

Evolution in the twentieth century

Joe Felsenstein

Sewall Wright and Evolutionary Biology. By William B. Provine. *University of Chicago Press: 1986. Pp. 545. \$30, £25.50.*
Evolution: Selected Papers by Sewall Wright. Edited and introduced by William B. Provine. *University of Chicago Press: 1986. Pp. 649. Hbk \$70, £59.50; pbk \$25, £21.25.*

EVOLUTIONARY theory in the 1960s and 1970s was dominated by optimization, by the search for the quantity evolution would maximize. The mean fitness of a population was not precisely what natural selection would maximize in a Mendelian genetic system, so perhaps if we did enough theory we could find out what was. The picture hanging on our wall was of R. A. Fisher, who had emphasized the importance of natural selection in large populations. The contributions of Sewall Wright were acknowledged by all, but were considered to be of secondary importance.

Theoretical population genetics then saw itself as a branch of applied mathematics, and in need of more mathematical rigour. The only data to which we paid attention were gene frequencies of electrophoretic polymorphisms. The kinds of data which morphologists, palaeontologists and most systematists collected were ignored.

By the end of the 1970s many of these evolutionists working above the population level saw the neo-darwinian synthesis as irrelevant to their needs. Punctuated equilibrium and even neo-lamarckian alternatives gained adherents. The resulting controversies over punctuated patterns of evolution and species selection mechanisms have revived interest in complex fitness surfaces and small populations. The evolutionary views of George Gaylord Simpson and Ernst Mayr, both influenced by Wright, have been important in these debates. All of which has led to a remarkable resurgence of the reputation of Sewall Wright.

It is unusual for the details of a theoretician's work to be so relevant 70 years after his views were formed. It is even more unusual for a major account of his work and its influence to appear in his own lifetime. Provine's thorough and thoroughly admirable examination of Wright's life and influence, which is accompanied by a very useful collection of Wright's papers on evolution, is the best we have for any recent figure in evolutionary biology.

Sewall Wright was born in 1889, and grew up in Galesburg, Illinois, one of a generation of talented and energetic intel-

lectuals from the prairies of Illinois and Wisconsin. One is reminded of people such as the poet Carl Sandburg and the photographer Edward Steichen; in fact, Sandburg married Steichen's sister, and Wright's father Philip was Sandburg's most influential teacher and first publisher (Sewall set the type and ran the press). Provine gives careful attention to these early years, and to the intellectual atmosphere in which Wright trained; his chapters on Harvard's Bussey Institution and on evolutionary theory after Darwin are worth the price of admission by themselves. Here, I was startled to discover how closely the present controversies over the relative importance of species selection and individual selection were paralleled by controversies at the turn of the century.

Provine also goes into detail — more



Early days — Sewall Wright in 1922.

than seems readable — on the physiological genetics which was Wright's main concern until his retirement. As a student learning two fascinating stories, on mammalian coat colours and mathematical genetics, I did not appreciate how closely they were bound together. One is the story of explaining a seemingly arbitrary array of colours by the concentrations and properties of enzymes. Part of its fascination is evolutionary: the appearance of the same genetic variants in different mammalian species (Himalayan in rabbits, Chinchilla in mice and Siamese in cats, for example). The other extends the genetic system to the population level, making predictions from the necessary regularities of the system of inheritance.

Only later did I come to realize that the same person, Sewall Wright, was central to both stories, and that coat-colour genetics was critical to the formation of his views on evolution. A list of Wright's PhD students (pp. 189–190) discloses few who concerned themselves with population genetics, but makes his influence on

American mammalian genetics palpable. He wrote major reviews of physiological genetics, and influenced Beadle and Tatum's famous work on *Neurospora* which led to the one gene — one enzyme hypothesis. Although Provine deals chiefly with Wright's evolutionary theories, he recognizes the importance of the work on gene action in coat colour in informing Wright's view of the role of gene interaction in the inheritance of quantitative characters.

