classes of molecules with interesting biochemical and pharmacological properties.

Further extension of our studies should involve the design of hitherto unobserved secondary structures of peptides. Judicious use of the stabilizing forces provided by the medium should allow one to stabilize energetically unfavorable conformations of the peptide bond, such as dihedral bond angles and even cis-peptide bonds which, in turn, should generate novel secondary structures.

On the basis of the available data it appears that peptides interact with their receptor macromolecules by a mechanism which is similar to that of information-bearing molecules of singular tertiary structure. In particular, the number of functional groups interacting with the receptor must be small and most of the amino acid components serve a purely structural role, namely, the proper positioning of the ligand functions.

References and Notes

1. E. T. Kaiser and F. J. Kézdy, *Proc. Natl. Acad. Sci. U.S.A.* **80**, 1137 (1983).
2. G. Barany and R. B. Merrifield, in *The Peptides*, E. Gross and J. Meienhofer, Eds. (Academic Press, New York, 1980), vol. 2, p. 3.
3. See, for example, T. Blundell and S. Wood, *Annu. Rev. Biochem.* **51**, 123 (1982).
4. Abbreviations for the amino acid residues are: Ala, alanine; Arg, arginine; Asn, asparagine; Asp, aspartic acid; Cys, cysteine; Gln, glutamine; Glu, glutamic acid; Gly, glycine; His, histidine; Ile, isoleucine; Leu, leucine; Lys, lysine; Met, methionine; Phe, phenylalanine; Pro, proline; Ser, serine; Thr, threonine; Trp, tryptophan; Tyr, tyrosine; Val, valine.
5. M. Schiffer and A. B. Edmundson, *Biophys. J.* 7, 121 (1967).
6. P. Y. Chou and G. D. Fasman, *Annu. Rev. Biochem.* **47**, 251 (1978).
7. C. Edelstein, F. J. Kézdy, A. M. Scanu, B. W. Shen, *J. Lipid, Res.* **20**, 143 (1979).
8. D. J. Kroon, J. P. Kupferberg, E. T. Kaiser, F. J. Kézdy, *J. Am. Chem. Soc.* **100**, 5975 (1978).
9. D. Fukushima *et al.*, *ibid.* **101**, 3703 (1979).
10. J. P. Segrest *et al.*, *FEBS Lett.* **38**, 247 (1974).
11. W. M. Fitch, *Genetics* **86**, 623 (1977).
12. A. D. McLachlan, *Nature (London)* **267**, 465 (1977).
13. D. Fukushima *et al.*, *Ann. N.Y. Acad. Sci.* **348**, 365 (1980).
14. S. Yokoyama, D. Fukushima, F. J. Kézdy, E. T. Kaiser, *J. Biol. Chem.* **255**, 7333 (1980).
15. W. F. DeGrado, F. J. Kézdy, E. T. Kaiser, *J. Am. Chem. Soc.* **103**, 679 (1981).
16. E. Habermann, *Science* **177**, 314 (1972).
17. E. Schröeder, K. Lübke, M. Lehmann, I. Beitz, *Experientia* **27**, 764 (1971).
18. W. F. DeGrado, G. F. Musso, M. Lieber, E. T. Kaiser, F. J. Kézdy, *Biophys. J.* **37**, 329 (1982).
19. J. W. Taylor, R. J. Miller, E. T. Kaiser, *J. Am. Chem. Soc.* **103**, 6965 (1981).
20. G. R. Moe, R. J. Miller, E. T. Kaiser, *ibid.* **105**, 4100 (1983).
21. G. R. Moe, in preparation.
22. W. Vale, J. Spiess, C. Rivier, J. Rivier, *Science* **213**, 1394 (1981).
23. S. H. Lau, J. Rivier, W. Vale, E. T. Kaiser, F. J. Kézdy, *Proc. Natl. Acad. Sci. U.S.A.* **80**, 7070 (1983).
24. J. W. Taylor, R. J. Miller, E. T. Kaiser, *Mol. Pharmacol.* **22**, 657 (1982).
25. J. W. Taylor, R. J. Miller, E. T. Kaiser, *J. Biol. Chem.* **258**, 4464 (1983).
26. J. Blanc, R. J. Miller, E. T. Kaiser, *ibid.* **258**, 8277 (1983).
27. S. H. Lau, private communication.
28. V. Bonnevie-Nielsen, K. S. Polonsky, J. J. Jaspan, A. H. Rubenstein, T. W. Schwartz, H. S. Tager, *Proc. Natl. Acad. Sci. U.S.A.* **76**, 3189 (1979), and references therein.
29. E. M. Ross and A. C. Gilman, *Annu. Rev. Biochem.* **49**, 533 (1980).
30. V. Bonnevie-Nielsen and H. S. Tager, *J. Biol. Chem.* **258**, 11313 (1983).
31. G. F. Musso, E. T. Kaiser, F. J. Kézdy, H. S. Tager, *Abstracts, Eighth American Peptide Symposium, Tuscon, Ariz., May, 1983.*

