

DESCENDED FROM DARWIN
INSIGHTS INTO THE HISTORY OF
EVOLUTIONARY STUDIES, 1900–1970

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CHAPTER 11

PAPILIO DARDANUS

THE NATURAL ANIMAL FROM THE EXPERIMENTALIST'S POINT OF VIEW

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INTRODUCTION

In 1930, German geneticist Richard Goldschmidt joined four of the most prominent English biologists at a dinner party at London's Athenaeum Club: J. S. Huxley, J. B. S. Haldane, R. A. Fisher, and E. B. Ford. Fifteen years later, in a paper regarding mimicry, genetics, and evolution, Goldschmidt imagined what may have happened if the conversation had turned to mimicry so many years before:

If the conversation and discussion had turned to the topic of mimicry I should probably have stated my views similarly to the contents of the following paper. Had this been the case, it would certainly have been a lively, if not heated discussion, but nevertheless one among friends. In such a spirit the following critical discussion is presented. (Goldschmidt, 1945)

Goldschmidt's paper provoked a vigorous attack from E. B. Ford, who suggested that the debate between micromutation and macromutation might be laid to rest through a detailed genetic analysis of a little known African swallowtail: *Papilio dardanus*.

P. dardanus was converted to a laboratory animal for a brief period. Its value depended upon its natural variability. It was the focus of a specific study to address a specific aspect of evolutionary biology, namely the evolution of defensive mimicry.¹ Scientists hoped that *P. dardanus* would help them determine the nature of genetic change: macromutation versus micromutation. Using *Papilio dardanus* as a lens, in

this chapter I examine the scientific discourse regarding evolutionary gradualism (continuous evolution via micromutation) versus saltationism (discontinuous evolution via macromutation). The central characters of my story are familiar; indeed, several of the major figures in the forging of the evolutionary synthesis play key roles. Also familiar is the topic of debate, namely, evolutionary gradualism versus saltationism. Less familiar (and little known in the history and philosophy of science) is the butterfly *Papilio dardanus*. In reconstructing the path of *P. dardanus* from natural entity to exemplary organism in the laboratory, I argue that certain organisms are so closely linked to the questions they answer that their utility drops once such questions have been answered. “Exemplar” is an apt term for *P. dardanus* in the story that follows.

Recently historians of the life sciences have recognized that we can learn from the organisms that scientists study (just as we can learn from studies of scientists themselves, their institutions, social contexts, and cultural contexts). As study objects, organisms define questions while simultaneously answering them (see Clarke & Fujimura, 1992; Kohler, 1994; Lederman & Burian, 1993; Provine, 1971; Rader, 1998, 2004; Travis, 2006). For the scientist, the organism becomes a tool that he or she uses to learn about the nature of life. The scientist asks, “What can this organism tell me about life? Evolution? Genetics?” As a historian, I see the organism in a very different light. For me, the organism is a lens through which to view the development of scientific ideas. The central question to my mind has to be, “What is the impact of the actual choices of biological material on the content of biological knowledge?” Yet, this question raises the consideration of its inverse: “How has biological knowledge affected the biological material examined by scientists?” As knowledge and the material develop, the answers and the questions can change.

Before launching into the arguments surrounding *Papilio dardanus*, it will be useful to situate this debate in its broader context of the history of evolution and genetics.² This term-laden and concept-laden conflict centered on the rate of variation in evolution. Darwin himself struggled with this problem.³ The issue was whether variation in nature occurred gradually in small discrete steps or whether variation happened suddenly in large leaps. Darwin believed that the latter type of variation (which he called “sports”) was too uncommon to be the mechanism of change on which natural selection operated. Instead, he identified small individual differences as the basis for change in evolution: “This way of looking at natural selection, that is, as operating upon individual differences, fit perfectly with Darwin’s idea of geological change derived from Lyell. With this mechanism evolution was necessarily a gradual and continuous process; yet great changes could be effected given time” (Provine, 1971, pp. 8–9).

Thomas Henry Huxley criticized Darwin for his commitment to the notion, *Natura non facit saltum* (“nature does not make leaps”). The gaps in the geological record prompted Huxley to suggest discontinuous variation (“saltations”) as the material for the action of natural selection. In a similar vein, William Bateson and Hugo DeVries both developed theories of discontinuous evolution. For his evidentiary base, Bateson looked to the expanding literature of evolution. DeVries (having rediscovered Mendel’s principles of genetics) developed his mutation theory to provide a genetic basis for evolution. “Mutation” (as DeVries coined the term) referred to the process by which new species had originated (Mayr, 1980, p. 742). R. A. Fisher (who figures prominently in the debates below) summarized the beliefs of

Bateson, DeVries, and the other geneticists at the turn of the century: “They thought of Mendelism as having dealt a death blow to selection theory, a particulate theory of inheritance implied [to them] a corresponding discontinuity in evolution” (cited in Mayr, 1980, p. 547).

Just after the turn of the century, biology was a discipline divided. This period has been called the “eclipse of Darwinism” (Bowler, 1983). Largent (this volume) has suggested “interphase” as an alternative. On one side, Darwinian naturalists believed that evolution occurred on the basis of discrete, gradual, individual, continuous variations (later, micromutation). On the other, Mendelian geneticists argued that mutation could produce rapid, discontinuous variations (later, macromutation), which would drive evolution. For one group of English lepidopterists and geneticists, an African butterfly named *Papilio dardanus* would serve as a focal point of debate.

Papilio dardanus, along with its polymorphic mimetic forms, provides an interesting point from which to view the development of evolutionary theory. Darwin recognized mimicry as the clearest example of how natural selection operates in nature after he read Henry Walter Bates’s (1862) essay on the theory of mimicry.⁴ Although the species description of *P. dardanus* appeared in 1870, many years passed before all of its forms were identified. Nevertheless, scientists and particularly geneticists recognized the significance of its complex polymorphism to evolutionary theory shortly after its initial discovery. Among biologists, there was a strong sense that a complete analysis of the genetics of *P. dardanus* would enable them to answer evolutionary questions. Moreover, since the debates regarding this butterfly spanned the evolutionary synthesis, a careful analysis of scientific claims should provide insights into how biology changed over the course of the synthesis.

E. B. POULTON AND *PAPILIO DARDANUS*

In 1906, E. B. Poulton (1856–1943) was an Oxford entomologist and one of England’s most prominent Darwinian evolutionists.⁵ He wrote one of the first reviews of the polymorphic mimetic forms within the many subspecies of *P. dardanus*, but the significance of the mimetic forms had been recognized by lepidopterists since 1869, when Roland Trimen published his descriptions of the mimics and their models. In naming one of the female forms of the subspecies *polytrophus* in honor of Trimen, Poulton noted the promise of *P. dardanus* to mimicry studies: “It is one of the most instructive if not actually the most instructive of all the female forms of *dardanus*; and I propose to call it *trimeni*, in honour of the great naturalist who solved the mystery, and laid a firm foundation for all future work upon the most interesting and complex example of mimicry as yet known throughout the world” (Poulton, 1906, p. 284).

