Genetics, Paleontology, and Macroevolution

Second Edition

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CAMBRIDGE
UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK
40 West 20th Street, New York, NY 10011-4211, USA
10 Stamford Road, Oakleigh, VIC 3166, Australia
Ruiz de Alarcón 13, 28014, Madrid, Spain
Dock House, The Waterfront, Cape Town 8001, South Africa

http://www.cambridge.org

First published 2001

Printed in the United States of America

Typeface Sabon 10/13 pts. and Franklin Gothic *System* QuarkXPress™ [HT]

A catalog record for this book is available from the British Library

Library of Congress Cataloging-in-Publication Data

Levinton, Jeffrey S.
Genetics, paleontology, and macroevolution / Jeffrey S. Levinton – 2nd ed.
p. cm.
Includes bibliographical references and index.
ISBN 0-521-80317-9 (hbk.) – ISBN 0-521-00550-7 (pbk.)
1. Macroevolution. 2. Genetics. 3. Paleontology. I. Title.
QH366.2 .L47 2000
576.8–dc21 00-052951

ISBN 0 521 80317 9 hardback
ISBN 0 521 00550 7 paperback

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CHAPTER 1

Macroevolution: The Problem and the Field

> The science of life is a superb and dazzlingly lighted hall, which may be reached only by passing through a long and ghastly kitchen.
>
> – Claude Bernard

The Process and the Field of Macroevolution

The return of macroevolution. The field of macroevolution embraces the excitement of seeking an understanding of the breadth of life. We have long desired to know how best to describe the diversity of life's forms and to explain how and why this diversity came to be. No mystery is more intriguing than why we have amoebas and horses, or dandelions and palms. The child's first walk in a meadow, when the child sees flowers and butterflies for the first time, can inspire the same wonder in the most sophisticated biologist walking those same tracks many years later.

We return to this perspective from many quarters of biology and paleontology, after many decades of asking far more restrictive questions that tended to put the process of evolution under a microscope. But now we are stepping back, to take in the broader view. The advances in molecular genetics and developmental biology in recent years have only increased our confidence that the nature of living systems can be understood mechanistically; we can now imagine the possibility of describing the difference between organisms in terms of their genes, gene products, and spatial organization. Such descriptions were beyond our grasp even 10 years ago, but now they are at hand, if still in fragments. The large-scale collation of fossil data and a new understanding of the history of the earth have brought similar increases of confidence among geologists and paleontologists. But we should not overlook some significant changes in fields such as systematics, and the crucial groundwork in population biology established through the advances of the neo-Darwinian movement and the Modern Synthesis. All these place us in position to answer questions that could not even be asked very seriously just a few decades ago.

Definition of the Process of Macroevolution

I define macroevolution to free it from any dependence on specific controversies and, more importantly, to define a field derived from tributaries that have merged from many sources. I define the process of macroevolution to be (Levinton 1983) *the sum of those processes that explain the character-state transitions that diagnose evolutionary differences of major taxonomic rank*. This definition of macroevolution focuses on character-state differences (defined in chapter 2) rather than on jumps, for example, from one taxon to another of great distance. The definition is noncommittal to any particular taxonomic level. I believe that one should eschew definitions of macroevolution such as (1) evolution above the species level (e.g., Eldredge and Cracraft 1980; Stebbins and Ayala 1981) or (2) evolution caused by speciation and selection among species (e.g., Stanley 1979). These definitions presume that major transitions can be analyzed properly only by examining speciation and other processes occurring at the species level and above, and they restrict our views toward alternative hypotheses. Worse than that, these definitions ignore the forest of organismal phenotypic breadth and focus on the trees of just one component of that breadth.

It is not useful to distinguish sharply between microevolution and macroevolution, as I will show in this volume. The taxonomic rank marking any dichotomy between microevolution and macroevolution would depend on the kind of transition being studied. Our impression of "major" degrees of evolutionary change is inherently qualitative and not fixed at any taxonomic rank across all major taxonomic groups. This is apparent when we consider transitions whose importance may rely on many characters, or just one. For the cichlid fishes, a synarthrosis between the lower pharyngeal jaws, a shift of insertion of the fourth levator externus muscles, and the development of synovial joints between the upper pharyngeal jaws and the basicranium may be necessary (but not sufficient) for the morphological diversification of species with differing food collection devices (Liem 1973). On the other hand, the evolution of the mammals involved a large number of integrated physiological and morphological traits, and these were acquired over a long period of time (Kemp 1982). Yet both fall well within the province of macroevolutionary change, because of the potential at least for evolutionary differences spanning large chasms of taxonomic rank.

A second reason for an unrestricted definition of the taxonomic level required to diagnose macroevolutionary change is the variation in higher level taxonomic splitting among major groups (Van Valen 1973a). There is no simple way of drawing an equivalence between families of mammals and mollusks; comparisons of rates of evolution between groups at "comparable" taxonomic levels (e.g., Stanley 1973a) are therefore usually invalid (Levinton 1983; Van Valen 1973a). This point is illustrated well by qualitative studies on hybridity and genetic and phenotypic distance within groups of species of similar taxonomic distance from different phyla. The taxonomist tends to use a qualitative threshold of phenetic difference to define significant evolutionary distance. Thus the ferret and the stoat were placed in different genera, even though they hybridize and produce fertile offspring. Crosses between congeneric species of frogs, however, do not usually produce viable, let alone fertile, offspring.

Perhaps the most unfortunate influence of taxonomic level in restricting our freedom in studying macroevolution is the presumption that crucial characters define specific taxonomic levels. This approach is a major organizing force for systematics today, despite the several decades since the 1970s when cladistic approaches have taken a more pluralistic view of the role of characters in defining evolutionary groups (clades) with common ancestry (see Chapter 2). This permeating influence derives from Cuvier's important notion of subordination of characters, which has survived through the centuries and has led systematists to accept the idea that specific traits define major taxonomic levels. Such thinking leads to unfortunate ideas as the "origin of orders," even though such a taxonomic level has been defined by an arbitrary character type.

The difficulty of gauging macroevolution by taxonomic distance is exacerbated by our current ignorance of the relationship between morphological and genetic divergence among distantly related taxa. By what proportion of the genome do chimpanzees and humans differ? Despite our available estimates of genetic differentiation from sequenced DNA and protein amino acid sequences, allozymes, and karyotypes, we cannot draw a parallel with our knowledge of morphological differences. We are crippled by this ignorance when seeking to judge how "hard" it is for evolutionary transition to take place. What is our standard of difficulty? Genetic? Functional morphological? Developmental? Worse than that, what if interactions among these three occur? At this point, we cannot even easily inject the notion of time in evolution. We may be able to estimate rates of change of a variety of entities (e.g., DNA sequence, body size, and the like), but we have no idea of whether evolution of a complex morphology, such as the rise of mammals, would be astonishing if it happened in one million years, or dizzyingly slow! If the Cambrian Explosion of eumetazoan life occurred in 10 million years, can we say that this was blazing speed or just an ordinary pace? We do not know.

