Book Reviews

PRIMATE ORIGINS: ADAPTATIONS AND EVOLUTION. Edited by Matthew J. Ravosa and Marian Dagosto. New York: Springer. 2007. ISBN 0-387-30335-9. $169.00 (hardcover).

During the late 1960s and early 1970s, a group of young, gifted, fiercely competitive evolutionary biologists began a protracted debate on the origins and composition of the Order Primates. Fred Szalay, Matt Cartmill, Bob Martin, and later Bob Sussman, keen naturalists all, came from different perspectives and knowledge bases, and the field ought to be thankful to them because in a few short years they helped to create a new evolutionary primatology. They transformed the moribund, scholarly primate morphology of LeGros Clark, where animals hardly seemed alive, into a vibrant empirical discipline tied into ecology and rooted in modern systematics and functional morphology. The effects are today seen in every corner of primatology and paleoanthropology, and they are evident throughout this unique and important book edited by disciples of the Cartmill and Szalay camps, respectively. More chapters than I can highlight in this limited space are not only technically sound and informative, but thoughtful too. They demonstrate a maturing awareness of the ambiguities involved in reconstructing the behavioral adaptations of deep-time taxa. That circumspection befits the cause, for *Primate Origins* also marks a turning point. Hereafter, it will be more difficult for textbooks to invoke visual predation as the genesis of primates—not that it was ever intended to be—and to ignore the crucial evidence plesiadapiforms provide about the primates' initiation into arboreality.

The original views of our quartet of protagonists are the foundation of this book. With apologies for oversimplifying, they are: 1) Szalay: In becoming arboreal, primates adapted via a feeding shift from a more insectivorous diet to one involving more plant parts, especially fruits. 2) Cartmill: The primate breakthrough was predicated on visually based predation, i.e., more efficient insect foraging in the terminal branches. 3) Martin: The first primates were not related to plesiadapiforms but were cheirogaleine-like, terminal-branch feeders living on fruits, exudates, and insects and relying on leaping and hindfoot grasping. 4) Sussman: Primates' success was based on their coevolution with flowering plants, which provided new resources, including plant parts and insect/animal foods.

Alas, 40 years later, with no Rosetta stone fossils to tie euprimates to their forerunners to everyone's satisfaction, we are still handicapped when trying to explain the adaptive transitions that are the central concern of *Primate Origins*. Some still keep plesiadapiforms in Primates, in spite of their often funny teeth, while others reject them or just sweep them under the archontan rug. This makes it hard for readers, as contributors sometimes talk past one another. There is no way to fix this problem, which is partly semantic and partly substantive, but it is one of the reasons why a synthesis is difficult to extract from the 23 chapters of this book.

While adaptation is the preeminent concept, *Primate Origins* does cover phylogenetic matters well. Much hinges on the paleontology of plesiadapiforms, a fast-moving field that has produced important new papers since this book was compiled. However, the spectacular fossils discussed by Bloch and Boyer are amazingly complete and prove plesiadapiforms to be highly diverse ecomorphologically. One, *Carpolestes simpsoni*, had a divergent, grasping, nailed hallux functionally similar to the arboreal tree shrew *Ptilocercus*, thus preadaptive to the powerful, grasping big toe of euprimates. No wonder Szalay gives some ground, saying plesiadapiforms may as well be classified in a sister order to the euprimates. The possibility that some plesiadapiforms were mitten gliders related to flying lemurs, Chris Beard's Primatomorpha hypothesis, is strongly challenged by Sargis and Godinot. Using the fossil record in a very different way, Bob Martin's team calculates that primates originated 90 Mya, 10 million years before euprimates. I find this deliciously ironic, as Martin has long been wary of the imperfections of the record and unimpressed by the anatomy of plesiadapiforms. However, they fit his new predictions by being the only potential gap fillers we have prior to 55 Mya, when we first encounter definitive primates.

To test Szalay's and Cartmill's hypotheses, four papers deal with cranial functional morphology, but there are none devoted to teeth. What a shame! Vinyard et al. conclude from experimental and biometric studies of tree shrew feeding and jaws that neither Szalay's proposed shift away from insects nor Cartmill's preference for the opposite trend can be falsified. Similarly, Ravosa et al. cannot explain the close eye-set and postorbital bar of euprimates as a consequence of predatory behavior, and Ross, Heesy, and colleagues concede that predation is only one of the possible adaptive explanations for the large, forward-facing orbits of primates, since eyes and ears cannot be decoupled as primary prey detectors. This theoretical position was staked out long ago by Szalay, and it is strongly echoed by Dagosto in her chapter on locomotion: biological roles are hard to pinpoint. Furthermore damage is done to a key idea of the visual predation hypothesis through experiments on lemurs and cats, which reveal that the postorbital bar does not keep chewing muscles from interfering with vision, though it might help fix an image by anchoring extraocular muscles more efficiently.

