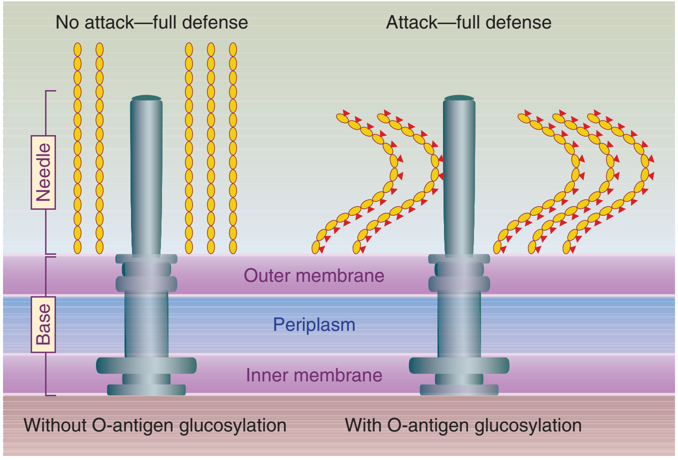


Shigella's sword and shield strategy. The pathogen *Shigella flexneri* causes disease by invading gut epithelial cells, a process mediated by effector proteins delivered by its plasmid-encoded type III secretion system (gray). The host responds to replication of *Shigella* inside gut epithelial cells with an aggressive inflammatory reaction. The bacterium defends itself against antibacterial inflammatory mediators by expressing at its surface a lipopolysaccharide containing O-antigen polysaccharide repeats (yellow). These repeats extend out from the bacterial cell surface, and may impede the ability of the needle tip to contact host cells. This dilemma is solved by a resident bacteriophage that adds one glucose residue (red triangle) to each of the repeating O-antigen units. Glucosylation causes a conformational change, from a more filamentous (**left**) to a more compact O-antigen structure (**right**). The more compact structure allows exposure of the needle tip, enabling invasion of gut epithelial cells to proceed without compromising the ability of the O-antigen polymer to protect the bacterium against host inflammatory mediators.

et al. study suggests that an inhibitor of Gtr-mediated O-antigen glucosylation in *Shigella* bacteria could ameliorate the symptoms of shigellosis by preventing delivery of type III effector proteins to gut epithelial cells of the host. The GtrV protein encoded by the bacteriophage operon catalyzes the transfer of a glucosyl residue via an α1,3 linkage to rhamnose II of the O-antigen unit (*9*). GtrV is an integral membrane protein, but its periplasmic loops are assumed to be functional because O-antigen modification is thought to take place in the bacterial periplasm. Developing bacterial virulence inhibitors that target periplasmic proteins is expected to be considerably easier than developing drugs against intracellular bacterial targets.

In enteropathogenic *Escherichia coli*, one of the translocated proteins, EspA, polymerizes to form an extension to the injectisome needle (*10*), eliminating the need to modify the lipopolysaccharide for contact with its host. The length of the needle seems to vary among different pathogens. For example, the needle possessed by *Salmonella* is longer than that of *Shigella* (*2*). In *Yersinia*, the length of the needle is governed by the size of the YscP protein (*11*). There is a linear relation between needle length and the number of amino acids in YscP. Even though the mechanism for this molecular ruler remains unknown, one end of YscP may be associated with the base and the other with the growing tip of the needle. When the YscP protein is fully stretched, a signal is delivered blocking further polymerization and preventing the needle from growing any longer. As Mota *et al.* (*12*) show on page 1278 of this issue, *Yersinia* bacteria with short needles are less effective at delivering the YopP effector protein into target cells than are those with normal-length or long needles (*12*). Thus, there is a minimum needle length required for operation of the *Yersinia* injectisome. The length of the needle correlates with the length of YadA, an adhesin-forming microfilament extending about 28 nm beyond the bacterial outer membrane. Mota *et al.* demonstrate that decreasing the length of YadA in the short-needle *Yersinia* mutants suppressed the translocation defect by decreasing the distance between the needle and the host cell. As the two new studies show, needle length in both *Yersinia* and *Shigella* has evolved together with other surface structures to allow the bacterial needle tip to interact with host cell membranes. Simultaneously, elegant mechanisms have evolved in these bacterial species to ensure that the adhesive and protective functions of other filamentous surface structures are not compromised.

