Early hominin diversity and the emergence of the genus *Homo*

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Summary - Bipedalism is a defining trait of hominins, as all members of the clade are argued to possess at least some characters indicative of this unusual form of locomotion. Traditionally the evolution of bipedalism has been treated in a somewhat linear way. This has been challenged in the last decade or so, and in this paper I consider this view in light of the considerable new fossil hominin discoveries of the last few years. It is now apparent that there was even more locomotor diversity and experimentation across hominins than previously thought, and with the discovery of taxa such as H. floresiensis and H. naledi, that diversity continues well into the genus Homo. Based on these findings, we need to reevaluate how we define members of the genus Homo, at least when considering postcranial morphology, and accept that the evolution of hominin bipedalism was a complex and messy affair. It is within that context that the modern human form of bipedal locomotion emerged.

Keywords - Hominins, Bipedalism, Homo, Locomotor diversity.

Introduction

The symposium at which this paper was given was entitled "What made us human". The answers to that question are of course myriad and multifaceted, and entirely depend on whether one is considering strictly our own species, Homo sapiens, or the hominin lineage as a whole. Look at our own species and one has to consider complex attributes linked exclusively to our relatively large brains, such as language or symbolic behaviour. Look at the entire hominin lineage and the picture becomes far cloudier. That having been said, one major behavioural attribute that arguably characterizes the entire lineage is bipedal locomotion and its associated anatomical modifications. All hominins possess features that show at least some indication of bipedality. The purpose of this paper is to discuss the evolution of this highly unusual form of locomotion within the context of the increasingly diverse and complex hominin clade. This will be done with particular emphasis on the foot, the only structure that comes into contact with the ground in bipeds, and thus one that is extremely reflective of locomotor behaviour.

The contemporary view of the hominin tree is that it is distinctly bushy. There are currently at least 23 taxa that are widely accepted as belonging to the hominini. Bipedalism is arguably the first major adaptation we see in hominins (Senut *et al.*, 2000; Zollikofer *et al.*, 2005; White *et al.*, 2009), and yet until about ten years ago it's evolution had largely been treated as a relatively linear affair. Some researchers, such as Robinson (1972) did argue that different hominin taxa living at the same time (*Australopithecus africanus* and *Paranthropus robustus*) had differing degrees of terrestriality in their locomotor repertoires, but the predominant view remained that that earlier, small brained hominins, such as *Australopithecus*, were bipedal much of time but retained some level of arboreality, the first members of the genus *Homo* has eschewed arboreality all together, and that the modern human condition (obligate bipedalism) was simply a matter of subtle modifications of the condition of basal *Homo*.

By the 1990s this position was becoming increasingly untenable, and in the following decade it was evident that within the context of greatly increased hominin taxonomic diversity, which was based entirely on craniodental features, a reevaluation was needed. The first modern paper to challenge this linear view of bipedalism argued, based on quantitative analyses of hominin foot bones, that there were at least two distinct experiments with the foot, one typified by Australopithecus afarensis, and one typified by Australopithecus africanus and Homo habilis (Harcourt-Smith & Aiello, 2004). It concluded that there was likely more locomotor diversity in the hominin clade than had been previously argued. It has been over ten years since that paper, and it is thus interesting to consider its conclusions within the context of the significant number of new hominin taxa that have been named and described since.

Locomotor diversity in early hominins

Early hominins (here defined as hominins living between approximately 7 and 4 Ma) are now well represented in the record thanks to significant discoveries over the last twenty years. The earliest, putative members of the clade, as one might expect, possess very few features that indicate bipedalism. At approximately 7 Ma in age, *Sahelanthropus tchadensis* has no published postcrania, but the digital reconstruction of the heavily crushed skull indicates an anteriorly positioned and horizontally orientated foramen magnum, the latter feature being especially important in indicating bipedality (Zollikofer

et al., 2005). The overall femoral morphology of Orrorin tugenensis also indicates bipedality (Richmond & Jungers, 2008) although the upper limb remains imply arboreality (Senut et al., 2001). The remains also come from a wide geographic area, perhaps making it difficult to be sure that they all represent the same taxon. The best represented of these early hominins, Ardipithecus ramidus, whose hominin status is now well established (Kimbel et al., 2014), possesses a postcranial skeleton dominated by features related to an arboreal lifestyle. However the pelvis, although distorted, suggests bipedality based on a number of features, including a prominent anterior inferior iliac spine, indicating a human-like attachment and function of the hip flexor *m. rectus femoris* and the iliofemoral ligament, a hip joint stabilizer