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Balzan Prize to Ernst Mayr

Stephen Jay Gould

In the public fanfare that accompanies the announcement of Nobel prizes, and in the exalted status conferred thereby upon recipients, we often forget that these premier awards are quite narrow in the scope of disciplines so honored. Entire fields are excluded. Thus, the second greatest revolution in the history of geology, the establishment of plate tectonic theory, has won no Nobel notoriety for its founders. The prizes pass over an entire style of scientific work, thus reinforcing a narrow and conventional stereotype about our shared enterprise.

The Nobel prizes focus on quantitative, nonhistorical, deductively oriented fields with their methodology of perturbation by experiment and establishment of repeatable chains of relatively simple cause and effect. An entire set of disciplines, different though equal in scope and status, but often subjected to ridicule because they do not follow this pathway of "hard" science, is thereby ignored: the historical sciences, treating immensely complex and nonrepeatable events (and therefore eschewing prediction while seeking explanation for what has happened) and using the methods of observation and comparison.

Evolutionary biology is a quintessential historical discipline. It has, since the mid-19th century, been continually in the forefront of science—both in its technical progress *in camera*, and in the public eye. Yet only once, when the definition of medicine was stretched to include the ethologists K. Lorenz, N. Tinbergen, and K. von Frisch, has an evolutionary biologist won a Nobel Prize.

Fortunately, the Balzan prizes, with their wider range, can rectify this situation and honor great historical scientists. In 1981, they cited a trio of geophysicists for work in plate tectonics: P. McKenzie, D. H. Matthews, and F. J. Vine. Last year, they honored the great plant physiologist K. Thimann. The Balzan prizes were first awarded in 1961 from a foundation established by Angela Lina Balzan to honor her father, Eugenio Balzan, former head of Italy's leading newspaper, *Corriere della Sera*. After designating two scientists (the ethologist K. von Frisch and the mathematician A. Kolmogorov), several scholars in the humanities, and leading fighters for "humanity, peace and brotherhood among peoples," the prizes were discontinued for 14 years and only reinstated in 1978. This year, and for the first prize designated in zoology, the Balzan Foundation has rightly selected our greatest living evolutionary biologist, Ernst Mayr.

Ernst Mayr was born and educated in Germany, receiving his Ph.D. in 1926 at the University of Berlin. Between 1928 and 1930, as an assistant at the Zoological Museum of the University of Berlin, he led three expeditions to study birds in various parts of New Guinea and the Solomon Islands. He emigrated to the United States in 1932, where he worked until 1953 as curator of birds at the American Museum of Natural History in New York. He then moved to Harvard as Alexander Agassiz Professor of Zoology at the Museum of Comparative Zoology, where he served as director from 1961 to 1970. As professor emeritus since 1975, Mayr has worked continuously and relentlessly at a pace that would exhaust most men half his age and

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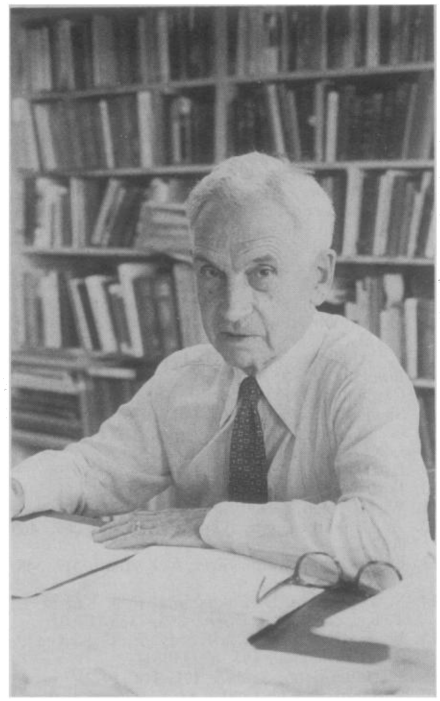
with a quality that is simply immeasurable.

