## Primate and Human Evolution

Susan Cachel

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**P**rimate and Human Evolution is an ambitious and broadsweeping attempt to set the issue of human evolution firmly within the context of its catarrhine substrate, while at the same time arguing that humans and their closest fossil relatives are remarkably different from other primates. It is this essential tension that Cachel aims to explore.

From its title it would be easy to assume that this is a textbook for undergraduates. As Cachel, however, warns in the opening sentences of her preface, it is not intended as such, nor should be seen as a textbook. Perhaps to emphasize the point still further, the opening paragraphs of Chapter 1 (The Primate Order) dispense with certain "conventions" that a textbook format might otherwise have followed. For instance, the term "hominin" is rejected, since in Cachel's belief, "the adaptations of humans and their fossil relatives are significant enough to warrant a family-level distinction."

The first three chapters cover issues such as the defining traits of primates, theory and historical impact of natural selection on understandings of the natural world, increased knowledge of heredity and variation due to genetic research, and essentialism versus population thinking. Also covered is a short history of primatology, where Cachel traces some of our thinking about non-human primates from antiquity to the Middle-Ages through to the Renaissance, describing the first encounters between Europeans and apes. A split in the history of primatology in terms of behavioral versus anatomical studies is discussed, followed by a section on the historical impact of the recognition of Australopithecines as fossil hominins. The third chapter summarizes the catarrhine fossil record, while also introducing the author's views on niche divergence and inter-specific competition, and (lack of) relationship between climate change and evolution.

In a particularly interesting chapter (4), Cachel discusses the evidence for speciation processes in extant primates. This begins with the author stating that, in her opinion, distinctions should not be made between living and fossil "species," and she rejects the notion that different species concepts should be applied in neontological and paleontological circumstances. Moving on to discussion of actual forces of taxonomic diversification, issues such as river barriers are considered, in particular, the evidence from New World monkeys. However, a point is made that the strength of a channel's current rather than width alone may be pertinent in determining whether water will form a "barrier" to primate colonization and gene flow. Potential parapatric

speciation in papionins also is discussed, although Cachel notes that as a general model of primate speciation (including hominins) such evidence tends to be contradictory to data originating from comparison with other mammals, which suggests that parapatric speciation is more frequently seen in mammals smaller than baboons. The second part of this chapter deals with the topical issue of extinction in extant primates. Primates have the highest proportion of endangered species amongst mammals, and Cachel draws several sobering observations regarding the probable fate of extant primates and fragmentation of their habitats. The chapter also discusses how issues such as habitat specialization, and diet and body size differentially affect extinction rates, making the point that certain macaque "weed species" have shown a greater resistance to speciation.

Chapter 5 discusses primate anatomy, venturing into functional morphology and ontogeny, while the sixth chapter discusses captive studies of non-human primates, particularly focusing on the issue of "aberrant behaviours" in captive subjects. If by now you are gaining the impression that Cachel is covering a lot of material rather quickly, you would not be mistaken, and indeed the density of information and pace of delivery is characteristic throughout remaining chapters. That said, the text is written in an engaging style, although, perhaps inevitably, such sweeping moves through wide-ranging material risk polemic. This is perhaps no more apparent than in a section of Chapter 5 discussing cladistic methodology and the study of adaptation. Several points Cachel makes regarding cladistic methodology (p.108) could be challenged. For example, she argues that cladistics only produces bifurcations when in fact polytomies will be produced in ambiguous situations. Likewise, she contends that character coding is always binary, and that continuous variation is not accommodated. As Rae (1998) has pointed out, this is not the case. There is no difference between quantitative and qualitative characters as far as cladistics is concerned. Cachel goes further than this, however, suggesting that cladistics may have led to a decrease of interest in functional morphology and adaptation. According to Cachel, because cladistic methods of phylogenetic reconstruction emphasize shared derived characteristics rather than overall similarity, and because homoplasy often is brought about by adaptation, "the adaptive significance of characters or traits is not important in cladistics." However, while cladograms certainly are not constructed solely with reference to phenetic similarity, Cachel ignores the fact that cladograms are informative about

those features that are homoplastic. Indeed, homoplasies that demonstrate similarity of form or property independently of phylogenetic association, provide the most secure evidence for adaptation (Harvey and Pagel 1991). In a footnote on page 127 Cachel suggests that "the furor mounted against adaptation ... may have been the biological equivalent of post-modernism." I would be surprised if I were not the only reader of this journal to be somewhat bemused to find cladistics implicated at the heart of a post-modernist plot.

In Chapter 7, Cachel lists 29 behavioral and anatomical traits that she sees as uniting all catarrhine species. She then uses this list to make a claim that while hominids, in Cachel's terminology, resemble catarrhines in many behavioral and anatomical features, hominids are truly distinctive from what she terms the "catarrhine substrate." The remainder of the book is largely dedicated to reinforcing this point, and arguing that, as a result, we must look elsewhere for models of why the particular hominin characteristics arose.

