TREE CLIMBING AND THE LOCOMOTIVE CONNECTION BETWEEN PAST AND PRESENT HOMININS

RAE DIAS

ABSTRACT

Bipedalism is considered one of the defining traits of past hominins and modern humans. It has long been assumed that the adaptation to bipedal locomotion came at the cost of tree climbing ability. Recent studies are showing that contemporary humans are still capable of tree climbing to acquire resources. The results of these studies suggest that tree climbing remained an important form of locomotion for certain species of past hominins and certain groups of humans today. In this way, tree climbing could represent a connection between humans in the present and to hominins in the past.

INTRODUCTION

Humans are the only species of living primates to move exclusively with an upright, two-legged bipedal posture. While other primates, such as chimpanzees, bonobos, and gorillas have the ability to walk bipedally and have been witnessed doing so, they are not obligate bipeds. In other words, walking upright is not their primary form of locomotion and so their skeletal and muscular systems have not specifically evolved for a bipedal posture and movement like we see in humans today. As a result, this highly specialized form of terrestrial locomotion is predominantly seen as one of the defining traits of a hominin, as well as a connection between modern humans and our evolutionary past. Due to this, the subject of bipedalism and its specific musculoskeletal adaptations have dominated paleoanthropological literature on hominin locomotion (Bramble and Lieberman 2004; Lieberman et al. 2006). This is not to say that the behavioural and physical shift towards bipedalism does not hold an important place in human evolution. Rather, the issue lies in that bipedal locomotion is given priority in anthropological research and so it influences what questions are asked about the locomotor abilities of likely human predecessors, such as *Australopithecus afarensis* and *Australopithecus africanus*. Despite the fact that fossil evidence shows that tree climbing was the dominant form of movement for our predecessors and other non-human apes for millions of years, tree climbing as an important type of locomotion in hominins has received minimal attention in these discussions. Any arboreal traits are often seen as mere encumberments to the bipedal model and unimportant traits by themselves (Kraft, Venkataraman, and Dominy 2014; Venkataraman, Kraft, and Dominy 2013). As Kozma and colleagues (2018) have pointed out, it is commonly thought that the ability to efficiently walk upright came at the *cost* of arboreal climbing. While it is certainly true that humans have lost many of the arboreal adaptations that would likely make our species more adept at tree climbing, recent research shows that humans are still capable of vertical tree climbing.

The main questions surrounding the lack of research into arboreality are twofold. Firstly, why do anthropologists place more emphasis on studying the emergence of bipedalism in past hominin species and frequently show a disinterest in exploring questions about the role that tree climbing could have played in hominin evolution? Secondly, why are not more questions being asked regarding the likely continued importance of tree climbing in both past hominins and in humans today? Despite modern humans being highly specialized for bipedal locomotion, experimental and ethnographic studies suggest that humans are still competent tree climbers (Kraft, Venkataraman, and Dominy 2014; Venkataraman, Kraft, and Dominy 2013). What is the significance of this dual-functionality? By asking more questions regarding the importance of tree climbing in both past and present humans, the rich diversity of human behaviour, such as the ability to adapt to living in a variety of environments across the world, can be better encapsulated and appreciated both within the academic realm and beyond it. In this way, meaningful connections can be formed *between* contemporary humans *and* hominins who may be our distant ancestors and relatives.

THE HISTORY OF BIPEDALISM INQUIRIES

Human bipedalism has captivated the interest of anthropologists and other scholars alike for over a century. Even before the discipline of anthropology had been established, the fact that humans stood and walked upright, unlike other apes, captured the interest of naturalists in the 19th century. In his article, “Stand and Be Counted: The Neo-Darwinian Synthesis and the Ascension of Bipedalism as an Essential Hominid Synapomorphy”, Tom Gundling covers the history of bipedalism inquiry, which will be summarized in the following section.

In 1809 Jean Baptiste Lamarck speculated on what might happen to a quadrupedal animal if they were forced to walk upright on their feet, and theorized that the big toe would presently become aligned with the other toes. While Lamarck’s general theory of evolution has long since been disproven, his above speculation is notably akin to that of discussions regarding the transition to bipedalism. In 1871, in *The Descent of Man*, Charles Darwin also describes a transition to bipedalism, although his theoretical approach was entrenched in natural selection and not the now infamous Lamarckism. He speculates that as predecessors to humans became more and more upright, their hands became more specialized for prehension and their legs and feet would have also changed for "firm support and progression" (Gundling 2012:187). A decade or so later, in Alfred Russell Wallace's *Darwinism,* he agreed that the transition to bipedalism and thus freeing up the hands was "the first major change associated with the human lineage" (Grundling 2012: 187-188). In reviewing the observations of Lamarck, Darwin and Wallace, Grundling (2012) concludes that their respective works agreed that bipedal locomotion was the first significant evolutionary step that set humans apart from an ape ancestor.

