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Challenges and perspectives on functional interpretations of australopith postcrania and the reconstruction of hominin locomotion

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Abstract

In 1994, Hunt published the 'postural feeding hypothesis' — a seminal paper on the origins of hominin bipedalism—founded on the detailed study of chimpanzee positional behavior and the functional inferences derived from the upper and lower limb morphology of the *Australopithecus afarensis* A.L. 288-1 partial skeleton. Hunt proposed a model for understanding the potential selective pressures on hominins, made robust, testable predictions based on *Au. afarensis* functional morphology, and presented a hypothesis that aimed to explain the dual functional signals of the *Au. afarensis* and, more generally, early hominin postcranium. Here we synthesize what we have learned about *Au. afarensis* functional morphology and the dual functional signals of two new australopith discoveries with relatively complete skeletons (*Australopithecus sediba* and StW 573 ‘*Australopithecus prometheus*’). We follow this with a discussion of three research approaches that have been developed for the purpose of drawing behavioral inferences in early hominins: 1) developments in the study of extant apes as models for understanding hominin origins; 2) novel and continued developments to quantify bipedal gait and locomotor economy in extant primates to infer the locomotor costs from the anatomy of fossil taxa; and 3) novel developments in the study of internal bone structure to extract functional signals from fossil remains. In conclusion of this review, we discuss some of the inherent challenges of the approaches and methodologies adopted to reconstruct the locomotor modes and behavioral repertoires in extinct primate taxa, and notably the assessment of habitual terrestrial bipedalism in early hominins.

Keywords: *Australopithecus*; Bone functional adaptation; Trabecular bone; Cortical bone; African apes

1. Introduction

Since the discovery of numerous *Australopithecus afarensis* postcranial remains at Hadar, Ethiopia, in the early 1970s (Taieb et al., 1974; Johanson and Taieb, 1976; Bush et al., 1982; Johanson et al., 1982), which built upon a collection of australopith fossils already uncovered in South Africa (e.g., Dart, 1925; Broom and Schepers, 1946; Broom and Robinson, 1949; Straus, 1948; Robinson, 1972), paleoanthropologists have increasingly focused on the inferences of posture and locomotion that can be drawn from fossil hominin (i.e., humans and their fossil relatives) skeletons. This focus on functional morphology led to contentious debates but also the development of new hypotheses, analytical approaches, and methods. Functional inferences have typically centered on understanding the form of bipedalism in which australopiths engaged and the relative importance of arboreality in their positional repertoire (e.g., Lovejoy, 1985; Stern and Susman, 1983; Susman et al., 1984; Senut and Tardieu, 1985; Latimer, 1991). Reconstructions of australopith locomotion and posture were made within the broader context of two foundational and longstanding evolutionary aims of paleoanthropology, 1) the identification of the primary locomotor behavior from which bipedalism evolved; and 2) understanding the evolutionary or selective process(es) leading to the establishment of hominin bipedal dependence. Multiple hypotheses about the primary locomotor behavior from which bipedalism evolved (e.g., Keith, 1923; Tuttle, 1969; Richmond and Strait, 2000) and the selective drivers of bipedalism have been proposed (e.g., Lovejoy, 1981; Darwin, 1987; Wheeler, 1991; Hunt, 1994), which remain contentious due to a paucity of Late Miocene and Early Pliocene hominin fossils and the virtual absence of an African ape fossil record (Crompton et al., 2008; Harcourt-Smith, 2010; Wood and Harrison, 2011; Andrews, 2020; Almécija et al., 2021; but see McBearty and Jablonski, 2005; Pickford et al., 2008). In the absence of fossil evidence near the time of the hominin-panin divergence, these hypotheses have traditionally relied heavily on functional interpretation of australopith anatomy, observations of extant primate postural and locomotor behaviors, and the influence of phylogeny. One such hypothesis is the 'postural feeding hypothesis' proposed by Hunt (1994) in "The evolution of human bipedality: Ecology and functional morphology" (see also Hunt, 1996). In this review, we use Hunt's (1994) seminal paper on the origins of hominin bipedalism as inspiration for how the australopith postcranium has influenced our hypotheses about the selective pressures surrounding hominin bipedalism and the value of living primate models and ecological context in our interpretation of hominin functional morphology. We start, with a brief review of the historical context in which Hunt's (1994) 'postural feeding hypothesis' was developed. We then further review some of the new australopith fossils discovered and new methods developed since 1994 that have helped paleoanthropologists to gain a better understanding of australopith diversity and make more informed functional inferences of the fossil morphology.