The most vital papers in the book may be those devoted to locomotion. One wonders if that is because *primates are locomotion*: end of story. We learn about the importance of grasping and the unusual diagonal-sequence, compliant gaits of primates, both key to balancing on small branches; and of the special primate shoulder and slender-fingered, long cheiridia that make this possible. Szalay and Dagosto clarify how their grasp-leaping hypothesis differs from Cartmill's and Martin's locomotor models of the earliest primates as fine-branch, deliberate quadrupedalists (branch creepers). Dagosto's fine piece, which is also one of her most outspoken, presses the point that acrobatic leaping is ineluctably tied with pedal grasping in the earliest fossil euprimates. How else to explain the form-function synergy of their long-legged, long-footed, deep-kneed hindlimbs with joints and muscles geared to rapid propulsion?

The papers by Shea and by Rasmussen and Sussman deserve close attention. Shea ties together arboreality, small body size, relatively large brain size, precociality, and small litters, as well as hallucial grasping—which he views as an infant survival tactic—to arrive at a profound statement on the importance of the novel brain–

body-size relationship, which vectored future primate adaptations. Rasmussen and Sussman flesh out the nuances of the fine-branch niche by comparing strepsirrhine feeding and locomotion to that of arboreal phalangeroid marsupials. They voice concern that Cartmill's visual predation hypothesis depended too much on lorises and cats, whose extreme orbital convergence—the norm for neither plesiadapiforms nor euprimates—occurred in concert with highly derived locomotor and predatory behaviors. Also important is Preuss's paper on how the primate brain evolved radical changes by integrating motor and cognitive aspects of looking and reaching, making primates more attentive in their use of the hand. I wonder if a similar integration extends to gross and fine motor control systems, and to visual, auditory, and tactile senses, which would produce an ideal neurological infrastructure for perceiving and managing the enormous inputs and outputs involved in negotiating the complex arboreal milieu.

So, where are we? Much further along than we were 40 years ago, but still confounded by biological complexity. Which of a structure's various biological roles has the greatest selective value? Which dominates the morphological compromises inherent in anatomical traits, complexes, and systems? This dilemma is particularly revealing in terms of the visual predation hypothesis. One of the beauties of this hypothesis has always been its specificity, which potentially makes it easy to falsify and modify. Although the idea's substrate and locomotory elements were rather broadly described, Cartmill was quite particular in stating the dietary emphasis and foraging behavior of his hypothetical ancestral primate. However, the details never fit well with the functional morphology seen in the fossil record, either of plesiadapiforms or early euprimates. No doubt they could walk amidst twigs and see and grab insects. However, nothing in the skeleton or dentition of adapiforms discloses exclusive capacities to do so; to the contrary, the least derived members look more like folivores, frugivores, and leapers. Likewise, the somewhat close-set eyes of the first euprimates, which must have improved stereoscopic vision, need not have been selected primarily for sighting insects. Even if the postorbital bar does enhance vision, there are no indicators suggesting that the selective purpose for the structure was to improve bug chasing and/or handling. As for the coeval fossil tarsiiforms, they prove the same point differently. Most of them are likely to have been visually directed predators and, consequently, evolved super-specialized morphologies to make that possible. As other workers have noted, there is a bit too much tarsier and loris embedded in the visual predation model, and neither of them resembles early euprimates or plesiadapiforms.

As in many mammalian orders, primate characters probably emerged along with a previously invisible niche as an ensemble of features that would become critical character complexes making a new lifestyle possible. These key characters, like the brain–body-size shift that predestined different primate lineages to evolve large brains convergently, also would have promoted future primates to do certain things. However, if the original breakthrough was visual predation, why did not the order evolve as an adaptive array of hunters? Why, instead, is predation so rare? Why, on the other hand, would frugivory have become almost universal? Yes, small-bodied primates often eat insects to meet their protein needs, but why are there essentially no small mammals, other than highly specialized ones like tarsiers and lorises, that are fundamentally and profoundly predaceous? This point is well made in Louise Emmons's monograph *Tupai* (2000), which is a must read for those interested in early primates.

