The legacy of early sickle cell anemia research cannot be underestimated. Pauling's grand vision of molecular biology and medicine has been realized to an extent he could never have foreseen, even if our therapeutic power does not yet match our understanding of the molecular basis of disease.


**References and Notes**

1. L. Pauling *et al.*, *Science* **110**, 543 (1949).
2. On Pauling's sickle cell anemia research: C. L. Conley, in *Blood, Pure and Eloquent*, M. M. Wintrobe, Ed. (McGraw-Hill, New York, 1980), pp. 319–371; L. E. Kay, *The Molecular Vision of Life* (Oxford Univ. Press, New York, 1993), pp. 256–259; T. Hager, *Force of Nature* (Simon & Schuster, New York, 1995), pp. 332–334. On its relation to racial ideology: K. Wailoo, *Drawing Blood* (Johns Hopkins Univ. Press, Baltimore, MD, 1997); and to clinical medicine: S. de Chadarevian, in *Molecularizing Biology and Medicine: New Practices and Alliances, 1910s–1970s*, S. de Chadarevian and H. Kamminga, Eds. (Harwood, Amsterdam, 1998), pp. 171–201.
3. Archives of the Eva Helen and Linus Pauling papers, Oregon State University.
4. V. M. Ingram, *Nature* **180**, 326 (1957).


PERSPECTIVES: EVOLUTIONARY BIOLOGY

# The Evolutionary Synthesis

**Nils Chr. Stenseth**

With his *Origin of Species* (*1*) Darwin enabled humans to be viewed as part of nature and provided a theoretical platform for rejecting the notion of a special creation. Today, no biologist questions the reality of evolution or that its mechanism is natural selection. Indeed, "nothing in biology makes sense except in the light of evolution" (*2*). Recently, the Royal Swedish Academy of Sciences awarded the 1999 Crafoord Prize to three giants in the field of evolutionary biology: Ernst Mayr (Harvard University, USA), John Maynard Smith (University of Sussex, UK), and George C. Williams (State University of New York at Stony Brook, USA). The Crafoord Prize (considered the Nobel Prize in fields for which no Nobel is awarded) was established in 1980 to promote basic scientific research in mathematics and astronomy, the geosciences, and the biological sciences (in particular ecology and rheumatoid arthritis). A conference on evolutionary biology that highlighted the contributions of the three prizewinners was held as part of the Crafoord ceremony.

The 1930s saw the emergence of the so-called "modern synthesis" (*3*) or "neo-Darwinism" theory of evolutionary biology. The "modern synthesis" integrated Mendelian genetics, systematics, paleontology, and ecology into a coherent theory of evolution that combined the theory of natural selection with the emerging understanding of how genes are transmitted from one generation to the next. With his *Systematics and the Origin of Species* (*4*), Mayr firmly established the modern synthesis. He promoted the idea of a "biological species," in which species are "groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups" (*4*).

The next important embellishment of Darwin's theory—the notion of evolution for the good of the species (*5*)—began to crystallize in the 1960s but was soon rejected, and the original Darwinian emphasis on the importance of the individual in the selection process was substantiated. The other prizewinners—George C. Williams and John Maynard Smith—contributed significantly to this rejection, as did William D. Hamilton (an earlier Crafoord Prize winner) (*6*, *7*). Of particular importance was Williams' book *Adaptation and Natural Selection* (*7*), which proposed that the evolution of a trait must confer an immediate selective advantage on an individual (generally in a group with other related individuals) rather than yield an ultimate long-term benefit for the group or species as a whole. Williams' pioneering work on the evolution of sex, senescence, and individually harmful social adaptations was based on this premise.

Taking a mathematical approach, Maynard Smith introduced game theory to the study of evolution. (Game theory postulates that the net benefit to an individual in a group of two or more depends on the behavior or strategies of the other individuals in the group.) He also introduced the notion of "evolutionarily stable strategies," that is, strategies adopted by an entire population that cannot be perturbed by other competing strategies (*8*). Game theory has proved fruitful for solving a broad range of evolutionary paradoxes, such as why the life histories (reproduction and survival) of organisms are so different, why evolution has maintained sex, the variety of animal behaviors that exist, and in particular why there is cooperation between individuals in a population.