He also notes that in 1951, Sherwood Washburn stated that the origins of modern humans began with the advent of bipedalism. Washburn's statement represented a paradigm shift in how researchers approached the study of fossils and human evolution, as Gundling notes that "[i]t is now incumbent on paleoanthropologists to demonstrate that any fossils claimed to be those of a hominid must display bipedal features" (206). With this conclusion in mind, one begins to understand why paleoanthropology's philosophical stance is so deeply rooted in asking questions about bipedalism, such as when this form of locomotion first became evident in the hominin lineage and the ways in which humans and their predecessors are physically adapted to this upright posture. Yet the study of the evolution of bipedalism is still filled with speculation, because postcranial fossils are not commonly found and when they are, they are often fragmentary or not easy to match to the cranial remains (Tuttle 1981).

THE BEGINNING OF TREE CLIMBING INQUIRIES

One of the key questions regarding the evolution of bipedalism is *how* the shift to this form of locomotion occurred. While this question has been pursued by anthropologists for over a century, a definitive answer has yet to be found. As early as 1900, Klaatsch speculated that vertical tree climbing might have been a pre-adaptive behaviour to bipedalism due to the enlarged size and shape of the human gluteus maximus (Stern 1972), which allows for powerful hip extension and the hyperextension needed for an upright stance. This speculation is particularly noteworthy because it appears to be the first proponent of what came to be formally known as the vertical climbing hypothesis some 70 years later. Before this hypothesis was formulated, research regarding past hominin locomotion attempted to answer questions focused on terrestrial forms of movement rather than arboreal modes. A common discussion for more than half a century was that terrestrial bipedalism arose from “arboreal giant apes" who became adapted to plantigrade quadrupedalism before transitioning to bipedalism (Tuttle et al. 1974: 390). This theory was put forward by Arthur Keith in 1903 and focused solely on lower limb adaptations, although it was later refined to include the argument by the palaeontologist Gregory (1916-49) that brachiating was a pre-adaptation to the upright position needed for bipedalism (Tuttle et al. 1974). This came to be known as the Keith-Gregory model. However, Keith later abandoned the brachiationist model in the 1940s, although Gregory and other scholars continued to argue for this hypothesis. The debate continued for several decades in various forms. Upon the advancement of biomolecular science in the 1960s, there was an abundance of evidence that showed that humans, chimpanzees, and gorillas were genetically similar to each other (Tuttle et al. 1974). In an attempt to include this genetic affinity into discussions regarding the evolution of bipedalism, Washburn proposed in the 1960s and 1970s that knuckle-walking had been a transitory locomotion phase between brachiation and bipedalism (Tuttle et al. 1974).

In the 1970s and 1980s, several scholars began to question this theoretical approach and an alternate hypothesis was presented that challenged the terrestrial knuckle-walker model: the vertical climbing hypothesis. The hypothesis states that “... protohominins adaptations for arboreal locomotion were later adapted for terrestrial locomotion, forming key precursors to bipedalism” (Bartlett et al. 2014: 125). Instead of a transitory knuckle-walking phase, there was a more direct transition from moving around in the trees to walking upright on the ground. Prost (1980) was one of the first anthropologists to attempt to empirically measure the field patterns of human and chimpanzee locomotion, and he observed that the lower limb patterns and trunk position of chimpanzee quadrupedal vertical climbing and human bipedal walking was remarkably similar. He suggested that a transitory, hominin-like species would possess upper limbs adapted to brachiating and a pelvis and lower limbs more human-like and adapted to bipedal walking locomotion. Given that australopithecines display this mixed morphology of arboreal and terrestrial traits, this would suggest that they were adapted to vertical tree climbing while also having the ability to be facultative bipeds and move about on the ground (Prost 1980).

