Ardipithecus ramidus: First Steps or Missteps in Human Evolution?

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Contenders for the title of "earliest human ancestor" or earliest **hominin** now date to the Late Miocene of Africa and include a 7 mya cranium from Chad (*Sahelanthropus tchadensis*) and 6 mya fragmentary remains (teeth and a few limb bones) from the Tugen Hills of Kenya (*Orrorin tugenensis*). Fossils from Ethiopia slightly younger in age but even more fragmentary have been attributed to *Ardipithecus kadabba*. Some scientists remain agnostic as to the hominin affinities of these three ancient species, and others dismiss them as pretenders rather than contenders. They are indeed primitive in most respects compared to later, undisputed hominins like the australopiths (for example, "Lucy" and her ilk), but I believe that current evidence awards them a place in the human career. Enter *Ardipithecus ramidus* from the Aramis region of Ethiopia – a 4.4 mya candidate, presumably the descendent of *Ar. kadabba*, and represented by a mother lode of specimens that span the skeleton from head to toe (including a remarkable partial skeleton of a female catalogued as ARA-VP-6/500).

In 2009, White, Lovejoy, Suwa and others described the "Ardi" skeleton in great detail and placed it within a broad, quantitative comparative context in print and via e-monograph in **Science** magazine. It was concluded that that "Ardi" was indeed a hominin (or "hominid" in the authors' preferred nomenclature). But it was a hominin unlike anything paleoanthropology had ever seen. Therein lies the crux of the debate over Ardi's phylogenetic position and locomotor adaptations (which themselves are inextricably linked in my mind): large body, small brain; small canines, apparent sexual monomorphism; grasping hands ***and*** feet, including a divergent big toe. But the skeleton also revealed features of the foot and bony pelvis that smack of bipedalism when compared to australopiths — and even when compared to more recent hominins. In other words, here was an exceedingly primitive bipedal hominin that was at home on the ground and in the trees, and it had solved the arboreal-terrestrial problem in a manner decidedly unlike that of knuckle-walking and suspensory chimpanzees. In light of the "Ardi" fossils, White and his co-authors now viewed chimpanzees and other great apes as highly specialized primates with their own independent evolutionary trajectories ; they were neither living fossils nor essential referents in modeling human evolution. Ardi was unique, and there simply were no good living analogues.

Shortly after the 2009 opus appeared, demurring points of view popped up in letters to the editors of **Science** and in invited commentaries published elsewhere. Scientific reporters had no problem finding skeptics (mea culpa). Rebuttals appeared and White and Co. held their ground. For many workers, bipedalism was one of the – perhaps ***the*** – ticket into the hominin club, and the bipedal signal seemed to be muted at best. Small canines were also claimed to exist in other fossil apes. Despite having read the descriptions and analyses, I also had my doubts. If

Ardi wasn't really a biped, then it probably wasn't a real hominin either – despite the fact that earlier cladistic analyses based largely on teeth had already placed it firmly at the base of a monophyletic group of extinct hominins and living humans. Much cognitive dissonance ensued, at least within me.

Although it may sound self-serving, there really is no substitute for seeing the fossils first-hand, and Tim White/Owen Lovejoy/Gen Suwa offered me and several of my collaborators that invaluable opportunity relatively recently, first in White's lab at UC-Berkeley (high resolution casts) and then in Addis Ababa at the National Museum of Ethiopia (the originals). We were allowed to study everything, and Suwa also provided access to micro-CT scans. My colleagues include Caley Orr, Matthew Tocheri, Sergio Almécija and Biren Patel, and our primary focus to date has been on the hands and feet of *Ardipithecus* and other early hominins. Our methods are diverse and include biomechanical modeling and three-dimensional morphometrics. Data collection continues on many fronts, and although our analyses to date are still preliminary, I will eat some crow and defend the proposition in my Dialogues presentation that the postcranial skeleton of *Ardipithecus ramidus* belongs unequivocally to an early bipedal hominin. Full disclosure: we are collaborating with White and Co., but that is not to say that we agree on everything with them or among ourselves. I take full responsibility for what follows.