1.1. Historical context of australopith locomotion and the emergence of hominin bipedalism

Hypotheses about the locomotor or postural behavior from which bipedalism emerged range from terrestrial knuckle-walking to arboreal vertical clinging or brachiation and from pronograde to orthograde postures (see reviews in Richmond et al., 2001; Harcourt-Smith and Aiello, 2004; Crompton et al., 2008; Senut et al., 2018). Keith (1903, 1923) was the first to explicitly propose hominoid-like, orthogradeancestor based on morphological features of the upper limb that are shared between humans and suspensory apes. Keith (1923) proposed three stages of hominoid evolution: a hylobatid-like ('hylobatian') ancestor that evolved into a larger-bodied African ape-like ('troglodytian') ancestor capable of orthograde climbing and terrestrial knuckle-walking, which in turn evolved into a bipedal (‘plantigrade’) hominin (see also Morton, 1926). Tuttle (1969, 1975, 1981; Tuttle et al., 1974) further developed Keith’s ‘brachiating’ hypothesis through the study of great ape hand postures and anatomy, highlighting the lack of anatomical evidence for a knuckle-walking phase in hominin evolution. Tuttle (1969:p. 960) proposed “that the ancestors of [hu]man probably engaged in some form of suspensory posturing and that they assumed bipedal postures very soon after venturing to the ground.” It is important to note that neither Keith nor Tuttle at this time had a conception of hominoid phylogeny [although the seminal research on hominid proteins by Goodman (1962, 1963) was published]. Tuttle (1969) supported a closer evolutionary relationship between *Pan* and *Gorilla* (and, in fact, grouped gorillas within in the *Pan* genus) to the exclusion of humans. Thus knuckle walking could be considered a synapomorphic behavior of African apes in his hypothesis that human bipedalism evolved from a suspensory ancestor.

With greater evidence and acceptance of the phylogenetic relationship between *Pan* and humans (Goodman, 1963; Sarich and Wilson, 1967; Miyamoto et al., 1987), Washburn (1967:p. 23) proposed, albeit with little morphological evidence, that hominin bipedalism evolved from a terrestrial knuckle-walking ancestor because it offers a logical ‘intermediate condition’ in which, as bipedalism is positively selected, the long upper limb can be used less and less. The terrestrial knuckle-walking hypothesis continued to gain support through comparative anatomy, notably synapomorphic features of the upper limb, wrist, and hand shared between humans and African apes (Marzke, 1971; Corruccini, 1978; Shea and Inouye, 1993; Gebo, 1992; 1996; Begun, 1993, 1994; Richmond and Strait, 2000; Richmond et al., 2001) and the identification of ‘knuckle-walking features’ in australopiths (McHenry, 1983; Richmond and Strait, 2000). Parsimony also played a key supporting role with the sentiment that knuckle-walking locomotion is too unusual to have evolved independently in *Pan* and *Gorilla* (Gebo, 1992, 1996; Begun, 1994; Richmond and Strait, 2000; Richmond et al., 2001). Although other hypotheses on the locomotor or postural origin of hominin bipedalism emphasize arboreality, most notably a vertical climbing origin supported by biomechanical similarities between primate vertical climbing and human bipedalism (Prost, 1980; Fleagle et al., 1981; Stern and Susman, 1981; Ishida et al., 1985; Senut, 1988), the terrestrial knuckle-walking hypothesis envisions a locomotor repertoire that also includes arboreal climbing and some suspension (Richmond et al., 2001).

