

Human Paleontology and Prehistory. Contributions in Honor of Yoel Rak

Assaf Marom and Erella Hovers (eds.)

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This book is a compilation of papers presented in honor of Yoel Rak's 70th birthday. It includes a bibliography of Rak's books and major publications. The volume begins with a forward by William Kimbel, who has been a friend and associate of Yoel Rak since graduate school. Besides reporting on a number of collaborations with Rak, Kimbel recounts Rak's discovery of the most complete skull of *Australopithecus afarensis* yet known—a large adult male, found at Hadar, Ethiopia, in 1992. A long preface by the editors introduces Rak's decades-long work as professor of anatomy at the Sakler School of Medicine at Tel Aviv University. The preface also gives a synopsis of each of the 19 chapters, emphasizing the need to know modern biology before paleoanthropological interpretation can begin. The editors also note something that is evident throughout the book: Rak sometimes emphasizes obscure points of fossil anatomy, and this may lead to controversial taxonomic and functional interpretations.

Tattersall begins by claiming that modern humans have experienced more change over the last two million years than any other living species. He uses non-human primates for comparison. I can think of a number of contrary examples in other mammals—for instance, baleen whales. And, in terms of body size, many mammal lineages show dramatic changes in body size since the beginning of the Holocene. Tattersall explains the presumed high rate of human evolution by material culture. Material culture affects human evolution not in the traditional sense of a biocultural continuum, but by fragmenting populations when the environment deteriorates. This occurs because culture permits the expansion of human populations into habitats that are marginal when environmental conditions are good. Populations collapse and fragmentation results when conditions worsen. Marginal habitats are abandoned, and local extinction takes place.

Neumann discusses Alfred Russel Wallace's invocation of supernatural factors beyond natural selection to explain human cognition and abstract thought. He notes that Wallace's view of the barrier between human and non-human animals was fueled by his respect for and admiration of tribal peoples in South America and Southeast Asia. This contrasts with Darwin's use of tribal peoples to fill the gap between non-human animals and civilized Europeans. Wool presents a survey of ideas about humans emerging from the natural world, controlling the natural world, and controlling their own evolution through eugenics.

Harrison discusses a turnover in the mammal fauna

at Laetoli, Tanzania, between 2.5–2.8 mya. A long table documents the change in mammal taxa. The faunal turnover occurred during a major climatic fluctuation, and was concomitant with the extinction of the hominin taxon *Australopithecus afarensis* and the emergence of *Paranthropus aethiopicus*. The paleoecological evidence is conflicting—many lines of evidence indicate increasing aridity, while East African lake levels indicate moister environments. The faunal evidence itself is conflicting—the paleoecology of the large mammals indicates drier habitats, but rodents, ostrich eggshells, and gastropods (land snails) indicate humidity and persistent woodlands. Harrison tries to reconcile these divergent reconstructions. Woodland, shrubland, and grassland mosaics existed in both periods. The signal of dominant woodlands and humid environments in the later period reflects the small scale, local evidence gleaned from micromammals, ostrich eggshells, and land snails. Harrison concludes that local habitat changes probably do not reveal complex ecological shifts leading to the appearance of new hominin species.

Holloway synthesizes the many controversies associated with the study of australopithecine brains in a well-illustrated chapter. He emphasizes that expert neuroanatomical knowledge is needed to interpret the evidence, regardless of the technique used to reconstruct the brain. Fine details of the sulci are almost impossible to retrieve—this is a major factor in the paleoneurological arguments. Many specimens of the australopithecine brain exist. Holloway continues to disagree with Falk about the identification of sulci. In the Stw 505 endocast, Holloway identifies a sulcus as the lunate, while Falk identifies it as the lateral calcarine. Holloway vehemently argues (as he has done for decades) that the brain of australopithecines has been reorganized in a hominin fashion, and that this rewiring precedes brain enlargement, because these taxa have a brain size that falls within the great ape range. Selection has not occurred on brain size alone; to consider only brain size is to ignore detailed neuroanatomical evidence. Both *A. afarensis* and *A. africanus* demonstrate a relative increase in the posterior parietal and temporal cortex. The brain of australopithecines was reorganized in a substantially different way from that of chimpanzees. Early *Homo* subsequently underwent reorganization of the frontal lobe.

