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Biomechanics and the origins of human bipedal walking: The last 50 years

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ABSTRACT

Motion analysis, as applied to evolutionary biomechanics, has experienced its own evolution over the last 50 years. Here we review how an ever-increasing fossil record, together with continuing advancements in biomechanics techniques, have shaped our understanding of the origin of upright bipedal walking. The original, and long-established hypothesis held by Lamarck (1809), Darwin (1859) and Keith (1934), amongst others, maintained that bipedality originated in an arboreal context. However, the first field studies of gorilla and chimpanzees from the 1960's, highlighted their so-called 'knucklewalking' quadrupedalism, leading scientists to assume, semi-automatically, that knucklewalking must have been the precursor to bipedality. It would not be until the discovery of skeletons of early human relatives *Australopithecus afarensis* and *Australopithecus prometheus*, and the inclusion of methods of analysis from computer science, biomechanics, sports science and medicine, that the knucklewalking hypothesis would be most robustly challenged. Their short, but human-like lower limbs and human-like hand indicated that knucklewalking was not part of our ancestral locomotor repertoire. Rather, most current research in evolutionary biomechanics agrees it was a combination of climbing and bipedalism, both in an arboreal context, which facilitated upright, terrestrial, bipedal walking over short distances.

1. Introduction

The past 50 years have seen great changes in the way that we interpret the human fossil record. Abundant fossil discoveries document morphological adaptation in evolution and new techniques have been developed to reconstruct locomotor biomechanics of fossil forms. In this Perspective, we review the temporal changes in our understanding of the origins of human bipedal walking.

1.1. Pre-1960: A very limited fossil record

Until the late 1960s, the general view, expressed by Lamarck (1809) and Darwin (1859) and by major early 20th century anatomists including Keith (1934), was that human upright bipedalism originated in an arboreal, not terrestrial context (reviewed *e.g.* by Crompton et al., 2022). In the 19th Century, little was known about relationships among the apes: the 'Anthropoid Apes' were grouped together as a unit and contrasted with 'Man' on the basis of possessing a prehensile, rather than a supporting foot (Owen, 1868). In 1894, Eugene Dubois published on the Trinil, *Pithecanthropus erectus* from Java, consisting of a partial

skull and femur. Dubois regarded this genus as a 'man-like ape', not 'early man'. It was not until 1921 that the first African hominin, 'Broken Hill Man' was discovered. Before that date, Central Asia was commonly regarded as the likely cradle of the human stock. (For a review of the early history of hominin palaeontology, see Boule and Vallois, 1957) However, Dart's 1924 discovery of the Taung child's skull in 1924, from which he named the genus *Australopithecus,* followed by others such as such as 'Florisbad Man' (1932) and Saldanha Man (1953), changed the focus of ideas on human origins from Asia to Africa.

1.2. 1960–1970: The emergence of the knucklewalking hypothesis

Early fieldwork on mountain gorillas (Schaller, 1963) and savannah chimpanzees (Goodall, 1968) reported high frequencies of *knucklewalking quadrupedalism*, where upper body weight is supported primarily on the middle manual phalanges. Washburn (1967), noting the close genetic relationship between chimpanzees and humans (*e.g.,* Chiarelli, 1967; Goodman et al., 1967) and, bipedal food-carrying behaviour in habitually quadrupedal captive great apes (Hewes, 1961), deduced that knucklewalking gave rise to bipedalism in early

hominins (early human ancestors and their close relatives). Washburn (1967), however, overlooked Hooton's (1946) argument that knuckle-walking in chimpanzees and gorillas was simply the constraining effect that a heavier upper body mass required to sustain habitual climbing in a quadrupedal posture. Nevertheless, Washburn's (1967) proposal led to a focus on studies of the mechanics of knucklewalking for much of the last 50 years. Tuttle (1967) claimed that many characteristics of the chimpanzee hand and wrist are adaptive for knucklewalking, and argued from cinematography of chimpanzee and great-ape dissections, that muscle masses and carpometacarpal joint surface geometry in African apes are biomechanically adaptive for sustaining the forces incurred in knucklewalking (Tuttle, 1969). Acknowledging that then-available fossil evidence for early-hominin hands lacked these features, he suggested that human ancestors diverged from those of other African apes before the emergence of knucklewalking adaptations.