Russell H. Tuttle is also particularly well-known for arguing that the upright upper body position and lateral flexion of the spine required for vertical climbing was a pre-adaptation for terrestrial bipedalism (Tuttle et al. 1974; Tuttle 1981). He also directly disagreed with the knuckle-walking hypothesis, instead arguing for a hylobatian model in which… "vertical climbing on tree trunks and vines and bipedalism on horizontal boughs were conspicuous components of their locomotor repertoire. They commonly stood bipedally while foraging in trees and employed bipedalism during intraspecific displays" (Tuttle 1981: 90). The vertical climbing hypothesis was explored further by a multitude of scholars in the 1980s, such as Stern and Susman (1981) and Fleagle and colleagues (1981). For example, Stern and Susman (1981) used electromyography (EMG) in an attempt to answer the question of gluteus maximus activation in non-human apes and humans. They found that in the powerful hip extension that is utilized during movements such as standing up from a chair or rising from a squatting position, the human gluteus maximus is activated in a similar way to the gluteus muscles in apes when they are vertically climbing (Stern and Susman 1981). They also found that the medial rotation of the thigh occurs in a similar fashion in both vertical climbing and bipedal walking. Stern and Susman (1981) interpreted this data to mean that climbing could have been a pre-adaptation to bipedal walking, which harkens back to Klaatsch's speculation in 1900.

While anthropologists have yet to reach a consensus regarding how bipedalism arose in hominins and what forms of locomotion were the predominant precursors to this behaviour, one thing remains clear from these findings and more recent paeloanthropological research: the locomotion repertoire of past ape and hominin fossils is likely to have been varied and complex, regardless of whether bipedalism arose from terrestrial quadrupedalism or tree climbing. For example, research on the foot of *Ardipithecus ramidus,* a 4.4 million year old fossil, suggests that this species used a mixture of terrestrial quadrupedalism similar to that of gorillas and chimpanzees, as well as tree climbing to move around (Prang 2019). Analyses of the mixed morphology of both arboreal and bipedal traits in *Australopithecus afarensis* and *Australopithecus africanus* (two hominin-like species from approximately 4 to 1 million years ago) also suggests that there was a great amount of locomotive diversity in past hominins (Georgiou et al. 2020; Ibáñez-Gimeno et al. 2017). This begs the following question: despite the fact that there is an abundance of experimental studies and evidence to support the vertical climbing hypothesis, why does climbing as an important part of hominin locomotor repertoire continue to be largely ignored in the anthropological literature?

DARWIN AND THE BIPEDAL APE

According to Tuttle and colleagues (1974), Darwin approached the subject of hominins prior to the modern human form with a great deal of caution. While he correctly hypothesized that the closest living relative to humans were the African apes (specifically gorillas and chimpanzees) and that Africa was the place in which geologists would find a common hominid ancestor, he was brief in his speculation as to what this common ancestor may have looked like and what selective forces acted on this ancestor (Tuttle et al. 1974). He did venture to describe them as "... hairy, bearded, tailed creatures that could move their pointed ears freely. They possessed prehensile feet with opposable great toes. The males had large canine teeth that were used as weapons. They were arboreal inhabitants of tropical or subtropical forests" (Tuttle et al. 1974: 389). Other than this description, Darwin and his contemporaries, Huxley and Haeckel, did not speculate further about the appearance of this ancestor or the evolutionary mechanisms by which these features developed. Perhaps they realized that it was difficult, if not impossible, to predict what a human ancestor would look like given they did not have the rich collection of hominin fossils and knowledge that anthropologists have access to today. In other words, they may have been exercising caution in order to avoid making incorrect inferences. Tuttle and colleagues (1974) also remark that these scholars instead focused their efforts on proving that humans had some sort of kinship with the great apes.

Yet while their intentions were well-meaning (in the pursuit of science, et cetera), the way in which they went about demonstrating this affinity was to the detriment of future tree climbing discussions. While Darwin was controversial for his time because he believed that humans were superior to other apes not in kind but in *degree*, he nonetheless saw humans as being above all other apes (Ingold 2004). Darwin believed that by attaining a higher intelligence humans were freed from natural instinct and thus transcended nature (Ingold 2004). As Ingold (2004) remarks, "Unlike the quadruped, with four feet planted solidly on the ground of nature, the biped is held down only by two, while the arms and hands, released from their previous functions of support and locomotion, become answerable to the call of reason" (318). This paper does not disagree that humans are complex in intelligence compared to other animals and that the process of walking upright on two feet did indeed free up the hands for more complex tool usage, et cetera. What this paper takes issue with is the belief that humans are superior to other apes because becoming bipedal "released" them from nature. By doing so, this approach attempts to sever the connection between humans and other species by viewing humans as "above" nature. In *Man's Place in Nature*, originally published in 1863,Thomas Huxley presents an illustration of the skeletons of a gibbon, an orangutan, a chimpanzee, a gorilla, and a human to demonstrate the anatomical changes made by humans to become bipedal (see Figure 1). Ingold (2004) argues that the illustration has been purposefully constructed to depict the human being's progression to bipedalism and to a position above the other apes and to the top of the animal kingdom. Indeed, when one examines the illustration and compares the relatively upright posture of the human to the other apes, the gibbon skeleton, followed by orangutan skeleton, stands out as having the most upright posture after the human. Yet instead of being placed closer to the humans to demonstrate this thought-provoking similarity, these two apes are placed as far away from the human skeleton as possible. While it is impossible to know for certain what Huxley intended by this order of skeletons, it is important to acknowledge that they might have been ordered in this fashion because at the time, orangutans and gibbons had already been classified into two distinct genera, while chimpanzees and gorillas were thought to be part of the same genus (Huxley 1894). Yet this still begs the question: why highlight the posture differences between the apes and humans instead of discussing the potential significance of their similarities? Why not discuss the meaning of these similar postures and what it might indicate about the role of tree climbing in hominin history?