My last justification for a definition based on genetic and phenotypic breadth is that it permits an expansion of previous evolutionary theory to embrace the larger-scale hierarchical processes (see below) and higher-level taxonomic variations previously ignored by the bulk of evolutionary biologists, except in passing or in gratuitous extrapolation from lower taxonomic levels of concern. It is my hope that my definition will eventually not be needed and that "macroevolution" will merge with "microevolution" to become a discipline without a needless dichotomy. The need for a discipline of macroevolution, in my view, is more to sell the expansion of approaches than to necessarily dismiss any previous theory.

The Scope of Macroevolution

The discipline of macroevolution should include those fields that are needed to elucidate the processes involved in accomplishing the change from one taxonomic state to another of significant distance. Macroevolutionary studies all must be organized around several basic questions:

1. How do we establish the phylogenetic relationships among taxa? What is the nature of evolutionary novelty and how do novel characters define the taxa we delineate?

2. How do genetic, developmental, and morphological components channel the course of morphological and genetic evolution?
3. What are the patterns of change and what processes regulate the rate of evolutionary change from one character state to another?
4. What environmental changes regulated the timing of evolutionary radiations and extinctions?
5. What is the role of extinction in the evolutionary potential of newly evolved or surviving groups?
6. What ecological processes regulate morphological and species diversity? To what degree do these effects have evolutionary consequences for any given group?

In the following chapters, I will try to support the following assertions:

1. Systematics is the linchpin of macroevolutionary studies. Without an acceptable network of phylogenetic relationships, it is impossible to investigate the possible paths of major evolutionary change (chapter 2).
2. The nature of evolutionary novelty is probably the most studied and still the most confused element of evolutionary biology. The presence of discontinuity in morphological state can be explained readily using the available data and theory of genetics (chapters 3 and 4). The mechanisms behind the discontinuities are more poorly understood and may relate to a complex interaction between genetic and developmental processes (chapter 4). The epigenetic processes are also subject to genetic control, and thus a spectrum of resultant morphologies can be discontinuous.
3. There is no evidence that morphological evolution is accelerated or associated with speciation, except as an effect of ecologically unique circumstances leading to directional selection. Intraspecific variation during the history of a species is the stuff of interspecific morphological differentiation (chapter 3). When it occurs, intraspecific stasis is affected mainly by gene flow, at a given time and stabilizing selection, over time.
4. Many genetic and epigenetic aspects of development are conserved in evolution. Early development is especially characterized by the use of widely conserved transcription regulators and other regulatory genes. Development, however, is widely labile, as is the order of appearance of expression in developmental genes. Although the expression of developmental genes can be used to trace homologies in closely related forms, developmental genes are a conservative set of elements that can be expressed radically differently in different organisms. Developmental genes are like the musical notes, and the organisms are like rock music, blues, and baroque music. This suggests that there are no profound constraints restricting evolutionary change. Nevertheless, certain early patterns of gene expression were incorporated early in animal evolution and were retained (chapter 5).
5. The nature of form is best understood within the framework of Adolph Seilacher's concept of *Constructional Morphology.* Constructional, Phylogenetic-Developmental, and Functional Morphological factors interact to determine form. This combination tends to make evolutionary pathways often eccentric and not conducive to predictions from "ground up" engineering approaches to optimality. Once historical constraints are recognized, however, optimality approaches can be used to gauge the performance of alternative morphotypes. Indeed, without such an approach, studies of adaptation would be vacuous (chapter 5).

6. Having understood the nature of variation, we find little evidence that the fossil record consists of anything more than the standard variation within populations that can be studied by evolutionary biologists. The process of macroevolution need not invoke paroxysmal change in genetics or morphology. The genetic basis of morphological change, nevertheless, involves a considerable variety of mechanisms. Morphological evolution is not the necessary *consequence* of speciation, though it may be a *cause* of speciation (chapters 3 and 6).
7. Baupläne are evolved piecemeal. Trends leading to complex forms consist of a large number of specific changes acquired throughout the history of the origin of the derived bauplan (chapter 6). Subsequently, however, stability is common. Some trends, such as a general increase in invertebrate predator defense and reductions in variation of morphologies, are probably due, to a degree, to the selective success and extinction of different taxa. Even though speciation rate is not related causally to the origin of the novelty, intertaxon survival, sometimes due to random extinction, has been a crucial determinant of the present and past complexion of the biotic world (chapter 7).
8. Although earth history has had a clear impact on diversification and standing diversity, patterns of taxonomic longevity may have had a distinctly random component. Major differences in biology may have consequences for rates of morphological evolution and speciation, but patterns of distribution within these groups may reflect random appearance–extinction processes (chapter 7).
9. Mass extinctions and radiations are a fact of the fossil record. But both are more easily recognized by changes in the biota than by any recognizable physical events. Means of distinguishing among current hypotheses of regulation of mass extinction and radiation are equivocal at best (chapter 7).
10. The Cambrian Explosion may have involved two phases. Molecular evidence suggests that the major animal groups diverged, perhaps as small-bodied forms or even as ciliated larvalike forms, about 800 to 1,000 million years ago. The sudden appearance of larger skeletonized body fossils and burrows at the beginning of the Cambrian is probably more of an ecologically driven event reflecting the evolution and radiation of crown groups (the modern phyla), rather than a time when the defining traits of the triploblastic metazoa arose, which was probably long over by Cambrian times (chapter 8).

Is macroevolution something apart from microevolution? Richard Goldschmidt instigated the dichotomous approach to macroevolution when he conceived of hopeful monsters that arose by means of speciation events (see below under Hierarchy and Evolutionary Analysis). The modern version of this beginning pictured a decoupling of microevolution from macroevolution (e.g., Stanley 1975), with the species level being the barrier through which any macroevolutionary change must penetrate. Although the specific notion of macromutations is restricted to only a few macroevolutionists (e.g., Gould 1980a), the notion of an evolutionary breakthrough has been associated with speciation events and their frequency. This point of view has made for an unfortunate battle royal, where victory would mean that the opposing group was irrelevant in evolutionary biology. If the microevolutionists win, then there is no such thing as macroevolution. If the macroevolutionists gain favor, then microevolution exists, but it is a minor part of a much larger set of evolutionary constructs. Macroevolutionist claims began by relegating microevolution to the ash heap of history (e.g., Gould 1980a). It made for great sound bites. Subsequent arguments have softened, only emphasizing the expansion of evolutionary theory offered by macroevolutionary considerations (Gould 1982a).