The role of arboreality has been central in the debate over early hominin functional morphology, and particularly that of australopiths, since the early 1980s, following the publication of the *Au. afarensis* fossils from Hadar (Taieb et al., 1974; Johanson and Taieb, 1976; Bush et al., 1982; Johanson et al., 1982). This debate stems from the duality of the *Au. afarensis*, and that of australopiths more generally, postcranium that can be broadly summarized as possessing human-like lower limbs and ape-like upper limbs. The functional interpretation of *Au. afarensis* morphology is typically divided into two camps that differ in the significance they grant to the ape-like morphological features, as aptly summarized by Daegling (2022; see also Ward, 2002). In the 'efficiency camp' researchers focused on human-like (i.e., derived) morphological features and biomechanical data to support the hypothesis that *Au. afarensis* had a bipedal gait similar to that of humans i.e., striding gait with extended hip and knee (Lovejoy et al., 1973; Lovejoy, 1975, 1978, 1988; Day and Wickens, 1980; White, 1980; Latimer, 1983, 1991; Ohman, 1986; Latimer et al., 1987; Latimer and Lovejoy, 1989, 1990; Crompton et al., 1998; Kramer, 1999). In this camp, *Au. afarensis* was reconstructed as fully committed to bipedalism because energetically costly bipedalism would not be positively selected, thus compromising any ability to climb competently. Arboreal behaviors were viewed as a trivial component of australopith positional repertoire.

In contrast, researchers in the ‘compromise camp’ incorporated both basal and derived morphology as well as biomechanical data to support the hypothesis that *Au. afarensis* engaged in a bipedal gait that was unlike that of modern humans and, instead, was compliant (i.e., bent hip and bent knee) and energetically costly (Senut, 1980; Stern and Susman, 1981, 1983, 1991; Feldesman, 1982; Jungers, 1982, 1991; Jungers and Stern, 1983; Schmid, 1983; Rose, 1984, 1991; Susman et al., 1984; Deloison, 1985, 1991, 1992; Tardieu 1986a, b; Susman and Stern, 1991; Duncan et al., 1994; Stern, 2000). This energetically costly bipedalism allowed *Au. afarensis* to be arboreally competent because trees were essential to, for example, foraging and avoiding predation (Susman et al., 1984; Preuschoft and Witte, 1991; Rak, 1991; Cartmill and Schmitt, 1996; MacLatchy, 1996; Schmitt et al., 1996, 1999; Ruff, 1998; Stern, 1999; also see below)

Numerous hypotheses have also been offered regarding the selective drivers underlying the origin of bipedalism (Rose, 1991, and references therein). These hypotheses are dependent not only on the functional interpretation of australopith morphology and on the form of positional behavior from which bipedalism evolved, but also the paleoecological context in which early hominins may have been living. Many of the initial hypotheses linked the origin of bipedalism to a savanna landscape, either the traditional view of an open, grassland savanna or a savanna-mosaic that includes areas of woodland (see review in Domínquez-Rodrigo, 2014). In an open landscape, bipedalism may have been an effective means of long-distance travel (Sinclair et al., 1986) or moving through patches of open terrain to reach woodland habitats (Rodman and McHenry, 1980; Isbell and Young, 1996; Potts, 1998). Others focused on the use of bipedalism for feeding in terrestrial, savanna-dwelling primates as a potential model for the selective driver of hominin bipedalism, all of which were grouped under the umbrella of the 'terrestrial feeding hypothesis' (Jolly, 1970; Rose, 1976, 1984; Wrangham, 1980). Jolly's (1970) 'seed-eater' model is particularly relevant to Hunt's (1994) 'postural feeding hypothesis' as it was the first time bipedal posture, rather than locomotion, was proposed as the selective target (see also Du Brul, 1962; Prost, 1980; Wrangham, 1980).