1.3. 1970–1980: Biomechanical studies of knucklewalkers

In support of the knucklewalking hypothesis, Tuttle et al. (1972; and see Tuttle and Basmajian, 1978) performed electromyography of gorilla forearm muscles during knucklewalking, concluding that they acted to support close-packed positions of the wrist and carpometacarpal joints. Jenkins (1972), and Jenkins and Fleagle (1975) studied bipedal walking in common chimpanzees using cineradiography, noting a more abducted, flexed posture of the swing-hip than seen in human bipedalism. Comparing chimpanzee wrist-joint morphology to that in then-known fossil apes, they conclude that suspensory and arm-swinging locomotion are unlikely to have antedated knucklewalking in ape evolutionary history, which tends to contradict Tuttle (1969). Zihlman and Hunter's (1972) calculations of joint torque about the hips of chimpanzees, an *Australopithecus* innominate and a size-matched human pelvis, stress a stabilizing role of the internal rotators in the latter two in upright posture. Following the then-current view of human origins, they interpret this as being beneficial to long-distance walking in the savannah. Energetic advantages of quadrupedal, versus bipedal, running were addressed by Taylor and Rowntree (1973) who compared oxygen consumption in each locomotor mode by chimpanzees and capuchin monkeys, revealing no significant differences.

1.4. 1980–2000: Challenges to the knucklewalking hypothesis

The discovery of the Laetoli G footprint trails (Leakey et al., 1976, some 3.6 million years old [MY]) provided a new source of data on early hominin gait. The first biomechanical analysis of their spacing by Alexander (1984), derived walking speeds resembling those of modern human "small-town" (i.e. unhurried) walking. However, the Laetoli G3 prints were made by adult australopiths walking with a child through soft volcanic ash. The predicted walking speeds presented by Alexander (1984), while fully representative of this condition, are unique to these individuals, only, and cannot be used to characterise or exemplify the walking speeds of an entire species (McClymont et al., 2021a).

Discovery of the one-third-complete skeleton AL 288-1 of *Australopithecus afarensis* (some 3.4 MY), the putative Laetoli trackmaker, and of StW 573 *Au. prometheus* (3.67 MY), led Susman (1983) and Clarke (1998) to observe that there was no evidence from their wrist, hands, or joint morphology, that could infer knucklewalking behaviour. Berge's (1994) calculation of torques about the hip of *Au. afarensis* under alternative muscle-attachment hypotheses, led her to conclude that the hip-joint would have been less stable, but more mobile than that of humans, favouring arboreal rather than terrestrial activity.

Senut (1980, 1981) observed that australopith elbow joints lacked the stabilization features expected in knucklewalkers and observed in chimpanzees. Ishida (1991) used techniques developed by Yamazaki and colleagues (1979, 1983) to model the costs of upright and 'slouched' (more commonly 'bent-hip, bent-knee' [BHBK]) bipedal walking. The parasagittal-plane model revealed that mechanical energy costs more