Is the dichotomy very useful? For one group to "win" conveniently ensures the irrelevance of the other to major contributions in evolutionary theory. The focus of this argument is at the speciation threshold of evolution. But I hope that the reader realizes already that there is much more to paleontological and neontological macroevolutionary arguments than the nature of speciation.

The focus of macroevolution. Macroevolution must be a field that embraces the ecological theater, including the range of time scales of the ecologist, to the sweeping historical changes available only to paleontological study. It must include the peculiarities of history, which must have had singular effects on the directions that the composition of the world's biota took (e.g., the splitting of continents, the establishment of land and oceanic isthmuses). It must take the entire network of phylogenetic relationships and superpose a framework of genetic relationships and appearances of character changes. Then the nature of constraint of evolutionary directions and the qualitative transformation of ancestor to descendant over major taxonomic distances must be explained.

The macroevolutionary foci I mention have been largely ignored by the founders of the Modern Synthesis in the past 50 years, who have been devising theories explaining changes in gene frequencies or small-scale evolutionary events, leaving it to someone else to go through the trouble of working in larger time scales and considering the larger historical scale so important to the grand sweep of evolution within sight of the horizon of the paleontologist. The developmental/genetic mechanisms that generate variation (what used to be called physiological genetics) have also been neglected until recently. Population geneticists assume variation but do not study how it is generated nearly as much as they worry about the fate of variation as it is selected, or lost by stochastic processes.

Evolutionary biology and astronomy share the same intellectual problems. Astronomers search the heavens, accumulate logs of stars, analyze various energy spectra, and note motions of bodies in space. A set of physical laws permits interpretations of the present "snapshot of the universe" afforded by the various telescopic techniques available to us. To the degree that the physical laws permit unambiguous interpretations, conclusions can be drawn about the consistency of certain observations with hypotheses. Thus, rapid and cyclical changes in light intensity led to the proof of the reality of pulsars. The large-scale structure of the universe inspired a more historical hypothesis: the big bang origin of the universe.

Does the evolutionary biologist differ very much from this scheme of inference? A set of organisms exists today in a partially measurable state of spatial, morphological, and chemical relationships. We have a set of physical and biological laws that might be used to construct predictions about the outcome of the evolutionary process. But, as we all know, we are not very successful, except at solving problems at small scales. We have plausible explanations for the reason why moths living in industrialized areas are rich in dark pigment, but we don't know whether or why life arose more than once or why some groups became extinct (e.g., the dinosaurs) whereas others managed to survive (e.g., horseshoe crabs). Either our laws are inadequate and we have not described the available evidence properly or no laws can be devised to predict uniquely what should have happened in the history of life. It is the field of macroevolution that should consider such issues. For better or worse, macroevolutionary biology is as much historical as is astronomy, perhaps with looser laws and more diverse objectives. If history is bunk, then macroevolutionary studies are ... well, draw your own conclusions!

Indeed, the most profound problem in the study of evolution is to understand how poorly repeatable historical events (e.g., the trapping of an endemic radiation in a lake that dries up) can be distinguished from lawlike repeatable processes. A law that states *an endemic radiation will become extinct if its structural habitat disappears* has no force because it maps to the singularity of a historical event. It is how we identify such events that matters. What we cannot do is infer that all unexplainable phenomena arise from such unique events. For example, if we postulate natural selection as the shaping force of all morphological structures, it is a cop-out to relegate all unexplainable phenomena as arising from unique historical events.

Hierarchy and evolutionary analysis. We need a context within which to study macroevolution. J. W. Valentine (1968, 1969) first suggested to paleontologists that large-scale evolutionary studies should use a hierarchical framework (e.g., Allen and Starr 1982; Eldredge 1985; Gould 1982a; Salthe 1985; Vrba and Eldredge 1984; Vrba and Gould 1986).

I use *hierarchy* in the sense of a series of nested sets. Higher levels are therefore more inclusive. There are at least two main hierarchies that we must consider: organismic-taxonomic and ecological. The organismic-taxonomic hierarchy can be ordered as:

> {molecules→organelle→cell→tissue→organ→organism→population→species→monophyletic group}

A variant of this hierarchy would include the substitution of *gene→chromosome→organism}* at the lower end. The ecological hierarchy would include: *organism→population→community.* There is no necessary correspondence, however, between levels of the ecological and organismic-taxonomic hierarchies.

Hierarchies can be used either as an epistemological convenience or as a necessary ontological framework for evolutionary thought. Both approaches have been taken in the past, sometimes within the same hierarchy. The standard taxonomic hierarchy is used commonly as a means to examine rates of appearance and extinction. Although different taxonomic levels may change differently over time, such studies do not assign special significance to these levels, as opposed to another set of levels that might also be studied (e.g., studying species, subfamilies, and families, as opposed to species, families, and orders). They are just conveniences whose ascending order of ranking may correlate with differences of response (e.g., Valentine 1969). On the other hand, some regard certain taxonomic levels as fundamental and of ontological significance. Van Valen (1984) sees the family level as a possible unit of adaptation. The species has been claimed to have great importance (Eldredge and Gould 1972). I and most neo-Darwinians see the organism as a fundamental level of the hierarchy, around which all other processes turn. If a given taxonomic level has meaning, it is because the traits of an organism can be traced to this taxonomic level.

If all processes could be studied exclusively with the smallest units of the hierarchy, then two conclusions would readily follow. First, it would not be necessary to study higher levels (i.e., there would be no macroscopic principles). Second, higher levels would be simple sums of the lower ones, with no unique characteristics of their own. The first principle might lead a geneticist to claim that once genes are understood, the entire evolutionary process could be visualized as gene–environment interactions, with no consideration of the properties of cells, organisms, species, or monophyletic groups. The second might lead a paleontologist to argue that patterns of ordinal standing diversity are a direct reflection of species diversity (e.g., Sepkoski 1978).

Taking the hierarchy as given, we can ask the following questions:

1. Can one learn about the higher levels from the lower?
2. Can one understand processes at a given level without resorting to knowledge of other levels?
3. Is there any principle of interaction among levels, such as unidirectional effects exerted by lower levels on higher levels (e.g., those of genes on individual survival) but not the reverse (the effect of survival of individual organisms on the future presence of the gene)?

The first question raises the issue of *reductionism,* a major area of controversy in biology (e.g., Ayala and Dobzhansky 1974; Dawkins 1983; Lewontin 1970; papers in Sober 1984a; Vrba and Eldredge 1984; G. C. Williams 1966, 1985; Wimsatt 1980). It is a common belief that all aspects of biological organization can be explained if the entire genome were sequenced and all the nature and sequence of all proteins were known. In parallel with this argument, several biologists have proposed the gene as the unit of selection and the primary target of understanding. A theory at the level of the gene would then be extrapolated to a theory of the entire genome. In one case (G. C. Williams 1966), the claim was a healthy antidote to the proposal that certain forms of evolution can be explained only at another level of the hierarchy, the population (e.g., Wynne-Edwards 1962).