References

1. R. Rosqvist, K. E. Magnusson, H. Wolf-Watz, *EMBO J.* **13**, 964 (1994).
2. A. P. Tampakaki *et al.*, *Cell Microbiol.* **6**, 805 (2004).
3. T. C. Marlovits *et al.*, *Science* **306**, 1040 (2004).
4. P. Cossart, P. J. Sansonetti, *Science* **304**, 242 (2004).
5. N. P. West *et al.*, *Science* **307**, 1313 (2005).
6. M. Hensel *et al.*, *Science* **269**, 400 (1995).
7. S. Guan, D. A. Bastin, N. K. Verma, *Microbiology* **145**, 1263 (1999).
8. A. M. Kauppi *et al.*, *Chem Biol.* **10**, 241 (2003).
9. H. Korres, N. K. Verma, *J. Biol. Chem.* **279**, 22469 (2004).
10. S. J. Daniell *et al.*, *Mol. Microbiol.* **49**, 301 (2003).
11. L. Journet, C. Agrain, P. Broz, C. R. Cornelis, *Science* **302**, 1757 (2003).
12. L. J. Mota, L. Journet, I. Sorg, C. Agrain, G. R. Cornelis, *Science* **307**, 1278 (2005).

10.1126/science.1109836

RETROSPECTIVE: EVOLUTION

Ernst Mayr (1904–2005)

Jerry A. Coyne

The death of Ernst Mayr at age 100 on 3 February marks the end of a scientific era. Mayr was the last living architect of the "Modern Evolutionary Synthesis," one of the greatest intellectual achievements of 20th-century biology. His 1942 book, *Systematics and the Origin of Species*, was, along with Theodosius Dobzhansky's *Genetics and the Origin of Species* (1937), largely responsible for the seminal achievement of the Synthesis. This was the demonstration that evolutionary patterns and processes in natural populations are consistent with Darwinian natural selection, the heredity mechanisms revealed by laboratory work in genetics, and the mathematical theories of population genetics.

It is not too much of an exaggeration to call Mayr the Darwin of the 20th century. Although nobody—least of all Mayr—would claim that his stature and achievements equaled Darwin's, Mayr nevertheless solved a major problem that eluded Darwin: the origin of biodiversity. Despite the title of his greatest work, Darwin made little contribution to understanding the origin of species. Rather, he explained the origin of features *within* species. Although others contributed to explaining how new species arise, Mayr and Dobzhansky get the most credit for synthesizing and revitalizing studies of speciation.

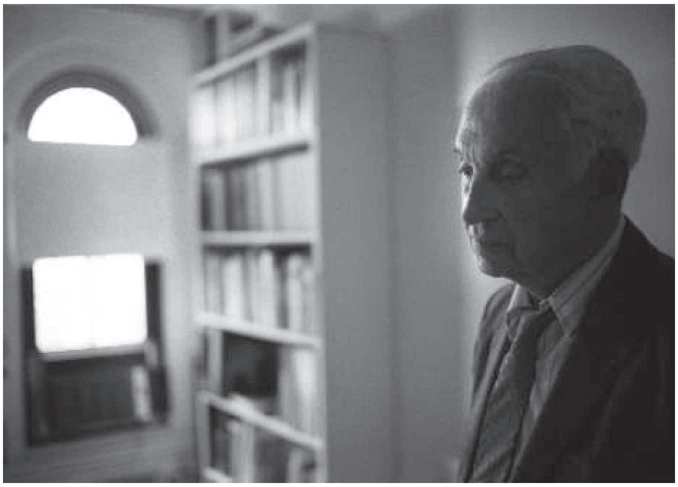
Mayr made three major contributions to understanding biodiversity. First, along with his colleague Dobzhansky, he recognized it as an unsolved problem. Why is nature divided into discrete groups—species—rather than forming an organic continuum? And how could the gradual and continuous process of Darwinian natural

The author is in the Department of Ecology and Evolution, University of Chicago, Chicago IL 60637, USA. E-mail: j-coyne@uchicago.edu

selection produce these discontinuities? Thus, Mayr made "the species problem" a central concern of evolutionary biology.

Second, in his "biological species concept," Mayr defined species as groups of interbreeding populations in nature, unable to exchange genes with other such groups living in the same area. Barriers to gene exchange—the so-called reproductive isolating mechanisms—include phenomena such as mate discrimination and sterility of hybrids. This characterization of species immediately made the study of speciation a tractable scientific problem: The origin of species thus became equivalent to the origin of isolating mechanisms.

Finally, in his theory of allopatric speciation, based on his observations as a naturalist and museum worker, Mayr showed how these isolating barriers could arise. Geographically isolated populations of a single species undergo independent evolutionary divergence, and reproductive barriers arise as a simple and accidental by-product of this differentiation. He thus showed that the origin of species involved well-known Darwinian processes, but processes that act in concert with geographic barriers.