Two years earlier, Poulton developed his ideas on speciation in his presidential address to the Entomological Society of London, now the Royal Entomological Society. To the legion stories of Darwiniana, we can now add a measure of Wallaciana. Less than a month before the address Alfred Russel Wallace sent to Poulton a bound volume of important papers regarding mimicry as a Christmas gift (Mallet, 2003). The papers included Bates (1862), Wallace (1865), Trimen (1869) paper on *P. dardanus*, and several of Poulton’s own papers.

Poulton called for genetic evaluation of the various subspecies and female mimetic forms of *P. dardanus*: “It would be of the highest interest to breed any of the sub-species

of *dardanus* through several generations: especially is this desirable in the case of *polytrophus*, which is certain to yield results of the utmost importance from many points of view” (Poulton, 1906, p. 296). Thus, Poulton recognized the potential of *P. dardanus*, but what were his views on the progress of evolution? Having studied Oxford’s extensive butterfly collections, Poulton explained the process of evolution (and mimicry) through the gradual accumulation of small differences (Kimler, 1983, p. 101). In 1908, he challenged opponents of Darwinian gradualism to explain mimicry: “How could a mutation create a painting? Explicitly, how could it draw on the wings of one butterfly the whole complicated and exquisite pattern of a leaf or another butterfly?” (cited in Turner, 1983, p. 133). In responding to this challenge, R. C. Punnett (1915) argued for the power of mutation and utilized *P. dardanus* to suggest that segregation of the polymorphic forms into Mendelian ratios implied that they arose by saltations. R. A. Fisher, E. B. Ford, and G. D. H. Carpenter sharply criticized Punnett’s views. Fisher noted that Mendelian segregation did not necessitate saltations, while Ford and Carpenter argued for evolutionary gradualism.

PUNNETT, MIMETIC BUTTERFLIES, AND SALTATION

In a full-length treatment of mimicry, R. C. Punnett (1875–1967) reviewed the complex polymorphism among the females of *P. dardanus*.⁶ While noting the promise of *P. dardanus* for studies of polymorphism, Punnett was concerned mainly with establishing a plausible mechanism for the development of mimicry in butterflies. To that end, he described the results of an elaborate Mendelian study of *Papilio polytes* (an Asian swallowtail). The study showed that the two mimetic forms of this butterfly segregated according to expected ratios of 3 heterozygous offspring to 1 homozygous. No intermediate forms arose during the study. Thus, each of the two distinct forms appeared to be under the control of separate, simple genetic alleles. Punnett believed that *P. dardanus* would follow the same rules of genetics allowing for a greater degree of complexity: “but the case here is complicated by the greater number of female forms. The data, too, are far more scanty than in the other two cases, but so far as they go there is nothing to preclude an explanation being eventually arrived at on similar lines” (Punnett, 1915, p. 90).

Punnett’s review of the *Papilio polytes* research prompted him to reevaluate the gradualist theory of the evolution of mimicry: “Now the most generally accepted hypothesis as to the formation of these mimetic resemblances supposes that they have been brought about through the gradual operation of natural selection accumulating slight variations” (Punnett, 1915, p. 90). The similarity between the simple Mendelian segregation of the two mimetic forms of *P. polytes* and studies of primulas and sweet peas convinced Punnett that gradual natural selection did not result in the two forms but rather that each form arose through a single mutation at the original locus: “Since the forms of the *polytes* female behave in breeding like the various forms of sweet pea and primula there is every reason to suppose that they arose in the same way, that is to say as sudden sports or mutations and not by the gradual accumulation of slight differences” (Punnett, 1915, pp. 91–92). Although others would apply this theory directly to the study of *P. dardanus*, R. A. Fisher, E. B. Ford, and other evolutionary biologists criticized Punnett for interpreting their empirical observations in a way that supported this saltationist view.

FISHER, FORD, AND CARPENTER: GRADUALISM
AND *PAPILIO DARDANUS*

In 1927, R. A. Fisher (1890–1962) attacked Punnett’s theory of evolutionary saltations in a paper entitled “On Some Objections to Mimicry Theory; Statistical and Genetic.”⁷ E. B. Ford would later call this paper the “true start of the modern evolutionary synthesis” (Ford, 1980, p. 338). After briefly reviewing Punnett’s claims, Fisher described and undermined the central argument: “The core of Punnett’s argument in favour of the production of mimetic forms by saltations lies in the Mendelian behaviour of the polymorphic females, for it is argued that these Mendelian factors must have arisen originally as mutations, and seeing that the different forms demonstrably differ by only single factor differences, these types must have sprung into existence each at a single leap. Convincing as this argument at first seems, we should, nevertheless, at once recognise our folly if we argued that because the sex difference in *Lebistes* is apparently determined by a single factor, therefore a female fish of that genus, with the appropriate adaptations of her sex had arisen by a single saltation from a male of the same species” (Fisher, 1927, p. 274)!

Drawing on examples from research on fish, rats, and butterflies, Fisher showed that while polymorphic forms of species might exhibit Mendelian behavior, this alone did not prove that such forms arose by single saltations. From this review, Fisher concluded that mimetic similarities evolved gradually: “The gradual evolution of such mimetic resemblances is just what we should expect if the modifying factors, which always seem to be available in abundance, were subjected to the selection of birds or other predators” (Fisher, 1927, p. 275).

It was E. B. Ford (1901–1988) who integrated Fisher’s claims for evolutionary gradualism with the genetic evidence given by *P. dardanus*.⁸ In 1933, Ford reviewed the subject of mimicry and its evolution with G. D. H. Carpenter (1882–1953) (Carpenter & Ford, 1933).⁹ In one example after another, *P. dardanus* provided the evidence for the authors’ evolutionary arguments. Carpenter and Ford contradicted Punnett’s notion of saltation without naming him. They noted that “elaborate mimetic adaptations” were controlled by a single gene, which must have appeared spontaneously as a mutation and “consequently it has been argued that the mimetic resemblances which it controls did so too” (Carpenter & Ford, 1933, pp. 106–107). Clearly, this is a reference to Punnett’s saltationist claim. They cited several examples of Mendelian segregation (including the female forms of *P. dardanus*) and asserted their gradualist explanation: “But we are none the less entitled to regard each of them as the product of slow and continuous evolution” (Carpenter & Ford, 1933, p. 107). In an earlier discussion about the shrinking gulf between the “Mutationist and the Darwinian explanations of Mimicry” and the differences between Mendelian and Darwinian variation, Carpenter and Ford cited a comment by Punnett that appeared to support a gradualist model: “An appearance of continuity in variation may be brought about by the interaction of a small number of definite factors upon one another” (Carpenter & Ford, 1933, p. 92). In *P. dardanus* this “continuity of variation” could be observed through extant transitional forms, thereby prompting the authors of *Mimicry* to write: “transitional stages still exist, and instead of being forced to decide what the stages in evolution must have been by study of allied

species we find the whole process exemplified in the flesh by forms living together” (Carpenter & Ford, 1933, p. 50).

