From Biped to Strider
The Emergence of Modern Human Walking, Running, and Resource Transport

D. Jeffrey Meldrum and Charles E. Hilton, Editors

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The papers in this edited volume were originally presented at a symposium during the annual meeting of the American Association of Physical Anthropologists, held in San Antonio, Texas, in 2000. Paleoanthropologists traditionally investigate the functional anatomy of early hominid locomotion and the degree of terrestriality exhibited by different species. The goal of this symposium, however, was to present a broad overview of the varieties of modern human locomotion, and the appearance of anatomical traits in the skeleton that are associated with an erect striding gait. The editors believe that questions about early hominid locomotion could be more productively addressed against a background understanding of locomotor variability gleaned from modern humans.

There are twelve papers in the book, including an introductory chapter by the editors and a concluding synthesis. Some of the chapters fall into natural sets. There are two papers on the origins of bipedalism, two papers on the Laetoli trackways, and two papers on mobility and resource transport in modern humans. There is a chapter on the functional anatomy of the foot and a chapter on the speed and cost of transport during bipedal locomotion. One paper compares body build and lifestyle in australopithecines and genus *Homo*, and one paper examines the biomechanical consequences of changing the proportions of leg segments in bipeds. The references are current, and there is an index. Some of the anatomical photographs are of poor quality; the anatomical photographs in one chapter are unlabeled, and lack a scale or orientation.

Hilton and Meldrum begin the volume by reaffirming the importance of obligate bipedality as the signpost of hominid status. However, they also introduce a major theme of the book by arguing that bipedal locomotion has continued to evolve since its inception. Marathon running, endurance walking, and long distance carrying of heavy burdens are important features of modern hunting-gathering groups. Hilton and Meldrum argue that these behaviors may have appeared only with the advent of genus *Homo*, and are still under significant selection pressure among living people following traditional lifestyles. In the shortest chapter in the book, McHenry summarizes the work of the other authors, but also presents a heavily referenced historical overview about research on bipedalism and its origins.

The chapters by Begun and Deloison deal with bipedal origins. Believing that molecular phylogenies that yield a chimpanzee-human clade offer an objective line of evidence independent from anatomy, Begun concludes that bipedalism evolves from knuckle-walking. Begun notes the powerful recent arguments by Dainton and Macho for two independent origins of knuckle-walking based on ontogenetic and kinematic differences between knuckle-walking chimpanzees and gorillas, but he uses this evidence to argue that such variability shows that knuckle-walking is a generalized form of terrestrial locomotion that does not depend upon a suite of derived traits. Begun includes a long discussion about the extinct chalicotheres (Order Perissodactyla)—terrestrial quadrupeds whose hook-like hands were held in a flexed digitigrade posture. His conclusion that humans evolve from a knuckle-walking ancestor is based on three points: molecular phylogenetic evidence of a chimpanzee-human clade, similarity in the forelimb anatomy of African apes and humans, and the structure of chalicothere hands. He believes that the African apes and humans evolved from an unknown Eurasian ape related to *Dryopithecus laietanus*. This ancestral species entered Africa between 8-10 mya and adopted a terrestrial mode of locomotion because of the spread of grasslands at this time. Examining fossil foot bones from Hadar and Sterkfontein, Deloison concludes that australopithecines show a mixture of both arboreal and bipedal features, although bipedalism here was different from that exhibited by genus *Homo*. She reconstructs a common ancestor of the extant hominoids as being an erect, bipedal, plantigrade creature with climbing abilities, and with forelimbs and hindlimbs of equal length. Three lineages develop from this ancestor, two of them being hominid lineages. Deloison thus views bipedalism as an ancient mode of locomotion that originally existed in conjunction with arboreal climbing. Australopithecines lose some arboreal traits, but the lineage leading to *Homo* loses more. Bipedal specializations evolve in human feet that are distinct from those of the australopithecines.