Although reductionism is often an object of scorn among evolutionary biologists (Wimsatt 1980, Gould 1982b), there seems to be much confusion about definitions. At least three concepts are often freely intermixed. First, reductionism may imply a *reducing science,* which can explain all phenomena in terms of a set of basic laws and units. In this conception of reductionism, biological constructs such as species, cells, and amino acids could be described completely in terms of the language and laws of physics. In evolutionary biology, the language and processes of Mendelian genetics might be substituted by the language and processes of molecular biology (Schaffner 1984). Second, reductionism is often used to imply *atomism,* where all phenomena of a science can be described effectively by laws involving the smallest ontological units. Thus, one might claim that the extinction of the dinosaurs could be explained with knowledge of their nucleotide sequences only. This is the type of reductionism often under attack by macroevolutionists (e.g., Gould 1983b; Vrba and Eldredge 1984). Some (e.g., Wimsatt 1980) attack reductionism as an *impractical attempt to explain phenomena in terms of the smallest ontological units of a science.* This does not imply that it is impossible to do so, only that it is so difficult that higher constructs of a hierarchy are more practical (Nagel 1961). This argument can also be made when, for adequate description of another science the use of a reduced science requires a myriad of complexities in language (e.g., translating Mendelian genetics into molecular genetics [Hull 1974]).

The confusion of these types of reductionism makes debate quite difficult. For example, geneticist Richard Goldschmidt was a reductionist of the reducing science kind (G. E. Allen 1974), even if he is remembered for immortalizing the distinct break of the species level. He believed that chromosomal effects could be reduced to physical laws. Yet, Vrba and Eldredge (1984) placed him on the side of holism. As another example, Wimsatt (1980) criticized the reductionist program, but only because it is impractical to explain many phenomena. From this argument alone, it would not be clear that he would reject the other two types of reductionism, if his objections to workability could be addressed. On the other hand, others find that certain levels have emergent properties, which are irreducible to lower levels of a hierarchy. This opinion, presumably, would also apply if a reducing science were available. In other words, if physics could subsume all biological processes, such individuals would criticize physics if it were atomistic. The attraction of both atomistic and reducing-science reductionism rests in their sweeping approach at explanation. If all scientific explanation could be accomplished with some minimal-level constructs in a single science, then we could achieve an essentially universal language. Keats decried Newton for reducing the poetic elegance of the rainbow to its vulgar prismatic colors. If, however, such a reduction were possible, then grouping concepts such as the rainbow would be superfluous. But can we find such basic elements and a set of relationary laws in science? Do we find emergent properties in higher hierarchical levels that cannot be defined in a language derived from the lower levels?

The dream of reductionism has never been achieved, nor does it seem likely that we will explain all by resorting to explanations using only the basic elements (Popper 1974). As we study different geometries, we learn that the detail lost in switching from Euclidean geometry to topology is superseded by whole new concepts that were never previously visible (Medawar 1974). In Euclidean geometry, shape is invariant and transformations and comparisons are based on angles, numbers of sides, and curvature about foci; topology ignores exact shape but maintains a sense of space and linear order. The transition from the former geometry to the latter involves a restriction of detail, but new concepts emerge. Thus, the notion of conic sections appears in the geometry of projection.

In evolutionary biology, the gene is often employed as the smallest unit of consideration, though recent discoveries of molecular genetics muddle this a bit.

Population genetics usually sees the fate of genes in terms of their contributions to fitness and stochastic processes. Complexities of genetic structure, such as epistasis and linkage, greatly complicate population genetic models. Yet it is a legitimate pursuit to ask how genes survive by virtue of their effects on the phenotype, although one might question the power of both our empirical tools and multilocus models to realistically attack population genetic problems (e.g., Lewontin 1974).

Most evolutionary biologists acknowledge a great deal of complexity in the effects of single genes on the phenotype and emphasize the complex interactions among genes. Most adhere to the principle that the organism, and not the gene, is the unit of selection (e.g., Dobzhansky 1970). The integrity of the organism and its internal interactions have been emphasized by Dobzhansky (1951), Lerner (1954), and Stebbins (1974), among others. Consider Stebbins's statement (1974, p. 302) of the limited evolutionary potential of the incorporation of new alleles:

> Mutations that affect these structures and processes have an adaptive value not in direct connection with genotype–environment interactions, but through their interactions with other genes that contribute to the structures or processes involved. In higher organisms, the majority of genes contribute in one way or another to these conserved structures and processes. The adaptive value, and hence the acceptance or rejection by natural selection of most new mutations, depends not upon direct interactions between these mutations and the external environment, but upon their interaction with other genes, and their contribution to the adaptedness of the whole organism.

This is not an appeal to mysticism. Stebbins merely acknowledged that genes serve to determine a functioning phenotype in a complex manner. Genes may very well be retained by virtue of their contributions to fitness, but there is an important hierarchical level, the organism, that also shapes the fabric of genetic organization. The organism is not the simple sum of its parts. It may well be that division of labor in some Hymenoptera serves the purpose of the survival of genes, but the phenomenon of labor division cannot be explained from the genes' mere presence.

The notion of levels is well entrenched within evolutionary biology, but the exact awareness of levels is not always present when evolutionary hypotheses are formulated. The effects of individual genes on fitness can be overshadowed by other processes, which are best considered as interactions of higher levels of the hierarchy with lower levels. Consider the many studies of regional gene frequency clines discovered by students of allozyme polymorphisms over the past few decades. Typically, one samples over a geographic–environmental gradient and finds a spatially progressive change in allele frequency at a locus (e.g., *Adh* for *Drosophila*). The distribution and abundance of the variant alleles have been studied by those interested in the question of natural selection. There is almost universal agreement that if the functional differences among allozymes could be related to fitness, then the problem of geographic variation would be solved. But is this true?

Effects within an evolutionary hierarchical system can be transmitted downward (Campbell 1974). For example, consider a step cline that transects a continent, with allele *a* nearly fixed in the east whereas *b* is fixed in the west. Suppose that a dramatic change in structural habitat (e.g., loss of the species' requisite food plant) drives to extinction the entire western part of the species. Owing to stochastic loss, the small remaining presence of allele *b* in the east fades out. The loss of the allele has nothing to do with effects of the locus on fitness; it is simply a consequence of selection at a higher level of hierarchical organization, the population. In all cases in which geography plays a role in genetic differences in a species, the difference between single gene selection and group selection can be similarly ambiguous (Levins 1970).

