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Susan Cachel
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Fossil Primates

Reconstructing the paleobiology of fossil non-human primates, this book is intended as an exposition of non-human primate evolution that includes information about evolutionary theory and processes, paleobiology, paleoenvironment, how fossils are formed, how fossils illustrate evolutionary processes, the reconstruction of life from fossils, the formation of the primate fossil record, functional anatomy, and the genetic bases of anatomy. Throughout, the emphasis of the book is on the biology of fossil primates, not their taxonomic classification or systematics, or formal species descriptions. The author draws detailed pictures of the paleoenvironment of fossil primates, including contemporary animals and plants, and ancient primate communities, emphasizing our ability to reconstruct lifeways from fragmentary bones and teeth, using functional anatomy, stable isotopes from enamel and collagen, and high-resolution CT scans of the cranium.

Fossil Primates will be essential reading for advanced undergraduates and graduate students in evolutionary anthropology, primatology and vertebrate paleobiology.

Susan Cachel is Professor of Physical Anthropology at Rutgers University. She has been on the Executive Committee of the Rutgers Center for Human Evolutionary Studies (CHES) since 2010 and a member of the graduate interdisciplinary Quaternary Studies Program at Rutgers since 2000. She has taught and performed research at the Koobi Fora Field School in northern Kenya, and she is currently a research associate of the Kenya National Museums (Nairobi). She was recently elected a Fellow of the American Association for the Advancement of Science for "incisive contributions to hominization theory, the role of nutritional fat in human occupation of high latitudes, and primate evolution." Her previous title, *Primate and Human Evolution*, was published by Cambridge University Press in 2006.

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To my family:

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PREFACE

While reading websites, blogs, newspapers, or popular magazines, one frequently encounters a statement like this: "The discovery of new human fossil X completely rewrites the textbooks!" Many editors would set this entire sentence in bold capital letters. Or, "New fossil primate is the first monkey . . ." or, "New higher primate is the first human ancestor." Such hysteria has become a normal part of press hyperbole. One expects that virtually every new primate or human fossil will completely rewrite the textbooks. But is it true? Dinosaur paleontology also receives a great deal of attention from both the public and the press. Do new dinosaur fossils mandate a complete rewriting of the textbooks?

A study has been conducted on both Old World higher primates (catarrhines) and dinosaurs, testing to see whether new fossils result in a complete re-vamping of evolutionary history—that is, do new fossil finds repeatedly rewrite the evolutionary history of a group? Tarver *et al.* (2010) discover that this is not true for catarrhine primates over the last 200 years of study. The basic outline of catarrhine evolution has remained the same since the early twentieth century. New dinosaur fossils, on the other hand, do continually and radically shift our understanding of dinosaur evolutionary history. Many new lineages have been discovered, and new fossils expand our understanding of the geographic expansion of dinosaurs. Our understanding of dinosaur evolution changes rapidly and wildly. Yet, fossils of new catarrhine primates result in virtually no change in the understanding of their fossil record and evolutionary history. Clearly, the mass media is unduly fixated on catarrhine primates. The principal reason for this is that humans are catarrhine primates, and the merest scrap of a new human fossil generates hysteria in the popular press. This also reflects a funding bias. Funding agencies are more apt to focus on primate (including human) paleontology, than paleontological work on other animal groups. Dinosaurs are clearly an exception—major dinosaur research programs have been funded by private donations alone.[1] This is why a test of whether new catarrhine primate or dinosaur fossils truly do rewrite evolutionary history is important. As a physical anthropologist, I am irreverent in pointing this out: dinosaur discoveries trump those of primates in terms of the advance of knowledge. Why study primates at all? Is this just stubborn single-mindedness, or a simple exercise in human vanity?

Testing whether new fossils necessarily rewrite evolutionary history (Tarver *et al.*, 2010) is important in a general sense. Our understanding of evolutionary patterns is not entirely dependent on the discovery of new fossils. This may be true for dinosaur history, which still has unknown dimensions. Primate history, on the

[1] For example, the research of Dr. John R. (Jack) Horner, Museum of the Rockies, Bozeman, Montana, on dinosaur paleobiology has been abundantly funded by private donations.

other hand, can be discerned from the fossils that we already know. Why should one write another book on primate fossils? A major reason is to establish that primates do, indeed, conform to the evolutionary processes that can be observed in other mammals. Traditionally, primate evolution is viewed as an inevitable progression from the lowest and least to the best of all. As T. H. Huxley first and famously phrased it, "Perhaps no order of mammals presents us with so extraordinary a series of gradations as this—leading us insensibly from the crown and summit of the animal creation down to creatures, from which there is but a step, as it seems, to the lowest, smallest, and least intelligent of the placental Mammalia" (Huxley, 1863:124–125). Huxley was mired in a deep debate about whether organic evolution had occurred at all, and can be excused some rhetorical flourishes. Since that time, however, many anthropologists and primatologists take the special status of the primate order as a given. The human-like or anthropoid primates, particularly the great apes, are especially revered, and debates now occur over whether they should be accorded the same legal rights as human beings. Yet, what does the fossil record show? Are primates subject to the same forces generating new species or determining species extinctions as other mammals? Have higher primates arisen independently in the Old and New Worlds? An overview of the primate fossil record immediately shows that major extinctions have occurred, including a recent major ape extinction. Some major researchers respond to this—I think indefensibly—by arguing that primate species have been continually expanding in number since the beginning of the order. Clearly, the prospects of primate extinction are emotionally disturbing. Other interesting questions arise: how many species of primates should one expect to see? How fast do primates evolve? Are climatic triggers important in primate evolution? What is primate niche structure like? What happens to primates isolated on islands? Do primates experience resource competition from their fellow primates? What place do primates have in community structure?

