuity of small genetic changes remains. But Goldschmidt accelerated, shifted gears, and finally proposed that these abrupt macroevolutionary changes are products of a genetic event different in kind from the micromutations underlying geographic variation—the systemic mutation, or chromosomal repatterning:

I derived the hypothesis that in addition to small or large mutations of genic loci, there exists a completely different type of mutation. I called this "systemic mutation," meaning that a reshuffling or scrambling of the intimate chromosomal architecture, which might occur rarely by chance, will act as a macromutational agent. This means that it will produce, suddenly, a huge effect upon a series of developmental processes leading at once to a new and stable form, widely diverging from the former. [1952, p. 96]

Finally, Goldschmidt came to deny the existence of the "corpuscular gene" altogether (1955) and to view all genetic changes as alterations in pattern. (In this system, "micromutations" became small and localized changes in pattern.)

Goldschmidt had made a clean and complete break between micro- and macroevolution, thus challenging the most important premises of the modern synthesis—continuity and extrapolation—and justifiably earning the enmity of a growing orthodoxy. *The Material Basis of Evolution* is the major work of his full-fledged heresy.

## II. A SELECTED PRÉCIS OF *THE MATERIAL BASIS OF EVOLUTION*

MANY of the great twentieth-century books in evolutionary theory have been exhaustive general summaries of entire fields (see Mayr, 1963 for the best example). Goldschmidt's book has a similar outward appearance; it ranges widely among topics and examples. But *The Material Basis of Evolution* is a work of different form: it is a long, partisan argument—sometimes repetitive, sometimes inconsistent—for a definite view of evolutionary processes.

Goldschmidt did not invent the words micro- and macroevolution, but he did popularize them. By microevolution, he referred to changes within local populations and geographic variation—in short, to all evolutionary events occurring within species. Macroevolution designates the origin of species and higher taxa. (Goldschmidt recognized, of course, that higher taxa must begin as new species, but he believed that the morphological jumps accompanying some events of speciation are so profound that descendant species must be designated as new higher taxa from their inception.)

For most evolutionists, this contrast between micro- and macroevolution can only be intergrading and indistinct because geographic variation, by intensification, leads to the origin of new species. But not for Goldschmidt. Viewing the two phenomena as products of distinct genetic mechanisms, he envisioned an absolute break between geographic variation and speciation. If continuity from micro- to macroevolution, with unity of genetic mechanisms throughout, is the primary belief of neo-Darwinism (as I believe it is; see quotes of Mayr and Dobzhansky on p. xiv), then no claim could be more unorthodox.

Goldschmidt had rekindled an issue that extended back to the earliest days of evolutionary theory. After all, Lamarck had contrasted



local adaptation, induced by "l'influence des circonstances," with progress up life's ladder, caused by "the force that tends, incessantly, to complicate organization." And Chambers, author of the anonymous *Vestiges*, had separated diversification within type from transition between types as products of different mechanisms of change. In an important sense, Darwin's greatest achievement was not merely to support evolution (as these worthy gentlemen had done before him), but to propose continuity between local changes that could be observed and made the object of controlled experiment and large-scale evolutionary changes that could not be seen directly. And now Goldschmidt, albeit in different guise, was resuscitating the old dichotomy just when modern Darwinians thought they had finally buried it for good.

The "long argument" of *The Material Basis of Evolution* can be briefly summarized:

1. Microevolution is all that Darwinians say it is: pervasive, adaptive, and integral to the success and spread of species.

2. Microevolution does not lead, by extension, to the origin of species. True species are separated by "bridgeless gaps." Microevolutionary change leads local populations into "diversified blind alleys."

3. New species arise by macromutation, not by the "accumulation of micromutations." The genetics of macromutation are different in kind from the point mutations underlying microevolutionary change. These "systemic mutations" involve fundamental repatterning of chromosomes. (Goldschmidt also attributes many abrupt shifts of phenotype to small genetic changes affecting developmental rates early in ontogeny; I shall discuss the potential inconsistency between systemic mutation and these alterations of rate below.)

4. The nature of developmental programs, with their alternate (and often discontinuous) channels of phenotypic expression and their regulative properties that direct major alterations into viable pathways, permits macromutation to be effective in the saltational genesis of higher taxa. (These arguments, the bulk of the book, have been generally ignored. I believe that they embody the part of Goldschmidt's argument with abiding value. They also counteract the caricatured dismissals of Goldschmidt's views and render them interesting and coherent, even if unacceptable today. In particular, they explain why monsters may be

hopeful and biologically well-functioning, and why macromutants may spread within local populations, even while breeding with conspecifics of normal phenotype.)