Although important for understanding the emergence of hominin bipedality, these taxa do not temporally overlap, and in the case of S. tchadensis and O. tugenensis are too poorly represented in the postcranium to sufficiently address questions relating to locomotor diversity in early hominins. In that respect it cannot be argued that there was locomotor diversity (or not) during the 7 - 4 Ma time period. The one interesting consideration, though, is the relationship between Ar. ramidus at 4.4 Ma and the earliest species of Australopithecus, Au. anamensis at 4.2 – 3.9 Ma. This latter taxon is argued to have had features in the lower limb indicative of habitual bipedalism (Ward et al., 2001). With a first appearance in the fossil record only 200,000 years after the 4.4 Ma date of Au. ramidus, it would have required a very fast rate of morphogenesis for Au. ramidus to have speciated into Au. anamensis. The alternative is that Ar. ramidus and Au. anamensis represent distinct evolutionary lineages, and that the two species may well have overlapped in time and space, thus indicating different experiments with bipedalism occurring in two different early hominin taxa. However, until further Au. anamensis remains are discovered (and critically from the same anatomical regions as we have for Ar. ramidus), this remains a somewhat speculative assertion.

Locomotor diversity in australopiths

Between 4 and 3 Ma we see a wealth of hominin remains that are predominantly assigned to the genus Australopithecus. The best know taxon from this time period, Au. afarensis, is wellrepresented throughout the skeleton. Although scholars have differed in their functional interpretations of the postcranium (e.g. Lovejoy et al., 1973; Lovejoy, 1988; contra Stern & Susman, 1983; Stern, 2000) the predominant view today is that this taxon was habitually bipedal (sometimes referred to as facultative bipedalism) but was not an obligate biped. Au. afarensis thus retained an arboreal component to its locomotor repertoire, as indicated by its curved manual and pedal phalanges and ape-like shoulder joint (Stern, 2000; Alemseged et al., 2006). Recently, new findings indicate that there were other, likely more arboreal hominin taxa living at the same time and in the same part of East Africa as Au. afarensis. The hominin foot from Burtele, Ethiopia (Haile-Selassie et al., 2012), dated to 3.3 Ma, is argued to have had an opposable hallux, thus indicating pedal arboreal grasping. It has long been argued that hallux opposability is not evident in Au. afarensis. Such a morphological condition would also be incompatible with the 3.6 Ma Au. afarensis set of hominin footprints at Laetoli, Tanzania, which are markedly human-like (e.g. Raichlen et al., 2010). Although the consensus view remains that the prints were made by that taxon (e.g. White et al., 1984), they have been argued to be incompatible with the pedal morphology of Au. afarensis (e.g. Tuttle et al., 1990, 1991; Harcourt-Smith & Hilton, 2005). The Au. afarensis foot, as represented by remains from Hadar, has an inflated navicular tuberosity and a low orientation of the sustentaculm tali on the calcaneus (Sarmiento & Marcus, 2000; Harcourt-Smith & Aiello, 2004; Harcourt-Smith et al., 2015). The former feature is indicative of a weight-supporting middle part of the medial foot (Elftman & Manter, 1935) while the latter feature suggests a low medial longitudinal arch (Morton, 1935). Architectural reconstructions of the medial column of the

Au. afarensis foot also support these findings (e.g. Berillon, 2003; DeSilva & Throckmorton, 2010). It follows, then, that the Laetoli trails may well represent a hominin taxon with a more derived foot than either that of *Au. afarensis* or the Burtele foot, thus pointing to even more variation in hominin foot form and locomotion in the 4 - 3 Ma time period.

