## Vignette: Genetics Edwardian Style

After a while I became something of an expert and was written to for advice on guinea pig habits and ailments. We got some new kinds, as we wanted to see not only how colour and brindling was inherited, but also long and short hair, and the whorls of show guinea pigs, though I never entered the show world....

Once, going out to feed them, I heard the scream for help, ran and found Titi, whose cage I always left open so that she could forage, her hackles up, facing a weasel, while her family scuttled for shelter in the hedge.... I snatched Titi up and the weasel looked at me with wicked little eyes, humped ready to jump. Knowing they go for the neck vein I was frightened, but held Titi tightly covered in my hands, feeling her poor little heart racing, and kicked out at the weasel with my solid school-boy shoes. It went away and I put Titi down to call to her family, gather them up and get back into her hutch. One had to look out, too, for owls and hawks, especially if any of my flock were in open-topped runs on the croquet lawn grass.

—*Naomi (Haldane) Mitchison*, in *Small Talk* (Bodley Head, 1973; reprinted in *As It Was*, Richard Drew Publishing, 1988)

unrelenting competition in nature drives diversity as he also believes it drives the growing British economy. Then arrives the letter from Wallace. Huxley, Hooker, and Lyell quickly arrange a joint presentation of the materials at the Linnaean Society because that was politically the group most likely to allow the event.

During the 1860s there is indeed a struggle between men of science and the clergy. They are fighting over social and professional status as much as ideas. Darwin's theory is but one element in the larger social dispute. Darwin's writings of the 1860s are really quite polemical. His volume on the cross-fertilization of orchids is a piece of natural theology in which natural mechanisms are developed without the hand of God present. The study of the domestication of animals displays his vast knowledge of breeding and his wide acquaintance with breeders. In *The Descent of Man* he returns quite openly to the materialism of the medical community in Edinburgh and London. Throughout these years Hooker rather than Huxley seems the more important friend.

During these same years Darwin becomes even more prosperous thanks to the wisdom by now of his own investments. He can leave his children well off. Illness continues to plague him. Natural selection is actually accepted by very few people. Even Huxley does not believe in it. Darwin becomes for all intents and purposes openly agnostic, though quietly so. There is a final illness and he dies. He is to be buried at Down, but his scientific circle intervene. His friends and admirers achieve the last bit of patronage for him as they petition the Dean of Westminster for a grave in the Abbey. It is a monument to the social respectability of professional science rather than to the radicalism of evolution by natural selection.

Notwithstanding the cohesiveness of this story, there are some omissions that are curious from a biography so determinedly revisionist. For all the discussion of Darwin's health, there is no discussion of his sexual activity or preoccupations. Despite the emphasis on the climate of political radicalism surrounding Darwin's experience, the biography displays an almost Victorian reticence about sexuality in the life of a man who wrote hundreds of pages about breeding, cross-fertilization, and sexual selection. Darwin clearly expended more professional and no doubt more private thought on sex than he did on politics. Desmond and Moore provide no consideration of Darwin's possible sexual encounters on the *Beagle* voyage, of the impact on his thought of the sexual relations in his marriage, or of the large number of children, including an unexpected one.

The discussion of Darwin's family life is warm and moving so far as the loss of his daughter is concerned. Yet there is little discussion of the relationship with Emma Wedgwood Darwin save ongoing regret over her religious orthodoxy. The latter was hardly unusual, nor is there any indication that it was extreme. Emma was the most constant figure in Charles Darwin's life. The marriage seems to have been happy. She deserves more attention.

The account of the decade of the 1850s is curious in two ways. Desmond and Moore tend to downplay the very real hesitancy that Darwin had about the validity of natural selection until it provided the same account of nature found in natural theology. Here as elsewhere they discount too much the long-term influence of the Cambridge experience and the influence of his clergyman-scientist friends. Furthermore, the Darwin-Wallace story is told with too little skepticism. The relevant letters are missing from Darwin's correspondence. Darwin and his friends moved as quickly as possible to assure his claim for originality and simply informed the deferential Wallace afterward. For all their concern with politics Desmond and Moore do not emphasize that Darwin, the landowner, and his middle-class friends were determined to see that the working-class Wallace received little attention. Wallace for his part displayed almost a textbook example of deference to his social betters.

Finally, in a work of radical history of science there is still a strongly Whiggish bias in discussing Darwin's opponents, and perhaps too much anti-clericalism. Many of Darwin's opponents struck important and not obscurantist blows. Indeed evolution triumphed in the second half of the century, but not natural selection. The authors would have served both Darwin and their readers better had they spun out the vast confusion over evolution that reigned by the time of Darwin's death.

Nonetheless, whatever the shortcomings, Desmond and Moore have written the best biography of Darwin since his son's.

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## Molecular Panselectionism

**The Causes of Molecular Evolution.** JOHN H. GILLESPIE. Oxford University Press, New York, 1991. xvi, 336 pp., illus. $35. Oxford Series in Ecology and Evolution.

It is 25 years since Motoo Kimura first proposed the neutral theory of molecular evolution. The theory asserts that variation in protein and DNA sequences within populations, and the evolution of sequence differences between populations, are mostly caused by chance fluctuations in allele frequencies due to finite population size (random genetic drift). As Kimura has stressed, this view of molecular evolution is in marked contrast with the conclusion of the modern evolutionary synthesis of the 1930s and '40s, that natural selection is the primary guiding force of evolution. Though Kimura recognizes the validity of this "panselectionism" for the evolution of mor-

phological or behavioral phenotypes, he has argued strongly that it should be abandoned at the molecular level.

