Removing Finalism from Developmental Biology

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Exploring Human Origins

Lowly Origin: Where, When, and Why Our Ancestors First Stood Up. Jonathan Kingdon. Princeton University Press, Princeton, NJ, 2003. 408 pp., illus. $49.50 (ISBN 0691050864 cloth).

The first systematic review of the anatomical differences between modern humans and the African apes, the chimpanzee and gorilla, was by T. H. Huxley in 1863. In an essay entitled "On the Relations of Man to the Lower Animals," which forms the central section of his book *Evidence as to Man's Place in Nature,* Huxley sets out his conclusion that the anatomical differences between modern humans and the chimpanzee and gorilla are less marked than the differences between the two African apes and the orangutan. Charles Darwin drew upon this evidence when, in 1871 in *The Descent of Man,* he suggested that the ancestors of modern humans were more likely to be found in Africa than elsewhere.

Developments in biochemistry and immunology during the first half of the 20th century allowed the search for evidence about the nature of the relationships between modern humans and the apes to shift from traditional gross morphology to the morphology of molecules. The earliest attempts to use proteins to determine primate relationships were made just after the turn of the century, but what Linus Pauling called "molecular anthropology" did not get into its stride until the early 1960s. Two scientists, Morris Goodman and Emil Zuckerkandl, made important contributions to this research. Goodman used techniques borrowed from immunology to show that the albumins of modern humans and chimpanzees were so alike that one could be confused with the other. Zuckerkandl employed enzymes to break hemoglobin up into its component peptides, and then used chromatography to demonstrate that the patterns made by the peptides from a modern human, a chimpanzee, and a gorilla were indistinguishable. A little later, Vince Sarich and Alan Wilson suggested that the modest differences in the serum protein albumin that separate modern humans from the living African apes may well have taken little more than 5 million years to accumulate.

By the late 1980s, advances in molecular biology meant that the differences between ape and human could be explored at the level of the genome. Studies of DNA hybridization confirmed that modern humans, chimpanzees, and gorillas were closely related, and subsequent DNA sequence analyses have confirmed Goodman's hunch that chimpanzees are more closely related to modern humans than to gorillas. Researchers cannot agree about the best way to calibrate the divergence of the chimp and human lineages. Estimates range from 5 million to 12 million years, with the early date having more adherents than the later one.

The impressive predictive power of biochemical methods contrasts with the dearth of fossil evidence about the history of the *Pan–Homo* clade. You will search the paleontological literature in vain for any fossils that are claimed to represent either the common ancestor of the

Pan–Homo clade, or of any creatures belonging to closely related clades. Nor will you find any fossil evidence that has been assigned to the chimpanzee part of the *Pan–Homo* clade. Most scenarios that purport to "explain" the origin of the human clade have either been refuted by paleoenvironmental evidence (e.g., taxa that almost certainly belong to our own, hominin, clade are not confined to savannah environments), or they are so far-fetched that researchers are loath to devote time to refuting them.

Jonathan Kingdon is not a member of the early hominin Mafia, and that alone makes him singularly well equipped to cast an eye over the thorny problem of human origins. He was talent-spotted by Julian Huxley, who, impressed by Kingdon's knowledge of the wildlife in Uganda's national parks, suggested that he should abandon teaching fine arts at Makerere University and switch to zoology. Thankfully, Jonathan Kingdon did not altogether abandon fine arts, and he is well known for combining his zoological and artistic talents in books that capture the essence and evolutionary context of African wildlife in a unique way.

The short title of Kingdon's latest book uses the last two words of Darwin's *Descent of Man.* Darwin ends the book by giving his readers a lesson in evolution and reminding them that "man still bears in his bodily frame the indelible stamp of his lowly origin." In case you miss the literary reference, the author helpfully subtitles the book "Where, When, and Why Our Ancestors First Stood Up." Scientists are supposed to eschew the "why" questions, but Kingdon sensibly casts these fetters aside and tackles the "why" question with gusto. Nor does he shy away from controversy.