Thus, the study of *P. dardanus* was beginning to realize its potential as an important example of the gradual evolution of mimicry. In 1936 and 1937, Ford published papers on the genetics of *P. dardanus* specifically and heredity in Lepidoptera generally. These works served to review the status of mimicry research and to identify areas for further research. In the earlier paper, Ford reviewed the various female forms of *P. dardanus* and their genetic relationships. Where information was lacking, he delineated specific experiments that would provide the necessary data. Although the subject of evolution (whether gradual or otherwise) fell outside of the scope of this paper, Ford laid the foundation for future genetic research on *P. dardanus* including eight discrete issues for consideration:

1. The frequency of multiple pairings in nature must be ascertained.
2. It will be of but little use to breed from captured females of *P. dardanus*.
3. All future work should be conducted on females bred in captivity and known to be mated with a single male only.
4. The same male should, if possible be mated to two or more virgin females of different forms.
5. Attention is drawn to Mr. C. F. M. Swynnerton’s discovery that this species can easily be forced to pair in captivity. This makes it quite possible to conduct work on the lines suggested above.
6. The theory of dominance-modification can be studied to great advantage in *P. dardanus*, by crossing the different subspecies. In this way, the genetic behaviour of given forms of female investigated when crossed with races in which they are rare or absent.
7. A special effort should be made to determine the relation of the mimetic to the male-like females, and of the tailed to the tailless mimics.
8. It should be established if the homozygous dominant class is rare or absent when any of the forms of this species segregate (Ford, 1936, pp. 463–464).

For breeding experiments to be significant, it would be necessary to carefully control the stocks of butterflies. To that end, Ford encouraged future researchers to concentrate their efforts on females bred in captivity. The most valuable data would be produced if virgin females of several forms could be mated with the same male. Ford noted that Swynnerton’s discovery that *P. dardanus* could be forced to mate in captivity facilitated all of these recommendations. The results of this research program would have a direct bearing on evolutionary arguments by providing data in specific areas designated by Ford.

From the specificity of the genetics of *P. dardanus*, Ford turned to the generalities of heredity in the Lepidoptera, offering a full review of the state of research on heredity in butterflies. Ford devoted the conclusion to the forms of *P. dardanus* which “provide by far the most complex example of mimetic polymorphism” (Ford, 1936, p. 495). As in “Genetics of *P. dardanus*,” evolution fell outside the scope of this paper, but Ford recapitulated Fisher’s argument against Punnett’s parallel mutations in model and mimic: “Though the patterns of model and mimic may be extremely alike in their general appearance, they are nearly always very distinct in their detailed

marking, the similar colours seem often to be produced by different pigments or in a different manner, and indeed the corresponding effects are generally attained by surprisingly diverse means” (Ford, 1937, pp. 466–467). Thus, Ford predicted that the mimetic color patterns could be controlled by different genes in different genera and species.

For a general theory of the evolution of mimicry, Ford returned to Fisher’s (1927) claims: “Consequently, when any mutation chances to give a remote resemblance to a more protected species, from which some advantage, however slight, may accrue, the deception will result in a gradual change in the *effects of the gene concerned*” (Ford, 1937, p. 497). A genotypic change through mutation may exhibit phenotypic change in the form of mimetic similarity, and the expression of the gene may change *gradually*. Ford’s argument continued: “But the gene itself is unchanged, and remains as a switch turning on one or another set of characters subject to genotypic variability and, consequently, susceptible of selection” (Ford, 1937, p. 497). Thus, Ford incorporated Mendelian segregation into his model of gradual evolutionary change. In a summary dismissal of Punnett’s theory of parallel mutation, Ford noted that intermediates could be found between alternative mimetic forms controlled by a single gene and that such aberrations were genotypic in nature: “Their existence is by no means in accord with the explanation of mimicry on the theory of parallel mutation. They do, however, represent precisely the type of variation which we are here postulating as providing a basis upon which selection may bring about gradual evolutionary change” (Ford, 1937, p. 497).

Of the scientists considered thus far, only Punnett described the rise of mimetic butterflies by saltationist leaps instead of gradual evolution based on small mutations. Individuals who were studying the genetics of *P. dardanus* (Poulton, Fisher, Carpenter, and Ford), all shared a commitment to evolutionary gradualism. Ford’s program for the analysis of *P. dardanus* promised to provide even more evidence for evolutionary gradualism. To continue, the debate (already dramatically one-sided) desperately needed new input. At the close of *Mimicry*, Carpenter and Ford issued a challenge to opponents to the concept of defensive mimicry: “Those who refuse to accept mimicry as a reality must propound an alternative or more suitable explanation to cover these facts” (Carpenter & Ford, 1933, p. 124). Their challenge received an answer, but not from an opponent to the “reality of mimicry.” Rather, the response came from one of the strongest voices in opposition to evolutionary gradualism.

GOLDSCHMIDT, SALTATION, AND *PAPILIO DARDANUS*

Richard B. Goldschmidt (1878–1958) was a German scientist skilled in zoology, biology, and genetics, who fled to the United States in 1936 to escape persecution by the Nazis.¹⁰ In 1945, he published a lengthy review of the research on the genetics and evolution of mimetic butterflies. Having spent 25 years studying the genetics of industrial melanism in moths, he was especially qualified in genetics, evolution, and Lepidoptera. He knew the English geneticists personally, and his review began with a preface about a dinner party at London’s Athenaeum Club 15 years prior with Huxley, Haldane, Fisher, and Ford (see Introduction). His position clear, Goldschmidt briefly sketched the debate over the evolution of mimicry citing Punnett, Fisher, and Ford as the primary contributors. He next reviewed the “Basic Facts of Mimicry,”

which included ecology, simple and sex-controlled polymorphism, parallel geographic variation, parallel behavior of sexual dimorphism, mimicry rings, variability of mimics, and genetics. *P. dardanus* and Ford's research figured prominently in Goldschmidt's descriptions of polymorphism, geographic variation, variability, and genetics.

Goldschmidt repeatedly noted the importance of Ford's research on *P. dardanus* as in this example from the variability of mimics: "The most important set of data is available for the African *P. dardanus* (fig. 2), data which has been assembled and extended by Ford (1937), who could use the huge material brought together by Poulton as well as that found in the great collections in England" (Goldschmidt, 1945, pp. 152–153). Similarly, Goldschmidt expressed his respect for Ford's mentor Poulton: "I should like to pay tribute to the memory of a great naturalist by mentioning that my interest in the subject [of mimicry] was first roused when, as a young student (in 1901) I had the privilege to listen to a brilliant expose of the subject by Professor Poulton" (Goldschmidt, 1945, pp. 152–153).

Having noted its importance, Goldschmidt methodically reviewed Ford's summary of heredity in the forms of *P. dardanus*. He created a simple table of the regions, subspecies, forms, and models of *P. dardanus* noted by Ford and included drawings of some of the forms. Part of Goldschmidt's compulsion to provide a comprehensive account of Ford's work on *P. dardanus* can be attributed to the recognized value of the work to genetics and evolution, but it also seems likely that Goldschmidt wished to demonstrate his command of the material evidence Ford used to support his claims.