Goldschmidt's chosen title, which strikes so many people as peculiar, accentuates the differences between his view and the tendencies of Darwinian argument. Just what does he mean by the *material* basis of evolution; could it be nonmaterial? Goldschmidt wished to focus on the constraints and opportunities provided by inherited genetics and development. "A change in the hereditary type can only occur within the possibilities and limitations set by the normal process of control of development" (p. 1). This theme, though unavoidably part of any evolutionary theory, has always been underplayed by strict Darwinians because a purely continuationist and adaptationist perspective deemphasizes the "internal" contribution of organisms to their own future change. If evolution is gradual and continuous, moving in any direction dictated by selective pressures of a changing environment, then developmental constraints play little role except as hindrances to be overcome by selection or as generators of nonadaptive and unimportant by-products of primary events. But, in Goldschmidt's view, changes are abrupt and not directly superintended by environment (though environment may reject them by conventional selection). The direction and extent of these changes are set, limited, and facilitated by inherited developmental pathways—the material basis of evolution:

What I propose to do is to inquire into the type of hereditary differences which might possibly be used in evolution to produce the great differences between groups, and the title of this book, accordingly, ought to be something like: The genetical and developmental potentialities of the organism which nature may use as materials with which to accomplish evolution. [p. 3]

Goldschmidt divided his book into two equal parts, labelled microevolution and macroevolution. The theme of the first half is ironic: although microevolution is all that Darwinians say, it has nothing whatever to do with the origin of new species. A study of this section immediately refutes one of the most common caricatures invented to refute Goldschmidt: that he was an unflinching typologist, a great "lab man" perhaps, but lacking the naturalist's feel for continuous variation.

Goldschmidt was always a naturalist first, a man who did as much work as anyone on geographic variation in the field. As Darwin used pigeons, so Goldschmidt invoked his own work in collecting natural populations of *Lymantria* throughout the world, recording the continuity and adaptive value of their variations, and bringing them to the laboratory to raise different races in controlled conditions for assessing the genetic basis of adaptation. We may not accept Goldschmidt's views about the restricted role of geographic variation in evolution, but they did not arise from ignorance of—but rather from immersion in—natural examples.

Goldschmidt begins by discussing single micromutants and their evolutionary effect, focusing upon industrial melanism in his beloved moths. He then moves to "local polymorphism"—the random and small-scale variation (as in breeds of domestic dogs, for example) that constitutes little more than noise at the larger and more important scale of adaptive geographic variation in *rassenkreise*.

The bulk of the first part, focusing upon his own work with *Lymantria*, discusses large-scale geographic variation in widespread species and the general concept of *rassenkreis*, or "circle of races." (This concept has been widely misunderstood by English-speaking evolutionists who have translated the word literally and then used it for a different concept to which the literal meaning seems to apply. In German, a "Kreis" need not refer to a literal, geometric circle, but to any collection of related elements, as in our English "circle of friends." Thus, *rassenkreis* is merely another name for a polytypic species, and that is all. It does not refer to a linear, spatial chain of races, whose adjacent members can interbreed and whose endpoints cannot, though this mistaken attribution is still common in the literature.)

Providing a foretaste of later arguments, Goldschmidt begins by stating Darwin's view that the subspecies of *rassenkreise* are incipient species and by announcing his later appraisal:

The taxonomists who worked upon these problems . . . have come to the conclusion that the geographic races are incipient species, that the formation of subspecies within a species over its geographic range (the *rassenkreis*) is the first and typical, even obligatory, step in the evolution of new species and

higher categories. There is no doubt that such a view is very attractive at first sight. . . . We shall begin our discussion with the facts pertaining to the rassenkreis as such and their analysis, and shall only proceed afterwards to the decisive point; i.e., whether this type of microevolution can lead beyond the confines of the species. [p. 30]

Goldschmidt's discussion of rassenkreise focuses upon the twin Darwinian themes of continuity and adaptive value. He regards clines that correlate with graded environments as the best demonstration of adaptation and cites several examples from *Lymantria*, primarily involving the timing of larval life (shorter in regions with cold winters or hot and dry climates). "It is just this set of facts by which it could be demonstrated that the seriation parallels climatic series in nature and by which it could be proven that the genetic differences are actually adaptations of the life cycle of the animal to the seasonal cycle in nature" (p. 60). Goldschmidt then extends the range of adaptation by emphasizing how many features of morphology (larval size, for example) are correlated with the physiological bases of environmental advantage (length of larval life, for example). "These examples demonstrate that what apparently is non-adaptational may turn out to be strictly adaptational if only the proper environmental factor and the proper physiological process can be located. Therefore I am inclined to consider all subspecific characters which vary in a cline parallel to a geographical, climatological, or other environmental cline . . . as, at least indirectly, adaptational" (p. 78). He refutes nonselectionist explanations of clines and rejects Lamarckian, while strongly supporting Darwinian, explanations for the "parallelism of subspecific clines" encountered in the ecogeographic rules of Bergmann and Allen.

He then discusses the genetic basis of geographic variation and defends the accumulation of small micromutations as its Darwinian source:

The decisive differences, which must have arisen by mutation, are based on groups of extremely small but additive deviations, as revealed by multiple-factor or multiple-allelic differences. These differences accumulate, beginning with differences between colonies of such a minor order that they can hardly be described, though each investigator knows them, and aggregating into the easily distinguishable quantitative differences separating actual subspecies. The

genetic picture, *within* the species, then agrees with Darwin's ideas. [p. 101, Goldschmidt's italics]

I have emphasized the sphere of Goldschmidt's Darwinism and quoted him at length because I wanted to illustrate that his apostasy at higher levels did not arise from an ignorance of Darwinian themes, but from a careful consideration of them and their defense at a level that seemed to him appropriate. But now the argument shifts.