An important chapter by Schmid examines the Laetoli trackways in detail. It provides a comprehensive history of discovery and research on the trackways, and includes digital maps of individual prints on the G trail. Schmid studied the original trackways when the conservators from the Getty Foundation re-excavated the footprint trails. Schmid admits to being stunned by the trackways, which he assumes were produced by three individuals belonging to the taxon *Australopithecus afarensis*. He had expected to find a plethora of ape-like traits in the prints and trackways. Instead, Schmid was amazed to find that they closely resembled modern human prints and tracks. This is an important admission because Schmid was the researcher who famously noted the non-modern body shape and form of the famous "Lucy" specimen (AL 288-1). Soft-tissue traits are preserved in the Laetoli trackways. Foot anatomy appears comparable to that of modern humans, and there are no signs of a prehensile foot structure. There is an adducted hallux, a functionally stable longitudinal arch, and short digits. One odd feature of the prints is the depth of the weight impression at the lateral part of the distal metatarsal area. Schmid also reports the results of preliminary experiments on bipedal weight transfer with 5-7-year-old children, in which these very short individuals were asked to walk with a fixed or rigid trunk. This created an "artificial amble gait," in which shoulders rotate to follow the movements of the ipsilateral pelvis. These children put greater pressure on the head of metatarsal V, thus mimicking the greater pressure exhibited on the lateral ball of the foot in the Laetoli trackways. Schmid then reconstructs this australopithecine gait. He argues that these people were certainly effective bipeds that could walk at a normal pace or stroll, but they could not run. Schmid argues that bipedal running is dependent on heavy respiration, which would be impossible in australopithecines. They could swing their arms, but their rigid thorax and lack of defined waist would restrict the degree of arm rotation, which needs to be strongly developed during running, and their shoulder girdle construction would prohibit elevation of the upper thorax during heavy breathing. Schmid thus argues that bipedal running first appeared when modern thorax morphology first appeared—that is, in genus *Homo*.

Meldrum investigates what effect the soft, ashy substrate might have had on the structure of the Laetoli prints. He does this by studying two footprint trails dating to 200 and 400 years ago left by habitually unshod humans in volcanic ash tuffs in Volcanoes National Park, Hawaii. Meldrum examined casts of the Laetoli trails and photographs made during the original 1978-1979 excavations. Both the Laetoli and Hawaiian trackways show variable gait angle and step width. However, in contrast to Schmid, Meldrum argues that the foot morphology of the Laetoli hominids was different from that of modern humans because a raised medial arch is not consistently present. Although the Laetoli hominids could engage in sustained bipedalism, Meldrum sees a tapered heel, transverse flexion at the mid-foot, an undeveloped ball of the foot, and relatively prehensile toes. Meldrum argues that a flat and flexible foot was characteristic for hominids through Neanderthal times—a medial arch occurs only in modern humans. Meldrum believes that considerable taphonomic alteration has occurred in the Laetoli trackways; this strong distortion accounts for the apparent similarity of the prints to those of modern humans. Berillon argues that the Laetoli prints do have a medial arch, although the orientation of the foot bone joints of *Australopithecus afarensis* in neutral position yield flat foot architecture. He consequently believes that very strong muscle activity must have occurred in order for plantar arching to take place. He points out that the muscles peroneus longus, peroneus brevis, tibialis anterior, and tibialis posterior have "huge" areas of insertion in the skeleton of *Australopithecus afarensis*. This taxon therefore had a unique form of bipedality in which longitudinal and medial arching was dependent upon strong muscle activity.

Gruss and Schmitt investigate whether the dynamics of bipedality are altered in living humans whose leg segments have different proportions. It is known, for example, that the human crural index (tibia/femur length) is affected by biological adaptation to external temperature. A high crural index is found in populations adapted to hot, arid conditions, and a low crural index is found in populations adapted to cold conditions. Biomechanical analysis leads one to expect that a relatively longer tibia should be associated with greater bending stresses at the knee, ankle, and along the tibial diaphysis. Twelve humans with different crural indices were investigated at walking speeds ranging from a slow stroll to a near run. Contrary to expectation, Gruss and Schmitt discovered that relative tibial length did not affect bending stresses. Instead, humans with a higher crural index walked with more flexed knees, and shifted the center of foot pressure forward. These results are applied to the 1.53 million year-old KNM WT-15000 *Homo erectus* specimen, whose crural index is at the upper range, even for tropical, arid-adapted modern humans. There is no sign of skeletal reinforcement at the knee joint, and so this specimen either resisted bending stresses with more muscular effort or used postural adjustments similar to those employed by the experimental subjects with high crural indices.

