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Book Review

Walking Upright. Edited by *Jens Lorenz Franzen, Meike Köhler, and Salvador Moyà-Solà*, Courier Forschungsinstitut Senkenberg 243, E. Schweizerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller): Stuttgart. 2003, 153 pp., EUR 29.90.

Walking Upright is the delightful product of bringing together 22 scientists from 10 countries and from a multitude of different intellectual disciplines whose passion is to understand the evolution of human bipedality.

The volume begins with "Principles of Upright Walking" from the master, McNeill Alexander (pp. 1–7) and is followed by 3 valuable papers on the biomechanics of upright walking by Preuschoft, Witte, Schilling and colleagues. Nakatsukasa and Hayama give results on effects of bipedality on the distribution of cortical bone in the femora of bipedal macaques. Watkins addresses the relationship between substrate use and hand bone proportions in a large comparative series. Isler reports on her studies of vertical climbing in gorillas and the significance of this form of locomotion to the origin of bipedalism.

Martelli and Schmid examine morphological features of the lumbar vertebrae that relate to the differences between obligate bipedal species and quadrupeds. They find that *Australopithecus africanus* and *Homo ergaster* had functionally significant traits of their lumbar vertebrae that were much like those seen in *H. sapiens*. However, the lumbar vertebrae of *Australopithecus afarensis* and *Paranthropus robustus* were different in these functionally significant characteristics and taken with other morphological features imply "... a different kinematic mechanism for the flexion-rotation movement of the pelvis" (p. 68).

This theme of different styles of early hominid bipedalism is explored further by Clarke's contribution on the Laetoli footprints, *Australopithecus* foot bones, and other related topics. He describes his extraordinary discovery of an associated skull and body in Member 2 of the Sterkfontein caves that appears to be 3.3 million years old. It clearly has bipedal characteristics,

but it also possesses many traits associated with arborealism. As one of the very few who actually excavated the 3.5 m.y. old human footprints of Laetoli, Clarke has a direct knowledge of their morphology. He points out many ape-like characteristics that fit with his interpretation of his 3.3 m.y. old "little foot" of Sterkfontein Member 2 as having ape-like characteristics. However, many others who have studied the footprints and/or seen "little foot" do not share this interpretation. To refine the analysis of footprints, Kullmer and colleagues present a "High resolution 3-D image analysis of ape, hominid, and human footprints" (pp. 85–91). They find that the Laetoli footprints have a more human-like morphology.

Walking upright requires special balance of the head and Spoor contributes "The semicircular canal system and locomotor behavior, with special reference to hominin evolution" (pp. 93–104). In theory the architecture of the inner ear should solve all mysteries about how the heads of our ancient relatives held their posture. Fortunately Spoor goes beyond simple explanation and arrives at the truly complex issue of how to interpret variations in the semicircular canal. Humans and *Homo erectus* differ from apes, but many other human species whose bodies are clearly specialized for bipedality including Neanderthals look more like modern apes.

One of the great difficulties of addressing the origin of human bipedalism is the fact that it appears to be a unique event in primate evolution. But it may not be entirely unique as Köhler and Moyà-Solà point out. *Oreopithecus* provides some valuable clues to the processes by which a hominoid may adopt an orthograde posture with hind limb modifications for balance on 2 lower limbs. There are many superb papers in this symposium, but this is a real gem. Like most of the volume it holds the highest standards of comparative morphology, but it goes on to place the organism in its evolutionary and environmental context. *Oreopithecus* lived on isolated islands and was subject to the evolutionary forces common to all mammalian species with limited area and resources, and reduced predation. This led to reduction in body size and increase in foraging efficiency. The key that makes it relevant to the study of human bipedalism is that it appears to be a hominoid that adopted ". . . slow bipedal locomotion, upright harvesting at shrub level . . ." and skillful hands (p. 111).

Although *Oreopithecus* appears to converge on human-like bipedality in some respects, it is not the direct ancestor of the human lineage. Senut takes on the task of reviewing the fossils that may be closer to the human line. She reviews the fossil evidence from *Proconsul* to the Middle Miocene forms such as *Kenyapithecus*, *Dryopithecus*, and *Equatorius*, and pays particular homage to *Nacholapithecus* with its apparent orthograde posture. This chapter is especially important because the author has been studying the fossil evidence for the origin of bipdality since the 1970s and is one of the

principles in the discovery and analysis of *Orrorin tugenensis*. The femora of this species appear to be the earliest (6 m.y.) evidence of human bipedality. Senut has long maintained the view that there was a diversity of locomotor patterns in early human species and her chapter is an excellent summary of her views on this subject and on the evolutionary history of diverse hominid lineages.

Of all the papers in this excellent symposium, the piece by Crompton and 11 colleagues is truly exceptional. It fairly presents alternative views to the nature of the precursor of hominid bipedalism and presents a strong case for "... arboreal hand-assisted bipedalism (and more broadly, orthograde scrambling) in ... [an] orthograde, long-armed, and short legged hominoid climber as the behavior most likely to have been exaptive for the adoption of habitual bipedalism" (p. 144). It stands as a well-reasoned hypothesis with a great deal of field and laboratory data behind it. I have have long favored a more African ape model and stubbornly refused to believe such heresy. But this "orangutanian model" provides a clear hypothesis worthy of critical testing.

The final chapter by Franzen provides a penetrating analysis of the path ahead. He critically evaluates 5 approaches including paleontology, cladistics, functional morphology, paleoecology, and constructional morphology. Franzen has decades of experience and has a keen eye for what kinds of approaches yield useful results. His critique of cladistics is particularly penetrating partly because he is well versed in what Willi Hennig actually said about the inappropriate use of his methodology to fossils.

One of the great challenges ahead in the study of the origin of human bipedalism is coming to understand the genetic control of development. Those magical 2% DNA differences between human and African apes have profound effects. The next Senckenberg Conference on Upright Walking would be enriched by inviting geneticists and developmental biologists who can bring us closer to understanding how changes in the genome lead to morphology characteristic of human bipedalism.

All who have curiosity about evolutionary history can be grateful to the Senckenberg Research Institute and particularly to Franzen and colleagues for organizing this and other symposia. It is a magnificent demonstration of how our science transcends national and disciplinary boundaries to promote understanding.

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