Cartmill and Brown discuss the anatomy of the gennuk (*Litocranius walleri*). Why? Because this African gazelle stands bipedally for long periods while feeding from trees and bushes. It fully extends its hips and knees while do-

ing so, and exhibits lumbar lordosis. Thus, the gerenuk becomes a test case for Hunt's postural feeding hypothesis, which argues that hominin bipedality arises when the proto-hominins engage in long bouts of foraging for food items that they seize by standing on the ground and reaching up into trees and bushes. Cartmill and Brown find no evidence of bipedal traits in the gerenuk pelvis and lumbar region. They therefore falsify Hunt's postural feeding hypothesis, and suggest that anatomical specializations for bipedality will evolve only when selection for habitual quadrupedalism declines.

Hylander addresses canine reduction in hominins, and explains it not by a relaxation of threat displays and sexual selection, but by greater bite force, and consequent greater mechanical efficiency of the jaws. That is, bite force is increased relative to muscle mass. Hylander first examines relative gape in catarrhines. He reviews his 2013 paper, presenting the original idea, and publishes raw data and statistics. He suggests that increased masticatory efficiency for exploiting new dietary resources that are difficult to chew may have been the ultimate driver of hominin canine reduction. Yet, he recognizes that changing forces of sexual selection may also have been operating.

Wood and Schroer review the genus *Paranthropus* from the point of view of systematics. In particular, they address whether the genus *Paranthropus* is distinct from *Australopithecus*, why different generic assignments were made for *Paranthropus aethiopicus* and *Australopithecus garhi* (in spite of both taxa being megadont and small-brained), what the relationship is between the geographically distinct *P. robustus* and *P. boisei*, and whether the genus *Paranthropus* is monophyletic. An extensive discussion of homoplasy, which reveals that the masticatory system is a "homoplasy ghetto" (p. 103), ends with the authors questioning the monophyly of *Paranthropus*. Daegling and Grine attempt to infer the feeding behavior and diet of *Paranthropus boisei* from the mandible. They conclude only that the diet of *P. boisei* required intense mastication. The type of food eaten cannot be inferred from the mandible. Glowacka, Kimbel, and Johanson examine growth in the mandible of *Australopithecus afarensis*, describing three new infant/juvenile specimens from Hadar, Ethiopia. Compared to common chimpanzees, *A. afarensis* is broadly human-like in its fast mandibular growth. The authors attribute this to canine reduction.

Rightmire describes the Middle Pleistocene crania from Kabwe and Petralona, providing the most detailed account of the Kabwe specimen since the late 1920s. He is particularly interested in the utility of cranial traits for taxonomy, and the phylogenetic relationships with European specimens from Arago and the Sima de los Huesos. Collard and Cross examine thermoregulation in *Homo erectus* and Neanderthals, concentrating on heat loss from the limbs. Heat loss results are based on Cross's previous work on estimating surface area from body segments and displacement distances from motion capture data on modern humans. Two *Homo erectus* specimens—the ectomorphic Nariokotome specimen and a specimen from Dmanisi—three Neander-

thals, five fossil modern humans, and six modern populations are used. Whole body heat loss results are consistent with Bergmann's and Allen's rules. The Dmanisi *H. erectus* specimen is more cold adapted than the Nariokotome individual, and European Neanderthals are more cold adapted than a Middle Eastern Neanderthal. Yet, proximal and distal limb segment contrasts do not follow Allen's rule—the distal limb segments do not promote greater heat loss in *Homo erectus* and the Neanderthals.