With the basic concepts of mimicry delineated, Goldschmidt examined the history of mimicry and evolution, placing particular emphasis on Ford and *P. dardanus*. He associated Bates, Wallace, Darwin, Muller, Haase, Weismann, Marshall, and Poulton with the discussion of mimicry as exemplary of evolution by selection of small aberrations. His counterpoint to this distinguished assemblage of evolutionists (and Darwinian or neo-Darwinian theory) came from Punnett and his saltation theory, which he described briefly before illustrating Punnett's objections to strict selection.¹¹ To establish the debate as current, Goldschmidt analyzed Fisher and Ford's responses to Punnett. With the exception of a single criticism of Ford's interpretation of a single ratio in his study of intermediate forms, Goldschmidt maintained a tone of balanced detachment throughout his discussion of the two schools of thought. Goldschmidt concluded the historical section of his paper with a summary of the chief arguments used by Fisher and Ford against Punnett's saltation theory:

1. Intrinsic improbability of sudden emergence of the mimetic pattern.
2. Availability of a neo-Darwinian conception of evolution by selection of modifiers (derived from Fisher's theory of origin of dominance).
3. The simple Mendelian basis thus would apply only to a switch reaction.
4. Genetic models for such a situation exist, namely inheritance of sex, of color in hooded rats, and some examples in Lepidoptera.
5. The relative numbers of mimics and models agree with selectionist expectations.
6. These expectations agree with facts indicating a greater variability of mimics where models are rare.
7. Parallel geographic variability is best explained by selection of modifiers.
8. The existence of intermediates is a proof of the presence of many otherwise invisible modifiers.

9. An explanation via parallel mutation in mimic and model is excluded because the similarity is only superficial (e.g., different chemistry of pigments). (Goldschmidt, 1945, pp. 160–161)

It was to these claims that Goldschmidt addressed his discussion and critique. Goldschmidt's extensive introduction with emphases on concepts in mimicry, Ford and *P. dardannus*, and historical background laid the foundation for his discussion, established his familiarity with the subject matter, and most importantly firmly rooted the argument in his own terms.

Despite his lengthy presentation of the neo-Darwinian interpretation of the evolution of mimicry in butterflies, Goldschmidt recognized that Punnett's views were more compatible with his own. His discussion, therefore, raised numerous problems with the gradualist explanation. One difficulty was the value of a small change to a mimic. Goldschmidt criticized Ford's reference to the selective advantage of a remote resemblance:

We must ask how remote the resemblance can be to have selective value. Can we really assume that the birds and monkeys and also mantids are such wonderful observers (or that some very clever ones among them are) to notice a 'remote' resemblance and to be repelled by it? I think that this is asking too much. (Goldschmidt, 1945, p. 162)

Other criticisms addressed *P. dardannus* specifically.

In discussing parallel geographic variation, Goldschmidt cited the example of *P. dardannus* and noted that mimics varied geographically according to their models and that this behavior was assumed to demonstrate the selection of modifiers in the origin of mimetic resemblance. However, there was a lack of genetic data from *P. dardannus* to support this assumption: "Unfortunately, no genetic experiments of crossing geographic races seem available (*except one reported by Ford, in which geographic difference was not represented*)" (Goldschmidt, 1945, p. 212, emphasis added). On a related issue, parallel mutation, Goldschmidt could not understand Ford's belief that a *Papilio* butterfly could not come to mimic a *Danaine* wing pattern through a single mutation (analogous to the mimicry in *P. dardannus* females). To Goldschmidt, the origin of such a pattern was undetermined and thus open to theoretical debate:

In my opinion, the unifactorial difference between one papilionid pattern and another mimetic one has no bearing whatsoever upon the genetic basis of the Danaine pattern. This might have originated in any conceivable way. It might be the product of a slow or a fast evolution, or of direct evolution or one with whatsoever detour; all of which we do not know, as long as it is not possible to analyze this pattern by crossing experiments. (Goldschmidt, 1945, p. 216)

Goldschmidt believed the origin of any pattern in a putative mimetic species to have no bearing on the potential for an existing pattern to mutate into a mimetic form. Nevertheless, he did suggest that crossing experiments could shed light on the problem.

One of Ford's strongest claims for evolutionary gradualism in *P. dardannus* rested on intermediate forms (note his comment above). Goldschmidt attacked this view and attributed the differences to incomplete sex control. Several facts supported this claim, such as the intermediates exhibited both the fluorescent yellow (present only in

P. dardanus males) and the dark pattern associated with mimetic females. This led to Goldschmidt's conclusion: "If one looks upon such facts as a geneticist and especially as a physiological geneticist, i.e., without any reference to theories of evolution, only one interpretation seems possible. The intermediates are the product of incomplete sex control on a genetic basis" (Goldschmidt, 1945, p. 220).

Goldschmidt returned once again to the inability of Fisher and Ford to accept the possibility of the development of a complicated mimetic pattern through a single mutation when he discussed the development of wing pattern. After briefly reviewing the basic wing pattern, Goldschmidt marveled at the number of patterns that could be derived through "splitting, fusion, disappearance, shortening, simplification or complication, and shifting of the main elements" (Goldschmidt, 1945, p. 222). Yet, the female forms of *P. dardanus* appeared to transcend such processes despite Goldschmidt's claim to the contrary: "In the *dardanus* case, the system is rudimentary in the normal form and relatively little changed in the mimetic wings except for a change in general appearance and the fusion of some elements" (Goldschmidt, 1945, p. 222). Finally, Goldschmidt used the analogy of seasonal dimorphism and the patterns of the forms of *P. dardanus* and noted that in principle they were no different.

At the close of his lengthy treatise, Goldschmidt declined to provide a summary and instead referred the reader to the chapter, but he restated his chief claim: "After reporting and discussing the significant facts, we came to the conclusion that Punnett's interpretation of mimetic polymorphism by mutation (saltation) agrees better with the facts than Fisher's neo-Darwinian theory" (Goldschmidt, 1945, p. 228). For Goldschmidt, saltation provided a simpler solution than neo-Darwinian gradualism, but his paper had ramifications beyond this idea. Like Ford, Goldschmidt had identified important areas for further research such as the genetics of similar geographic races. Moreover, the reaction to his assertions would prompt the pursuit of answers to the questions posed by Ford as they contributed to this debate.