The question of considering levels of the hierarchy without resorting to explanations at other levels is of equal importance in evolutionary investigations. This can be as much a practical issue as a philosophical one. In an empirical study of diversity in the fossil record, for example, higher taxonomic levels may be more tractable than lower ones. Valentine (1968) was a pioneer among paleontologists in considering hierarchies from a paleoecological point of view. If hierarchies are "nearly decomposable" (Simon 1962), different taxonomic levels might respond variously to the same environmental processes. But if higher-level constructs are mere aggregates, one might study the abundance of taxonomic families over geological time without needing to count species.

But the response of families to aspects of earth history differ from the response of species. Families are, of course, constructs of species and therefore may have responses that can be predicted from the aggregated species of each family. The family level might, however, correspond ecologically to adaptive zones and therefore have its own unique response (e.g., Simpson 1953, Van Valen 1984). It is crucial in any hierarchical analysis of a system to understand (1) to what degree it is decomposable and (2) if the hierarchy is decomposable, the nature of the differences of response of different hierarchical levels to different processes.

Consider, for example the pattern of first appearances of phyla versus those of families (Valentine 1968). Phyla show a distinct peak in the rate of first appearances early in the Phanerozoic. Families appear and disappear continuously throughout the Phanerozoic. One might argue that phyla represent major turning points in the history of life: As a response to a series of open environments, developments of major evolutionary consequence came first. By contrast, family-level divisions may represent minor evolutionary changes that came and went in response to minor changes in earth and biotic history. Certain measures will have entirely different meanings at different levels of the hierarchy. The measure of individual productivity is fecundity; at the species level, however, speciation rate would be the appropriate measure. *Fecundity* and *speciation* have entirely different meanings, because speciation decouples two entities from further reproductive connection, whereas an organism's offspring would still be part of the same interfertile population unit. *Extinction* also has different meanings. At the organismal level, death does not necessarily entail the loss of given genes from the population; in the case of species extinction, it almost invariably does. At the level of the monophyletic group, entire character complexes will be lost.

Although generalizations about the interactions within hierarchies are difficult to make, certain evolutionary hypotheses are phrased most profitably in terms of a regularity of interaction within a hierarchical framework. Riedl (1978) argued, for example, that an ordering principle of evolution is "burden," which is the effect on the whole organism of a given evolutionary change. He argued that natural selection is a confrontation between the external aspects of the environment with the internal interactions of the organism. Evolution emerges from the continuing interaction between internal organismal organization and the effects of the external environment (Schmalhausen 1949). As such, the nature of internal order (we will not define this precisely for the moment) at a given time in a taxon's history is part of the measure of response to selection. This leads to the following hypothesis. With the evolution of increasing internal order, the functional burden, encumbered by any given response to natural selection, increases and "with this a new lack of freedom called canalization also increases" (Riedl 1978, p. 80). In hierarchical terms, Riedl (1978) argued that as the evolution of increasing internal order (presumably of development) proceeds, any new effect of selection on any part of the system (e.g., gene) will have increasing effects on the entire system (e.g., developing embryo). Thus, he predicted that the tightness of effect from the lower to the upper part of the organismal hierarchy will increase with evolutionary time.

Jacob (1977) has proposed a related hypothesis, based on a presumed hierarchical structure of organization within the living organism. "Highly evolved" organisms are not perfectly evolved machines at all. Rather, the process of evolution acts in the way that an engineer tinkers with an invention while "improving" it. This leads to machines and organisms that have a peculiar set of internal constraints that can be explained only by history. As Darwin (1859) recognized, the process of evolution via natural selection should build up complex and imperfect organisms with limited abilities to deal with environmental change. "Nor ought we to marvel if all the contrivances in nature be not, as far as we can judge, absolutely perfect. The wonder indeed is, on the theory of natural selection, that more cases of the want of absolute perfection have not been observed" (Darwin 1859, p. 472).

Hierarchies are thus the natural framework for the study of the evolutionary process. Having the wrong gene could conceivably extinguish a phylum. Extinguishing a phylum could, by accident, extinguish a gene. The hierarchical approach allows the organization of research programs to tackle such questions that are historical in nature.

In the context of hierarchies, the macroevolutionist critique of Modern Synthesis rests in the belief that selection at the level of organism and levels beneath is inadequate to explain the entirety of evolution. This is predicated on the belief that processes relating to larger groups can result in evolutionary change. The principal example of such a process is the balance of speciation and extinction, which might produce biased morphological change (Eldredge and Gould 1972, Stanley 1975). This claim is not at odds with the presence of selection at lower levels of the hierarchy. Rather, it suggests an expansion of possibilities in the explanation of evolutionary trends. At the least, one can argue intuitively that extinction strongly affects the relative proportion of taxa and, therefore, the spectrum of morphologies. Because habitat destruction is often a major source of extinction, it is not very controversial to claim that extinction would not be tightly linked to individual genes in many cases. What would be controversial is to argue that such processes caused the evolution of complex morphological structures such as the cephalopod eye. Here, neo-

Darwinians would stand firm in ascribing such an evolutionary process to natural selection working on the interactions of genes and the organism.

The Role of Type in Evolutionary Concepts

Typology and evolution. The problem of macroevolution has always been regarded as the problem of the origin and evolution of types and the present gulf between them. A type is a class whose members share a certain set of defining traits. Such a definition implies gaps between types, or at least discrete differences in the sets of traits that define the different types. If you don't believe in types and gaps, then you don't worry much about major evolutionary jumps, but the belief in types, among species or among higher taxonomic constructs (e.g., baupläne) will lead you toward a deep concern about discontinuities in evolution.

We should distinguish among three sorts of typologies that permeate the study of biology:

- *Essentialist type or idealistic type:* The type has a fixed immutable essence. Minor variation is possible within the type.
- *Modality descriptor:* The type is of a modal form, defined by the overall properties of a population. Intermediate stages between the types are possible but uncommon, at least at present.
- *Saltatory type:* The type has a fixed set of properties, but it is changeable into other discrete types only via a saltatory process. Intermediate stages would be claimed not to exist or to ever have existed.

The deep-seated belief in types derives from an *essentialist* philosophy, which views the world as a series of entities defined by their respective essences. The ordering of these entities is usually associated with a teleological view of the universe. In the biological context, species are viewed as constant and immutable. Aristotle thought of natural selection but dismissed it in favor of a world of teleology and types. Certainly the deep-seated belief in essentialism, commonly held by as disparate a set of intellectual luminaries as Aristotle, Bacon, Mill, and Cuvier, would have tended to freeze all scientific notions of the potential mutability of species (see Hull 1973). To Cuvier, for example, species were perfectly adapted to a specific environment. If the environment were eliminated or altered over time, the immutability of the species would ensure its extinction, making transitional changes inconceivable.