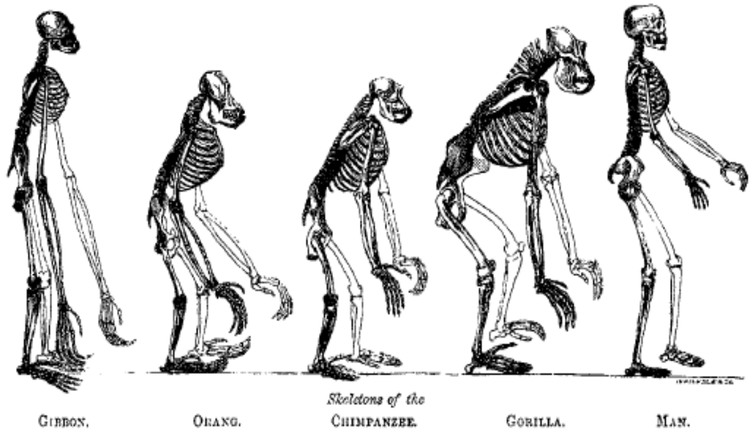

Figure 1 - Anatomical comparison of human and ape skeletons, from Huxley's (1894) Man's Place in Nature Source: Ingold, 2004:316.

AUSTRALOPITHECINE LOCOMOTION

It is clear that arboreal and bipedal locomotion have a complex relationship with one another. Yet the challenge still lies in answering the questions of *how* and *when* the shift to bipedalism occurred in hominins (Prost 1980). Disagreements have also arisen over the timing and nature of the emergence of habitual bipedalism, partially because there are differing interpretations regarding the extent to which the shift towards bipedalism affected tree climbing ability (Kraft, Venkataraman, and Dominy 2014). While these are not easy questions to answer and anthropologists have amassed a number of theories as previously discussed, one thing remains clear. The emphasis on bipedalism has led to a dichotomous relationship between arboreal-terrestrial forms of locomotion in comparative primatology and paleoanthropology research (Kraft, Venkataraman, and Dominy 2014). This philosophical stance in anthropology has limited what questions are being asked regarding tree climbing. By placing the utmost importance on the presence of bipedal traits in fossils, arboreal traits are often not treated as significant. When anatomical signs of bipedalism are found in the fossil record, such as ankle and foot similarities between contemporary humans and *Australopithecus afarensis*, the possibility of tree climbing still being an important part of the species' locomotor repertoire is dismissed (Kraft, Venkataraman, and Dominy 2014). Instead, there is the assumption that if humans or past hominins climbed trees, they did so in an inept and awkward fashion (Kraft, Venkataraman, and Dominy 2014). Yet did the shift to a bipedal locomotion actually come at the expense of climbing ability?

Anthropologists have contentiously argued over the answer to this question, such as when it comes to the morphology of *Australopithecus afarensis* (Venkataraman, Kraft, and Dominy 2013). This is due to the fact that *Australopithecus afarensis* has a mixture of traits we would generally classify as bipedal or arboreal. For example, this early hominin shows lower body adaptations to bipedalism, such as a rigid ankle, an arched, non-grasping foot (Venkataraman, Kraft, and Dominy 2013), a long femoral neck (Georgiou et al. 2020), a relatively broad sacrum (Kimbel and Delezene 2009), and a shorter ischium (Kozma et al. 2018). Yet this species also shows a variety of upper limb arboreal adaptations, such as long, curved fingers and a cranially oriented glenoid fossa (Venkataraman, Kraft, and Dominy 2013). This mixture of bipedal and arboreal traits has resulted in decades of debate regarding the locomotory behaviours of *Australopithecuafarensis* and of other species of *Australopithecus,* such as *Australopithecuafricanus* and *Australopithecu. sediba* (Georgiou et al. 2020). Given the presence of these more "primitive" arboreal traits, Ibáñez-Gimeno and colleagues (2017) point out that there are two main interpretations regarding the locomotory behaviour of *Australopithecu. afarensis*. The first one suggests that the arboreal traits were no longer functional or adaptively significant but merely retained in the species' morphology due to a lack of strong selection pressures against it. These arboreal traits are seen as "primitive retentions" (Ibáñez-Gimeno et al. 2017:789). The second interpretation posits that these traits are still present because they were being selected for by the environment and so were still functionally relevant to the behaviour of the hominin (Georgiou et al. 2020; Ibáñez-Gimeno et al. 2017). It has also been noted that the divergent upper body and lower body morphology of some hominins might represent a selection for *both* arboreal and bipedalism locomotion (Georgiou et al. 2020).