2. Hunt (1994) and the 'small-tree postural feeding' hypothesis

Within the historical context described above, Hunt (1994) recognized that feeding behavior is a logical selective target for changes in hominin positional behavior, but none of the previously proposed feeding hypotheses adequately accounted for the dual functional nature of the *Au. afarensis* postcranium. Hunt, instead, proposed the 'small-tree postural feeding hypothesis' based on extant chimpanzees as behavioral models to interpret the selective pressures on the early hominin postcranium (see also Hunt, 1996). The foundation of his hypothesis was the behavioral and ecological study of 26 habituated adult chimpanzees from the Mahale Mountains and Gombe of western Tanzania. Similar to studies of baboons (Rose, 1976, 1984, 1991), Hunt (1994) found that bipedalism was rare in comparison to other locomotor and postural behaviors, but when used, it was most often adopted as a posture during feeding (80% of bipedal bouts) rather than as as locomotior behavior for traveling. Bipedalism was used both on the ground and in trees, but when foraging for fruit from short trees while on the ground, chimpanzees were able to reach higher fruits, use both hands for fruit gathering, and to eat the fruits faster.

Hunt's (1994, 1996) postural feeding hypothesis aimed to reconcile the presumed contradictory functional signals across the *Au. afarensis* skeleton: an ape-like upper body advantageous for arboreal arm-hanging and more human-like lower body that he interpreted as indicating habitual but 'less than optimal' bipedal locomotion (i.e., more energetically costly) compared with humans. Although the modern human bipedal economy (i.e., a low energetic cost during bipedalism) is not necessarily the appropriate benchmark (Daegling, 2022), Hunt (1994, 1996) highlighted the importance of considering the energetic economy (or what Hunt often called 'energetic efficiency') of bipedalism, both postural and locomotor (see also Rodman and McHenry, 1980; Steudel, 1996). The postural feeding hypothesis aimed to explain *Au. afarensis* morphology holistically as 'fully-evolved' hominins adapted for a unique positional repertoire rather than as intermediate, 'half-evolved' bipeds (Hunt, 1994:p. 199) (of course, these terms used by Hunt (1994) were not meant as teleological or to imply evolution is goal-oriented). In doing so, Hunt (1994, 1996) synthesized two of the arguably most plausible hypotheses at the time for the origin of bipedalism: the hylobatid hypothesis and the terrestrial feeding hypothesis.

We find Hunt's (1994) paper to be inspiring because it 1) uses the careful study of extant ape behavior as a model for understanding potential selective pressures on hominins, 2) makes robust predictions based on functional morphology, biomechanics, and locomotor economy that can be (and since have been) tested, and 3) presents a hypothesis that aims to explain the dual functional signals of the *Au. afarensis* and, more generally, early hominin postcranium; all of which are just as relevant, if not more so, today as they were nearly 30 years ago.

Here we review the key questions regarding functional interpretation of the australopith postcranium, what we have learned about *Au. afarensis* functional morphology since Hunt's paper was published, and the dual functional signals of two new australopith discoveries with relatively complete skeletons (*Australopithecus sediba* and StW 573, referred to by some as *Australopithecus prometheus*). We follow this with a discussion of the advances in three research approaches used to draw inferences about early hominin behavior (and the past more generally): 1) the study of extant apes as models for understanding hominin origins; 2) measurement of bipedal gait and locomotor economy in extant primates to infer the locomotor costs from the anatomy of fossil taxa; and 3) the study of internal bone structure to extract functional signals from fossils. We end with a summary of the current challenges in paleoanthropology for reconstructing (locomotor) behaviors, including (but not only) the evolution of hominin bipedalism.

