# COMMENTARY

# EVOLUTIONARY BIOLOGY: PUZZLE SOLVING OR PARADIGM SHIFTING?

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PHILOSOPHER of science Thomas Kuhn (1970) suggested that scientific activity can broadly be divided into two phases: "normal" science and paradigm shifts. Normal science uses established frameworks of reference (paradigms) to solve specific problems, or puzzles, within those frameworks. Paradigm shifts occur when the puzzle-solving capability of the reigning paradigm becomes insufficient, precipitating a situation of crisis, which is resolved by the adoption of a new framework. It is a sort of punctuated equilibria theory of scientific discovery.

For example, so-called Ptolemaic astronomy had accounted for the positions of the planets since classical Greece (although Ptolemy himself lived later, in the 2nd century CE). Yet, by the time of Copernicus (16th century), and shortly thereafter because of the detailed astronomical measurements of the positions of the planets carried out by Tycho Brahe, a crisis had ensued. It took Copernicus, Brahe, Galileo, and finally Kepler (who had the fundamental insight that the planets not only orbit around the Sun—as Copernicus and Galileo had argued—but that they do so in elliptical, rather than circular, orbits) to complete the shift. Copernican-Galilean-Keplerian astronomy still represents the modern paradigm in the field.

It has always been difficult to apply Kuhn's ideas to biology, since fundamental new discoveries (e.g., the structure of DNA in 1953) have enriched the framework introduced by Charles Darwin, and that Theodosius Dobzhansky (1973) correctly identified as the paradigm in light of which everything else makes sense in biology. Indeed, the Modern Synthesis of the 1930s and 1940s can better be seen as an augmentation of Darwinian theory rather than a shift to a new framework. Even Stephen Jay Gould (2002) acknowledged that intellectual developments since the Synthesis are best understood as further ramifications of the twin Darwinian insight of descent with modification and natural selection as the explanatory principles of the history and diversity of life on Earth.

A cursory examination of the oral presentations and posters on display during the recent Evolution meetings, held at Stony Brook University, New York, 23–27 June 2006, and

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hosted by the Society for the Study of Evolution, the American Society of Naturalists, and the Society of Systematic Biologists, confirms the idea that evolutionary biology is healthy, and busy with puzzle solving. A lot of puzzle solving. Titles of sections at Evolution 2006 included "natural selection and contemporary evolution," "phylogenetic theory and methods," "adaptation," "speciation," "behavior and social evolution," and "comparative biology," to name a few. The societies' sponsored symposia included "species delimitation," the rather mysterious-sounding "alternative perspectives on evolutionary dynamics" (on modeling of complex phenomena such as the evolution of quantitative traits or of genome structure), "the evolution of behavioral phenotypes," "geographic gradients and species richness," and "integrative studies of evolutionary processes." (There was also a much-needed symposium on the threat of Intelligent Design creationism, but that is a different matter.) All of this is very exciting, but it has also become standard fare both at professional meetings and in technical papers. So, is evolutionary biology—almost 150 years after the publication of Darwin's *Origin of the Species*—busy just at puzzle solving, or are there new major ideas on the horizon?

Maybe it is a bit of both. I did not see anything at the Evolution 2006 meetings that smelled of paradigm shift. (Then again, these are recognized only after the fact, and even then not without considerable controversy among historians and philosophers of science.) But, I did hear several talks that promise major developments in the way we think of biological evolution, as well as how we go about connecting our empirical investigations to the corresponding conceptual frameworks (see Pigliucci and Kaplan 2006).

Some of the most interesting work I saw presented at Evolution 2006 actually dealt with well-known problems. For example, Kathleen Engelmann and Michael Purugganan (New York University) used the model system *Arabidopsis thaliana* to seriously address the perennial question of how to bridge the gap between our understanding of epistasis as a molecular phenomenon (gene products physically interacting with each other) versus the classic statistical, population-level treatment that is used in evolutionary theory. It turns out that a connection between the two can be made, but it is very complex, likely system-specific, and requires a lot of work. Megan Phifer-Rixey and collaborators (University of Pennsylvania) addressed another "well-known" evolutionary staple, natural selection. Surprisingly, almost a century and a half after the introduction of the concept by Darwin, we still have relatively few detailed studies of it. Phifer-Rixey's multipronged approach to understand the possible adaptive nature of shell color polymorphism in *Littorina obtusata* is a model of how such things ought to be done, by eliminating alternative explanations one by one, building what philosophers call a "consilience" of evidence that leads to a likely causal inference.

Yet another example of novel work within a well-established framework was represented by Abby Drake and collaborators' (University of Manchester) study of the evolution of dogs from wolves. The common wisdom—unchallenged for decades—was that artificial selection (Darwin's analog for his concept of natural selection) had arrived at dog breeds via neoteny, a type of heterochronic change from which a "juvenilization" of the phenotype results. But Drake and coworkers actually gathered quantitative measures of the skulls of wolves and 17 breeds of dogs, from which it appears that most dog breeds actually arose by simple proportioned dwarfism. As Thomas Huxley (Darwin's bulldog) would have put it, here is yet another example of a beautiful theory killed by an ugly fact.

At Evolution 2006 there were also talks that hinted at entirely new ways of looking at things, which, while again not exactly mandating a paradigm shift, may in fact require at least the rewriting of large sections of our textbooks. An example was the talk by Christina Richards et al. (Stony Brook University) on the possibility that epigenetic inheritance systems may play a role in the variation and evolution of natural populations, in particular of invasive species. Stay tuned for much more about the potential interplay between genetic and epigenetic inheritance (e.g., Jablonka and Lamb 2005). Similarly, Alex Badyaev (University of Arizona) provided one of the first convincing examples that genetic accommodation actually occurs in nature. The process has been proposed (e.g., West-Eberhard 2003) as a potentially crucial bridge between the immediate ability of organisms to respond to changes in the environment (phenotypic plasticity, see Pigliucci 2001) and the long-term genetic changes that more classically define the evolutionary process (Futuyma 1998).

Does all of this mean that a much-heralded "new synthesis" in evolutionary theory is around the corner? I think so, because new empirical and conceptual developments continue to enrich evolutionary biology far beyond the intellectual horizons delineated by Dobzhansky, Mayr, and Simpson, among others. However, as Gould (2002) has persuasively (if far too exhaustively) argued, we will see further growth from the foundations established by Darwin, not a fundamental rethinking of Darwinism. This means that evolutionary biology will keep defying Kuhn's model of paradigm shifts and, in the process, clearly distinguish the modus operandi of biology from that of physics.

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