than doubled in BHBK walking. They concluded that long-distance walking would select strongly for adoption of upright posture. However, Nakatsukasa et al. (2004) found that energy consumption in Japanese macaques trained in bipedal walking was 20–30% higher in bipedal than quadrupedal gaits. Similarly, Preuschoft and Witte (1991) calculated effects of the short-legged *Au. afarensis* AL 288-1 (see. Stern and Susman, 1983) on muscle costs and mobility, concluding that, while short-legged proportions facilitated changes of direction and pace, it did not facilitate long-distance walking. Schmitt (2003) concluded from experimental studies of joint excursions and vertical ground reaction forces (vGRFs) that compliant gaits allow attenuation of vGRF shocks, arguing that compliant gaits would, therefore, have been favoured in early hominins with (putatively) smaller, less-stable joints. Sellers et al. (2003) developed a forwards-dynamic modelling system using evolutionary robotics, generating stable upright bipedal gaits with maximum efficiencies within 15% of experimentally derived, modern human values. Later Sellers et al. (2004) used this system to predict optimal patterns of muscle contraction and bipedal gait in *Au. afarensis*, matching them to the footfall patterns of the Laetoli footprint trails to estimate likely speeds. This research indicates that the bipedalism demonstrated by the Laetoli hominin was fully competent.

Dainton and Macho's (1999) comparison of the dimensions and ontogeny of carpals in *Pan* and *Gorilla,* identified differences in hamate and capitate dimensions, suggesting that the hand is more heavily loaded on the ulnar side in *Gorilla*. This implies that knucklewalking is not kinematically consistent in the two genera, and hence likely, independently derived. Richmond and Strait (2000) responded by claiming that *Au. anamensis* KNM ER 20419 and *Au. afarensis* AL 288-1 distal radii display a mechanism for locking in hyperextension in knucklewalking as seen in chimpanzees.

One issue rarely addressed by proponents of the knucklewalking hypothesis is, if hominins arose from knucklewalkers, why did they abandon knucklewalking? Early on, Wheeler (1985) argued that bipedal posture and losing body hair was a response to insolation in open savannah. But by the end of this period, Hunt's (1991) consideration of the mechanics of forelimb suspension, led him to suggest that ground-based feeding from small trees drove the adoption of upright posture (1996). Now, even proponents of a knucklewalking origin (*e.g.* Richmond et al., 2001), set the transition to bipedal walking not in an open-savannah context, but in woodland-savannah, and combined with arboreal climbing.

1.5. 2000–2010: Studies of the mechanics of BHBK and knucklewalking gait

However, some continued to argue for knucklewalking underpinning the origins of human bipedalism. Knucklewalking chimpanzees, when they do occasionally walk bipedally, adopt a 'bent-knee, bent-hip' (BHBK) posture, with flexed hip and thigh. This has lead many to think that early human ancestors would have walked in the same way when they first became bipedal. Thus, for example, Schmitt (2003) argued that early hominins would have favoured BHBK gaits because of morphological constraints, namely joint mobility limitations. Since Steudel-Numbers and Tilkens (2004) found that short-legged humans incurred greater costs: the short legs of *Au. afarensis* might suggest there might have been greater costs in erect bipedalism than BHBK gaits. However, Carey and Crompton (2005) found a 50% increase in basal metabolic rate, a doubling of metabolic energy costs, blood lactate production and raised core temperature in BHBK over upright walking of adult humans. Such an inefficient gait is most unlikely to have been selected for, and indeed would most likely have been the subject of intense negative selection.

Drapeau and Ward (2007) showed that while *Au. afarensis* had relatively short metacarpals compared to ulnar length, both common and pygmy chimpanzees have uniquely long metacarpals, indicating a period of isolated evolutionary and/or developmental history. Also in