These views, set out and defended by Mayr in a series of papers continuing until his death, reenergized work on speciation and made it a respectable field—and a contentious one. Some biologists have denied the reality of species, argued about whether the biological species concept is a proper definition, and asserted that species have arisen without geographic barriers. Opposition to Mayr also stemmed from his forceful and uncompromising style of argument (I once heard him say, "I'm not dogmatic, I'm simply *right*!"). Nevertheless, Mayr's ideas form the core of modern views of speciation, are accepted by most evolutionists, and have inspired much recent work. In 1963, Mayr revised and extended his theories in perhaps his most famous work, the magisterial *Animal Species and Evolution*. The "big green book," written in his characteristically elegant and lucid prose, was responsible for turning many students, including myself, into evolutionary biologists.

Such broad acceptance, however, does not extend to what Mayr called "perhaps the most original theory I have ever proposed": that of founder-effect speciation. This idea derived from Mayr's observation that birds on isolated islands often diverged spectacularly in their appearance. Mayr believed that in most cases speciation involved the movement of a few individuals into a geographically isolated area, followed by what he called a "genetic revolution"—a drastic alteration of the genome involving changes in many coadapted genes. Although this theory was once influential, and contributed to Niles Eldredge and Stephen Gould's theory of punctuated equilibrium, it has fallen on hard times owing to a lack of field and laboratory evidence and to the presence of alternative explanations (such as new environments) for the divergence of isolated populations.

Mayr's career also showed striking parallels with Darwin's. Both became naturalists in their youth, Darwin specializing in beetles and Mayr in birds. Both started medical school, but abandoned this study to return to their avocations. Both went on expeditions that critically influenced their later work: Darwin had his *Beagle* voyage, and Mayr a 2.5-year trip to New Guinea and Melanesia (from 1928 to 1930) underwritten by his mentor Erwin Stresemann and Lord Rothschild. Like Darwin, who carefully monographed his barnacles, Mayr's work was informed by close acquaintance with variation in nature. His observations on the variation and distribution of birds, recorded in nearly 300 papers, led directly to his theory of geographic speciation, and culminated in the publication (at age 97!) of the monographic *Birds of Northern Melanesia: Speciation, Ecology, and Biogeography*. Written with Jared Diamond, this is one of the best books on any aspect of bird biology.

Finally, both Mayr and Darwin achieved their fame largely through synthesizing an enormous and scattered group of facts that supported their theories. Mayr readily admitted that the biological species concept and allopatric speciation had been suggested by earlier workers, and even drew attention to their contributions in his historical writings. Nevertheless, the great influence and authority of *Systematics and the Origin of Species*, and of *Animal Species and Evolution*, derive from the collection and collation of a vast amount of data from biogeography, systematics, and genetics.

Mayr was a polymath, and one cannot do justice to his many other accomplishments in this limited space. He wrote 25 books and nearly 700 papers, all while performing curatorial duties, first at the Berlin Museum, and later at the American Museum of Natural History and Harvard's Museum of Comparative Zoology. His many writings on systematics (including *Principles of Systematic Zoology* in 1969) helped bring taxonomy into the modern era, replacing the haphazard naming of species, subspecies, and varieties with a more rigorous approach based on the appreciation of naturally occurring variation within species.

He helped found the Society for the Study of Evolution in 1946 and became the first editor of its journal, *Evolution*. His long-standing interest in the history and philosophy of biology yielded many books and papers including, in 1982, *The Growth of Biological Thought*, a history of organismal biology that is required reading for evolutionists. He founded *The Journal of the History of Biology* in 1967. His major contributions to the philosophy of biology were his analyses of species concepts, and his relentless attacks on the reductionism of philosophers who tried to analyze biology as if it were physics. Finally, Mayr remained an avid ornithologist throughout his life, writing field guides, checklists, and describing more species of birds (26) than any other living person.

As he approached the century mark, Mayr retained his critical faculties and productivity, publishing prolifically long after many scientists have retired to devote themselves to reconciling science and religion. He finally acknowledged his advancing age, priding himself on outliving his fellow evolutionary synthesist Sewall Wright (who died in 1988 at the age of 99) and joking that his dwindling years made him afraid to buy unripe bananas. In the end, his body betrayed him, developing terminal cancer, but Mayr faced death bravely and serenely. He died having received a multitude of honors and awards, but the greatest honor of all was his legacy to evolutionary biologists, many of whom are enormously influenced by his work despite never having met him. At the end of his hundredth-birthday symposium at Harvard's Museum of Comparative Zoology last May, Mayr stood up and addressed those who came to pay him tribute. "I've had a wonderful life," he said. And so he did.

10.1126/science.1110718