While these debates continue in the anthropological literature today, recent research utilizing three-dimensional (3D) modelling software technology has shown that locomotion in the past was highly variable between hominin species. For example, Georgiou and colleagues (2020) analyzed 3D scans of the trabecular (internal bone structure) of the femur (upper leg bone) of one specimen classified as *Austraolopithecus africanus* and a second specimen who is thought to have either been an early *Homo* member or a *Paranthropus robustus* member. The results show that the *Australopithecus africanus* specimen's trabecular bone pattern is actually more similar to a modern human's patterning, while the unknown / possible early *Homo / Paranthropus robustus* specimen's pattern is more similar to an ape's trabecular bone, specifically that of a bonobo. These patterns indicate that *Australopithecus africanus* was an obligate biped, while the other specimen regularly adopted a highly flexed position typical of arborealism. There are several particularly interesting aspects about these results. Firstly, the results suggest that *Australopithecus africanus* did not engage in arboreal locomotion as much as was previously thought. On the one hand, this may appear to fit into the first interpretation described by Ibáñez-Gimeno and colleagues (2017), that arboreal traits are merely remnants from a form of locomotion no longer used, although importantly, they still maintained the ability to climb trees. On the other hand, the unknown / possible early *Homo / Paranthropus robustus* specimen's results may provide support for the second interpretation as described by Georgiou and colleagues (2020) and Ibáñez-Gimeno and colleagues (2017), that the presence of arboreal traits suggests that they were still being selected for because they provided some kind of benefit or advantage in that particular hominin's environment. It is also particularly interesting that the unknown specimen is geologically *younger* than the *Australopithecus africanus* specimen, yet it exhibits more evidence of regularly engaging in some form of tree climbing. While this could be seen as evidence that the specimen belongs to the *Paranthropus* genus as opposed to *Homo*, one must keep in mind that the only evidence for arboreality in this genus has been found in a scapula, a humerus, and a radius (Georgiou et al., 2020). It is also possible that an early *Homo* specimen could exhibit arboreal traits, as another *Homo* specimen called the Olduvai Hominid exhibits arboreal adaptations as well (Georgiou et al., 2020). With these results, as well as the diverse mixture of arboreal and bipedal traits in other hominins such as *Australopithecus sediba*, *Homo naledi*, the Burtele foot, and *Ardipithecus ramidus*, the authors' results suggest that there was a great amount of locomotor diversity in the hominin fossil record and that the shift to bipedalism was not as linear as once thought (Georgiou et al., 2020).

CONTEMPORARY HUMAN TREE CLIMBING

There is an area of anthropology that has largely been overlooked in discussions regarding the significance of tree climbing in hominin evolution: modern human tree climbing. Despite the fact that there are many groups of modern humans (especially hunter-gatherers) around the world who frequently engage in tree climbing to acquire resources, they have been largely ignored in discussions regarding the evolution of hominin locomotion and behaviour (Kraft, Venkataraman, and Dominy 2014; Venkataraman, Kraft, and Dominy 2013). Due to the difficulties of inferring locomotory behaviour from fossils (due to lack of preservation of soft tissues such as muscles, tendons, and ligaments), modern human tree climbers are particularly relevant in helping to shed light on hominin arboreality (Venkataraman, Kraft, and Dominy 2013). Given that they are definitive proof that humans are fully capable of climbing trees, at least for the purposes of acquiring resources, this data is particularly relevant in trying to answer the question of whether bipedalism resulted in a trade-off in climbing abilities. That being said, it is unlikely that any anthropologist would argue that humans are as deft and skilled in the trees as the other great apes.