The period between 3 and 2 Ma is extremely meagre for East African material, although the 2.5 Ma remains from Bouri, Ethiopia, indicate a hominin that might have had slightly elongated hind limbs (Asfaw et al., 1999). In South Africa, however, the numerous well-known remains attributed to Au. africanus and Au. sediba (and possibly other species of Australopithecus) indicate combinations of postcranial morphologies that are distinct from both those in east Africa and also from each other. Outside those at Makapansgat, some of the oldest remains of South African Australopithecus are those belonging to the skeleton Stw 573 ("Little Foot"), from Member 2, Sterkfontein (Clark, 1998). The dating of this skeleton has been the subject of considerable disagreement, and although a review of that research in conjunction with new dating methods place it between 2.6 and 2.2. Ma, the most recent findings indicate that it is more likely to be aged to 3.2 Ma (Granger et al., 2015). If as old as 3.2 Ma, the Stw 573 skeleton has a combination of features in the foot entirely different to the contemporary Au. afarensis remains from Hadar (Harcourt-Smith & Aiello, 2004). If Stw 573 is younger, it still represents a distinct pattern from Au. afarensis, and given that it has a more primitive talo-crural joint, it either indicates a reversal in morphology from Au. afarensis to Au. africanus, or two distinct lineages with different types of mosaicism in the foot (Harcourt-Smith, 2002). Elsewhere in the skeleton the relative size of the long bone joints in Au. africanus and Au. afarensis are argued to be broadly alike (e.g. McHenry, 1986; Dobson, 2005), although there are also argued to be distinctly different muscle attachment configurations in the pelvis (Haeusler, 2001). Haeusler (2001) in fact asserts that the older Au. afarensis was more human-like in its mode of bipedalism that the more recent Au. africanus.

The recently described Au. sediba remains point to a late species of South African australopith completely distinct in its postcranial skeleton and gait from other contemporary hominins from the region (Au. africanus and Paranthropus robustus) in having a pelvis that shares a number of important features with those from the genus Homo, such as shorted ischia and more vertically orientated ilia (Kibii et al., 2011). Given the relatively small brain size of Au. sediba, this is a strong indication that selection for obligate bipedalism in this taxon was a more likely reason for a more *Homo*-like pelvis than anatomical reconfiguration to accommodate larger-brained neonates during parturition. However, the leg and foot of Au. sediba are mosaic and are argued to indicate a hyperpronating form of bipedalism distinct from that of both early Homo and other species of Australopithecus (DeSilva et al., 2013).

Little can confidently be said about the postcranial morphology of the genus *Paranthropus*, although Robinson (1972) argued that the extensive remains from Swartkrans, South Africa, indicated a locomotor repertoire that was more terrestrial than that of the contemporary *Au. africanus*. In east Africa the recent discovery of new *Paranthropus boisei* postcrania at Olduvai Gorge, Tanzania (Domínguez-Rodrigo *et al.*, 2013) indicates that that taxon may have had powerful and large forelimbs, perhaps indicating some degree of arboreality. This is distinct from the more gracile upper limb remains attributed to contemporary early *Homo* from northern Kenya (Leakey *et al.*, 1978; Aiello & Dean, 1990).

Locomotor diversity in the genus Homo

Until the last ten years or so the earliest member of the genus *Homo* with associated postcranial elements, *H. habilis*, was argued by most to have been an obligate biped (e.g. Day & Naiper, 1964; Susman & Stern, 1982). Recent finds have challenged that assertion. Ruff (2009) has shown that the OH 62 partial skeleton retained ape-like structural properties in its long bones, and the taxonomic affinities of much of the Olduvai postcranial material have been challenged (Constantino & Wood, 2007). New discoveries have also expanded the locomotor diversity within the genus. While the postcranium of H. ergaster and H. erectus is predominately humanlike, analyses of the upper limb indicates that the position of the scapula and the degree of humeral torsion in these taxa falls outside the modern human range (Larson, 2009, but see Roach & Richmond, 2015). This would have had implications for arm and trunk movement during bipedal walking, perhaps leading to a gait different from that of modern humans. More drastically, the diminutive remains of H. floresiensis has a shoulder configuration unlike that of modern humans (Larson et al., 2007), a long foot relative to the leg, a hallux shorter than in humans and a foot lacking a medial longitudinal arch (Jungers et al., 2009). In combination these features would have resulted in a gait definitively different that of modern humans, and would likely have impaired complex bipedal behaviours such as running. Most recently the H. naledi remains from South Africa (Berger et al. 2015), although lacking a geologic age, indicate further experimentation with bipedalism within Homo. The foot is largely humanlike (although it has phalanges more curved than in modern humans) (Harcourt-Smith et al., 2015) whereas the shoulder joint has a cranially orientated glenoid, and highly curved manual phalanges, both adaptations to arboreal climbing (Berger et al., 2015). Given that the H. naledi talus is far more derived than that of OH 8 (if that belongs to H. habilis), and the cranial morphology is closer to basal Homo than not, this indicates a different suite of locomotor adaptations in H. naledi compared to its likely closest relatives, H. habilis, H. ergaster and H. erectus. Recent descriptions of fempostcranial remains from northern Kenya (Ward et al., 2015) support this assertion. The remains are argued to be Homo-like, but possess femoral midshaft and pelvic inlet morphologies distinct from those found in African H. erectus, indicating that at 1.9 Ma there were at least two distinct postcranial morphotypes in east Africa attributed to the genus Homo. How these differences relate

to potentially different types of bipedal locomotion will need to be further explored.