FORD'S RESPONSE AND CALL FOR GENETIC ANALYSIS OF *PAPILIO DARDANUS*

Before recounting the response of the neo-Darwinians, it might prove useful to recall Goldschmidt's *Preface* where he envisioned a conversation about mimicry with the assembled scientists. The image of congenial debate within the cozy ambience of a London club contrasts sharply with the tone of Ford's response. After a brief recapitulation of his own and Fisher's original skepticism that mimetic polymorphism could arise through fortuitous mutations in separate species and a review of relevant genetic work (including his 1936 study of *P. dardanus*), Ford noted that Goldschmidt's account contained many errors of both fact and theory. In response to Goldschmidt's doubt in the selective advantage of a slight resemblance, Ford wrote: "The point of view which requires a limen [threshold] of advantage before selection can become operative is, of course, well known to mathematical evolutionists and long ago disproved" (Ford, 1953, p. 67). Moreover, Ford suggested that large mutations generally had a deleterious effect upon the organism: "Consequently, the mutants with big effects, to which Goldschmidt appeals, will generally be unusable" (Ford, 1953, p. 68).

With respect to *P. dardanus*, Ford raised several important problems in Goldschmidt's critique. He refuted Goldschmidt's notion that intermediates were the

product of incomplete sex control on a genetic basis by noting that intermediates of both sexes had appeared in breeding experiments with an intermediate female. More generally, he remarked: "Moreover such variation is well known without any apparent connection with sex" (Ford, 1953, p. 69). Drawing on Carpenter (1946), Ford also criticized Goldschmidt's defense of parallel mutation. Goldschmidt claimed that the models for mimics were generally related: "it does not occur that one female form mimics a *Danaine* and another a poison-eater *Papilio*" (Goldschmidt, quoted in Ford, 1953, p. 70). In considering *P. dardanus*, Ford conceded the absence of "poison eater *Papilios*" in Africa, but, he commented: "while the majority of mimetic females copy Danaidae, one of them, *planemoides* Trim., mimics a member of the Acraeidae; a complete contradiction of Goldschmidt's statement" (Ford, 1953, p. 70). Carpenter, who had originally noted this inconsistency, also objected to Goldschmidt's characterization of wing patterns: "Arguments about mimicry based on the statement that the pattern systems of different families of butterflies are in reality not very different are useless for dealing with a wider aspect of mimicry" (Carpenter, 1946, p. 279).

Ford recognized, however, that he did not have concrete evidence to respond to Goldschmidt's claim that future genetic research would reveal that the differences between geographic races of mimics (and models) will be of a multiple allelic character involving the locus controlling the mimetic pattern. Resolving this issue would become the task of C. A. Clarke and P. M. Sheppard. But how did Goldschmidt respond to Ford's extensive critique of his view? Specifically, he did not. But in his autobiography there is a comment that expressed his convictions regarding his views as expressed in his *Material Basis of Evolution*:

I returned to my heretical views on macroevolution and Neo-Darwinian evolution and tried to prove the necessity of macroevolution via macromutation. I extended my argument especially to the aspect of the organism's ability to change its development in to new directions, and built up a strong argument for my ideas. I certainly had struck a hornet's nest. The Neo-Darwinians reacted savagely. This time I was not only crazy but almost a criminal. There were, of course exceptions, like the deep thinker Sewall Wright, who criticized my work objectively and has recently moved much nearer to my views. And again the number of evolutionists who try at least to find a place for my views in evolutionary thinking is increasing. I am confident that in twenty years my book, which is now ignored, will be given an honorable place in the history of evolutionary thought. (Goldschmidt, 1960, pp. 323–324)

These are hardly the words of a defeated scientist. Despite attacks from all sides, Goldschmidt remained true to his convictions. Even Goldschmidt's prediction proved prophetic when in the 1980s scientists and, to a greater extent, historians of science, began to acknowledge Goldschmidt's central role in the stimulation of debate regarding the evolutionary synthesis.¹²

Literally since Roland Trimen completed the species description of *P. dardanus* and its mimetic forms in 1869, scientists were convinced that it would provide a useful example of mimicry and its evolutionary significance. In supporting that claim, Poulton suggested that experimental breeding of any of the subspecies would prove interesting. He also noted that mutation was unlikely to explain the evolution of mimicry (in *P. dardanus* and other species). Punnett agreed that breeding experiments would prove useful, but he contradicted Poulton by arguing that mutation and Mendelian

segregation offered a simpler explanation for the development of the polymorphic forms. Although Punnett cited research on *P. polytes*, he suggested that his findings were applicable to *P. dardanus* also. Fisher, Carpenter, and Ford all used *P. dardanus* as an exemplar of evolutionary gradualism. Nevertheless, their claims were theoretical rather than empirical. Ford developed a research program based on *P. dardanus* emphasizing specific considerations, as well as the advantages of the butterfly as an experimental organism (particularly that it could be forced to mate). Like his English counterparts, Goldschmidt developed a theoretical argument based in part on *P. dardanus*, but he sided with Punnett in the view that the mimetic forms had arisen through mutation (saltation). Any hope of resolution depended on an infusion of new empirical research (based on Ford's research program).

CLARKE AND SHEPPARD ANALYZE *PAPILIO DARDANUS*

P. M. Sheppard (1921–1976) and C. A. Clarke (1907–2000), two geneticists from the University of Liverpool, determined to collect evidence to distinguish between the theories of evolutionary gradualism and evolutionary saltation.¹³ To accomplish this, they began a systematic evaluation of the genetics of *P. dardanus* following E. B. Ford's program for study. Even before they could begin crossing experiments, they had to remake *P. dardanus* as a laboratory animal. Beginning with wild stock of four forms of the race *P. dardanus cenea* in 1954 (one year following the publication of Ford's critique), Clarke and Sheppard controlled crosses by hand mating a single male with several females. Then they kept the broods from the different females separate. After they tabulated the resulting offspring, they concluded that the data confirmed the view that the difference between two of the mimetic forms (*hippocoonides* and *cenea*) was controlled by a switch mechanism, which reduced the probability of getting intermediate forms (Clarke & Sheppard, 1959, p. 250).

While the purpose of this initial study was to obtain genetic information in preparation for making race crosses, Clarke and Sheppard noted progress toward their ultimate goal for the research: "The *P. dardanus* data do not throw any light on whether the mimicry evolves gradually or whether it arrives at a single step, as suggested by Goldschmidt, for no race crosses have yet been made. However, a cross between the form *hippocoonides* from East Africa which mimics *Amauris niavius dominicanus* with *hippocoon* from the West coast which mimics *Amauris niavius niavius* would give the appropriate information" (Clarke & Sheppard, 1959, p. 251). They also predicted what the results would be according to each of the hypotheses: "On Goldschmidt's view, the two mimics should differ by a pair of allelomorphs, while according to the other hypothesis the difference should be multifactorially controlled" (Clarke & Sheppard, 1959, p. 251). *P. dardanus* had been remade as a laboratory animal and as such Clarke and Sheppard could conduct the breeding experiments that would enable them to test the alternative hypotheses. With the hypotheses and predicted results thus established, the geneticists only needed to make the appropriate crosses and note the results to validate one or the other theory of the evolution of mimicry.