There is presently a substantial schism in the early hominin Mafia family. The West Coast side of the divided family takes anagenesis (the process by which one species evolves into a new species) as its null hypothesis. According to this view, all fossil hominins belong to a single lineage of time-successive taxa unless proved otherwise. The null hypothesis of the East Coast faction is quite different. Recognizing that the evolutionary history of most other mammals is complex and "bushy," this faction holds that even if we were sure that the existing hominin fossil evidence faithfully represented all the diversity that has ever existed, we could not reconstruct the branching pattern with any confidence because it, like that of most mammalian taxa, is too bushy. Thus the prejudice of the East Coasters is a form of uniformitarianism: It rests on the essential similarity of evolutionary branching patterns in different taxa. In this view, a simple linear explanation of human evolution flies in the face of a more complex comparative reality.

The West Coast branch of the family accuses their East Coast relatives of being unscientific, and of doing "X Files" paleontology. The East Coast family are generally more tolerant of their West Coast colleagues and, even when provoked, their harshest criticism is that the West Coasters tend to interpret the world in too simplistic a fashion. Jonathan Kingdon has never been a fence sitter, and in this instance he comes down unequivocally on the side of the East Coasters. He cites evidence of many living animals that show at least as much, and probably more, taxonomic diversity than that envisaged by the East Coasters. His scenario is as follows. The ancestor of the *Pan–Homo* clade returned to Africa from Asia about 10 million years ago. By this time it was much less dependent on trees for its habitat, and Kingdon thinks that its niche was, or became, that of a ground-dwelling ape, trunk erect and carefully sifting through the forest floor for foodstuffs. The taxonomic diversity some see in the hominin fossil record would have come from the effective isolation provided by the patchwork quilt of eight or so major lake basins scattered across Africa.

Kingdon has read widely and wisely. There are a few glitches in his book: Most of the sensation in the face travels with the three divisions of the trigeminal nerve, and it is the mammalian middle ear, not the inner ear, that has complex homologies with the jaws of earlier vertebrates. But these are trivial concerns, and the confusions are uncharacteristic. The text is riddled with evidence that Kingdon is one of the few people who have the breadth of interests and the practical knowledge of contemporary African wildlife to comment authoritatively about the ecology and diversity of its flora and fauna.

In Chicago's excellent Field Museum, there was (and maybe still is) an exhibit about Africa. To try and convey the sheer size of that continent, an outline of Africa has been traced on the floor. Within it, to scale, are the outlines of many other parts of the world that we routinely think of as big (e.g., North America, India, Australia). Jonathan Kingdon's *Lowly Origin* does justice to the immense task of trying to convey the actual and potential complexity of the evolutionary history of Africa's fauna. The West Coasters think we are close to knowing all there is to know (at least in terms of taxonomic diversity) about the early stages of human evolution, whereas the East Coasters think, at least in relation to the early stages, that we are just beginning to scratch the surface of the fossil evidence. Kingdon's book shows the value of the perspective of a careful student of "old-fashioned" natural history. The author does not claim to have found the answer to human origins. The real message of the book is the rich contextual evidence it provides. Wise students of human evolutionary history would be well advised to think carefully about that message.

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REMOVING FINALISM FROM DEVELOPMENTAL BIOLOGY

The Development of Animal Form: Ontogeny, Morphology, and Evolution. Alessandro Minelli. Cambridge University Press, Cambridge, United Kingdom, 2003. 323 pp., illus. $75.00 (ISBN 052180851 cloth).

In the preface to his engaging and groundbreaking book, Alessandro Minelli points out that "most of the steam pushing the new engine [of evo-devo] is coming from developmental biology rather than from evolutionary biology." He continues: "Developmental biology is rapidly transferring to evolutionary biology a wealth of precious data and concepts, which are revolutionizing our current views on homology, body plans, and the origin of evolutionary novelties" (p. xv). With his book, the evo-devo engine switches tracks; abundant facts, concepts, and problems from comparative morphology and the study of postembryonic development generate powerful new "steam" for future research.

Minelli proposes nothing less than a paradigm shift in the field of evo-devo, one that moves the field of developmental biology from finalism (what he terms an "adultocentric" view) to a truly developmental view. Finalism is thinking about development as the program by which an egg becomes an adult, and it is this outlook that Minelli seeks to remove from developmental biology (evolutionary biology, he argues, has already expunged finalism). Some examples are necessary to understand adultocentrism, and he weaves these throughout the book. I found two of them particularly compelling.