The problem of the biological concept of type gains modern relevance through the theory of evolution, particularly that espoused in Darwin's *On the Origin of Species by Means of Natural Selection* (1859). The pre-Darwinian notion of the perfection of design being a manifestation of the work of God accepted the types as perfectly adapted designs. It is in the post-Darwinian morass of species mutability that the essentialist notion of types takes on a nonscientific connotation. Perfection and perfect adaptedness gave way to the "law of the higgledy piggledy," as Herschel called it. Organisms were often out of step with their environment and natural selection culled out less well adapted variants. Successive forms were not necessarily perfect, according to Darwin; they only happened to be the fittest of the lot.

Aside from a decidedly nonteleological abandonment of perfection, Darwin's theory concluded that species were mutable. Darwin's conception of evolution presumed that every pair of ancestral and descendant forms comprised the end towers of a bridge of a (not necessarily evenly) graded series of intermediates spanning the chasm. Gaps between successional fossil forms could be explained by two possible shortcomings of the data of paleontology: (1) the new species arose via a string of intermediates in a small and isolated population not preserved in the fossil record and (2) the series of intermediates could not be preserved owing to frequent gaps in the fossil record. If only the gaps could be filled, then we would find our intermediates. Was Darwin right? We will discuss this issue in chapter 6. Whether right or wrong, Darwin clearly was antitypological.

The transitional period between the dominance by typological idealists such as English morphologist Richard Owen and the new generation of evolutionists led by Darwin and Huxley was a bit more muddled than is generally realized (see discussions in Desmond 1982; Ospovat 1981). Although Owen vigorously opposed the godless role of chance and the purposeless force of natural selection, he nevertheless came to believe in extensive gradual change from a primitive ancestor, all within a general archetype. The archetype, however, contained an essence that was to be revealed among the members by the study of homology. Thus, he saw vertebrate evolution as a gradual process and even managed to find a transitional form, *Archegosaurus,* that obliterated the gap between reptiles and fish. Owen's (1859) reconstruction of the evolution of the Vertebrata even included a concept of branching and was therefore decidedly close in spirit to Darwin's (1859) hypothetical phylogeny diagram and Haeckel's later attempts at phylogenizing in the *Generelle Morphologie* (Bowler 1976).

By contrast, Thomas Huxley, "Darwin's bulldog," held at first to a typological view of species that probably derived from his adherence to Charles Lyell's concept of nonprogression in evolution (Desmond 1982, p. 90). This viewpoint led him to believe, despite evidence to the contrary, in the early Paleozoic origin of mammals, and in *persistence,* a concept that allowed no major progressive evolutionary trends. This latter belief was in conflict with that of Darwin, his idol, who said "I cannot help hoping that you are not quite as right as you seem to be" (quote in Desmond 1982, p. 86). In this context, Huxley's prepublication warning that Darwin's *Origin* was too enthusiastically against saltation seems more derived from confusion and mixed loyalties than prescience. In a way, Huxley's belief in persistence was more inimical to the establishment of evolutionary trends with empirical evidence than was Owen's idealized archetype, within which some evolutionary change was accepted.

An association of phyletic gradualism with nineteenth-century liberalism (Eldredge and Tattersall 1982; Gould and Eldredge 1977) is an oversimplification. One associates a belief in slow progress with this period in history. But Darwin was not part of the mob: He eschewed the notion that evolution was to be understood as progress toward higher forms. Darwin's belief in slow evolution may indeed have derived from the Victorian belief in slow progress, but the notion of continuous gradational transformation was held in many non-Darwinian quarters in the mid-nineteenth century. Owen strongly believed in phyletic gradualism and was clearly associated with the forces of privilege and station. It apparently served his purpose to believe in evolutionary radiation, however, because it weakened the position of the followers of Lamarck (Desmond 1982, p. 69). His notion of transmutation had limits, and they were those that fit safely within a theistic philosophy. Darwin's conception of nature, red in tooth and claw, was, if anything, repugnant to the Victorian zeitgeist.

Huxley spoke clearly for the new emerging class of individuals whose station was to be recognized by their own efforts. Yet, until the late 1860s, he stood intransigently opposed to evolutionary progress while, at the same time, he fought vigorously for the working class and worked actively to help install a new generation of meritocratic professionals. As Ospovat (1981) wisely noted, the notion of phyletic evolution, with an inferred directional series of gradational forms, would have developed even if Darwin's *Origin* had never been published! The notion of gradualism came from the morphological tradition and did not originate with Darwin. Think of Lamarck, whose notion of gradual change and inevitable evolutionary directionality through acquired inheritance might have been the accepted paradigm of evolution had Darwin and Wallace not come along. As Riedl (1978) noted, even Goethe's philosophy, so clearly typological, allowed for extensive variation within the type (see also Sherrington 1949).

Essentialism ends with the rise of population thinking. The history of progress of twentieth-century biology can be broken down into four discrete periods. The terms I use to describe them are used disparately.

Mutationist–biometrician debate. The mutationist-versus-biometrician period covers the first two decades of the twentieth century, contemporary with the rediscovery of Mendelian variation and the early investigation of chromosomes. Two schools of thought were popular. The *biometricians,* led by such luminaries as Pearson, Galton, and Weldon, had by this time developed a battery of statistical techniques to analyze natural variation in populations. In contrast, the rediscovery of Mendelian transmission inspired another school of thought, led by deVries, Bateson, and Morgan (at first), to emphasize the discontinuous mutations found in laboratory experiments. This school saw *mutationism* as the stuff of evolution and rejected natural selection on existing variation (Bateson 1894). The belief in quantum jumps from one type to the next by mutation versus a belief in natural selection on continuous variation was a false dichotomy. The controversy hampered the growth of population genetics for a decade (see Huxley 1940; Provine 1971). The belief in steplike differences between types (mutations) froze our outlook on natural variation. We now appreciate that mutations occur at all levels of variation and that their presence in steplike transitions is far from being incompatible with the theory of natural selection. Mutation is understood as the source of variation on which natural selection can act.

Neo-Darwinian period. Covering the approximate interval 1920 through 1937, the neo-Darwinian period was marked by the survival from the past century of a host of now-defunct hypotheses such as Lamarckism and orthogenesis. But, most importantly, Sewall Wright, J. B. S. Haldane, and R. A. Fisher laid the foundations for genetic analysis of traits and genetic changes in populations. The power of natural selection was discovered, starting from an initial report by Punnett (1915), and a debate arose about the relative importance of stochastic versus deterministic effects in population genetics. All three of the neo-Darwinian triumvirate, however, seem to have believed firmly in the preeminence of natural selection (Mayr 1982a; Provine 1983). A series of intense debates on the role of drift in small populations were extremely important in focusing attention on several empirical systems, such as *Panaxia* and *Cepaea* (Provine 1983).