At the end of May in 1959, Clarke and Sheppard submitted three papers to the journal *Heredity*. Each drew on their genetic analysis of *P. dardanus* and each provided decisive empirical evidence for accepting Ford's theory of the gradual evolution of mimicry. Moreover, the papers clarified Ford's theory with theoretical details. In

“The Evolution of Mimicry in the Butterfly *P. dardanus*,” Clarke and Sheppard briefly reviewed the history of the evolution of mimicry from Bates and Darwin to Ford, before reporting the results of crossing the South African *hippocoonides* form with the West African *hippocoon* form. The second generation (F₂) and first backcross¹⁴ to *hippocoonides* did not segregate clearly into the original or first generation forms. In addition, Clarke and Sheppard recorded many grades of intermediates. Furthermore, the characters that distinguished the *hippocoon* and the *hippocoonides* forms segregated and appeared variable in expression. Considering these results, Clarke and Sheppard concluded: “We are therefore led to the conclusion that *hippocoon* and *hippocoonides* do not differ by a pair of allelomorphs but by a minimum of three and probably many more than three loci” (Clarke & Sheppard, 1960b, p. 166).

By crossing individuals of other forms (*cenea*, *trophonius*, *planemoides*, as well as *hippocoon* and *hippocoonides*), Clarke and Sheppard demonstrated that the allelomorphs controlling these forms produced a poorer resemblance to the model when they were crossed with a race that did not possess the particular mimic. They also considered the tailed forms of *P. dardanus*, which occurred in Abyssinia and Madagascar and postulated the evolution of dominance under disruptive selection (an idea they explored in the first paper). But how did these findings relate to the two theories of the evolution of mimicry?

Clarke and Sheppard noted that the genes under their consideration did not produce perfect mimicry, so according to Goldschmidt’s theory an allelomorph associated with mimicry would have to occur in a favorable gene-complex and that selection would have to be very powerful to maintain the mimetic resemblance. Since mimetic forms of *P. dardanus* occurred wherever models occurred commonly, Goldschmidt’s appropriate gene complex must have occurred when a mutant was available in the areas where models were common. Based on their genetic evaluation, Clarke and Sheppard claimed: “anyhow at the present time, such suitable gene complexes do not occur” (Clarke & Sheppard, 1960b, p. 172). They also cited J. V. Z. Brower’s (1958) findings on the advantage of imperfect mimicry to respond to Goldschmidt’s skepticism of such an advantage. In summarizing their analysis, Clarke and Sheppard concluded: “The results support the view that the original mimetic resemblance produced by a new mutant is enhanced by the selection of modifiers and when perfected the pattern is stabilised by selection” (Clarke & Sheppard, 1960b, p. 172). Thus, as both Goldschmidt and Ford predicted, *P. dardanus* provided decisive evidence in explaining the evolution of mimicry. That evidence supported Ford’s gradualism over Goldschmidt’s saltation.

Having spent nearly five years researching the genetics of *P. dardanus*, Clarke and Sheppard accomplished more than the successful defense of gradualism. The genetic analysis enabled the scientists to advance additional theories regarding the evolution of mimicry. In evaluating the forms of *P. dardanus*, Clarke and Sheppard found that the mimetic-color patterns were comprised of simple elements such as the distribution of black on the fore-wings and on the hind wings as well as variations in the ground color of the pale areas of both wings. Such relatively simple variation prompts the geneticists to suggest a super-gene: “It therefore seems possible that the apparent multiple allelomorphous series controlling the colour-pattern in all forms investigated is really a super-gene in which various combinations of linked allelomorphs control each pattern” (Clarke & Sheppard, 1960c, p. 182). Lincoln Brower has suggested

that these supergenes were misinterpreted by Goldschmidt to be macromutations (Brower, 1992, p. 9).

When Clarke and Sheppard crossed races of *P. dardanus* from the African mainland with the nonmimetic *meriones* race from Madagascar, they noted considerable variability among the first generation (F1) and even greater variability in the second generation (F2). Such variability suggested to Clarke and Sheppard that each race had a coadapted gene complex, which ensured a low degree of variability in the phenotypic expression of the major genes, all of which was disturbed by crossing disparate races. Their conclusion from this evidence indicated the stabilizing effect of natural selection:

The crosses reported in this paper therefore supply yet more evidence that the pattern in *P. dardanus*, whether one considers the mimetic or non-mimetic patterns, is stabilized by natural selection which results in a highly co-adapted gene complex, so that the major genes produce the most advantageous effects. (Clarke & Sheppard, 1963, p. 412)

To support their conclusions, Clarke and Sheppard included photographs of the distasteful models, the mimics from the same areas, and the “broken down” backcrosses (see Figure 11.1).

Clarke and Sheppard addressed many of the areas of research identified by Ford (1936). And as Ford had predicted, this resolved many of the complexities of mimetic polymorphism. Indeed, *P. dardanus* had also lived up to Poulton’s expectations as “the most interesting and complex example of mimicry as yet known throughout the



Figure 11.1. Clarke and Sheppard’s (1963) decisive image from *Evolution*. Top row: The distasteful models. Center row: *P. dardanus* female mimics from the same areas. Bottom row: The breakdown in mimicry, which occurs in the cross between the South African race and the race *meriones* from Madagascar. Figure from C. A. Clarke & P. Sheppard, “Interactions between major genes and polygenes in the determination of the mimetic patterns of *Papilio dardanus*,” 1963, *Evolution*, 17, pp. 404–413. Reprinted with permission.

world.” Clarke and Sheppard recognized the historical significance of their work, as well, when they identified an allelomorph controlling the amount of black in wing pattern in *hippocoonides* and cited Trimen’s (1869) theory that mimicry in *P. dardanus* had been based on an extension of the black costal margin of the forewing (Clarke & Sheppard, 1960c, p. 180). Ford, who had participated in much of the research and debate over *P. dardanus*, would synthesize the new evidence in his own discussions of evolution, genetics, and mimicry.

FORD SUMMARIZES

In 1964, Ford published *Ecological Genetics*, a full-length treatment of the process of genetics in nature. It seems fitting that he dedicated the work to the memory of his friend and colleague, Fisher. Ford devoted an entire chapter to *P. dardanus* and the evolution of mimicry. His tone in the introduction bordered on joyful (given the constraints of academic prose). The full effect cannot be captured without quoting it nearly in full:

No species with the possible exception of *Hypolimnias bolina* and *Pseudacraea eurytus* provides such complex examples of mimicry as *P. dardanus*. It is, moreover, particularly well fitted to throw light upon the evolution of these resemblances since they occur in a number of distinct geographical races. Most fortunately therefore this is the very butterfly in which the genetics of polymorphism, both mimetic and non-mimetic, have been most fully investigated. The credit for that work is to an outstanding degree due to C. A. Clarke and P. M. Sheppard. They have overcome great difficulties in obtaining the necessary stocks and in breeding these largely tropical and sub-tropical insects in Liverpool on an extensive scale. Their analysis of the results so obtained has verified the theory of mimicry based upon the concept of polymorphism described in Chapter Six and has provided a secure foundation for it.¹⁵