In the first, Minelli posits that the evolutionary origin of the skeleton and cuticle (chapter 2) in vertebrates and ecdysozoans was for a developmental purpose: the control of mitosis in the epidermis (in the absence of cilia to control it) and hence the control of growth and thus of body size. Because ciliated cells in metazoans cannot divide, they are removed from the lineage of proliferating cells and take on a morphostatic role—that of maintaining the animal's shape. In animals in which cilia are lost (vertebrates and ecdysozoans), Minelli proposes that other cell types/tissues (bone/cartilage and cuticle) evolve to maintain body shape. The adultocentric view is that the skeleton and cuticle evolved for locomotion and protection in the adult; the developmental view is that they evolved to make the developing animal more predictable, stable, and robust.

In the second compelling example, Minelli argues against the adultocentric concept of "provisional scaffolding" (chapter 6), the view that the patterning of early development is a scaffold for later development. Cartilage precursors of long bones, for example, typically are viewed as necessary scaffolds for subsequent ossification. Minelli argues that we must reverse this perspective: What is interpreted as a developmental scaffold is actually a structure that is in congruence with a particular developmental stage. Thus, cartilaginous skeletal elements would be interpreted as present in early development because they are congruent with the developmental dynamics of that stage and not because they will be useful for later ossification. The criteria by which such congruence can be recognized, however, are unclear.

Biologists remain fascinated by the magic numbers of animal body segments and regions (tagmata), and Minelli boils down the problematic issues surrounding their comparisons and homology assessments in chapters 4 and 5. He considers at length the very low upper limit (approximately six) of differentiated parts in any given series or body dimension (e.g., the number of tagmata in an animal's body, the number of kinds of body segments in a polychaete or fingers in a tetrapod limb). This discussion will be of considerable interest to developmental biologists whose work focuses on a segmented model such as *Drosophila.* In chapter 10, the final one, he weighs in on the side of partial homology (that a feature may be homologous to more than one other feature) and stresses the relative nature of this concept.

One of Minelli's goals was to "inject... into the lively arena of evo-devo biology a number of facts, concepts, and problems that have failed, until now, to find the place they deserve in today's debates and research agenda." These are a few of his thought-provoking ideas:

- Complex and circuitous genetics may underlie geometrically simple patterns. Insect tracheae and mammalian lungs, for example, have different specific genetic controls at different branching levels.
- The syncytial nature of early blastoderm in *Drosophila* and other insects is not an adaptation to a particular way of patterning, but an adaptation for speedy development.
- The high number of genes that encode transcription factors is similar in animals with different body plans because these genes effectively stabilize form.
- The processes of pattern formation are phylogenetically more recent than many or most pathways of cell differentiation, but the pathways are delayed in development until after body patterning (which refutes recapitulation, the concept that development parallels evolution).

Minelli views the cell as the basic unit of development. Understanding cell properties and functions, such as cell size, cell cycle length, and cell number, is key to understanding the emergence, complexity, and patterning of multicellular systems (chapters 6 and 7). Development is thus defined as the "complex networking of cellular behaviors and mechanisms influenced by the expression of genes." Instead of regarding development as a global property of the organism, Minelli emphasizes the high degree of local autonomy that cells and other subsystems (modules) hold within an organism as it develops. Minelli's considerations of the robustness of the network of interactions existing among cells and subsystems, and the degeneracy (as opposed to redundancy) of these interactions, are up-to-date from a molecular standpoint.

Perhaps the most important chapter in *The Development of Animal Form* is chapter 8, in which Minelli addresses questions of axes and symmetry in a new context. He first asks what the main body axis is, and he demonstrates, by comparing a planarian with a ventral mouth and no anus to polypoid bilaterians and gastropods, that it is not easy to define. This brings him to a discussion of an idea generalized from A. S. Romer: the "dual animal," composed of two segmental systems that are largely patterned independently. Most of us find it easy to distinguish between the body axis of an animal and its appendages, but Minelli's view may be a surprise: The vertebrate tail, he argues, is an appendage and not part of the main anterior-posterior body axis. His arguments rest on the fact that the tail, like paired limbs, has only ectodermal and mesodermal derivatives. Minelli builds the concept of axis paramorphism, that is, the idea that appendages are duplicates of the main body axis (without endoderm). Structural correspondence between the main body axis and appendages is demonstrated by two observations: (1) that the degree of segmentation in the body axis is frequently mirrored in the appendages and (2) that many trends simultaneously affect the anterior-posterior axis of the body and the proximal-distal axis of the appendages. He thus extends an answer to the question of why fishes have not evolved paired fins posterior to the anus: The tail is an appendage, like the fins themselves.