Modern synthesis. The Modern Synthesis period starts with the publication of Theodosius Dobzhansky's seminal work *Genetics and the Origin of Species* and culminates with the famous conference at Princeton University in 1947 (see Jepsen, Mayr, and Simpson 1949). The theoretical advances made during the neo-Darwinian movement were incorporated into systematics, ecology, and, to a degree, paleontology. Older concepts lingering in evolutionary biology, such as orthogenesis and Lamarckism, were discarded. Along with Dobzhansky, Ernst Mayr, Bernhard Rensch, George Gaylord Simpson, and Ledyard Stebbins were crucial contributors. The period was marked by a harmony never seen before or since. Of course, the neo-Darwinians were still actively contributing to evolutionary theory, and Sewall Wright contributed to the Princeton conference. Ernst Mayr (1982a) has argued that they did not influence the Modern Synthesis, but both Dobzhansky's (1937) and Simpson's (1944) texts show strong influence from theoretical population genetics (e.g., Provine 1983; Laporte 1983).

From the beginning of this period, all architects of the Modern Synthesis followed their neo-Darwinian forebears in believing in the primacy of natural selection in shaping evolution. A few nagging examples of claimed random variation – for example, inversion polymorphisms in *Drosophila* – turned out to be strongly selected (e.g., Dobzhansky 1948a, 1948b). This only strengthened the general feeling for the importance of natural selection. Gould (1983a) argued for a "hardening of the Modern Synthesis" and suggested that factors other than natural selection were actively suppressed. As the founders of the neo-Darwinian movement and its architects all believed in the primacy of natural selection from the beginning, it seems contradictory to conclude that any "hardening" could have taken place (Levinton 1984). Gould saw the 1930s as a time of pluralism; if orthogenesis and Lamarckism were what he had in mind, we could have lived without this pluralism. The further move of the Modern Synthesis toward population thinking and experimental approaches was the healthiest episode in the twentieth-century history of evolutionary biology.

Postsynthesis period. As in any historical period following a major congealing, the postsynthesis period is marked by disarray. At first, the Synthesis came to dominate natural history. But two movements have directed current trends in the study of evolution. Wynne-Edwards's claim (1962) that group behaviors arise from group selection became a major concern. G. C. Williams's (1966) attack on this overall hypothesis attempted to restore the primacy of individual selection and an orientation toward the study of genic level natural selection. This response was contemporary with W. D. Hamilton's explanation of altruism in terms of benefit to the individual and was followed by the sociobiology movement (e.g., E. O. Wilson 1975), which has been the source of intense debate and criticism (Segerstråle 2000). Following the elucidation of the gene-protein specification process, a large degree of genic protein polymorphism was discovered (Harris 1966; Hubby and Lewontin 1966; Lewontin and Hubby 1966). This was surprising to the majority, who, from predictions of theory and experience with laboratory variation, saw gene loci in natural populations as relatively invariant, with rare mutants of low fitness. From this came the neutral theory of evolution, the first credible theory that incorporated stochastic processes to explain variation in living systems (see Kimura 1983). Of course, many selectionist explanations for molecular variation have been tendered as well (see chapter 3), but the issue has not yet been resolved. Newer methods have allowed the investigation of selection at the level of DNA sequences.

The Modern Synthesis, a period during which genetics, systematics, and population genetic theory blended into a supposedly harmonious neo-Darwinian view of evolution (Mayr and Provine 1980), was also a time when typological thinking was under attack. Mayr (1942), in particular, was a great pioneer in exposing the traditional methodologies of systematists as basically typological. He wrote:

> The taxonomist is an orderly person whose task it is to assign every specimen to a definite category (or museum drawer!). This necessary process of pigeon-holing has led to the erroneous belief among nontaxonomists that subspecies are clear-cut units that can be easily separated from one another. [Mayr 1942, p. 106]

and:

> The species has a different significance to the systematist and to the student of evolution. To the systematist it is a practical device designed to reduce the almost endless variety of living beings to a comprehensible system. The species is, to him, merely one member of a hierarchy of systematic categories. [Mayr 1942, p. 113]

Even Darwin, although believing that at least some species were in the process of changing and that certainly all species were mutable, held a rather practical view of delineating species:

> In determining whether a form should be ranked a species or variety, the opinion of naturalists having sound judgement and wide experience seems the only guide to follow. [Darwin 1859, p. 47]

These quotes reflect a traditional reliance of systematists on the presence of types. But it is not always clear whether this reliance stems from essentialism or from a practical attempt to classify the world's creatures. It is doubtful that twentieth-century systematists adhered to an essentialist concept of species. More likely, they incorporated some intuitive notion of statistical recognition among modes between more continuous morphological gradation. In the period preceding the Modern Synthesis, most systematists saw species as distinct and definable by characteristic differences that arose by some sort of nonadaptive process (see Gould 1983a; Provine 1983).

The Modern Synthesis substituted a new concept of species for older concepts. The modern biological species concept (Dobzhansky 1935) defined speciation as a stage in a process "at which the once actually or potentially interbreeding array of forms becomes segregated into two or more separated arrays which are physiologically incapable of interbreeding." Although this concept has been modified and redefined in terms of the fitness of hybrids versus that of intrapopulation crosses, the basic concept has survived and is still widely regarded as a natural definition of species, although the suggested mechanisms of species formation are varied (see chapter 3).

The new definition of *species* has carried with it a more sophisticated concept of type, based on a process that produces modality of form rather than on an inherent and undefinable essence or the expectation of saltation. The biological mechanism of reproductive isolation ensures the possibility that the forms of two daughter species can go their separate ways. It acknowledges a materialistic basis behind the ability of both native peoples and systematists to arrive at nearly the same species divisions. As Dobzhansky claimed:

> ...the living world is not a single array of organisms in which any two variants are connected by an unbroken series of intergrades, but an array of more or less distinctly separate arrays, intermediates between which are absent or at least rare. [Dobzhansky 1937, p. 4]

Dobzhansky's notion of type as modality is committed to the mechanism of speciation through reproductive isolation and certainly eschews the notion of essence. A well-known critique of the reality of the biological species concept (Sokal and Crovello 1970) also avoids the issue of essentialism; it simply attempts to criticize the utility of the Dobzhansky–Mayr biological species concept to practicing systematists and claims the importance of phenetic similarity in systematic work. Typology as essentialism is properly absent from their arguments.