Kraft, Venkataraman, and Dominy (2014) observed that human tree climbers typically move more slowly and cautiously in the trees than other apes such as chimpanzees. Yet it has been pointed out that given the various forms of locomotion in chimpanzees that have been extensively studied (such as their quadrupedal knuckle-walking, tree climbing, and facultative bipedalism), to overlook modern tree climbers is to overlook the full range of human locomotor capabilities (Venkataraman, Kraft, and Dominy 2013)). The fact also remains that these hunter-gatherer groups are sufficiently successful at acquiring food by way of tree climbing without the assistance of technology (Kraft, Venkataraman, and Dominy 2014) and that it forms an important part of their locomotor repertoire that they are willing to expend valuable energy on. This activity has fitness consequences both in the form of risks and rewards, which begs the question: why do humans climb trees? Worldwide, hunter-gatherer groups go to great lengths to acquire honey, for example, as it is an extremely high-energy resource (Kraft, Venkataraman, and Dominy 2014; Marlowe et al. 2014; Venkataraman, Kraft, and Dominy 2013) as well as other resources such as fruit, nuts, seeds, and palm products (Kraft, Venkataraman, and Dominy 2014).

Kraft, Venkataraman, and Dominy (2014) go into great detail regarding the various aspects of human tree climbing behaviour and the rewards and risks associated with it. For example, they describe how honey is also a sought-after resource because it is nutrient-dense, preserves for a long time, and has antimicrobial and antiviral effects, amongst other properties. Honey can even have sociological significance, such as in the case of the Mbuti people in the Ituri Forest in the Democratic Republic of Congo, where it is used to maintain and foster social relations. In some groups, such as the Sekai in Malaysia, if a man is a good climber he is seen as a more appealing prospective husband. It is also interesting to note that human climbers appear to climb higher on average than great apes during honey acquisition, despite the fact that it is an extreme dangerous activity with often fatal consequences. Worldwide, tree climbing is also a strategy employed in hunting activities. For example, the Efe hunter-gatherers of the Democratic Republic of Congo perch in trees in order to ambush duikers who feed on the fallen fruit on the forest floor, and the Batek people of Malaysia move within the trees (and up to forty meters in the canopies) in order to hunt animals such as birds, monkeys, bats, and rats using blowguns. The Hadza people of Tanzania also sometimes use trees to stash meat from hunting. While it is known that non-human primates also use trees as a form of protection against predators, such as by nesting and sleeping in trees, this behaviour appears to be less analogous with humans, although the Ache people of Paraguay have been known to climb trees in order to avoid a charging predator.

Yet despite the rewards, tree climbing has high morbidity and mortality risks. Given the great heights that are sometimes climbed, such as in order to attain honey (sometimes as high as 51 m in the tree canopy), the consequences of falling out of the trees are often fatal. While the data is sparse regarding the types of non-fatal injuries sustained by human tree climbers, evidence of long-bone trauma in non-human primates that is consistent with falling has been found. Previous studies have shown that in countries such as Papua New Guinea and Nigeria, tree fall-related injuries accounted for a significant portion of hospital admissions, and it is known that falling from significant heights can result in injuries to the spine, legs, arms, and internal organs. Therefore, one can see not only that the rewards of tree climbing in certain hunter-gatherer groups are seen to outweigh the often-fatal risks associated with this form of movement, but that humans are proficient enough at tree climbing that they are extremely successful at repeatedly using trees to acquire resources.

Now that is has been established that certain groups of humans frequently engage in tree climbing for resource acquisition, the following question must be asked: how might this behaviour inform studies regarding tree climbing in fossil hominins? More specifically, what do we know, and what do we *not* know, about tree climbing morphology in modern human tree climbers, and are there connections between their morphology and past hominins? Given that the skeletal morphology of human tree climbers does not appear to reflect the morphology that we see in arboreal apes, what might this say about soft tissue plasticity in humans and potentially in fossil hominin species? While more data from human tree climbers needs to be collected before appropriate comparisons can be made with other living primates and hominins, Kraft, Venkataraman, and Dominy (2014) point out that studies on skeletal morphology associated with tree climbing ability in humans could allow for inferring climbing behaviour in the fossil record, something that is not typically easy to do in paleoanthropology. Venkataraman, Kraft, and Dominy (2013) discuss the Twa people in Uganda, who use extreme ankle dorsiflexion during climbing. The position of their ankles during climbing is comparable to the dorsiflexion seen in chimpanzees; an action that anthropologists had previously assumed was not physically possible in our species. The advantage to this position of the ankle is that it places the climber's center of mass closer to the tree and thus lowers the energy expenditure and the risks of vertical ascent (Venkataraman, Kraft, and Dominy 2013). Yet the dorsiflexion seen in the Twa climbers is not reflected in the skeletal morphology of their ankle, but rather in plasticity of their soft tissues. The ankle joint is a complex system of bones, ligaments, and muscle, all of which contribute to ankle flexibility (Venkataraman, Kraft, and Dominy 2013). This finding is particularly significant when considering the morphology of *Australopithecus* specimens, as this genus has a distinctively non-arboreal foot and ankle (Venkataraman, Kraft, and

Dominy 2013). As the authors demonstrate with their study of the Twa people, morphological adaptations to climbing do not necessarily have to be a skeletal change, but rather can be changes in the soft tissue. Therefore, this soft tissue plasticity, as well as the overall competence of human tree climbers, must be taken into account when paleoanthropologists are formulating their questions regarding the role of arborealism in past hominins.