In the next section, on "limiting features of subspecific variation," Goldschmidt asks whether extreme members of rassenkreise approach the status of separate species. In an argument that I regard as often forced or inconsistent (see next section), he argues that neither facts of fertility nor isolation lead to the belief that extreme subspecies can become separate species. He admits that extreme subspecies of a rassenkreis may exhibit lowered fertility, but argues that the causes of their partial incompatibility are not the stuff of which true species are made. He argues that many extreme subspecies (or very closely related sympatric populations) can be induced to produce fertile offspring in the laboratory even if they do not do so in nature (thus brushing by the fact that populations who don't, even if they can in artificial circumstances, are still reproductively isolated). He allows that isolation may induce less orderly and adaptive variation than that displayed by continuous clines, and he admits that isolation may accentuate the amount of variation; but "there is no reason, at least as far as the factual material goes, to suppose that isolation makes subspecies develop into species. . . . Isolation or no isolation, the subspecies are diversifications within the species, but there is no reason to regard them as incipient species" (p. 136).

Goldschmidt ends this section by reemphasizing that Darwinism "works perfectly within the limits of the species" (p. 139) and by questioning the value of population genetics not on any mathematical basis, but on the falsity of its Darwinian premise:

The most brilliant mathematical treatment is in vain if the biological rating of the material is not correct. I am of the opinion that this criticism applies also to the mathematical study of evolution. This study takes it for granted that evolution proceeds by slow accumulation of micromutations through selection,

and that the rate of mutation of evolutionary importance is comparable to that of laboratory mutations, which latter are certainly a motley mixture of different processes of dubious evolutionary significance. If, however, evolution does not proceed according to the neo-Darwinian scheme, its mathematical study turns out to be based on wrong premises. [pp. 137–38]

In his final section on “the species,” Goldschmidt argues for “bridgeless gaps” between true species. Microevolution works down by “diversifying the primary form either by adapting the species genetically to diverse conditions of the environment . . . or by a diversification which is more haphazard and nonadaptational. . . . In all cases the diversification could be subdivided almost without limit down to differences between individual colonies” (p. 139). But the primary forms themselves—the species—must arise all at once, for they are separated by bridgeless gaps:

If subspecies are considered to be incipient species which only need isolation to become species, such a merging of one rassenkreis into another must be observable. . . . If, however, subspecies are nothing but an intraspecific diversification which adapts the species, at least in the majority of cases, to definite conditions within its area of distribution, the limit between two species or rassenkreise ought to be in the nature of a hiatus, an unbridged cleft. . . . Most of these species are, as every earnest inquirer will find, in their natural areas of distribution rather circumscribed products, which do not live in any extensive connubium with congeners of other species. The bridgeless gaps . . . remain to be explained. [pp. 142–43]

Species, Goldschmidt argues, are separated by genetic differences distinct in kind from the accumulated micromutations that produce rassenkreise; they “turn out to involve a chromosomal reorganization” (p. 181). Moreover, “species differences are differences of the whole developmental pattern” (p. 180). New species are fundamentally different animals, not extremes of an intergrading series. Thus, Goldschmidt ends the first part of his book with a paragraph in italics:

Microevolution by accumulation of micromutations—we may also say neo-Darwinian evolution—is a process which leads to diversification strictly within the species, usually, if not exclusively for the sake of adaptation. . . . Subspecies are actually, therefore, neither incipient species nor models for the

origin of species. They are more or less diversified blind alleys within the species. The decisive step in evolution, the first step toward macroevolution, the step from one species to another, requires another evolutionary method than that of sheer accumulation of micromutations. [p. 183]

In the second part, entitled "macroevolution," Goldschmidt searches for this "other evolutionary method" behind the origin of species and higher taxa. This part contains two rather different discussions; the first (pp. 184–250), shorter and more controversial, on systemic mutation and the nonexistence of "corpuscular genes"; the second (pp. 250–396), more extended and full of holistic insight about the nature of integrated organisms, on the constraints and opportunities of developmental systems and the potential macroevolutionary result of mutations affecting early development.

Goldschmidt centered the first discussion upon a pet theme—the nonexistence of corpuscular genes—that occupied more and more of his time and rendered him more and more controversial as the years wore on; (his last book, *Theoretical Genetics* (1955), contains his most developed and extreme statements). The progression was, perhaps, inevitable, but it led Goldschmidt so far beyond the pale for many colleagues that his points of value, and the real problems that elicited his novel solutions, often sank from sight.