Mayr's early work focused on the descriptive taxonomy and biogeography of the Pacific birds that he had observed and collected on his expeditions. These labors culminated in a large volume that took 10 years to write and that Mayr proudly and rightly displays as his finest work—the *List of New Guinea Birds* published by the American Museum in 1941. People who do not understand the nature and purpose of taxonomic work might dismiss such a volume as a simple compilation, requiring immense patience and hard work to be sure, but reflecting no superior intellectual skill. But each species is a separate puzzle, a little exemplar of scientific methodology requiring hypothesis, test, and comparison for a resolution of range and a definition of content. As Mayr proceeded, he sharpened his notion of species as fundamental units in nature and deepened his understanding of evolution, finally emerging as a thorough Darwinian from the eclectic and partly Lamarckian tradition that he had learned in Germany.

These taxonomic studies in ornithology led directly to the general work in evolutionary theory that has established Mayr's worldwide reputation. He stands firmly among the handful of great biologists who, from the mid-1930's until the Darwinian centennial celebrations of 1959, established from preceding chaos a paradigm of evolutionary thought known as the "modern synthetic" theory. Darwinian perspectives so dominate evolutionary thought today that most people assume it was so in the beginning, and is now, and ever shall be—right from the *Origin of Species* in 1859. But while Darwin convinced all thinking people that evolution had occurred, he was not notably successful in advancing natural selection as its mechanism. The rediscovery of Mendel initially fostered chaos, not resolution, as the early geneticists advocated macromutation as an alternative to slow and continuous natural selection. In 1922, in a famous article in *Science* (20 January, p. 55) the great British geneticist William Bateson wrote: "When students of other sciences ask us what is now currently believed about the origin of species we have no clear answer to give. Faith has given place to agnosticism." Thus, in helping to establish the modern synthetic theory, with mutation as a source of variation and natural selection as the primary agent of evolutionary change, Mayr became an architect of one of our century's most important scientific achievements.



Ernst Mayr [Photo by M. K. Kelly]

In 1942, Mayr published the first of three great books (most of us would leave this world content if we could write just one adequate volume), *Systematics and the Origin of Species*. This work played a pivotal role in the developing synthesis by integrating one of the classical subdisciplines of natural history with the neo-Darwinian core of the new theory. Later in the decade, G. G. Simpson performed the same task for paleontology and G. L. Stebbins for botany, as the synthesis drew more and more fields within its orbit. At the same time, Mayr also played a key role in the organizational side of evolution's advance. He was a founder in 1946 and first secretary of the Society for the Study of Evolution. He also served as first editor of its journal, *Evolution* (from 1947 to 1949), where he established its continuing reputation as the leading periodical in our field.

Mayr's distinctive intellectual contribution to the synthesis lies squarely with his work on theories of speciation—the production of diversity. Ironically, although Darwin called his great book the *Origin of Species*, and although the diversity of Galápagos mockingbirds inspired some of his first musings about evolution, Darwin said rather little about speciation—the production of diversity by the branching of phyletic lines. He doubted the reality of species (as merely momentary configurations along a gradient of constant change), and focused in any case upon the process of evolutionary transformation within lineages, not on the production of new lineages by branching. This emphasis continued, unconsciously abetted no doubt by one of the deepest biases in Western thought—our desire to view history as progress. The study of diversity and its production received decidedly short shrift from nearly all major evolutionary thinkers. A tradition even arose for viewing speciation as a kind of biological extravagance, quite unrelated to the fundamental path of progress. Julian Huxley wrote, for example: "Species formation constitutes one aspect of evolution; but a large fraction of it is, in a sense, accident, a biological luxury, without bearing upon the major and continuing trends of evolutionary process."

Mayr put speciation right back at the center of evolutionary thought, where it so clearly belongs. In helping to establish the "biological species concept," he sought a definition of species—as interacting units reproductively isolated from other populations—that would make them real objects in nature, not the artifices of a taxonomist's compilation. This concept has emerged as a centerpiece of disciplines as diverse as ecology and behavioral biology, where so much of interest involves the interaction among species seen, at least in spatiotemporal moments, as objective units.

The establishment of species as real objects also requires a coherent theory for their origin. Before Mayr, and largely because the subject received so little attention, most evolutionists, when they thought about it at all, held vaguely sympatric ideas about speciation (in sympatric speciation, new forms arise in the same geographic region as their ancestors). But Mayr's work on Solomon Island birds had pressed upon him the importance of geographic isolation as a precondition to speciation. When populations are spatially separated from their ancestors, they are better able to accumulate enough genetic differences to become new species by the primary criterion of reproductive isolation. Mayr added to this basic hypothesis of allopatry (speciation in geographic regions separated from ancestors) the important idea that such isolated populations are usually very small, and peripheral in location with respect to the ancestral range (for peripheral environments often differ sharply from those in the center of the ancestral range, thereby enhancing selective pressures for change). Mayr developed this concept of speciation in small, peripherally isolated populations into his distinctive theory of peripatric speciation. Forty years later, and buoyed by his continuous, spirited defense, this theory has not only held up remarkably well as by far the major mode of speciation in nature, but has also been unusually fruitful in extension and implication.