Minelli's well-edited, well-referenced, and nicely illustrated volume is the first evo-devo book in recent decades to be written by a comparative evolutionary morphologist. His appealing style of prose is illustrated by this example: "We must dispose of the idea that housekeeping genes evolved once and forever, in a remote aeon, and are now continuing to perform their job 'at the service' of a separate and still evolving company of 'higher level' developmental genes. The whole system and all its components are evolving without rest" (pp. 24–25). This important book should be read by every graduate student whose work touches either or both of the fields of developmental and evolutionary biology. It is not simply a rich collection of comparative data (though I did pull various pearls of factual information into course notes); most important, it is a rich source of fresh ways of viewing animal body plans, development, and developmental genomics. I think that the ideas in this book will, as the author hoped, stimulate interest in research on a broader assemblage of taxa, their body "syntax," and a host of overlooked features, and perhaps begin to shift our perspective from an adultocentric to a developmental view of biology. To understand the puzzles of the diversity of animal forms and development, Minelli points out that we need not only molecular developmental genetics but also the theoretical tools of updated comparative morphology. As a comparative developmental morphologist, I could not agree more.

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FOLLOWING PENGUINS

The Adélie Penguin: Bellwether of Climate Change. David G. Ainley. New York, Columbia University Press, 2002. 310 pp., illus. $59.50 (ISBN 023112306X cloth).

The Adélie penguin (*Pygoscelis adeliae*) is one of the most appealing and well studied of all bird species. Dave Ainley explains why in a delightfully written volume that is certain to please the amateur birder, the polar traveler, and the serious academic ornithologist. *The Adélie Penguin: Bellwether of Climate Change* also updates the earlier, now out-of-print book on Adélie penguins by Ainley and colleagues (1983).

Between 1960 and 1970, up to 5000 juvenile penguins were flipper-banded each year to build up a population of known-aged birds. As one of my Johns Hopkins University doctoral students, Dave Ainley inherited most of this population when the birds were nearly 8 years of age; he did a magnificent job of analyzing the data and moving the research forward to produce what is now one of the most important long-term avian population studies. He returned recently from his 25th visit to Antarctica and the Southern Ocean, still following the Cape Crozier population.

His book has an interesting title. Dictionaries define *bellwether* as "a wether or male sheep that leads the flock, usually bearing a bell" or "a person or thing that takes the lead; e.g., 'Paris remains the bellwether of the fashion industry.'" Climate change does not happen overnight. Thus, the title is a good one, something that may make people realize that continued long-term research on Ross Island, Antarctica, where a simple ecosystem prevails, is justified.

Apart from the acknowledgments, the book has eight chapters. The first presents an extremely thorough introduction to the early research on the Adélie's natural history. The book is worth its price for this chapter alone. Chapter 2, "Marine Ecology," is equally valuable: It summarizes the bird's marine ecology (118 references) and reports new information from an area of research that has seen much progress since the publication of *Breeding Biology of the Adélie Penguin* (Ainley et al. 1983), thanks to the development and miniaturization of high-tech equipment to study diving and foraging behavior. Another important advance has come from the Holocene history of the Adélie population, including genetic differentiation of populations that comes from the dating of penguin bones in extinct and extant colonies.

The professional ornithologist will find the next few chapters useful. Chapter 3, "Breeding Populations," lists every known Adélie colony and summarizes their geographic distribution and population size. "The Annual Cycle," chapter 4, looks into the basic chronology of the penguin's nesting and population dynamics. In chapters 5 and 6, covering the occupation and reoccupation periods, Ainley brings in material from his 1983 book, presenting it in context with a great deal of additional material from other researchers.

Chapter 7, "Predation," emphasizes that of the three listed predators of Adélie penguins—the killer whale, the leopard seal, and the skua—only the leopard seal is a really significant predator. The skua is a scavenger and preys mostly on fish at sea. "Demography," chapter 8, updates *Breeding Biology* (Ainley et al. 1983). An important conclusion is that flipper bands, used in earlier studies, induced mortality during the first year after banding (as one might expect), but not thereafter. The banded population was declining 3 percent more rapidly than the unbanded one, which was declining at about 4 percent per annum during the 1960s and early 1970s.