When asked about the locomotor repertoire of *Ardipithecus*, Tim White is said to have quipped: "If you wanted to find something that moved like these things, you'd have to go to the bar scene in *Star Wars*." Alien locomotion notwithstanding, the skeleton of Ardi is a fascinating mosaic of features that reflects a successful adaptation to life both in the trees and on the ground. If we are to judge by the new Burtele hominin foot from Ethiopia, it appears that aspects of this mixed configuration persisted for over a million years. The big toe (hallux) is a divergent grasping digit, but the other toes exhibit a geometry seen elsewhere only in later, unequivocal bipeds – long straight metatarsal shafts with marked "doming" of the head coupled with a corresponding angulation (dorsal canting) of the proximal pedal phalanges. This permits and reflects extreme dorsiflexion of the lateral toes during push off in bipedal walking. We have quantified this feature, and it is unique to bipedal hominins. Although the bony pelvis is crushed, important regions require no reconstruction: the distance between the hip joint and the sacroiliac joint is short as in fossil hominins and modern humans, thereby moving the center of gravity closer to the hip joint. If the reconstructed iliac blade orientation is accurate, the gluteal muscles used in lateral balance during bipedalism are also very favorably positioned. No living or fossil ape has this pelvic anatomy (in other words, a hominin-like false pelvis attached to an ape-like true pelvis). Another feature linked to upright posture ("orthogrady") is the forward position of the foramen magnum. Limb proportions in *Ardipithecus* are similar to those of "Lucy" (*Au. afarensis*) and are therefore also compatible with a bipedal gait of some sort. We conclude that *Ardipithecus* was indeed a biped.

Those features above linked to bipedalism are derived and can be added to the tally of craniodental character states that make *Ardipithecus* a "cladistic hominin". We see nothing in the

locomotor skeleton that would disqualify Ardi from being a possible ancestor of either australopiths and/or the Burtele hominin, but confirming bona fide ancestor-descendent relationships in the fossil record is not a simple task. There are numerous other postcranial similarities between *Ardipithecus* and later hominins like the australopiths, but we are still pondering the polarities (primitive or derived) of many of these features. These include the overall shape of the metacarpals and proximal hand phalanges, shape of some of the wrist bones (for example, the lunate), and relative hand length (short). Miocene "apes" represent a plausible ancestral morphology or starting point from which one might derive an early hominin such as *Orrorin* or *Ardipithecus*, but none of them, including the famous Italian ape *Oreopithecus*, are sufficiently hominin-like to argue that Ardi is just another aberrant ape. We conclude that *Ardipithecus* was indeed a hominin.

Recent research has demonstrated that modern humans, even with bodies specialized for bipedal walking and running, are still agile climbers. However, compared to *Ardipithecus*, it is clearly no contest. Its skeletal anatomies, especially its hands and feet, reflect and facilitate a real commitment to climbing and arboreality. That is not to say that these early hominins rival living chimpanzees in climbing capabilities or exhibit any specializations for highly suspensory behaviors. But they probably were very flexible and versatile in the trees despite their large body size. Use of both hands and feet together in quadrumanous clambering seems highly likely. If they were indeed upright or orthograde in general and bipedal when on the ground, it seems probable to me that arboreal bipedalism was also practiced, with and without assistance by the hands. Hoisting, bridging, and even occasional below-branch movements might have been parts of their positional repertoire. However, we find no compelling evidence for knuckle-walking, digitigrade quadrupedalism or palmigrade quadrupedalism when in the trees or on the ground. Finally, there is no need to invoke open habitats and grasslands as driving forces or prerequisites for the early evolution of bipedalism. *Ardipithecus* links bipedalism directly to forested habitats, and it may prove to be the case that bipedalism first emerged in the trees and was then co-opted for terrestrial travel. Crow doesn't taste so bad after all.