Collectively, the three prizewinners have participated in the two greatest advances in evolutionary biology this century: the establishment of the modern synthesis and the realization that individual selection is more important than group selection. Mayr was instrumental in incorporating evolutionary thinking into systematics and biogeography; Williams and Maynard Smith laid the foundation for what is called the adaptationist program. This program states that evolution can be primarily explained in terms of natural selection maximizing fitness under existing environmental conditions.

Mayr continues to work on philosophical and historical issues within evolutionary biology (*9*). Maynard Smith has recently started to study the evolution of bacteria (*10*), and Williams continues his work on aging and has advocated the application of evolutionary thinking to medicine (*11*). An important development in the last 10 years has been the study by Maynard Smith, together with Eörs Szathmáry (*12*), of the "major transitions"—that is, the changes in complexity of organisms through evolution—and their attempt to develop a common theory to explain the evolution of eukaryotes, sex, multicellularity, colonial life, and culture. The three prizewinners have not only contributed enormously to the field of evolutionary biology, but have actively participated in bringing Darwinian thinking to a very broad audience (*13*).


**References and Notes**

1. C. Darwin, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (Murray, London, 1859).
2. Th. Dobzhansky, *Am. Biol. Teach.* **35**, 125 (1973).
3. Important contributors to the modern synthesis were Th. Dobzhansky (1900–1975), G. G. Simpson (1902–1984), S. Wright (1889–1988), R. A. Fisher (1890–1962), and J. B. S. Haldane (1892–1964).
4. E. Mayr, *Systematics and the Origin of Species* (Columbia Univ. Press, New York, 1942); *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, MA, 1963); *Principles of Systematic Zoology* (McGraw-Hill, New York, 1969).
5. V. C. Wynne-Edwards, *Animal Dispersion in Relation to Social Behaviour* (Oliver & Boyd, Edinburgh, 1962).
6. W. D. Hamilton, *J. Theor. Biol.* **7**, 1 (1964); see also J. Maynard Smith, *Nature* **201**, 1145 (1964).
7. G. C. Williams, *Adaptation and Natural Selection* (Princeton Univ. Press, Princeton, NJ, 1966); see also *Natural Selection: Domains, Levels and Challenges* (Oxford Univ. Press, Oxford, 1992).
8. J. Maynard Smith, *Evolution and the Theory of Games* (Cambridge Univ. Press, Cambridge, 1982).
9. E. Mayr, *Proc. Am. Philos. Soc.* **139**, 317 (1995); see also *The Growth of Biological Thought: Diversity, Evolution, and Inheritance* (Harvard Univ. Press, Cambridge, MA, 1982).
10. J. Maynard Smith *et al.*, *Nature* **349**, 29 (1991); J. Maynard Smith *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **90**, 4384 (1993).
11. R. M. Nesse and G. C. Williams, *Why We Get Sick* (Times/Random House, New York, 1995).
12. J. Maynard Smith and E. Szathmáry, *The Major Transitions in Evolution* (Freeman/Spektrum, New York, 1995); *The Origins of Life: From the Birth of Life to the Origin of Language* (Oxford Univ. Press, Oxford, 1999).
13. E. Mayr, *This Is Biology* (Harvard Univ. Press, Cambridge, MA, 1997); *One Long Argument: Charles Darwin and the Genesis of Modern Evolutionary Thought* (Harvard Univ. Press, Cambridge, MA, 1991); G. C. Williams, *Plan and Purpose in Nature* (Weidenfeld & Nicholson, London, 1996); J. Maynard Smith, *The Problems of Biology* (Oxford Univ. Press, Oxford, 1986).


The author is in the Department of Biology, University of Oslo, Post Office Box 1050 Blindern, N-0316 Oslo, Norway. E-mail: n.c.stenseth@bio.uio.no

## References and Notes

[10] **How Clonal are Bacteria?**
John Maynard Smith; Noel H. Smith; Maria O'Rourke; Brian G. Spratt
*Proceedings of the National Academy of Sciences of the United States of America*, Vol. 90, No. 10. (May 15, 1993), pp. 4384-4388.
Stable URL:
http://links.jstor.org/sici?sici=0027-8424%2819930515%2990%3A10%3C4384%3AHCAB%3E2.0.CO%3B2-I