He began with the search for a macroevolutionary mechanism other than accumulation of micromutations. Since inversions, translocations, and other chromosomal changes can exert a marked effect upon phenotypes in the absence of any alteration within genes, point mutations cannot be the only source of evolution. "In these cases there is no indication that anything has changed but the serial order of the constituent parts of the chromosome" (p. 188). If new species represent fundamentally new developmental programs and if individual point mutations exert local and minor effects (except in cases of massive pleiotropy or mutations affecting early development), then perhaps the "different" genetics behind speciation involves a fundamental reordering of chromosomal pattern. In such a mechanism evolution would find a device for the rapid and wholesale transformation that accompanies speciation. Goldschmidt named these hypothetical changes of general chromosomal patterns "systemic mutations."

For a long time I have been convinced that macroevolution must proceed by a different genetic method. . . . A pattern change in the chromosomes, completely independent of gene mutations, nay, even of the concept of the gene, will furnish this new method of macroevolution. . . . So-called gene mutation and recombination within an interbreeding population may lead to a kaleidoscopic diversification within the species, which may find expression in the production of subspecific categories. . . . But all this happens within an identical general genetical pattern which may also be called a single reaction system. The change from species to species is not a change involving more and more additional atomistic changes, but a complete change of the primary pattern or reaction system into a new one, which afterwards may again produce intra-specific variation by micromutation. One might call this different type of genetic change a *systemic mutation*, though this does not have to occur in one step. . . . Whatever genes or gene mutations might be, they do not enter this picture at all. Only the arrangement of the serial chemical constituents of the chromosome into a new, spatially different order; i.e., a new chromosomal pattern, is involved. [pp. 205–06]

With systemic mutation, Goldschmidt felt that he had escaped “the dead end reached by neo-Darwinian theory” (p. 203). “The systemic pattern mutation—as opposed to gene mutation—appears to be the major genetic process leading to macroevolution; i.e., evolution beyond the blind alleys of microevolution” (p. 245).

But Goldschmidt went further. We have definite physical evidence for the causes of repatterning, but what do we know of so-called gene mutation beyond the fact of localization on chromosomes? This localization does not imply that the gene is a physical “corpuscular entity.” Why have two parallel systems—chromosomal repatterning and gene mutation—one that we understand in physical terms and one that merely exists as a name for ignorance? Citing no less an authority than William of Occam, Goldschmidt argues that, in the absence of direct evidence for genes as “things,” we should restrict ourselves to the objects we know and interpret “point mutation” as localized and small-scale pattern change: Why not accept “the viewpoint, which in my opinion is daily becoming more probable, that actually no particulate genes exist, but that all mutations are based on very small pattern changes” (p. 203)? Goldschmidt cites Occam’s motto as the last word in his book: *Frustra fit per plura quod fieri potest per pauciora* (In vain we do with



many things what can be accomplished with fewer). Goldschmidt began by separating change in pattern from mutations in genes and ended by denying genes themselves. Of "the classical atomistic theory of the gene" (p. 209), Goldschmidt wrote: "It is this theory which blocks progress in evolutionary thought. . . . We have already foreshadowed the twilight of the gene" (p. 210).

The second discussion, entitled "evolution and the potentialities of development," is in one sense complementary, but in another curiously contradictory, to the first. It includes two topics: norms of reaction (or "reactivity" in Goldschmidt's phrase) and mutations affecting early development. After writing with such joyous abandon about the twilight of the gene, Goldschmidt brings point mutations right back to develop a different, and more acceptable, theory of macroevolution by small genetic changes that produce marked phenotypic effects by acting upon developmental rates in early ontogeny. (I wonder if Goldschmidt wrote the two parts of his second half at different times, or if he put the entire book together in haste.) Others noted this inconsistency, and Goldschmidt himself commented later (1955, quoted in Frazzetta, 1975, p. 116), "I have been reproached for not having made clear in my book *The Material Basis of Evolution* whether I was speaking of systemic mutation (scrambling of the chromosomal pattern) or of ordinary mutations of a macroevolutionary type, and of being confused myself on what I meant."

The constraints and opportunities of developmental systems is the common theme of this second discussion—and it must be so because Goldschmidt has now dropped wholesale alteration of chromosomal pattern (systemic mutation) for macroevolution by small mutations of large impact. How can ordinary mutations be amplified in their effect to produce major, discontinuous changes in phenotype? Goldschmidt answers that they can only do so by "playing off" the inherited developmental program. If that program is so constructed that small alterations in timing can shift development into radically different, but still viable, channels, then small inputs can generate cascades leading to large effects. In this theme, Goldschmidt's lifetime of work on physiological genetics, rate genes, and reaction velocities achieved its integration with evolutionary theory.