After describing Wright's years at Harvard (1912–1915), the US Department of Agriculture (1915–1925) and the University of Chicago (1925–1955), Provine devotes most of the rest of the book to Wright's views on evolution and their influence. There are some surprises. For example, in the course of an extended consideration of Wright's "shifting balance" theory of evolution Provine argues that Wright changed his views substantially in the 1940s. Wright himself denies this, but Provine's evidence, largely drawn from Wright's papers, seems incontrovertible. Before 1940, he points out, systematists believed that differences between species were of little or no adaptive significance. Wright's theory, originally developed with animal breeds in mind, could be applied to natural populations by supposing that random differences arose between species by genetic drift, and that selection between species utilized these to produce a net adaptive response. Provine believes that evolutionary biologists during the 1920s and 1930s did not understand the role of between-group selection in Wright's theory, that they understood him to be saying that genetic drift was the primary agent of evolution.

After 1940, as systematists and population geneticists reinterpreted species differences as being largely adaptive, Wright modified his theory. He brought it closer to the original animal-breeding model by having the random differences arise between local populations rather than between species. Provine finds evidence that this unadvertised change of views was a source of much confusion, playing a role in the famous post-war disputes with Fisher and Ford.

The controversies with Fisher are given careful attention. Provine takes pains to point out the reasons why these two came to disagree so completely about the evolutionary forces operating in nature, despite their agreement on most of the mathematical details. As long as we lack a comprehensive picture of the patterns of gene interaction and population structure in a wide range of species, the views of Fisher and Wright will form opposite poles of microevolutionary theory. One pole emphasizes optimization by natural selection in large populations with additive effects of genes, the other interaction of genes and interaction of natural selection and genetic drift. ▶

I was surprised, too, to find how much of Wright's time during the 1930s and 1940s was taken up analysing Theodosius Dobzhansky's data for his famous series of papers on the "Genetics of Natural Populations", and how dependent Dobzhansky was on Wright's suggestions and analyses. Provine's treatment is extensive and illuminating, and indicates the underlying objectives of many of Dobzhansky's papers. Indeed, Provine's book will be an excellent starting point for a study of Dobzhansky's papers; through it the new student in evolutionary biology may be able to appreciate that genetic variation was once much more difficult to find and measure than it is today.

As the title indicates, *Sewall Wright and Evolutionary Biology* concentrates upon Wright's views and influence on evolutionary biology, and is not a general account of Wright's life or science. Although Wright's work on mathematical genetics is mentioned, Provine devotes little space to it. A symptom of this is the omission of the five essential "systems of mating" papers of 1921 from the collection of papers. On the mathematical theory Provine makes a few false steps. After pointing out that there are three logically distinct versions of Wright's concept of a fitness surface, he argues forcefully that these are logically unconnected, that Wright has spread confusion by using two of the notions interchangeably, and that population geneticists mistakenly assume that the two notions are related. Provine is mistaken in this: you really *can* derive the gene frequency adaptive surface from the genotype adaptive surface by taking a weighted average.

Wright's personal life is treated, but only rather briefly and circumspectly. Many population geneticists have Sewall Wright anecdotes, most of which do not appear in Provine's book. I did not find my favourites: "Sewall Wright And The Coffee Cup", "Sewall Wright Penniless In Berkeley" and "Sewall Wright Lectured On Genetic Drift". To his credit Provine does mention the most famous of all, noting both Wright's denial and the numerous people who claim to have seen him absent-mindedly erase a blackboard with one of his guinea pigs.

Twenty years ago I happened to be the person who first suggested to Provine that he should interview Sewall Wright (Provine was surprised to hear that Wright was still alive). Now I'm glad I did, because the result is a remarkable book. As we face the interesting possibility that Wright will be the keynote speaker at his own centennial celebration, his influence on evolutionary biology is greater than it has ever been. We will be listening to that speech with more than just polite attention. □

Joe Felsenstein is a Professor in the Department of Genetics, University of Washington, Seattle, Washington 98195, USA.

Redouté requiem

Sandra Raphael

Wonders of Creation: Natural History Drawings in the British Library. By Ray Desmond. *The British Library: 1986.* Pp.240. £25.

A Redouté Treasury: 468 Watercolours from Les Liliacées of Pierre-Joseph Redouté. Text by Peter and Frances Mallary. *Dent, London/Vendome Press, New York: 1986.* Pp.228. £40, \$50.