Several contributors to *Primate Origins* accept that we cannot rely on single-character definitions or adaptive explanations and note that key characters and capacities were added to the primate lineage sequentially. (Ah, phylogeny!) To me, this anticipates a new phase of research that resurrects the plesiadapiforms as central players. After a long period when their fossils were poorly known and thus highly contentious, the richness of new material should move researchers beyond obsessing over the auditory bulla as a primate diagnostic character. Now, we have pretty much the whole body to work with. What better place to look for phylogenetic and adaptive clues to the origins of the world's foremost, nonvolant arboreal navigators? To toss these fossils aside because they do not meet the expectations of euprimate-based reconstructions is to believe we can understand the "after" without appreciating the "before." True, there is room for other orders to displace plesiadapiforms as primates' sister group: the tupaiid radiation is still poorly known and much of Asia and Africa is unexplored. However, these new fossils are not the scraps that plesiadapiforms once were.

There is a tacit acknowledgement in *Primate Origin*s that we will be guessing at these riddles for a long time to come. Where and when we will discover the right fossils to reveal a more complete picture remains to be seen. However, the necessary foundations and perspectives for continuing the quest are laid out in *Primate Origins,* thanks to the editors, who saw fit to revisit the lines of inquiry established by Fred, Matt, Bob, and Bob. And for that we thank them all.

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THE INVISIBLE SEX: UNCOVERING THE ROLE OF WOMEN IN PREHISTORY. By J. M. Adovasio, Olga Soffer, and Jake Page. New York: Smithsonian Books. 2007. 302 pp. ISBN 0-061-17091-7. $19.95 (cloth).

In this book, Adovasio and colleagues aim to challenge the male-centered stories that, via countless images and museum dioramas, dominate public ideas of prehistory. They do this through an entertaining popular account of prehistory in which females are central to human evolution and women have important roles. This is a highly qualified team: Page is a science writer, while Adovasio and Soffer are experts in North American and Eastern European prehistoric archaeology. The latter

authors' documentation of very early evidence for perishable materials gave a new dimension to the Upper Palaeolithic record of Europe.

The book spans an enormous time period, from the earliest hominins to the Neolithic revolution; later prehistory is absent. Part 1 outlines the fossil record from Africa and Eurasia and explores theories of the evolution of bipedalism and language. Part 2 covers the appearance of anatomically modern humans and the archaeological transition in Africa and Europe and focuses in more detail on the Middle Upper Palaeolithic of Eastern Europe. The scope of Part 3 is the colonization of the rest of the world, with chapters devoted to the genetic evidence and the early record from Australia, northern Eurasia, and North America. It finishes with a very brief outline of the early Neolithic.

The authors focus first on the role of female biology in human evolution. For example, Chapter 3 includes an interesting discussion of changes in the mechanics of human childbirth, including the anatomy of the pelvis, the role of midwifery, and the hormone oxytocin. This makes it clear that changes in female anatomy and physiology were central in the development of a large human brain. The authors first address gender roles in prehistory in their discussion of the Middle Upper Palaeolithic of Europe. For example, Chapter 8 starts with a vivid reconstruction of everyday life at Dolní Vestonice I, in the Czech Republic, showing women involved in a wide range of craft and ritual activities. This leads to a fascinating discussion of the archaeological record, including the evidence for weaving, basket making, and cordage. Drawing on their knowledge of this technology, the authors describe patterning on some of the Gravettian Venus figurines as painstakingly carved representations of apparel. The focus on activities other than hunting large game and making stone tools provides a useful counterbalance to the gender bias in prehistoric archaeology. Based on this evidence, the authors argue that women produced most, if not all, of these artifacts, as well as ceramics and clothing and also suggest that some women had a high status marked by specific garments. However, given the text's description of variation in the ethnographic record for the division of labor in these activities, the link between activity and gender comes across as rather a broad generalization.

The tendency to generalize is apparent elsewhere in the book: for example, in the conclusion that women were responsible for the domestication of virtually all species of plants. While this provides a strong narrative, it is one that can be easily undermined by counterexamples from the ethnographic and archaeological record. In addition, limiting discussion of gender roles to a relatively late period reinforces a dualistic view of human prehistory. This seems a missed opportunity to use insights from evolutionary ecology, which provides a framework for understanding patterns and variation in the sexual division of labor, including that of earlier hominins.

Writing an entertaining and informative popular account of prehistory, and particularly the Palaeolithic period, is hard to do. Not only are there the usual problems for experts addressing a lay audience, such as how to present controversial arguments, but the data are also astoundingly sparse and hard to interpret and not in themselves very interesting unless you are a flint freak. The style of this book is chatty and playful, and some of the cheekier asides made me laugh out loud. The varied research interests of the authors provide a novel perspective on some of the same old sites and fossils and introduce some new examples. One quibble is that the authors generally provide little in the way of maps, dates, or chronological framework, making it rather hard to take in all of the information. Overall, this is a well written, engaging popular account of early prehistory. But by incorporating more variation, the authors could have made a stronger argument for the importance of women in prehistory.

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