CONCLUSION

For the past two centuries, scholars have been asking questions regarding how our unique behaviour today (that is, bipedal locomotion) connects us to hominins that lived millions of years ago. Cross-species comparisons between humans and other apes led scholars to try to identify which physical traits set humans apart from all other animals, and how these traits might have arisen in the evolutionary process. One of the most apparent differences between humans and apes, and in fact all other animals, is that humans habitually and exclusively (or so it was thought) walk upright on two feet. Due to this observation, this form of locomotion and thus the anatomical adaptations associated with it are treated as the defining trait of hominins both past and present. Thus, when a fossil discovery is made one of the first questions to be asked is whether the specimen was bipedal or not. The skeleton must exhibit an adaptation to bipedalism in order to be classified as a hominin and to be considered either a possible direct ancestor or cousin species of modern humans. The great importance placed on bipedalism since the writings of Charles Darwin in the 19th century has greatly influenced the theoretical framework in which many paleoanthropologists formulate their research questions. This biased perspective has led to the frequent dismissal of other forms of locomotion being important in hominin locomotion studies, such as tree climbing. When a fossil exhibits a mixed morphology of bipedal and arboreal adaptations, it is commonly assumed that the specimen was either clumsy or awkward at tree climbing (Kraft, Venkataraman, and Dominy 2014) or that the arboreal traits are vestiges from a past arboreal lineage that has yet to be selected against by the environment. One of the main limitations that paleoanthropologists face is that it is impossible to entirely and definitively reconstruct the behaviour of fossil hominins. While this is true of any discipline that strives to study past human behaviour, this is a particularly challenging aspect of paleoanthropology because soft tissues such as muscles, ligaments and tendons do not preserve in fossils, and no cultural artifacts are typically found with older fossils such as *Australopithecus*. This means that answering questions regarding the behaviour of these hominins, such as what their locomotive repertoire was, is inherently difficult. Yet there are promising areas of research that are attempting to both mitigate these limitations and that are asking questions that consider a more comprehensive range of locomotion in hominins. In the past ten years, anthropologists have also been calling attention to the fact that there are groups of humans worldwide who frequently engage in tree climbing to acquire resources (Kraft, Venkataraman, and Dominy 2014; Venkataraman, Kraft, and Dominy 2013), some of whom demonstrate soft tissue plasticity in response to selection for climbing trees more efficiently. All of these studies have significant implications for future studies regarding fossil hominin locomotion, as they prove that specimens who show more adaptations to a particular form of locomotion such as bipedalism do not necessarily experience any apparent trade-offs when engaging in another form of movement such as tree climbing. These studies, as well as future inquiries, will help address the areas of ambiguity in paleoanthropology, such as whether bipedalism did actually come at the cost of tree climbing ability, and how the transition from a predominantly arboreal locomotion to a terrestrial locomotion occurred.

REFERENCES

Bartlett, Jamie L., Bonnie Sumner, Richard G. Ellis, and Rodger Kram. 2014. Activity and Functions of the Human Gluteal Muscles in Walking, Running, Sprinting, and Climbing. *American Journal of Physical Anthropology* 153(1): 124–31. https://doi.org/10.1002/ajpa.22419.

Bramble, D. M., & D.E. Lieberman. 2004. Endurance running and the evolution of Homo. *Nature*, 432(7015): 345–352. https://doi.org/10.1038/nature03052

Fleagle, John G., Jack T. Stern, William L. Jungers, Randall L. Susman, Andrea K. Vangor, and James P. Wells. 1981. Climbing: A Biomechanical Link with Brachiation and with Bipedalism. *Symposium of Zoological Society of London* 48: 359–75.

Georgiou, Leoni, Christopher J. Dunmore, Ameline Bardo, Laura T. Buck, Jean-Jacques Hublin, Dieter H. Pahr, Dominic Stratford, Alexander Synek, Tracy L. Kivell, and Matthew M. Skinner. 2020. Evidence for Habitual Climbing in a Pleistocene Hominin in South Africa. *Proceedings of the National Academy of Sciences* 117(15): 1-8. https://doi.org/10.1073/pnas.1914481117.