The argument based on norms of reaction invokes the idea that there exists both an enabling and a constraining force and that the interplay of these forces allows "mutations affecting early development" to produce viable and fundamentally altered phenotypes. The multiplicity of developmental pathways permitted by a single genotype defines the enabling force. Often, Goldschmidt demonstrates, discontinuous phenotypic changes of macroevolutionary magnitude can be generated by environmental manipulation of a constant genotype. Phenocopies that mimic or duplicate the effects of gene mutations can be made by perturbing environments of development, often in minor ways. Since these perturbations induce changes in rates, genes themselves must act in similar, quantitative ways. Small doses of hormones may enhance or inhibit metamorphosis and produce the macroevolutionary effect of neoteny in an unaltered genotype. In this case, the potentialities of development are not alternate pathways, but sequential and profound transformations in ontogeny, whose suppression or induction produces a radically altered adult. "In other words," Goldschmidt writes (p. 260), "within a constant genotype the potentialities of individual development may include a range of variation of the same phenotypic order of magnitude which otherwise characterizes large evolutionary steps based upon changes in the genotype. The norm of reaction thus shows what paths are available for changes in the genotype (mutations in the broadest sense) without upsetting normal developmental processes."

The creative constraining force is embodied in the last phrase—"without upsetting normal developmental processes." If shifts to alternate pathways simply discombobulate the system, then all monsters will be hopeless. Many intricately complex systems simply fall apart or change in injurious ways under the impact of perturbations. But organic systems are regulated to accommodate impacts by minimal change and to integrate changes into canalized and viable pathways. Goldschmidt cites a range of phenomena illustrating organic "buffering," from regeneration of amphibian limbs to reaggregation of sponges after dismemberment into cells. Monsters may indeed be hopeful because strongly altered phenotypes will, when regulation is effective, be integrated within still viable developmental systems. (Goldschmidt's

critics often conflated systemic mutation with “hopeful monsters.” But note that Goldschmidt discusses hopeful monsters (pp. 300–93) only under the heading of norms of reaction and mutations affecting early development. The phrase is not pure whimsy or nonsense. Goldschmidt granted hope to his monsters *because* regulation can integrate certain large alterations of phenotype into viable systems of development; moreover, the large alterations themselves are extensions or modifications of inherited developmental channels produced by changes in rates within established systems.)

If such “play” exists within constant genotypes, imagine what mutational change might accomplish. And so Goldschmidt reaches his final topic, “mutations affecting early development.” Goldschmidt, who codified the concept of “rate genes,” had long emphasized the quantitative nature of gene action. “The genetic material controls the velocities of production, and the time of action, of the determining stuffs which control differentiation. The proper timing of these processes is the decisive feature in the general control of development” (p. 263).

If mutations affect the timing of crucial early stages in development, they may initiate a cascade of consequences inherent within the norm of reaction and channeled into viable pathways by organic regulation. “A single mutational step affecting the right process at the right moment can accomplish everything provided that it is able to set in motion the ever-present potentialities of embryonic regulation” (p. 297).

Goldschmidt’s general themes include D’Arcy Thompson’s vision of reducing complex forms to few generating parameters (whose small quantitative alterations, beginning early in growth, can lead to major changes of adult phenotype) and the phenomena of homeosis and rudimentation discussed as small changes that induce large effects by switching an organism into developmental pathways already contained within its genome’s norm of reaction. His specific examples are all of the same form (and not really adequate in missing a crucial step of the usual argument for saltation, as I shall discuss on p. xxxv): phenotypes that arise as teratologies or as products of environmental perturbation within one species have become the normal forms of related species; since these phenotypes can arise (or be experimentally induced) abruptly

in species that do not normally produce them, they probably arose by macromutation in related species defined by their fixation (see pp. 304, 306, 331, 353, 356, 360, and 376). In the moth *Orgyia*, for example, the normal antennae of males are identical with those of aberrant intersexual males in the closely related *Lymantria* (p. 304). The fly *Termitoxenia* "has minute rudimentary wings of a very peculiar type" (p. 333), but they are identical with reduced wings intermediate between halteres and normal wings in two homeotic mutants of *Drosophila*.

Thus, the primary agents of macroevolution may be small mutations acting early and shunted through developmental systems adapted for responding to perturbations by channeling changes into viable alternative pathways:

The physiological balanced system of development is such that in many cases a single upset leads automatically to a whole series of consecutive changes of development in which the ability for embryonic regulation, as well as purely mechanical and topographical moments,\* come into play; there is in addition the shift in proper timing of integrating processes. If the result is not, as it frequently is, a monstrosity incapable of completing development or surviving, a completely new anatomical construction may emerge in one step from such a change. [p. 386]

Constraints of development have their creative side; small mutations may be potent forces for abrupt and extensive change if they can commandeer this creativity by acting early in development and not forcing developmental systems beyond their breaking point. The hopeful monster is a creature bearing such mutations. He, and his cousin (or twin) the systemic mutant, are agents of macroevolution and exterminating angels of the Darwinian hope that all evolution might be rendered as the promoted and accumulated product of small, adaptive changes that we observe in the field or produce by selection in the laboratory.

### III. CRITIQUE AND APPRECIATION

WHATEVER private doubts Goldschmidt may have harbored, his almost overbearing self-confidence permitted no public airing. Of his heterodox \*D'Arcy Thompson's theme.

views, he wrote, "I am certain that in the end I shall turn out to have been right" (1960, p. 307). Although we are now only infinitesimally closer to that end, and although Goldschmidt's star may again be on the rise among evolutionists, I doubt that his major book will ever achieve total approbation. It contains too many inconsistencies and includes at least two poor arguments at crucial points. I do, however, believe that its general vision is uncannily correct (or at least highly fruitful at the moment) in several important areas in which conventional Darwinian theory has become both hidebound and unproductive.