2006, Isler et al. demonstrated that, uniquely among apes, the segment-inertial properties of common chimpanzees showed a remarkable match between pendular periods of the forelimb and hindlimb, indicating optimisation for a mechanically effective quadrupedal gait. Inevitably, this would only be selected for on stable and continuous substrates, *i.e.*, in terrestrial rather than arboreal contexts. Some workers resisted the idea of chimpanzees as derived: Orr (2008) used computerized tomography to track 3D carpal motion in chimpanzees and orang-utans. Observing that in common chimpanzees, the scaphoid supinates on the capitate in midcarpal extension, causing close-packing of the mid-carpus, he claimed features of early hominin hands indicated a similar mechanism, *contra* Susman (1983) and Clarke (1998). But Kivell and Schmitt (2009) presented data on the frequency and development of claimed 'knucklewalking features' of the wrist joint. They found that they are not unique to knucklewalking primates, not all present in gorillas, and show different ontogeny in chimpanzees and gorillas: thus knucklewalking in chimpanzees and gorillas is functionally distinct and knucklewalking is not a unitary phenomenon. Further, Sockol et al. (2007) carried out metabolic, kinematic, and kinetic studies of quadrupedal and bipedal walking in chimpanzees, finding that energetic costs were lower in some individuals during bipedalism than knucklewalking. Again, using inverse-dynamic modelling, Wang et al. (2004) found that required muscle power per unit distance is higher in BHBK than erect walking. However, unlike forwards- dynamics, inverse-dynamics does not drive motion using muscle power, and *Australopithecus* might have moved in a different way to humans. Thus, using forwards-dynamic modelling, which does not suffer from this limitation, to simulate walking in AL-288-1, Sellers et al. (2004) found that the metabolic cost of locomotion increases by nearly 38% in BHBK walking.

In modern human walking, efficiency depends on extended postures of the hip and knee. This produces characteristic, double-humped vGRF curves which show a heel strike transient, and out-of-phase oscillations of the potential and kinetic energies of the body centre of gravity. These allow 50–70% (depending on mode of calculation) of the energy expended in one stride to be conserved into the next. Crompton et al. (2008) found that, while common chimpanzees walking bipedally produce single-humped vGRFs, and hence conserve little or no energy from one stride to the next, in some 25% of sequences, bipedally walking orang-utans produce at least mildly double humped curves. Orang-utans are of course primarily arboreal apes, engaging in a diverse spectrum of locomotor modes and like all other non-human apes, have relatively short legs (Thorpe and Crompton, 2006), so this finding is highly pertinent to the origins of erect bipedalism. Some of the latest findings on locomotor anatomy pertinent to this discussion, but which are not in the biomechanics purview of this paper are reviewed in eg. Alemseged, 2023; Clarke et al., 2021; Crompton et al., 2021; DeSilva et al., 2019; Grine, 2013, and other papers in the same volume; Heaton et al., 2019 and Ward et al., 2019.

1.6. 2010-present: Modern experimental and modelling approaches to the origins of human bipedal walking

Two recent experimental biomechanics studies using human participants investigate characteristics of arboreal locomotion in human ancestors. First, Johannsen et al. (2017) modelled effects of unstable forest support on human bipedal stability. Participants stood on a springboard while watching video of swaying branches, which destabilized them as much as wearing a blindfold, aligning with the results of much earlier, and thus necessarily much less sophisticated studies (*e.g.* Lee and Lishman, 1975). But, when subjects were permitted to make contact with rigid supports using their fingertips, balance was greatly enhanced, and thigh-muscle activity decreased by up to 30%. In support of this evidence, Halsey et al. (2016) used human parkour athletes to investigate effects of learning on the efficiency of horizontal movement through simulated arboreal environments. They found that familiarity with the simulated arboreal course allowed the athletes to substantially reduce

their energy expenditure. Significantly, those with greater arm-spans (including chest breadth) and shorter legs (*i.e.*, more 'australopith-like') were particularly able to reduce their costs.

In an interesting combination of experimental and modelling approaches, O'Neill et al. (2017) compared human and chimpanzee muscle capacities, showing that chimpanzees have about 1.35 times the muscle dynamic force and power output of humans, because of their higher myosin heavy chain fibre content and longer muscle fibres. They speculate that the human lineage has progressively reduced these capacities since the lineages split, and reference the greater similarity of *Ardipithecus ramidus* to non-human African apes in forelimb/hindlimb length ratios than humans. Whilst it is certainly true that early hominins including *Australopithecus* had shorter hindlimbs than members of genus Homo, and likely engaged in more arboreal activity, it does not follow that the muscle dynamics seen in modern chimpanzees were the ancestral form. Both chimpanzees and humans have been evolving since the split. Thus, the features of modern chimpanzee muscle dynamics referred to could equally well have evolved in chimpanzees since the split, as have been lost in the hominin lineage.