Both Ghiselin (1975) and Hull (1976, 1980) argued that if species are to be treated as classes (e.g., *Homo sapiens*) with a set of members (e.g., Martin Luther), then the class becomes effectively immutable and just as essentialist as pre-Darwinian notions of species or higher taxa. Hull (1976) recommended that a species be regarded as an entity with spatial-temporal and genetic continuity. As such, it effectively became an individual, bearing a proper name – that is, the specific name. The border between one species and another under this approach could be arbitrary, although Hull accepted that mechanisms such as Mayr's (1963) theory of speciation might tend to sharpen the borders between species. This individualistic concept is therefore not essentialist.

The old essentialist notions of type still pervade our thinking. The typological approach, transformed into an evolutionary guise through the late nineteenth century by great morphologists such as Gegenbaur, initiated a research program that accepted the concept of evolution yet stuck closely to an idealistic system. Coleman (1976) noted (p. 172), "Seemingly new organisms could always continue to appear [via evolution] in the world of objective reality, but the idealistically inclined morphologist claimed the power to discern the unvarying form or forms to which these appearances properly belonged." Thus, although evolution was taken to be the grand justification for the study of comparative morphology, a residual belief in typology prevented a study of variation and focused study on homology, with no consideration of process. This led the field of comparative morphology toward academic disaster in the twentieth century and prevented advancement relative to nonessentialist-dominated fields such as population genetics and molecular biology (Coleman 1976). This does not mean, however, that baupläne do not exist – only that a subtle essentialism has inhibited our capacity to study their possible materialistic basis.

An appropriate point of departure for the study of transitions in evolution was succinctly outlined by Dobzhansky. Two groups of organisms in two-dimensional space have a gap between them. Did one give rise to the other? If so, then why is the gap present? Is it hard to traverse? What is the pathway of the traverse? How fast was the change effected? These questions arise and can be approached objectively only when the mutability of the "types" is admitted and evolutionary relationships can be determined. Characters and their mapping on cladograms are the key to avoiding types.

The mind-set of typology is not limited to arguments over taxonomic categories. Even the functional morphologist can be led to types, with intervening gaps where no intermediate is to be found. D'Arcy Wentworth Thompson revealed his prejudice in the following passage from his *On Growth and Form*:

> A "principle of discontinuity," then, is inherent in all our classifications, whether mathematical, physical, or biological, and the infinitude of possible forms, always limited, may be further reduced and discontinuity further revealed. . . . The lines of the spectrum, the size families of crystals, Dalton's atomic law, the chemical elements themselves, all illustrate this principle of discontinuity. In short nature proceeds "from one type to another" among organic as well as inorganic forms; and these types vary according to their own parameters, and are defined by physical-mathematical conditions of possibility. In natural history Cuvier's "types" may not be perfectly chosen nor numerous enough, but "types" they are; and to seek for stepping stones across the gaps is to seek in vain, for ever. [Thompson 1952, p. 1094]

In the passages preceding this quotation, D'Arcy Thompson argued that the nature of growth and function had most probably erased much of the vestiges of morphology that might be used to reconstruct phylogeny. Thompson's views are reminiscent of those of the anti-Darwinian Mivart (1871), who also likened the differences among forms to the laws of crystallization. His typology is clearly quite different from that of the essentialists and quintessentially the opposite of Gegenbaur's. He believed, nevertheless, in some mechanism or axiomatic condition that underlies a typological system. Are the stepping-stones never to be found?

Macroevolution and the Fall of Goldschmidt

Hopeful monsters and hopeless mooting. Studies of macroevolution tend to either idolize or denigrate the role of the geneticist Richard Goldschmidt. I find myself in between the extremes. He is best remembered for *hopeful monsters* (Goldschmidt 1933, 1940), those few monstrosities that he claimed to be the stuff of major species-level saltations in evolution. He relied on hypothetical chromosomal mutations that accumulated cryptically in populations until a threshold was breached, propelling the phenotype across an unbridgeable gap. Most of these new phenotypes were hopeless, but the rare success was the progenitor of a new species. This work has not withstood the test of time and was at variance with the fact and theory contemporary with its proposal and all that we have learned since. But Goldschmidt's work includes a more visionary thread attempting to integrate genetics, development, and evolution, which was largely ignored until the 1990s, despite other standard-bearers for the approach (e.g., Waddington 1957, 1962).

After a long and successful career, Goldschmidt – a Jew – was dismissed from his academic position in Berlin. After leaving Nazi Germany, Goldschmidt came to the United States and settled at the University of California, Berkeley. Among his important works in English are *Physiological Genetics* (1938) and *The Material Basis of Evolution* (1940). The latter brought him into disfavor with his contemporaries, so much so that he wrote a bitter reprise to start his 1945 (a, b) papers on the evolution of Batesian mimicry in butterflies.

Why was Goldschmidt so isolated from the pillars of the neo-Darwinian period and the Modern Synthesis? He proclaimed that "The neo-Darwinian theory of the geneticists is no longer tenable" (Goldschmidt 1940, p. 397). He argued that "there is no such category as incipient species. Species and the higher categories originate in single macroevolutionary steps as completely new genetic systems" (ibid., p. 396). The first part of the book, entitled "Microevolution," described the nature of geographic and within-population variations in a species. The second part denied that this was the stuff of transspecific evolution. His adherence to this strong point of view is exemplified in his endorsement of the contemporary work of the paleontologist Otto Schindewolf (1936), who had proclaimed that the first bird had hatched from a reptile's egg.

Both of Goldschmidt's books displayed a strong empirical approach to the nature of variation and the varied relationship between development and genetics. But his final prescription for solving the mystery of mysteries, as Herschel described the origin of species, was dogmatic and simplistic: saltation. Goldschmidt admired simplicity – "a simplistic attitude is not a flaw but the ideal goal for a theory in science" (Goldschmidt 1940, p. 399).

Despite the apparent simplicity, Goldschmidt's views were based on a false dichotomy between broader-scale chromosomal mutations and point mutations, which were presumed to be the neo-Darwinian basis for evolutionary change. Neo-Darwinians took variation for granted and made no strong distinction between single genes and larger genetic constructs, so long as they obeyed Mendelian rules. Goldschmidt's claims that neo-Darwinians believed solely that races were incipient species are also at variance with the many saltatory mechanisms of speciation that had been previously proposed (see Templeton 1982). In sum, Goldschmidt's characterizations of the neo-Darwinian movement were inaccurate caricatures.

Goldschmidt felt that the population geneticists of the day were too faithful to the notion that genes were independently acting entities. Some discoveries, such as the notion of position effects of genes, strengthened his suspicion of the genic theory. This feeling might have stemmed from his training, which emphasized development and physiological function, as opposed to transmission genetics (G. E. Allen 1974). His interests in physical science might have also given him the standard 1930s philo-