Ford regarded the research of Clarke and Sheppard as validation of his own research and theories. He devoted the rest of the chapter to a description of the races of *P. dardanus* and the genetic studies of Clarke and Sheppard along with yet another recapitulation of the theories put forth by Punnett and Goldschmidt. Although Ford considered *P. dardanus* genetics to have been well investigated, there were aspects that required further study. For example, Ford recognized Clarke and Sheppard’s work on the control of wing-pattern via an allelomorph as strong evidence for the control of mimetic polymorphism via a super-gene, but he sought clearer evidence: “For precise proof of that contention we have to await the occurrence of a cross-over within the unit itself (such as that which has produced the homostyled primrose by reconstruction of the super-gene controlling the pin and thrum phases). However, this may well have become a very rare event, perhaps down nearly to mutation frequency” (Ford, 1964, p. 242). Even in the conclusion of this chapter, Ford suggested subjects requiring further study. After crediting Clarke and Sheppard with validating Fisher’s 1927 explanation, Ford recommended the subject for future research: “Evidently the time has now come for further studies on the ecology of mimicry in the field, carried out in the light of these studies” (Ford, 1964, p. 246). With this statement, Ford suggested that *P. dardanus*’s utility as a lab animal had run its course. For new insights into the biology and evolutionary significance of mimetic forms, scientists (naturalists to be

more precise) needed to conduct field studies of the butterfly. Thus, the career of *P. dardanus* as a model organism had come full circle from Fisher and Ford's hypotheses to Clarke and Sheppard's experiments to Ford's suggestion that field studies would yield still more information on its evolution.

Ecological Genetics underwent several revisions as Ford incorporated new material. In 1975, he reported that Clarke and Sheppard had examined the genetics of *Papilio memnon* and *Papilio polytes* and found similarities with polymorphism in *P. dardanus* and additional information on the formation of super genes, thereby reinforcing the results of the earlier work on *P. dardanus* (Ford, 1975, p. 306). Finally, with an eye to the future, Ford noted the successes of J. V. Z. Brower, L. P. Brower, M. Rothschild, and T. Reichstein in the areas of ecology of mimics and their models and ecological chemistry (Ford, 1975, p. 313).

Although the life of *P. dardanus* as an experimental organism ended as the stocks bred by Clarke and Sheppard died off, its life as a model organism continued as Ford and others continued to cite its value in answering questions of evolutionary biology. In 1994, C. Frederik Nijhout showed that the super-gene hypothesis was flawed and that simpler genetics could explain the phenotypic variability of the mimetic forms of *P. dardanus*, but he encouraged further experimental studies of the butterfly. Moreover, as Clarke and Sheppard predicted, the study of mimicry advanced with the pursuit of complexes for which field study proved more tractable. Examples of such field studies include the western butterfly, *Battus philenor* (Fordyce & Nice, 2003), and the large Latin American genus, *Heliconius*, and mimics (Turner, 1983).

CONCLUSION

This essay has traced the impact on evolutionary theory of a single species of butterfly, *Papilio dardanus*, from its initial promise as a model organism to the realization of that promise as an exemplary case in the history and science of mimicry and evolution. I have attempted to provide a balanced representation of the ideas of the butterfly geneticists, whether they supported the neo-Darwinian model of gradual change or the saltational model of large-scale mutations. Rather than portraying scientists as right or wrong, victorious or vanquished, I have shown the scientific process as the integration of theory and research with the end result of clearer resolution. In the case of *P. dardanus*, the clash between two theories stimulated theoretical debate. Yet, empirical research ultimately resolved issues and transcended the conflict.

In *Papilio dardanus*, scientists recognized the natural organism as a valuable tool in the study of evolution when it was first described. Its original use as an excellent demonstration of the selective advantage of mimetic forms gradually changed as scientists co-opted it to develop the case for evolutionary gradualism. But the use of *P. dardanus* became even more specialized when Ford and Goldschmidt both cited the polymorphic forms of *P. dardanus* to support gradualism and saltation, respectively. Both called for the genetic analysis of the butterfly. To conduct genetic studies of *P. dardanus*, Clarke and Sheppard first remade the butterfly as a laboratory animal through carefully controlled pairings.

As predicted, experimental genetics provided concrete evidence to support one theory of the evolution of mimicry over the other. E. B. Ford's synthetic *Ecological Genetics* restored *P. dardanus* to its proper place within a much larger machine by recognizing the organism's context in nature and by situating the tool's role in evolutionary

theory. By 1975, when Ford published *Ecological Genetics*, *P. dardanus*'s career as an experimental organism had long since ended, but the butterfly continued to serve as a model organism in textbooks. Recently, scientists have called for its resurrection as an experimental lab animal.

Moreover, the evolutionary story of the mimetic forms of *Papilio dardanus* parallels the unification of biology around the evolutionary synthesis. It was clear from the original 1869 description of mimetic forms that the species could shed light on the evolution of mimicry. Yet, such theoretical promise required empirical support, as both Ford and Goldschmidt noted. By the time Clarke and Sheppard fashioned a laboratory animal out of wild stocks of various *P. dardanus* forms, genetics had become an important part of evolutionary biology; the lab was as important as the field for the resolution of problems in evolution (Kohler, 2002). While the genetic analysis seemed to vindicate the views of the evolutionary gradualists, their work in fact provides a striking example of the power of unification in biology, as theorists and empiricists came to cooperate (Smocovitis, 1996).

Finally, the status of *P. dardanus* as a model organism may seem rather minor, though it yielded valuable results during its brief career as an experimental animal. For the most part, historians of science have confined their studies of model organisms to the most prominent examples such as *Drosophila* and *C. elegans*, both of which sat at the center of decades of research. Nevertheless, the story of *P. dardanus* suggests that the notion of a model or exemplary organism can be broadened to include less celebrated examples of animals in the lab or the field that served to answer discrete, albeit important, questions in ecology and evolution. It is also an interesting example of revealing greater complexity than had been anticipated. The evidence that the various genes must be linked to form the mimetic forms tied *P. dardanus* to the emerging body of literature on *Cepaea nemoralis*, *C. hortensis*, and the discovery of "supergenes" controlling color and banding pattern. This led to hypotheses about the evolution of linkage itself (and to quantitative hypotheses about the evolution of sexual reproduction through its role in breaking linkage groups) and to theories for entire genome evolution and genome structure. The genome went from constraint to product of evolution, in part due to work on organisms like *P. dardanus*.¹⁶

One of my core questions at the outset of this essay was, "What is the impact of the actual choices of biological material on the content of biological knowledge?" In studying the story of *P. dardanus* as evolutionary exemplar, it has become clear that the butterfly has yielded valuable insights into the evolution of mimicry, the pace of evolutionary change, the role of supergenes in evolution, and even genomic evolution.