Pearson and Sparacello examine midshaft shapes and robusticity of the humerus, radius, femur, and tibia in Middle Eastern Neanderthals, fossil modern humans from Skhul and Qafzeh, and a global sample of Holocene humans. They attempt to discern behavioral differences between Neanderthals and fossil modern humans in the Middle East. The Levantine Neanderthals resemble European Neanderthals and modern human agriculturalists and intensive foragers by showing severe and demanding use of the upper limb—it is the fossil humans from Skhul and Qafzeh that are the outliers. Because long bone structure reflects habitual physical activity, this implies that the Skhul and Qafzeh individuals did not engage in activities that strongly stressed the upper limb. Weinstein-Evron and Zaidner discuss the Acheulo-Yabrudian and Mousterian industries from Misliya Cave at Mount Carmel. The Mousterian occurs in a quick transition, which is characterized by the production of blades, points, and flakes using the Levallois technique. There is a wealth of Mousterian artifacts and faunal remains dated to over 160,000 years B.P., and behavior is similar to that detected in the late Mousterian. The authors infer that a population increase and migration into the site may have been responsible for the arrival of the Mousterian.

Harvati and Lopez use geometric morphometrics to analyze the Tabun C2 mandible, which is generally considered to belong to a Neanderthal, but which may also represent a Neanderthal/modern human hybrid—it has a retromolar gap as well as a mental eminence. The authors find that the specimen resembles neither Neanderthals nor modern humans. They are reluctant to infer hybridization, because the anatomical signs of hybridization are not well known. Bailey, Weaver, and Hublin use Bayesian statistics on non-metric traits to separate Neanderthal and modern human teeth. They then examine early modern human teeth from West Asia and Africa, and discover that these teeth are already dentally modern. Yet, material from North and South Africa exhibits the most primitive traits, even though there is no evidence of Neanderthals and modern humans coexisting there. The authors believe that their methods cannot be used to detect hybridization. However, given that the Oase 1 specimen has a 98% probability of being an Upper Paleolithic modern, and the Oase 2 specimen has a 97% probability of being a Neanderthal (Bailey et al.: Appendix A), signatures of hybridization may exist in the non-metric dental traits. This mixed signal conforms to the ancient DNA evidence of hybridization from Oase.

Freyer discusses hyoid anatomy and the controversy over Neanderthal language. He notes that the 3.3 million

year old hyoid from the infant Dikika *Australopithecus afarensis* is ape-like with a laryngeal air sac, while Neanderthal hyoids from Kebara, Sima de los Huesos, and El Sidrón are like those of modern humans. Frayer also argues that his work showing oblique scratches on the labial side of Neanderthal incisors and canines indicates handedness in Neanderthals, and thus brain lateralization associated with language. Been et al. create a 3D virtual reconstruction of the spine from vertebrae T1-S5 in the Kebara 2 Neanderthal. They analyze spinal curvature, and discover that this specimen had a more vertically oriented sacrum and less lumbar lordosis than the average modern human. This individual may have been adapted to carrying heavy loads and intense use of the upper body. This individual may also consequently have had a shorter stride length and slower walking speed than most modern humans. Hypolordotic modern humans contribute to this reconstruction.

Caspari, Rosenberg, and Wolpoff first discuss the changing position of Neanderthals in ideas about human evolution since the nineteenth century. They then pay particular attention to the Neanderthal pelvis and body shape, population structure, and survivorship curves. The authors concur with Rak's often-repeated mantra that Neander-

thals are different from, but not inferior to, modern humans. They conclude that Neanderthals may have been a distinct subspecies, even though human subspecies do not exist now. But did a Neanderthal race exist in the past? Ancient DNA reveals fine details of population structure. The authors argue for the validity of the subspecies designation as a synonym for race, given that Neanderthals had complex population structures and contributed different genes to living human populations in different combinations.

In summary, this book presents new and expanded data sets on fossil humans, especially australopithecines and Neanderthals. Chapter contributors read like a Who's Who in current paleoanthropology. The illustrations are beautiful, providing fine anatomical and archaeological detail. Anatomical coverage is extensive, ranging from the dentition, cranium, mandible, and hyoid to the limbs, pelvis, and spine. Archaeological discussion focuses on Israel. All of the authors show a genuine fondness and admiration for Yoel Rak. This is succinctly expressed by Frayer (p. 236): "...while we often disagreed about some things, Yoel could not have been more congenial nor as courteously dismissive of my ideas. All my best to a first class person and scholar."