Kozma et al. (2018) compared dimensionless mechanical advantage about the hip in monkeys, extant and fossil apes, the early (4.4 MY) hominin *Ardipithecus ramidus* (see Lovejoy et al., 2009), two later australopiths, *Au. afarensis* and *Au. africanus*, and modern humans. They found that the short ischium of humans offers a greater range of hip extension, at the cost of extensor moments, and *Au. afarensis* and *Au. africanus* essentially agreed with the human condition. *Ar. ramidus*, however was intermediate to the case in living apes, where the longer ilium provides greater extensor moments, but less mobility. Kozma and colleagues describe the living apes as having a 'crouched gait' as a consequence. However, this is incorrect for both orang-utans and gorillas, which can walk fully upright for short distances (see *eg.* Thorpe and Crompton, 2006; Watson et al., 2009; Goh et al., 2017), despite the stiff lumbar region reported by Lovejoy and McCollum (2010). Holowka et al. (2017) investigated chimpanzee and human bipedal walking and found that humans had a greater range of motion through stance, because of dramatic midfoot plantarflexion and adduction which they thought prepared the foot for push-off.

Gruss et al. (2017) assessed 3D kinematics of walking in humans and found that those with wider pelves take longer strides at different velocities, but with less hip-extension, than others. They concluded that the wide australopith pelvis could have offset short legs and enhanced efficiency. Using inverse-dynamics to model joint force, torque and work during simulated bipedal walking in humans and nonhuman apes, Wang et al. (2014), found that the gorilla foot is dynamically most like that of humans. This agrees with Schultz's (1963) finding that of all great apes, the gorilla foot was most similar in anatomy to that of humans. Through forwards-dynamics modelling, Goh et al. (2017) found that the mechanical effectiveness of gorilla bipedalism in extended postures is not reduced by hip adaptations for climbing large vertical supports in highly flexed postures. Rather, (Goh et al., 2019) gorillas correspond with other non-human apes and differ from humans, in their greater capacity to exert flexor moments about the distal interphalangeal joints of the foot. Wiseman et al. (2020) performed a mathematical model of the constraints imposed by articular cartilage in the AL 288-1 hip joint, and found that the joint was capable of the mobility needed for both arboreal climbing and erect bipedal walking. Analysis of the now 93% complete skeleton of StW573 *Au. prometheus*, which includes a brain endocast, carotid canals and inner ear mechanism shows that cranial blood perfusion was very limited compared to *Homo* and the inner ear tuned for a 3D, arboreal environment, not for extensive movement on the ground (Beaudet et al., 2019, 2020) These are consistent with a pectoral girdle and long upper limb clearly adapted for arboreal motion, but a short lower limb combined with a human-like knee joint (see Heaton et al., 2019; Carlson et al., 2021, and Crompton et al., 2021).

Finally, modern interpretations of the topology of digitised fossil footprints deliver useful information on biomechanical parameters such