Consideration of locomotor diversity in the genus *Homo* within light of increased taxonomic diversity

Although beyond the scope of this paper, it is worth briefly considering how we define the genus Homo within the context of increased hominin postcranial and associated locomotor diversity. Many of the traditional characters used to define Homo have been challenged or reevaluated over the last twenty years (e.g. Wood & Collard, 1999), and recently several finds have contributed to this process. We now know that stone tool production (Harmand et al., 2015) and possible hominin tool use (McPherron et al., 2010) predate the emergence of the genus Homo. Brain size increase is also an increasingly problematic criterion to use (Spoor et al., 2015) which leaves two major usable criteria: the dental apparatus and the locomotor skeleton. New finds that push back the earliest evidence of the genus (Villmoare et al., 2015) indicate that a reduced dentition predates other bony adaptations in the jaw of early Homo, making dental modification a robust criterion for membership of the genus, although it is also evident that there was considerable diversity in dental and gnathic morphology between early Homo taxa (Spoor et al., 2015). Postcranially, there are now new species of Homo with locomotor adaptations indicating either a different type of bipedalism to that of modern humans (e.g. H. floresiensis), or a retention of some arboreality in the locomotor repertoire (e.g. H. naledi).

Given these problematic and confounding factors, obligate and, more importantly, modern human-like, bipedalism should perhaps not be used as a criterion for membership of the genus *Homo*. Instead, a combination of postcranial traits and archaeological evidence that clearly indicate a distinct behavioural shift in activity patterns, landscape use and resource acquisition (including materials for tool-making) should be considered more closely. This is especially important within the context of the earlier date for the emergence of *Homo* that coincides with a shift to more open and arid habitats (DiMaggio *et al.*, 2015).

Conclusions

Based on current evidence from the foot it is now clear that there was considerable variation in fossil hominin pedal anatomy (Fig. 1). Given that the foot is the only structure to interact with the substrate in bipeds, this likely indicates variation in the "types" of bipedalism found in different fossil hominin taxa Though the evidence is meagre for early hominins, by 4.2 Ma it is apparent there may have been two distinct locomotor modes, in Ar. ramidus and Au. anamensis respectively. These two patterns continue throughout the Pliocene, as evidenced by the Au. afarensis remains and Burtele foot (Haile-Selassie et al., 2012). The potential incompatibility of the Au. afarensis foot and the Laetoli footprints indicates possible further variation in that time period. The early Pleistocene Au. sediba remains point to experimentation with a Homo-like pelvis in late South African Australopithecus, in combination with a reconstructed gait unique to the genus. In early Homo we now see an increased diversity in postcranial anatomy and associated locomotor behavior, which indicates a continuation of locomotor experimentation late into the hominin fossil record (as indicated by H. florsiensis). New finds suggest at least two distinct postcranial morphotypes at 1.9 Ma (Ward et al., 2015), and H. habilis and *H. naledi* are argued to have retained a degree of arboreality in their locomotor repertoires, while H. floresiensis would have had a gait markedly distinct from that of modern humans (Jungers et al., 2009). It follows, then, that it is perhaps necessary to reevaluate obligate, human-like bipedalism as a meaningful diagnostic criterion for membership of the genus Homo.

It is thus from a broad spectrum of locomotor experimentation that modern human bipedalism emerged. While this may be confusing to some, it largely supports what we know for many other aspects of the human condition, that the story is complex and diverse.

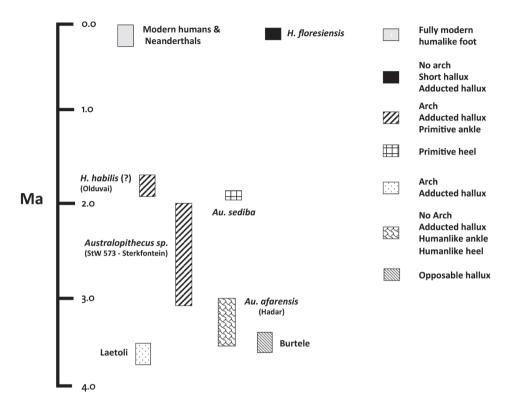


Fig. 1- A graphical summary of pedal anatomical variation in the hominin fossil record.

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