The theory of peripatric speciation became the centerpiece of Mayr's second great book, *Animal Species and Evolution* published in 1963. Whereas the 1942 book had been provocative and initiating, this definitive work of 800 pages masterfully integrated everything that the triumphant synthesis said or implied about species. Theodosius Dobzhansky called it "a truly great work, which will remain a landmark in the biology of our age."

This book, and Mayr's unrelenting crusade for neo-Darwinism in general and the peripatric theory in particular, exerted an enormous influence over all students of my generation. I will wager a great deal that any compilation would trace a majority of new concepts that we now cherish or debate to Mayr's (often indirect) inspiration. If I may cite just one example in the way of personal witness: when, in the late 1960's, Ernst took me on as coteacher of the advanced seminar in evolution that he had previously shared with G. G. Simpson, he told me that their classroom debate had always centered on the concept of species—Mayr plugging for a "nondimensional" view of species as real entities, Simpson for the artificial character of species as arbitrary segments of evolving lineages. I dismissed this debate as a mere semantic quibble, reasoning that, for the moment, species were as Mayr stated and, over geological time, as Simpson opined. But the idea kept rattling about in the recesses of my mind—Ernst was just too smart to identify a debate about words as a key separation between two great thinkers. Finally, after much discussion with Niles Eldredge (who had seen the implications more clearly), I realized in a kind of flash that two fundamental world views were at stake: either evolutionary change accumulates primarily in events of *branching* speciation (which are geologically instantaneous at the characteristic peripatric rate, however slow in terms of our short lives), or evolution is largely the story of more gradual change *within* phyletic lineages. Mayr's insights therefore led, when translated into geological terms, to the theory of punctuated equilibrium.

As if all this were not enough (*Dayenu*, as my grandmother would have said), Mayr took on a new profession in midcareer and has achieved enough in it to merit such a prize for this "afterthought" alone. He became a historian of science, focusing on his own beloved field of evolution and the historical side of biology in general. He has written famous general papers on Lamarck's thought, Darwin's development of the idea of natural selection, and, in an important challenge to Kuhn's model of scientific revolution, on the establishment of Darwinism. His colleagues in the history of science honored him with a festschrift on the occasion of his 75th birthday.

Then, during the past 10 years, at an age when most people have finished their original work, or turn inward to write an autobiography, Mayr embarked on the most ambitious project of his career—a thorough survey of the history of evolutionary biology, culminating in 1982 in his third great book, *The Growth of Biological Thought*. It is a grand and curious work, not an objective history in the term's usual sense, but an embodiment of Mayr's personal vision extended through time. It is, as one historian remarked, not a secondary source, but a primary source. I say this not as a criticism, but as a tribute to the finest kind of inspired writing. As the great historian Herbert Butterfield said in his *Whig Interpretation of History*: "The historian may be cynical with Gibbon or sentimental with Carlyle; he may have religious ardor or he may be a humanist. . . . It is not a sin in a historian to introduce a personal bias that can be recognized and discounted. The sin in historical composition is the organization of the story in such a way that bias cannot be recognized."

Mayr's book tends to view the entire pageant of historical biology as a great battle between Platonic "essentialists" who focus on unvarying types or, if evolutionarily inclined, must view the process as saltation from one essence to another, and "population thinkers" who understand that variation is irreducible reality and become receptive to a Darwinian model of change. This 2000-year struggle culminated in the triumph of population thinking in the modern synthesis, with Mayr's own work as a prominent contribution. And then I finally understood. *The Growth of Biological Thought* is Mayr's autobiography, writ large.

About 2 years ago, I attended a graduate student's talk on some arcane matter in evolutionary systematics. Mayr was there, and he joined the subsequent discussion with a vigor and definiteness that was simply intimidating. Initially, I became annoyed that he would so assert his authority against such a younger colleague. But then I understood that I had it all backwards and that I was seeing the essence (pardon your least favorite word, Ernst) of Mayr's greatness. He remains so in love with his subject, so enthusiastic about its promise and intellectual content, that he couldn't hold back. He was arguing with all the verve of a graduate student because, by God, he remains one himself in heart, energy, and commitment.

Ernst Mayr is a marvel and an inspiration to us all.