*The Material Basis of Evolution* will always be shrouded in ambiguity, as, I suppose, every irreverent masterpiece must be. I believe that it contains a number of weaknesses gathered under two general headings. I also believe that other aspects of the same headings define its greatest strengths.

The two dubious themes both represent areas in which Goldschmidt had an important insight, but pushed and extended it well beyond the bounds of acceptability. In carrying his campaign against the "corpuscular gene" into the pages of his book, Goldschmidt introduced a red herring (made more offensive by the conscious red flag of his colorful pronouncements) that led people to angry dismissal and to a disregard for his cogent arguments about the integration of developmental and gene function. (This attempted reconstruction of theoretical genetics was, of course, central to Goldschmidt's world view; in this book, however, it played a diversionary role and alienated scores of geneticists who otherwise had no rooted antipathy to his macroevolutionary ideas.)

Goldschmidt's views were not quite as heretical as he made them sound. He did not deny the heuristic value of treating localized modifications of the genome as if they represented the alteration of particles on a string, even if (in his reality) they represented small examples of repatterning—but he didn't bother to place the disclaimer in this book. Later, in 1946, he wrote:

There has been much misunderstanding of our conclusions. There is, of course, no doubt that the chromosome has a serial structure and that localized changes of this structure, the mutant loci, can be located by the cross-over method. There is no doubt either that these localized conditions of change can be handled

descriptively as separate units, the mutant locus or gene, and that for all descriptive purposes the extrapolation can be made that at the normal locus a normal gene exists. Further, there can be no doubt that almost all genetical facts can be described in terms of corpuscular genes, and that a geneticist who is not interested in the question of what a gene is may work successfully all his life without questioning the theory of the corpuscular gene. [Quoted in Dodson, 1960, p. 225]

Not only did he push a good insight too far, but he also brought other important points down with it. By continually conflating the unacceptable systemic mutant (though aspects of this concept have merit too) with the small mutation that has macroevolutionary impact by affecting early development, he led people to dismiss his important material about the potential for macroevolution inherent in constraints and opportunities of developmental systems. The colorful terminology of hopeful monsters also led to easy and unconsidered dismissal, as people falsely linked these putative macroevolutionary agents with rejected systemic mutants, whereas Goldschmidt specifically labelled them ‘hopeful’ because the regulative properties of development might channel small impacts upon early embryology into viable pathways of major phenotypic effect.

As his second dubious theme, Goldschmidt carried a good insight too far by advocating an absolutely clean break in principle and kind between micro- and macroevolution. In numerous haughty phrases about ‘blind alleys,’ ‘dead ends,’ and ‘twilights,’ he argued that microevolution has nothing whatever to do with the origin of species and that a completely different style of genetic change (chromosomal re-patterning versus micromutational accumulation) underlies speciation. Could any statement be more calculated to arouse Darwinian ire?

The current debate about macroevolution (Eldredge and Gould, 1972; Stanley, 1979; Lewin, 1980) indicates strong support for Goldschmidt’s gut feeling that extrapolation of small-scale adaptive change within local populations will not encompass all of evolution. But I doubt that any current critic of the modern synthesis would hold that no species can ever arise by an intensification of geographic variation, that saltation is the major (or only) mode of origin for new species, and (especially)

that microevolution provides no insights, but only diversions and delusions, for our understanding of evolutionary trends and the origin of new *Baupläne*.

Moreover, Goldschmidt supported his concept of an absolute break between levels by two poor arguments at key points. The first occurs in part I, when Goldschmidt must face the intermediary cases that seem to exist in fair abundance between geographic variation and speciation—imperfectly separated local populations with impaired interfertility. By arguing that these extreme members of rassenkreise do not approach species, Goldschmidt engages in an almost frantic special pleading. When he must acknowledge impaired fertility, he argues that it is not of the sort that produces true reproductive isolation in speciation; it is “a more or less freakish type of microevolution of the nature of a blind alley within the confines of a species” (p. 128), he states in one place. When he encounters the intermediate situation of two entities that interbreed in some parts of their range but not in others (see pp. 155–68 on “the border cases”), he proclaims them mere members of a single rassenkreis because the fact that they do in some places reflects their compatibility, while the fact that they don’t in others merely records a current state, not a potential. Here Goldschmidt wins his own argument by definition. He has precluded the very possibility of acknowledging intermediacy by admitting populations to full membership in an ordinary rassenkreis if they interbreed anywhere, and setting them up as separate species if they interbreed nowhere.

The second poor argument pervades part 2, for Goldschmidt fails to invoke the central claim—and still an indispensable one, I think—of the classical argument for saltation. All Goldschmidt’s illustrations of potential saltation involve fixed characters of species that are present as mutants, teratologies, or environmentally induced phenocopies of related species. In other words, he shows that pathways of development *could* permit the expression of these phenotypes in single steps. But *could* isn’t *must*, and the simple fixation in some species of phenotypes that represent deviant pathways of development in related taxa does not establish their saltatory origin. For as Lande (1980) and others have emphasized recently, the accumulation of modifiers can lead to the crossing of phenotypic thresholds under gradual selection.