Gundling, Tom. 2012. Stand and Be Counted : The Neo-Darwinian Synthesis and the Ascension of Bipedalism as an Essential Hominid Synapomorphy. *History and Philosophy of the Life Sciences* 34(1/2): 185-210. https://www.jstor.org/stable/43831772

Huxley, Thomas H. 1894. *Man's Place in Nature, and Other Anthropological Essays*. London: Macmillan.

Ibáñez-Gimeno, Pere, Joan Manyosa, Ignasi Galtés, Xavier Jordana, Salvador Moyà-Solà, and Assumpció Malgosa. 2017. Forearm Pronation Efficiency in A.L. 288-1 (Australopithecus Afarensis) and MH2 (Australopithecus Sediba): Insights into Their Locomotor and Manipulative Habits. *American Journal of Physical Anthropology* 164 (4): 788–800. https://doi.org/10.1002/ajpa.23319.

Ingold, Tim. 2004. Culture on the Ground: The World Perceived through the Feet. *Journal of Material Culture* 9 (3): 315–40. https://doi.org/10.1177/1359183504046896.

Kimbel, William H., and Lucas K. Delezene. 2009. 'Lucy' Redux: A Review of Research on Australopithecus Afarensis. *American Journal of Physical Anthropology* 140 (49): 2–48. https://doi.org/10.1002/ajpa.21183.

Kozma, Elaine E., Nicole M. Webb, William E.H. Harcourt-Smith, David A. Raichlen, Kristiaan D'Août, Mary H. Brown, Emma M. Finestone, Stephen R. Ross, Peter Aerts, and Herman Pontzer. 2018. Hip Extensor Mechanics and the Evolution of Walking and Climbing Capabilities in Humans, Apes, and Fossil Hominins. *Proceedings of the National Academy of Sciences of the United States of America* 115 (16): 4134–39. https://doi.org/10.1073/pnas.1715120115.

Kraft, Thomas S., Vivek V. Venkataraman, and Nathaniel J. Dominy. 2014. A Natural History of Human Tree Climbing. *Journal of Human Evolution* 71: 105–18. https://doi.org/10.1016/j.jhevol.2014.02.002.

Lieberman, D. E., D. A. Raichlen, H. Pontzer, D. M. Bramble, & E. Cutright-Smith. 2006. The human gluteus maximus and its role in running. *Journal of Experimental Biology*, 209(11): 2143–2155. https://doi.org/10.1242/jeb.02255

Marlowe, F. W., J. C. Berbesque, B. Wood, A. Crittenden, C. Porter, & A. Mabulla. 2014. Honey, Hadza, hunter-gatherers, and human evolution. *Journal of Human Evolution*, *71*, 119–128. https://doi.org/10.1016/j.jhevol.2014.03.006

Prang, Thomas Cody. 2019. The African Ape-like Foot of Ardipithecus Ramidus and Its Implications for the Origin of Bipedalism. *ELife* 8: 1–17. https://doi.org/10.7554/eLife.44433.

Prost, J. H. 1980. Origin of Bipedalism. *American Journal of Physical Anthropology* 52 (2): 175–89. https://doi.org/10.1002/ajpa.1330520204.

Stern, Jack T., and Randall L. Susman. 1981. Electromyography of the Gluteal Muscles in Hylobates, Pongo, and Pan: Implications for the Evolution of Hominid Bipedality. *American Journal of Physical Anthropology* 55 (2): 153–66. https://doi.org/10.1002/ajpa.1330550203.

Stern, Jack T. 1972. Anatomical and Functional Specializations of the Human Gluteus Maximus. *American Journal of Physical Anthropology* 36 (3): 315–39. https://doi.org/10.1002/ajpa.1330360303.

Tuttle, Russell, Karl W. Butzer, and Bennett Blumenberg. 1974. Darwin's Apes, Dental Apes, and the Descent of Man: Normal Science in Evolutionary Anthropology. *Current Anthropology* 15 (4): 389–426. https://doi.org/10.1086/201494.

Tuttle, Russell, H. 1981. Evolution of Hominid Bipedalism and Prehensile Capabilities. *Philosophical Transactions of the Royal Society of London* 392(1057), 89-94. https://www.jstor.org/stable/2398646 (Accessed April 2020).

Venkataraman, Vivek V., Thomas S. Kraft, and Nathaniel J. Dominy. 2013. Tree Climbing and Human Evolution. *Proceedings of the National Academy of Sciences of the United States of America* 110 (4): 1237–42. https://doi.org/10.1073/pnas.1208717110.