Another reason to examine fossil primates is that primates, along with birds, are often the only creatures still studied as whole animals in university curricula—veterinary schools excepted. The remainder of the animal world is now often reduced to the study of molecules, cells, DNA, or genes. Furthermore, as whole animals, primates are embedded in tropical ecosystems. Anyone concerned about the fate of these ecosystems and their preservation will be concerned about primates. Living primate species (the sifaka, the muriqui, the orangutan) often stand as heraldic figures that animate the worldwide fight for conservation of other endangered species or habitats.

An additional reason to study fossil primates is that they remain one of the last groups where traditional vertebrate paleontology can be taught and practiced. Many university geology departments have abandoned the teaching and study of vertebrate fossils altogether, except for teaching an introductory course on dinosaurs. Invertebrate paleontology has economic significance in stratigraphic analysis, dating, climatic research, and petroleum exploration—this will never be the case for vertebrate fossils, because they are too rare. Universities and museums are disbanding their vertebrate collections. Vertebrate curators are no longer needed. Many researchers fear that vertebrate paleontology will itself become extinct as a science. “I believe that the fate of the paleontologist is in jeopardy. Where are the specialists who will focus on the new fossils still to be recovered, and where will they be trained? Perhaps more importantly, where will they be employed?” (Reed, 2011:77).

One might think that primate history, anatomy, and morphology are immune to this trend, because of the medical importance of studying human anatomy and functional morphology. Unfortunately, many medical schools in the USA are abandoning the traditional study of gross anatomy through dissection. Instead, they increasingly rely on computer software programs that teach anatomy through simulated dissections. Thus, the fate of the human anatomist may also be in jeopardy. Should one applaud this? Can medical personnel be adequately trained without reference to cadavers? Can they appreciate the vast array of variation and variability that living humans encompass if they only study computer simulations of ideal human anatomy? In addition, physicians still receive virtually no training in evolution, and, for over 30 years, have roundly rejected the call for introducing it into basic medical science (Ewald, 1980). A later call for a “dawn of Darwinian medicine” never saw the sun rise on this endeavor (Williams & Nesse, 1991). Yet, the concept of evolutionary medicine, based on natural selection, adaptation, and population-level differences in humans, would revolutionize medicine by altering merely descriptive or mechanistic approaches to disease. Evolution is capable of offering powerful new explanations for alterations in human life-history variables such as growth, reproduction, and lifespan, as well as the onset of ageing, and disease.

In summary, although the focus of this book is primate evolution, I also intend it to be a resource for those interested in both exploring evolutionary processes, as well as the broad shape and pattern of mammal evolution. Along the way, I will emphasize the possibility and utility of studying function and behavior from the remains of fossil animals. I will reinforce the general importance of studying evolution and functional anatomy in biology, as well as in other disciplines, such as conservation biology and medicine.

Finally, I introduce a novel perspective on primate and mammal evolution by interjecting new research into the narrative on the genetic bases for anatomical shape and form. This new research, called evolutionary development, promises to unveil mysteries about the appearance of new anatomical structures. Without knowledge of evolutionary development, paleontologists could merely describe novel structures and compare them to similar structures in living animals. Paleontology was description and phylogeny, the attempt to reconstruct ancestor-descendant relationships between fossil organisms. The origin of anatomical innovation remained a mystery. But the genetic bases for new anatomical structures are now becoming clear. Evolutionary development is therefore becoming the linchpin between evolutionary processes affecting variation within populations and the grand procession of life as revealed by classic paleontology. Thus, there is continuity between evolution at the level of individuals in populations (microevolution), and evolution at the level of the origin of new families, orders, and classes of animals (macroevolution). This firm linkage between microevolution and macroevolution represents a break from paleontology during the 1980s and 1990s, when some major figures (e.g. S. J. Gould, N. Eldredge) argued that microevolution was caused by relatively weak processes like natural selection, and was decoupled from macroevolution, which was largely directed by unpredictable accidents and catastrophes.

The future importance of evolutionary development to human and non-human primate evolution is indicated by a major symposium mounted at the 2012 annual meeting of the American Association of Physical Anthropologists: "Finding our inner animal: Understanding human evolutionary variation via experimental model systems" (Young & Devlin, 2012). Papers presented at this symposium illustrate how morphology and adaptation can be studied through experimental comparative anatomy and comparative genomics. The way in which natural selection affects variation in the body size, teeth, skulls, and limbs of humans and non-human primates is examined through animal experimentation. The results are used to generate and test hypotheses about evolution. Thus, adaptation and evolution can sometimes be studied by experimentation. This counters the arguments of skeptics who state that the study of adaptation and functional morphology in fossils or in living organisms is nothing more than a series of ad hoc stories (Gould & Lewontin, 1979).