The classical argument for saltation, on the other hand, requires a claim for the *inviability of conceivable intermediate states*. The fact that a phenotype arises discontinuously as a teratological mutant in one species does not prove that it cannot be built gradually in other circumstances. Interesting claims for phenotypic saltation have always invoked the inconceivability of intermediary stages in an evolutionary sequence—as in the torsion of snails, Frazzetta's snakes with a split maxillary (1970), and Long's rodents with inverted cheek pouches (1976). Mivart's old argument (1871) about the inviability of "incipient stages of useful structures" seems as sound as ever, and Goldschmidt fails to use it.

The strengths of Goldschmidt's argument, and the power of his vision, also invoke the same two themes, but divested this time of Goldschmidt's extended claims for them. It must be said, first of all, that many of Goldschmidt's points are not nearly so extreme or unthinking as the usual caricatures depict them. He did not argue that all chromosomal repatterning between species must arise in a single step. Rather—and he says so repeatedly, not merely as a disclaimer in one hidden footnote—he imagines that much repatterning occurs gradually and sequentially with no (or minor) outward effect upon phenotypes. The systemic mutant is the step, usually a large one to be sure, that provokes the crossing of a phenotypic threshold. "This new genetic system, which may evolve by successive steps of repatterning until a threshold for changed action is reached, produces a change in development which is termed a systemic mutation" (p. 396). Moreover, he did not ignore, as many critics have charged, the problem that hopeful monsters must spread through populations by interbreeding with individuals of normal phenotype. In arguments still invoked by modern models of chromosomal speciation (White, 1978; Bush, 1975), Goldschmidt (p. 207) specified the conditions of inbreeding and lack of strong selection against heterozygotes that would permit the phenotypes of hopeful monsters to spread and reach fixation. Finally, since the hopeful monster is not a phenotypic absurdity reflecting a fundamentally altered genotype, but the product of small genetic changes regulated by inherited developmental pathways into viable phenotypic channels, it is not the deviant "basket case" that any "right thinking" normal form



would reject, or that would invariably produce even more bizarre heterozygote offspring.

If I may epitomize the first theme as “the material basis of macroevolution” and the second as “hierarchical levels of evolution,” we may begin to assess the strengths of Goldschmidt’s vision. For the first, Goldschmidt’s denial of the corpuscular gene may be unacceptable today,\* but the problems in conventional thinking that led him to propose it remain acute. As a man trained in classical morphology and embryology, Goldschmidt developed a professional sense that animals must be viewed as integrated wholes and that our organic world of divergent *Baupläne* cannot be rendered by models of strict, gradual continuity in transformation. As a mechanist at heart (see p. 398), he groped and struggled for a holistic but material concept of the genetic basis for such integration (see p. 218).

The systemic mutant may represent a misguided attempt, but the insight that inspired it has fundamental validity. Under strict Darwinism, with its emphasis on adaptive, gradual change guided by natural selection, organisms move where selective pressures push them. In Galton’s metaphor (see Gould, 1980, pp. 128–29), organisms are spheres pushed by the pool cue of natural selection along preferred paths constructed by environments (for the table is not smooth). Accumulated micro-mutation becomes a viable mechanism for all evolutionary change. But if organisms are polyhedrons, then they “push back” and resist change, can only alter in certain directions, and flip from one stable system to another when they do change. Natural selection may still be the only pool cue, but the “internal” factors of organic integration constrain and direct the possible paths of pushing. The polyhedron may slide on its current facet in adapting to local environments by micromutation, but the flip from facet to facet, or macroevolution, may require other styles of genetic change.

Constraints of developmental programs define the facets of Galton’s polyhedron and suggest that flips and slides—or macro- and mi-

\*The Watson-Crick model in its original form demolished Goldschmidt, but part of his claim may hold in our modern world of split and overlapping genes. Still, history of science must reject the anachronistic method of evaluating people according to the number of times they are vindicated by good and unanticipated later fortune.

croevolution—may not represent a pure continuum. Most of Goldschmidt's book discusses these developmental constraints and opportunities. His vision of a difference between macro- and microevolution is rooted in this theme that got lost in the strict Darwinian shuffle.

We do not now accept Goldschmidt's notion of a strict separation between the genetics of slides and flips. Galton's polyhedron implies the theme of developmental constraints, but does not require a different genetics for flips—since ordinary mutations can induce flips by exciting developmental switches, inducing a movement across thresholds, or acting early in development with cascading consequences. (Goldschmidt recognized all this, but submerged it in his later enthusiasm for systemic mutation.) Still, even the idea of different genetic styles has caught on again, though not in Goldschmidt's extreme form: witness Carson's open and closed systems (1975), the current emphasis on structural vs. regulatory genes (King and Wilson, 1975; Wilson et al., 1975), renewed emphasis upon rapid chromosomal speciation vs. micromutational change within species (White, 1978), and awakening interest in evolutionary aspects of development and such classic heterochronic phenomena as neoteny (Gould, 1977b; Alberch et al., 1979, the Dahlem conference on development and evolution held in Berlin, May, 1981).