Chapter 9, "The Bellwether of Climate Change," comes to grips with the book's title, offering some fascinating hints on how Adélie populations may change in the future. Ainley details the way in which the Adélie natural history patterns (egg laying, breeding success, survival, etc.) have evolved in relation to sea ice cover at various times of the season. In relation to global warming, I was hoping to learn more about the increase in chinstrap penguins (*Pygoscelis antarctica*) at the expense of the Adélie along the Antarctic Peninsula. The chinstrap breeds one month later than the Adélie, nests on steeper slopes, usually molts on land instead of in the pack, and is more dependent on open water (Sladen 1955). I found some interesting comparisons in chapter 6 but not in chapter 9.

The art by Lucia deLeiris is superb and could have easily replaced the rather poor photographic reproductions that, out of the many thousands that must have accumulated in 40-plus years, should have all been outstanding. Substituting a hardback photographic cover for a paper cover was excellent, but again the photos displayed could have been more relevant to the title of the book. My only other small complaint is the inconvenience of each chapter having a separate bibliography. Of the 560 total references listed, many are duplicated. One bibliography would have saved space and been easier to use.

I cannot resist quoting a section of Ainley's introduction where he so eloquently describes the Adélie penguin coming ashore, as I have so many times witnessed and filmed on the beaches of Cape Crozier:

> I have always been amazed at the vivid change in demeanor each time an Adélie comes ashore. The act takes incomparable athleticism. It's as if the penguin knows that all the cards are stacked against it, if not this time then certainly the next; if not the leopard seal, then huge waves; if not heaving blocks of ice, then an ice foot necessitating a leap of two or more meters. The penguin lands ashore in a bad mood, exasperated and seemingly oblivious to what the beach has to offer. Then as it shakes the water from its feathers, its awareness of the colony and of purpose seems to take over. It is only then that the penguin completes the transformation from marine to terrestrial creature. Off it goes, unquestioning and unvarying, sometimes even muttering almost inaudible renditions of calls it will use to greet mates or chicks.

A final word about the long-term bird population studies exemplified by this book. Five decades ago it was the amateur independent individuals who led the way, such as Richdale (1957), who studied yellow-eyed penguins (*Megadyptes antipodes*) and the royal albatross (*Diomedea epomophora*), and Margaret Nice, who examined the song sparrow (*Melospiza melodia*). It took a great deal of persuasion to get government agencies to sustain long-term funding for the biological sciences, as they willingly did for the physical sciences. For example, a researcher would not, could not, spend millions of dollars on a telescope and then abandon it after a few years. Two Johns Hopkins University projects that I was privileged to help activate, Lance Tickell's doctoral study on albatrosses on Bird Island, South Georgia, in 1958 and our study at Cape Crozier in 1960, have so far survived, but not without some early gaps due to lack of funding.

The albatross research continues under the watchful eyes of John Croxall, of the British Antarctic Survey, and, as presented in this book, the Adélie research continues under Ainley. But both of these birds are in trouble. The ice, home for the Adélie, is diminishing. The wandering albatross (*Diomedea exulans*), a bird that has evolved to mature at more than 10 years of age, lays only one egg and has a breeding cycle of 18 months; once abundant, it is now becoming endangered because of adverse commercial fishing methods. Yet many birds are proving to be longer-lived than we ever had thought. A wandering albatross has been recovered at age 41; one of Chan Robbin's laysan albatrosses (*Phoebastria immutabilis*), when rebanded in 2002, was 51 years old. Charles Huntington's study on Kent Island, New Brunswick, has followed a 36-year-old Leach's storm-petrel (*Oceanodroma leucorhoa*). One of our Cape Crozier south polar skuas (*Catharacta maccormicki*) reached the age of 38 in 2003. All these are long-distance travelers. Only with continued long-term research can we keep track of all of these bellwethers.

Had it not been for Dave Ainley and the mass of data we all helped to collect during the early days, our Cape Crozier study (Ainley et al. 1983) would have never seen print. Now he has done it again. Jolly good show, Dave. Keep up the good work, and continue to inspire young potential researchers to continue your work as you age. Long-term population studies should continue with all the support they need.

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