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NOTES

1. For a recent analysis of biological mimicry, see Joron & Mallet (1998).

2. For complete reviews of theories on the rate of variation in evolution, see Provine (1971) and Mayr (1980, 1991).
3. Each generation of scientists and many individuals coined their own terms for synonymous or slightly different phenomena. I have attempted to define terms in the scientists' own language (Table 1).
4. Cited in Brower (1992, p. 4). For an expansive review of the history of mimicry, see Kimler (1983).
5. Sir Edward B. Poulton (1856–1943) studied at Oxford during the 1870s and remained at the university for the remainder of his professional life in entomology. He was knighted in 1935,

Table 11.1. Terms

<i>Polymorphism</i>	Ford, 1945 Ford, 1964	The occurrence together in the same locality of two or more discontinuous forms in such proportions that the rarest of them cannot be maintained merely by recurrent mutation.
<i>Micromutation</i>	Mayr, 1980	A minor genetic change that appears in an offspring that is slightly different from its parents.
<i>Macromutation</i>	Mayr, 1980	A pronounced genetic change that appears in an offspring that is significantly different from its parents.
<i>Parallel mutation</i>	Goldschmidt, 1940	The recurrence of mutations that produce similar changes in different plants and animals.
<i>Gradualism</i>	Mayr, 1991	A theory that evolution progresses by gradual modification and not by the sudden origin of new types (saltations).
<i>Saltation</i>	Mayr, 1991	The assertion that new types of organisms originate by the sudden origin of a single new individual, which becomes the progenitor of this new kind of organism.
<i>Discontinuous variation</i>	Mayr, 1980	The spontaneous occurrence of an occasional individual that falls outside the normal range of variation of the known species.
<i>Continuous variation</i>	Mayr, 1980	Individuals of the same species differ from each other in size, proportions, intensity of coloration, and many other characteristics that can either be measured or graded.
<i>Dominant/dominance</i>	Ford, 1945	A gene that obscures the action of its allelomorph (the recessive) when present with it in the heterozygous state.
<i>Recessive</i>	Ford, 1945	A gene whose action is obscured by its allelomorph (the dominant) when present with it in the heterozygous state.
<i>Segregation</i>	Ford, 1945	The recovery of the original types in definite proportions in subsequent generations, when individuals exhibiting contrasted characters have been crossed.
<i>Sex-controlled inheritance</i>	Ford, 1945	Characters that can only be manifested in one or the other sex. The genes producing them may be carried either in the sex-chromosomes or in the autosomes.
<i>Backcross</i>	Ford, 1945	A mating between a heterozygote and the recessive homozygote.
<i>Supergene</i>	Ford, 1964	A tightly linked group of genetic loci controlling several characters that effectively segregate as a single gene.

- There is no complete biography of Poulton; although, see Carpenter (1944). For an overview of museum entomology at Oxford, see Smith (1986).
6. Reginald C. Punnett (1875–1967) initially studied medicine at Cambridge, but soon focused on zoological morphology. After working in the natural history department at the University of St. Andrews, he returned to Cambridge to become a demonstrator in morphology. He eventually met William Bateson with whom he collaborated on several projects. In 1910, Punnett succeeded Bateson in a Professorship at Cambridge. The two geneticists cofounded and coedited the *Journal of Genetics* in 1911. His most renowned contribution may be the Punnett Square for determining the ratio of dominant to recessive phenotypes. G. H. Hardy clarified Punnett's ideas regarding Mendelian segregation with the equation: $pr = q^2$, which Punnett initially called Hardy's Law, but the formula soon became known as the Hardy-Weinberg principle or the Hardy-Weinberg equilibrium. See Crew (1967) for a biography and bibliography. For a detailed examination of Punnett's views on selection, see Kimler (1983).
 7. Sir Ronald Aylmer Fisher (1890–1962) was a gifted mathematician from an early age. He studied mathematics and theoretical physics, completing his degree in 1912. Over the next 20 years, Fisher developed the reputation as Britain's leading statistician, but he became interested in genetics and in 1933 accepted the Galton Professorship of Eugenics at the University College London. After a decade in that position, he became Balfour Professor of Genetics at Cambridge. Fisher was knighted in 1952. For a full-length biography of Fisher, see Box (1978) and Gridgeman (1972).
 8. Edmund Briscoe Ford (1909–1988) was a student of Julian Huxley's at Oxford and after he completed his studies he remained at Oxford to become Professor of Genetics and to organize a leading group of geneticists. Through Huxley, Ford met R. A. Fisher in 1923 and the two became close friends and collaborators. They visited one another regularly at their respective universities (Ford would later remark that Fisher visited no one else at Oxford), see Clarke (1995), Ford (1980), Kimler (1983), and Box (1978).
 9. Geoffrey Douglas Hale Carpenter (1882–1953) studied medicine at Oxford and served in Africa as a member of the Colonial Medical Service from 1910 to 1930. During this time period, Carpenter specialized on sleeping sickness and the tsetse fly. Having already published *Mimicry* with E. B. Ford in 1933, he served as Hope Professor of Entomology at Oxford from 1938 to 1948.
 10. Richard B. Goldschmidt (1878–1958) studied at the University of Heidelberg and the University of Munich and he later taught at Munich. In 1913, he became the director of the Genetics Department of the newly established Kaiser Wilhelm Institute for Biology in Berlin. One of his extensive studies examined industrial melanism in moths of the genus *Lymantria*. In July 1936, Goldschmidt accepted a professorship at the University of California at Berkeley where he spent the rest of his life working on the genetics of *Drosophila*. For additional material, see Goldschmidt (1960), Stern (1967), and Dietrich (1995).
 11. Goldschmidt took exception to Dobzhansky's characterization of saltation theory as "cataclysmic theory," which to Goldschmidt implied something damnable or irrational, like a deluge or catastrophe (Goldschmidt, 1945, p. 155).
 12. For a critical reevaluation of Goldschmidt's claims, see Gould (1980, 1982). The latter appears as the introduction to the 1982 reissue of Goldschmidt's above referenced classic, *The Material Basis of Evolution* (New Haven: Yale University Press). For a review of Goldschmidt's critical role in the evolutionary synthesis, see Dietrich (1995).
 13. Phillip MacDonald Sheppard (1921–1976) had been one of E. B. Ford's students at Oxford during the 1940s. He spent a year in Ford's lab after completing his doctorate and another year in Dobzhansky's lab in the United States. In 1956, he accepted a position at the University of Liverpool where he joined his friend and collaborator, Cyril A. Clarke (Clarke, 1977). Sir Cyril Astley Clarke (1907–2000) studied medicine at Oxford. He worked as a consultant physician in Liverpool from 1946 to 1958, when he joined the staff of the University of Liverpool. Clarke and Sheppard made significant contributions to the fields of butterfly genetics and human genetics. After years of research in butterfly genetics, the two scientists studied

- Rhesus babies (rH-positive fetuses in an rH-negative mother) and discovered how to prevent spontaneous abortion; see Daintith (1994).
14. Backcross: the mating of a heterozygote and the recessive homozygote (see Table 11.1).
 15. Ford (1964, p. 223). In subsequent editions, the first line read: "Few species provide such complex examples of mimicry as *Papilio dardanus*" (Ford, 1975, p. 284).
 16. I am grateful for Joe Travis for this crucial insight.

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