Wonders of Creation contains a selection of illustrations of plants and animals from manuscripts and drawings in various departments of the British Library, with a few pictures from printed books added to demonstrate the changes in style and taste described in the text. The choice seems to have been made almost at random in an attempt to include something for everyone, from flowers and trees, to birds, fishes, snakes, terrapins, rhinoceroses, koala bears, beetles, spiders and Stamford Raffles's "hairy-nosed otter". The sources range from mediaeval manuscripts to nineteenth-century drawings. The coloured plates (nearly 50 of them) are at the back of the book, each with its own short description, while the black-and-white illustrations are used to break up a short text that gives a rather pedestrian survey of the development of illustration as an aid to the descriptive work of naturalists.

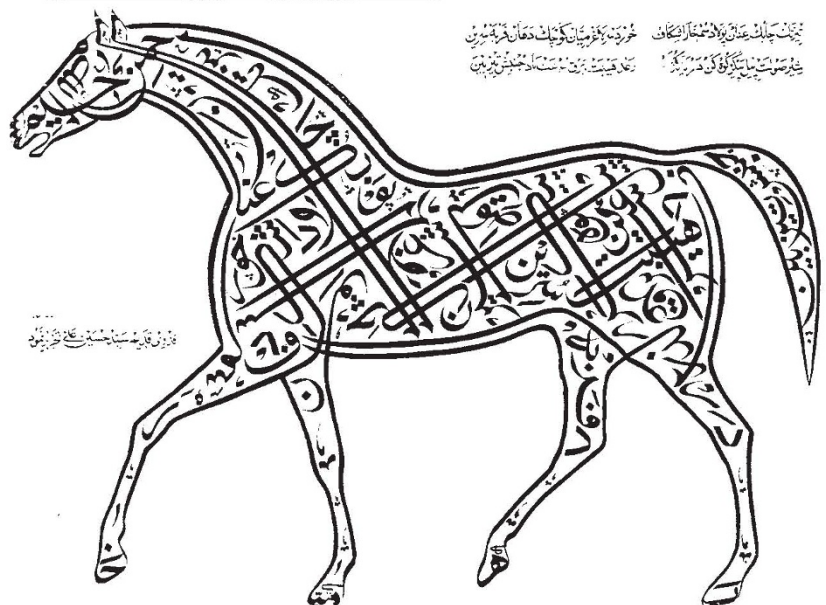
The British Library collections in this field are quite rich, but it seems perverse to isolate them from the complementary and even richer hoards in the Natural History Museum in Kensington and the Print Room of the British Museum, still under the same roof as the British Library. In

spite of the book's restrictions, the beauty of many of the pictures, oriental or European, will surely please browsers.

On 20 November 1985 Sotheby's in New York sold for \$5.5 million the Empress Josephine's copy of Pierre-Joseph Redouté's *Les Liliacées* (1802–1816), 16 volumes containing 468 original watercolours on vellum as well as the printed text. *A Redouté Treasury* is a revised version of the sale catalogue, with colour photographs of the drawings of plants of the lily family and related groups rearranged and supplemented by a longer introductory essay and botanical notes.

Although *Les Liliacées* was sold as a single lot, it has since been dismantled by its buyer, a "breaker" who specializes in taking apart colour-plate books and selling their illustrations piecemeal. This process is sad enough when its subject is a relatively ordinary book, but when it is applied to one that is unique it becomes a bibliographical scandal. Redouté's drawings for *Les Liliacées*, possibly his masterpiece, were bought by his patron Josephine, whose garden at Malmaison provided many models for the artist. The drawings were inherited by Josephine's son, and all but 19 of them were bought by an American dealer, Edward Weyhe, in Zurich in 1935. Now they have been sold again. The drawings have been taken out of their fine bindings, so that this example of a great artist's greatest work has now been scattered and will never again be seen whole. *A Redouté Treasury* may be seen as a requiem for a French national treasure, now ruined. □

Sandra Raphael, 18 Argyle Street, Oxford OX4 1SS, UK, was the natural history editor of the new Supplement to the Oxford English Dictionary, the last volume of which was published earlier this year.



Piety in art — an example of Tughra calligraphy. The opening verses of the Koran start at the horse's mouth, while the rest of the text praises the physical qualities of the animal.