Drawing on some of her earlier work (Cachel 1994), the author argues that what makes humans distinctive from other catarrhines is "natural history intelligence." She takes some time to discuss how her use of the phrase "natural history intelligence" differs from that of Mithen (1996), who previously used similar terminology. For Cachel (p.159), "[n]atural history intelligence corresponds to fluid intelligence, highlighting the importance of planning, predicting, and manipulating items in the nonsocial environment." Stone tools, appearing in East Africa 2.6 Mya, indicate the presence of such distinctive cognitive and behavioral traits in early hominins, Cachel argues. To reinforce her point, she devotes part of the chapter to discussing problems with the alternative "Machiavellian intelligence" or "social brain" hypothesis to hominin intelligence, whereby many cognitive capacities are seen as resulting from selection associated with social interactions and political maneuverings. Indeed, Cachel posits that competitive social pressures and Machiavellian interactions may even militate against attentiveness to events outside of the social sphere, potentially inhibiting the evolution of the features she sees associated with "natural history intelligence." Cachel (p.171) even argues that less status striving and social competition among bonobos (Pan paniscus) compared with P. troglodytes, might result in greater natural history intelligence capacities in bonobos, and it is argued that this hypothesis may be supported by captive studies. However, this point is left under-explored. Why, for instance, do bonobos show less tool-use in the wild? Do wild bonobos show more evidence of "planning, predicting, and manipulating items in the nonsocial environment" than do wild chimpanzees? In the final pages of the chapter (pp.180–184), Cachel argues that because social carnivores exhibit elaborate cooperative feeding, food sharing, and food caching, they may make better models than non-human primates for understanding the selection pressures underlying natural history intelligence. The point that more distantly related taxa may make more appropriate models for understanding selective

forces in hominins is one that the author repeats at several points in following chapters.

Chapters 9–12 delve into issues such as primate sociality, body size and its effect on behavioral ecology, and the nature of the fossil record. In Chapter 13, Cachel takes on the thorny issue of hominin bipedalism. Despite the fact that the book is not designed as textbook, this is one chapter that may be useful for tutors of undergraduates to use as potential reading material when introducing some of the issues surrounding this debate. Chapter 14 marches through the hominin fossil record from the earliest fossil candidates to the origin of anatomically modern humans, while Chapter 15 discusses some of the history, and what Cachel sees as potential pitfalls, of using baboons as models for human evolution.

In Chapter 16, Cachel discusses the importance of Paleolithic archaeology in understanding human evolution. There is a short history of changing attitudes to Paleolithic artifacts, followed by the nature of the earliest archaeological traces in the form of the Oldowan, and evidence for use of bone tools in the Pleistocene. Again, in dealing with all of this material Cachel makes a plea to look outside of primatology (particularly hominoids) in order to identify the important aspects of human evolution, and possible selective pressures and associated adaptive responses. Cachel is particularly scathing of what has come to be termed "chimpocentrism," and at one point (p. 373) states "that it is fundamentally wrong to assume that hominids during the Plio-Pleistocene or any earlier time were behaving like bipedal chimpanzees." Although an appeal for the use of non-primate models for studying hominin evolution is well-reasoned, it is her dismissal of primate taxa as sources of hypotheses and as appropriate models with which I suspect some readers will find issue. As Cachel herself warns in her preface (p. xv), such arguments identify her as "an apostate from primatology."

In the final part of Chapter 16, Cachel draws together the foregoing issues to present a "hominization model." The trigger of her model is reduced intra-group competition and, as the author notes, this is a stark contrast to alternative models that posit environmental change as the initial catalyst of "hominization." Cachel argues (p. 346) that if environmental change was "all that was needed for hominid origins, then the first hominids should have emerged as part of the early to middle Miocene hominoid radiation." For Cachel, reduced intra-group competition leads to parallel developments in increased terrestrial behavior and sentinel behavior, and increased natural history intelligence capacities. In turn, these factors instigate the main elements of "hominization" such as tool behavior, dietary change, increased levels of carnivory, etc. The chapter ends with a brief discussion of how the model may be tested in the future.

The range and breadth of topics covered in this lengthy book are undeniably impressive, and Cachel certainly dares to be different. There are forays into artificial intelligence, speciation, primates as models (and non-models), neuroanatomy, the origins of sociality, the evolutionary implications of body size, the possible impact of diet on sexual dimorphism, taphonomy, bipedalism, *Hox* genes, tool use, technology, ... the list goes on. And all interspersed with condensed histories of primatology and palaeoanthropology. However, given the wide-ranging discussion, the reader has to work hard to maintain semblance of the overriding argument, despite what is generally a highly readable style. Such breadth also leads to an inevitable lack of depth on some issues. Indeed, I have glossed over many individual points with which I may have wished to quibble (if not contest). I leave it to those who go on to read the book for themselves to find their own, for in a volume as broad as this, there are sure to be many.

If book titles are supposed to provide a précis, then a title that aims to take in many of the most controversial topics in discussions surrounding the evolution of primates and humans under a single cover is extremely ambitious—some may even say too ambitious. The book is wide-ranging and thought-provoking as a result, albeit with the noted tendency, at times, to be a little under-developed in cogen-

cy of argument. For those of us who believe that a book should be, perhaps, primarily for stimulating, educating, and entertaining, the question raised is simply whether I enjoyed Cachel's book and learned something from it? Undoubtedly yes, and I believe others also will, although they probably will wish to draw breath as they reach the book's close.

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