In *The Causes of Molecular Evolution*, John Gillespie presents a radically different case. Whereas the neutral theory asserts that changes in DNA and protein sequences are due to the same evolutionary mechanism (drift), Gillespie argues that drift is important only for the so-called "silent" changes in DNA sequences, that is, those not affecting the amino acid sequences of proteins. Differences in protein sequences are claimed to be predominantly under the control of natural selection. The obvious objection, that attempts to observe selection on naturally occurring protein variants have mostly been inconclusive, is met by noting that very small selection coefficients are sufficiently large to allow selection to take control but would be undetectable experimentally. Gillespie points out, however, that amino acid variants segregating in natural populations, and amino acid differences between species, frequently have effects on physiologically relevant properties of the proteins concerned and suggests that it is plausible that such differences can be subject to natural selection. In some cases, the evidence for selection is convincing. But these are comparatively rare. The link between the relatively frequently observed kinetic differences between different forms of the same enzyme and fitness is not secure, since the effect of the activity of a single enzyme in a pathway may be greatly dampened by the properties of the pathway as a whole. This line of argument thus seems inconclusive to me.

Gillespie's review of information on variation and evolution at the DNA level indicates that the notion that silent nucleotide changes follow the neutral model stands up well to rigorous scrutiny. The lower levels of variation and slower rates of evolutionary change for nucleotide site changes that alter protein sequences make sense if these often cause deleterious changes in protein function, resulting in their prompt elimination by selection. The amount of variation between different lineages in the rate of evolution over long time periods for silent sites is approximately in line with the classical neutral expectation. In contrast, Gillespie's analysis suggests that there is often a highly significant excess variance in rates of evolution for amino acid replacements. Overall the variance is about eight times that expected on neutrality. His interpretation is that the evolution of a given protein follows an "episodic clock"—that is, millions of years without change are interspersed with brief bursts of evolution, in which two to four amino acid substitutions occur.

The core of the book is an attempt to interpret this pattern in terms of the mathematical theories of selection that Gillespie has developed over the past 20 years. This involves over 100 pages of abstruse derivations. Two models of the episodic clock are produced. The "mutational landscape" model imagines that an environmental challenge to a population can be met by the fixation of new mutations at a given locus. Given a finite set of possible alleles that can be ordered with respect to their fitness in the new environment, the population responds by successively substituting alleles with higher fitnesses, until a state is reached when further change would require more than one mutational step for a higher level of fitness to be reached, whereupon change at the locus ceases. The other model assumes that allelic variation is maintained by environmental fluctuations affecting fitness. Occasionally a large change causes a particular allele to become fixed, which may differ from the initial allelic state by several mutations. Either process ensures that each episode of change involves only a limited number of substitutions, consistent with the results of the sequence analyses.

My overall verdict, as an evolutionary biologist who is not intimately involved in research in this area, is that the case for selection is persuasive but not conclusive. Two difficulties occur to me. First, the episodic-clock interpretation is consistent with, but not demanded by, rate variation. Rates could vary over time but in a steadier fashion. If this were the case, then the interpretation of rate variation as a consequence of neutral substitutions changing the selective constraints operating on a protein might seem plausible. Second, the selection models themselves do not necessarily lead to the episodic clock: there is no guarantee that the pattern of environmental variation in selection pressures is episodic on the long time scale that Gillespie's interpretation requires. It is thus not clear that a strong case for selection can be built on rate variation alone. A weakness of the book is that no research program is offered for further testing of the rival theories.

John Gillespie has thought harder than anyone else about the subtleties of the ways in which natural selection can bring about variation and evolution at the molecular level, and he has an enviable command of the theoretical and empirical literature on molecular evolution. His book therefore deserves the careful attention of everyone interested in this field. The sections reviewing the data are well written and informative. Readers should be warned, however, that the theoretical sections are extremely demanding. They assume considerable familiarity with technicalities of population genetics theory, and there is a tendency to develop the theory first and tell the reader of its relevance later. The connection between the data and many of the details of the models is tenuous, and a more effective book could probably have been written if these details had been pared down.

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## Astronomical Oddities

**Unusual Telescopes.** PETER L. MANLY. Cambridge University Press, New York, 1992. xviii, 221 pp., illus. $39.95.

Amateur and professional observational astronomers alike maintain a strong interest in the design and development of telescopes, for they are the means by which celestial objects are detected. Without telescopes, the appreciation of the objects of the universe would be subject to the limitations of the human eye; with them, the heavens are revealed in increasing refinement as the power of the telescope and detector increases.

In *Unusual Telescopes*, Peter Manly goes beyond the fundamentals of the history, principles, and basics of telescope design and construction to present a potpourri of designs he considers unusual—telescopes that are nonstandard in at least one aspect. This book is aimed principally at amateur astronomers familiar with the principles and practice of the construction of telescopes of modest aperture, but because of the variety of telescopes described and the engaging nature of the descriptions the book should appeal to a broader audience as well. Engineers involved in projects of modest to large scale will find interesting ideas and approaches here, along with sketches of designs that have or have not received widespread adoption and the reasons why. Professional astronomers like myself may be drawn to the descriptions of several interesting or unique designs in use at professional observatories, perhaps understanding for the first time why a particular telescope is as productive (or as expensive) as it is.

Manly describes an extremely broad assortment of telescopes, including over 150 designs. These vary from the bentwood telescope of Weyman Reams, an 8-inch, *f*/8.3 telescope that looks "more like furniture than the scientific instrument it really is," to telescopes mounted on the roofs of cars for easy portability to dark sites (in one case arranged so that the observer sits in comfort inside the car and views through an