as: stride length, body proportions, foot shape and speed of the track-maker (Alexander, 1984; Reynolds, 1987; Kramer and Eck, 2000; Sellers et al., 2004; Raichlen et al., 2010; Masao et al., 2016). However, accurately predicting species-wide characteristics from fossil footprint trails is impossible given the tiny sample sizes available (McClymont et al., 2021b, 2022), sedimentological effects (Bates et al., 2013a; Bates et al., 2013b), the fossilisation process, and neurobiological systems degeneracy. But using a combination of experimental measurements of foot-pressure in humans and non-human great apes, pedobarographic statistical parametric mapping (pSPM), and forwards-dynamic modelling to simulate foot pressure during erect and BHBK gait, Crompton et al. (2012) showed that the Laetoli prints are typical of upright walking, and very similar to modern humans. Hatala et al. (2016) found that modern habitually barefoot humans produce footprints in which statistically significant patterns of biomechanical function may be discerned. However, comparison of fossil footprint scans from Laetoli (*Au. afarensis*), Ileret, Kenya (early *Homo*), Walvis Bay, Namibia (Holocene, *Homo sapiens*) and modern *H. sapiens* using pSPM (McClymont et al., 2021a), found no statistically significant differences between these footprint sites – spanning 3.66 MY – that were not accounted for by sedimentological effects (Bates et al., 2013a; Bates et al., 2013b). A lack of statistical support from footprint analyses for species-unique locomotor modes in early hominins, is consistent with other studies which demonstrate fully upright bipedalism in *Au. afarensis* (Sellers et al., 2004; Raichlen et al., 2010). High step-to-step variability in foot pressures of modern humans walking at a range of speeds shows that neither robust statistical differences (McClymont et al., 2016), nor habitual walking behaviour can be determined from small sample sizes (<50, McClymont et al., 2021b). These findings are all consistent with the expectations afforded to a biological system by the natural selection pressure of neurobiological system degeneracy (reviewed in *e.g.* Seifert et al., 2016). Viewed from this perspective, the high range of variation and intra-species overlap evident in foot bone morphology, foot pressure and locomotor mode in the hominin lineage, can be seen as natural selection's solution to sustaining effective, efficient and adaptive locomotion over mixed woodland and grassland terrain (McClymont et al., 2022). Degeneracy sustains robusticity, correlates positively with complexity, thereby increasing adaptability (Whitaker and Bender, 2009). We identify degeneracy as the underlying mechanism driving species-overlap in distribution and magnitude of foot pressure in all great apes (and see Vereecke et al., 2005; Crompton et al. 2010; Bates et al., 2013a and DeSilva et al., 2013 for examples of variability in foot pressure in apes and humans). The hands and feet are particularly subject to degeneracy, having many units (carpals + metacarpals/tarsals + metatarsals and phalanges) which exhibit instantaneously unique interactions with each unique step taken, yet still produce a consistently similar, if not identical, external pressure outcome after hundreds of steps are recorded and compared (i.e.*,* for the foot, intended foot pressures, see; McClymont et al., 2016). The significance of neurobiological degeneracy is only recently being recognised in hominin palaeontology, as is evident, for example by contrasting the intensity of the debate between Latimer and Lovejoy (1989) and Susman and Stern (1991), on the significance of the narrow calcaneal cross-section of *Au. Afarensis*. However neither party considered how resulting external forces may be affected by the morphology of all the other bones in the foot. However, in 2020, Zipfel and Wunderlich, comparing foot bones in Sterkfontein australopiths, noted that it must be considered that the external effects of distinctions in the morphology of bones between species, may be offset by other distinctions elsewhere in the foot. This is another important acknowledgement towards understanding the complexity and variability of our bipedal past.

2. Conclusion

The last 50 years of hominin evolutionary biomechanics have thus seen a contextual shift, from a terrestrial, savannah origin hypothesis to one where upright walking evolved much earlier and in an arboreal context. Consequently, knucklewalking has been nearly universally abandoned as the likely locomotor mode of the human/chimpanzee common ancestor, and increasingly replaced with recognition that we come from a long line of highly variable bipeds. Motion analysis within evolutionary biomechanics has experienced its own evolution in line with technological advancement in this computer age. An ability to virtually reconstruct the motion of our ancestor has arisen from a rich foundation of motion analysis in sports science, medicine and bioengineering. In particular, computer simulation studies, some of which we have cited, have as a side benefit taken us from still photographs, to virtual models we can experience.

CRediT authorship contribution statement

Robin Huw Crompton: Writing – review & editing, Writing – original draft, Conceptualization. **William Sellers:** Writing – review & editing, Writing – original draft. **Keith Davids:** Writing – review & editing, Writing – original draft. **Juliet McClymont:** Writing – review & editing, Writing – original draft.

Declaration of Competing Interest

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