Carrier introduces the longest chapter in the book with a photograph that dramatically juxtaposes a pit bull and a greyhound. These adult male dogs have the same body mass, but very different body proportions. The pit bull has been bred to fight, and the greyhound has been bred to run. Carrier argues that a similar dichotomy existed among Plio-Pleistocene hominids: australopithecines evolved to fight, and members of genus *Homo* evolved to run. Australopithecine body build is characterized by high sexual dimorphism, very robust, long forelimbs, short hindlimbs, and a very wide pelvis. Carrier believes that dispensation toward fighting determined forelimb length and robusticity. The center of gravity was low, and a wide pelvis conferred lateral stability during aggressive bipedal encounters. In contrast to Kramer (this volume), who argues that australopithecines were slow speed foragers, Carrier believes that the australopithecine hindlimb was too muscular for slow walking. This muscular hindlimb allowed australopithecines to engage in rapid twists, turns, and short distance sprints. Carrier reconstructs the following behavioral scenario. Polygynous adult male australopithecines exhibit a high level of sexual dimorphism, and engage in aggressive male-male encounters emphasizing violent use of the hands and forelimbs in a bipedal stance. Weapon use by *Homo* eventually replaces forelimb fighting. Furthermore, because *Homo* can dissipate body heat through evaporative cooling of sweat, and can uncouple locomotion from respiration, distance running and walking is possible. Genus *Homo* is thus characterized by "both greatly increased distance transport and increased lethality in a lineage that was already specialized for fighting." (155-156). Somewhere, Raymond Dart is smiling.

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Kramer first enumerates the many variables that are affected by locomotion: energy, heat, efficient foraging, range, speed, endurance, fatigue, predator avoidance, and the carrying of burdens. Using a modeling technique that computes mass specific mechanical power and cost of transport for body segments, she concludes that australopithecines were efficient bipeds, but they walked slowly and could carry only minimal burdens. Members of genus *Homo* could walk rapidly and carry heavy burdens. The same analysis applied to modern humans reveals that human females are more efficient than males at slow walking speeds, but males are more efficient at high speeds. Genus *Homo* thus appears to be specialized for rapid walking that covers longer distances, and for carrying heavy burdens. Modern humans demonstrate these differences in locomotion and resource transportation: females are better adapted for traveling long distances with heavy loads and males are better adapted for fast travel.

This biomechanical analysis underlying sexual dimorphism is borne out by two chapters with ethnographic and archaeological evidence from modern humans. Hilton and Greaves study Pumé foragers on the seasonally flooded savannahs of Southwestern Venezuela. They find that sex affects travel distance and the transportation of food resources. Females carry heavy food burdens, occasionally exceeding their own body weight; males are more mobile throughout the year, but transport lower weights. Older females consistently collect and carry food that averages 30 percent of their body weight, about twice as much as younger females do and about five times as much as males do. Older females are responsible for collecting and carrying the bulk of the food during critical periods of resource stress. Ogilvie examines cross-sections of the femoral diaphysis in three Amerindian populations from the American Southwest. The sample spans the transition to agriculture in this area, ranging from mobile hunter-gatherers to early agriculturalists, to sedentary late agriculturalists. Foraging males and females show virtually no differences in cortical bone thickness or robusticity. During the transitional period, cortical bone thickness in females dramatically declines as mobility declines. This signals the beginnings of a sexual division of labor with a shift towards food production by females. Cortical bone thickness declines in both males and females during the late agricultural period as dependence on maize increases.

In summary, this fine volume is an up-to-date compendium of ideas about the origins of bipedalism, locomotion in Plio-Pleistocene hominid species, the appearance in modern humans of long distance running and walking, and the ability to transport remarkably heavy burdens during endurance walking. The book is written for a technical audience, and it presents much original material. There are pronounced differences of opinion, especially with regard to interpretation of the Laetoli trackways. This would confuse undergraduates and might limit the book's use as an undergraduate text. Yet, because it presents original data and new interpretations, researchers or advanced graduate students will certainly profit from reading this volume.

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