

Humans and Primates: New Model Organisms for Evolutionary Developmental Biology?

If the animals in George Orwell's *Animal Farm* had been biologists, they might have proclaimed that while all organisms are unique, some are more unique than others. Perhaps with some justification, we humans often apply that essentialist view to our own especially interesting phenotype. We are the only striding, tailless bipeds; we have absurdly long ontogenies for our body size; our brains are approximately six times the size predicted for a mammal of our body mass; we are capable of complex language, planning, theories of mind, and so on. The list could go on, and we all have our particular favorite unique human attributes (sweat glands, penis size, etc.).

Human uniqueness is worthy of study for many reasons, both practical and intellectual, and there has been no lack of interest, speculation and research on the evolution of our peculiar phenotypes. However, very little of this research has been on development. For the most part, research on human evolution has focused on elucidating the fossil record, and quantifying patterns of variation (both genetic and phenotypic). There have been myriad studies of the evolution of human and primate ontogeny, including several recent volumes. But most of these studies have been fundamentally about understanding how patterns of ontogeny changed (e.g., via heterochrony analyses) rather than understanding the genetic mechanisms that underlie these changes. In other words, the evolutionary developmental biology ('evo-devo') revolution remains rarely applied to human and primate evolution.

There are several reasons for this unfortunate state of affairs. The most obvious is that we are not obvious model organisms for experimentation. We cannot manipulate human development in the way we can a mouse or a chick or a zebrafish. Primates are also problematic experimental models from both moral and practical points of view. Another problem is structural: human and primate evolutionary research has often occurred in the context of anthropology rather than biology departments. While well versed in anatomy, archaeology, and evolutionary theory, many paleoanthropologists do not have the specialized

training in developmental biology and genetics necessary to do evo-devo. In addition, infrastructure and funding for basic research in human evolution is very minimal compared to what is available for developmental biologists.

But these are problems that must be seen as challenges not excuses. As a field, evo-devo is vitally important for studying human and primate evolution because of the importance of studying process. Phenotypic patterns are the result of developmental processes. If we do not understand the processes that generate them, then we will not really be able to test hypotheses about what happened in human evolution.

In addition, we have drastically underestimated our own potential as a different kind of model animal for evolutionary developmental biology. We know an incredible amount about the human genome, human genetic variation, and human physiology and anatomy. We have a fantastic and well-studied fossil record of human evolution that is uniquely accompanied by an archaeological record that preserves information on behavior unavailable for any other species. Our nonhuman primate relatives are well studied for most of these categories (including the complete chimpanzee genome), providing a rich set of relevant comparative data. And new genetic techniques enable us to study candidate genes of relevance to human evolution in other species such as the mouse. In short, biologists should consider looking at humans and primates both as a means and an end to studying the evolution of development.

With this goal in mind, we have assembled a series of papers on human and primate evo-devo. So far, human and primate evo-devo is a small field. Even so, we were regrettably unable to entice everyone working on the subject to contribute. Nonetheless, the papers that follow should provide some ideas and perspectives on an array of topics interesting to a wide range of biologists.

—Daniel Lieberman