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ESSAY

Darwin Still Rules, but Some Biologists Dream of a Paradigm Shift

By DOUGLAS H. ERWIN

Is Darwin due for an upgrade? There are growing calls among some evolutionary biologists for just such a revision, although they differ about what form this might take. But those calls could also be exaggerated. There is nothing scientists enjoy more than the prospect of a good paradigm shift.

Paradigm shifts are the stuff of scientific revolutions. They change how we view the world, the sorts of questions that scientists consider worth asking, and even how we do science. The discovery of <u>DNA</u> marked one such shift, the theory of plate tectonics another.

Many scientists suffer from a kind of split personality. We believe that this is the most exciting time to be working while yearning for the excitement of a revolution. What ambitious scientist would not want to be part of a paradigm shift? Not surprisingly, this yearning occasionally manifests itself in proclamations that a revolution is at hand.

To understand the current tumult it helps to understand how our evolutionary framework developed. It was constructed from the 1930s to 1950s by early geneticists, paleontologists and others, who disagreed about the efficacy of natural selection in driving evolutionary change (Darwin's big idea) and about the nature of the underlying genetic variation upon which natural selection could act. What they came to agree on was called the modern synthesis, and it established an intellectual zeitgeist that continues today, and has been continually adapted, in the best evolutionary fashion, to encompass new discoveries.

That synthesis holds that mutations to DNA create new variants of existing genes within a species. Natural selection, driven by competition for resources, allows the best-adapted individuals to produce the most surviving offspring. So adaptive variants of genes become more common. Although selection is often seen, even by biologists who should know better, as primarily negative, removing poorly adapted individuals, Charles Darwin understood that it was a powerful creative tool.

It is the primary agent in shaping new adaptations. Computer simulations have shown how selection can produce a complex eye from a simple eyespot in just a few hundred thousand years.

In the past few years every element of this paradigm has been attacked. Concerns about the sources of evolutionary innovation and discoveries about how DNA evolves have led some to propose that mutations, not selection, drive much of evolution, or at least the main episodes of innovation, like the origin of major animal groups, including vertebrates.

Comparative studies of development have illuminated how genes operate, and evolve, and this places less

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emphasis on the gradual accumulation of small genetic changes emphasized by the modern synthesis. Work in ecology has emphasized the role organisms play in building their own environments, and studies of the fossil record raise questions about the role of competition. The last major challenge to the modern synthesis came in the 1970s and 1980s as my paleontological colleagues, including the late <u>Stephen Jay Gould</u>, argued for a hierarchical view of evolution, with selection occurring at many levels, including between species.

Transitions between species documented by the fossil record seemed to be abrupt, perhaps too abrupt to be explained by the modern synthesis. If this were generally true, it could render irrelevant much of natural selection occurring within species, because just as mutations are produced randomly with respect to the needs of a species, with selection shaping these into new adaptations, new species might evolve randomly with species selection shaping them into evolutionary trends. This challenge was greeted with less than fulsome praise by evolutionary biologists studying changes within species. The resulting hubbub has yet to fully die down. But the newer work cuts closer to the core of the modern synthesis, and is potentially more revolutionary, because it addresses the fundamental question of how really new things happen in the history of life. What brought about the origin of animals, or the invasion of land?

The Achilles' heel of the modern synthesis, as noted by the philosopher Ron Amundson, is that it deals primarily with the transmission of genes from one generation to the next, but not how genes produce bodies. The recent discoveries in the new field of evolutionary developmental biology, or evo-devo, that the gene Pax-6 controls the formation of eyes in mice and humans, Nkx2.5 heart formation, and a suite of other genes the formation of the nervous system, has provided a means to investigate the genetic and developmental mechanisms influencing how the form of organisms has evolved, not just their genes. Perhaps the most exciting area in evolution is in exploring how rewiring the circuitry of genes produces different arthropod appendages, or wingspots on butterflies.

Eric H. Davidson, a colleague of mine at CalTech, has dissected the network of interactions between the genes that build the gut of sea urchins and starfish during development. When he compares these gene networks, there is a core of about five genes whose interactions are essential to forming the gut, and which have been preserved for some 500 million years.

One advantage developmental biologists have over paleontologists is that they can experiment on the development of these animals. Most of the genes in this network can be removed, and the developing embryo finds a way to compensate. But these five core genes, which form what Davidson calls a kernel, cannot be modified: change any one of them and no embryo forms at all. There is no reason to think that there was anything unusual about how this kernel first evolved some 500 million years ago (before sea urchins and starfish split into different groups), but once the kernel formed it locked development onto a certain path. These events, small and large, limit the range of possibilities on which natural selection can act. These questions about mechanism were not even being asked under the modern synthesis.

The failure to consider how biodiversity grows reflects an even more troubling flaw in the modern synthesis: it lacks any real sense of history. This may sound odd, as evolution is about history. A geologist would describe evolutionary theory as uniformitarian: "The present is the key to the past." This is the principle we use that by understanding how processes operate today we can understand past events. Evolutionary theory assumes that the processes we can study among fruit flies disporting themselves in a laboratory capture the broad sweep of

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evolutionary change.

But just as the erosive power of a river changes the future options for the course of the river, so evolution itself changes future evolutionary possibilities. This can happen in simple ways, as termites construct their own environment by building termite mounds. These mounds may last for dozens or hundreds of years and provide a sort of ecological inheritance for generations of termites.

The first cyanobacteria turned carbon dioxide into oxygen and set off a revolution that completely changed the chemistry of the oceans and atmosphere. Most species modify their environment and this often changes how selection affects them: they construct, at least in part, their own environment. As evolutionary biologists we have little understanding of what these processes mean for evolution.

Does all this add up to a new modern synthesis? There is certainly no consensus among evolutionary biologists, but development, ecology, genetics and paleontology all provide new perspectives on how evolution operates, and how we should study it. None of these concerns provide a scintilla of hope for creationists, as scientific investigations are already providing new insights into these issues. The foundations for a paradigm shift may be in place, but it may be some time before we see whether a truly novel perspective develops or these tensions are accommodated within an expanded modern synthesis.

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