We will not return to Goldschmidt's extreme view that all speciation is different in genetic kind from microevolution; classical Darwinian continuity works in many cases, and many species are separated by relatively minor genic differences. But the origin of new *Baupläne* requires the reorganization of developmental systems, the flips between facets that Darwinians deemphasized and Goldschmidt knew were important. Goldschmidt's vision was sound, his solution too extreme.

On the second theme of hierarchical levels, Goldschmidt was again too extreme in asserting a "bridgeless gap" (if I may borrow his phrase for another context) between micro- and macroevolution, or geographic variation and speciation. For him, microevolution led only to blind alleys and operated by genetic mechanisms playing no role in speciation; therefore it illuminated nothing of interest about macroevolution. This is a depressing claim indeed, for it renders useless for most purposes the most extensive, and the only directly observable, data that we have about evolution—small-scale change within local populations. Hopes for a unified and general theory of evolution fade.

But the only more depressing claim is unity bought at the high price of ignoring a vital aspect of evolution. I believe that the Darwinian modern synthesis achieved this spurious unity by submerging the concept of levels and opting for an extrapolationist vision that reduces all macroevolution to microevolution extended. Goldschmidt's levels were too distinct and noninteracting; but better this perhaps than no levels at all.

I believe that we may achieve a unified and more general evolutionary theory by combining parts of both visions: the acknowledgment of levels that Goldschmidt demanded, with the Darwinian belief in a unity of processes across these levels. The notion of hierarchy does not demand separate causes, for the same set of causes may produce different results in acting upon the disparate phenomena of distinct levels (Gould, 1980; Eldredge and Cracraft, 1980). Moreover, the levels are not separated by impenetrable barriers, but by interacting boundaries that permit extensive leakage and feedback. Speciation doesn't need a distinct genetics to be meaningfully different from microevolution. If microevolution is fundamentally a process of adaptation, and if reproductive isolation (speciation) is the mere by-product of divergent selection upon two isolated populations, then we have smooth continuity and the modern synthesis is vindicated. But if reproductive isolation often arises first, then speciation merely provides an opportunity for subsequent divergent adaptation—and speciation is not microevolution extended. Speciation becomes a recognizable level of evolution—distinct from adaptive diversification within populations—without requiring a distinct set of genetic causes. Eldredge and Cracraft (1980) write:

Speciation is not, fundamentally, a process of adaptation. Therefore, a theory emphasizing adaptation at its core cannot properly be extrapolated smoothly from the level of microevolution to the level of macroevolution. The conflict with the syntheticist form of macroevolutionary theory, which is a direct, wholesale extrapolation of within-species, microevolutionary theory, arises from the necessary obliteration of species as the basic evolutionary units in the syntheticist view. [p. 326]

Likewise, if most species do not change appreciably following their geologically rapid origin, then large-scale evolutionary trends are not microevolution extended, but must represent a higher-order sorting out

of speciation events themselves (Gould and Eldredge, 1977; Stanley, 1979). But again, we have no separate genetics for evolutionary trends, only a distinct operation of ordinary processes.

In conclusion, I believe that Goldschmidt made a profound (deep, not large) and interesting error in supporting his cogent vision that evolution must be viewed as a hierarchy of levels. As a mechanist, he apparently felt that a claim for difference must be supported by something concrete and material. He understood that micro- and macro-evolution were different, and he therefore sought a distinct genetic basis for the two processes. He proposed one without enduring success.

But I believe that legitimate differences may arise for reasons more abstract than definite mechanistic causes; they may, as in this case, be the product of similar causes working within a set of phenomena arranged as distinct hierarchical levels. If I may make an analogy: the eighteenth-century preformationists postulated a homunculus within the egg because they correctly understood that a formless egg could not unerringly generate the same complex phenotype again and again. In their world, form meant definite concrete structure—and they had no alternative but to postulate actual parts or organs of the next generation within the ovum. Their vision was right; the egg cannot be formless. But we now know that its inherent structure, though still material of course, is a thing more abstract than actual parts—namely, coded instructions for building the parts.

The systemic mutant, the saltatory origin of nearly all new species, may be rejected, but Goldschmidt's vision was sound—and it supplied (or rather resupplied) an essential ingredient that strict Darwinism had expunged from evolutionary theory: the idea that evolution works through a hierarchy of distinct levels with important independent properties (however strong the ties of feedback that Goldschmidt denied). Thus, when I place Goldschmidt in the balance during the year of his own predicted triumph, I find him not victorious, but weighted equally with his self-proclaimed Darwinian opponents. He occupied his pan virtually alone; the other pan contained a cast of thousands. If he has truly balanced them, then he is a weighty man indeed—and his book, which I now invite you to read, will stand as an enduring document, however flawed.

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