3. New fossil evidence: The early years

Over 40 years of debate about the reconstructed positional behavior of *Au. afarensis* (i.e., the ‘efficiency camp’ vs. ‘compromise camp’; see above) has been driven, at least in part, by differences in the functional importance one attributes to ape-like vs. human-like features found throughout the australopith postcranium (Stern, 2000; Ward, 2002, 2013; Daegling, 2022; Fig. 1). In a simplified scenario, derived, human-like features of the australopith lower limb offer clear phylogenetic polarity and a direct biomechanical link to function (Lauder, 1996), which reveals their biological role for bipedal movement (Bock and van Wahlert, 1965; Weishampel, 1995). These derived features, or their biological role—in this case, bipedal posture and locomotion— can be inferred to have conferred fitness benefits to those individuals better able to deal with the mechanical demands of terrestrial bipedality. On the contrary, primitive, ape-like features can be considered 1) selectively neutral or stabilized retentions from an ape-like ancestor that are not directly linked to function (e.g., retained via pleiotropy or other ontogenetic mechanisms), 2) positively-selected retentions that are functionally significant and play a biological role—in this case, arboreality; or 3) positively-selected exaptations that are functionally significant for a new biological role, such as manipulation (Fig. 1). In the 1980s and 1990s, interpreting the functional significance of *Au. afarensis* morphology was done largely within the comparative context of extant great apes, modern humans and, less frequently, geologically younger fossil hominins (e.g., Jungers, 1982; Stern and Susman, 1983; Susman et al., 1984; Latimer and Lovejoy, 1990), making phylogenetic polarity of features and their functional interpretation more challenging. Older (putative) hominins with postcranial remains prior to 4.0 Ma were not uncovered until mid-1990s or later (e.g., Leakey et al., 1995; Senut et al., 2001; Lovejoy et al., 2009a; White et al., 2009; Macchiarelli et al., 2020; Daver et al., 2022; but see Patterson and Howells, 1967), and thus debates about the functional significance of certain aspects of australopith morphology were fueled by a 'black box' of hominin evidence between 4–7 Ma. Below we briefly review (putative) fossil hominin evidence prior to the first appearance of *Au. afarensis* that has been uncovered since 1994.

The earliest species of australopith, *Australopithecus anamensis* (4.2–3.8 Ma), was announced in 1995 based on fossils from Kanapoi, Kenya (Leakey et al., 1995) with additional specimens also from Allia Bay, Kenya (Leakey et al., 1998, Ward et al., 1999, 2001, 2013) and Asa Issie, Ethiopia (White et al., 2006). Although there are few postcranial remains, all can be generally described as being similar in morphology to *Au. afarensis*, but larger in absolute size (Ward et al., 1999, 2001; White et al., 2006). The proximal and distal tibia show several features distinctive to bipedal locomotion, including an expanded proximal end with concave condyles and a vertical tibial shaft that is orthogonal to the talar joint (Leakey et al., 1995; Ward et al., 1999). The femoral shaft lacks a linea aspera, similar to the morphology found in *Au. afarensis*

A.L. 288-1, and has remarkably thick cortical bone (White et al., 2006). The distal humerus lacks morphology specific to African apes and although some have noted distinctive *Homo*-like features (Senut and Tardieu, 1985; Baker et al., 1998; Senut, 1999), more detailed studies show the most morphological similarities to *Au. afarensis* (Feldesman, 1982; Lague and Jungers, 1996). Like the femur, the humerus also has notably thick cortical bone (Ward et al., 2001). The radius is long, suggesting elongated forelimb proportions similar to those of *Au. afarensis* (Heinrich, 1993; Ward et al, 2001). A dorsal ridge on the distal radius has been interpreted as limiting radiocarpal joint extension, implying evidence of a knuckle-walking origin for hominin bipedalism (Richmond and Strait, 2000; but see Ward et al., 2001). The capitate has a radioulnarly broad proximal head with a large lunate articulation, similar to some other australopiths, but the radially-facing second metacarpal facet is similar to that of extant African apes and unlike that of other hominins (McHenry, 1983; Leakey et al., 1998, Ward et al., 2001; Lovejoy et al., 2009b, Macho et al., 2011). *Australopithecus anamensis* manual phalanges are curved to a similar degree as *Au. afarensis* (Ward et al., 1999), but the intermediate phalanx from Asa Issie is described as being longer for its breadth than those from Hadar (White et al., 2006).

Insert Figure 1 here

Ardipithecus (5.8–4.4 Ma) is currently the best known (putative) hominin prior to *Au. afarensis* (White et al., 1994, 1995, 2009; Haile-Selassie, 2001; Haile-Selassie and WoldeGabriel, 2009; Lovejoy et al., 2009a, b, c; Simpson et al., 2019). There are two species: the older *Ardipithecus kadaba* (5.8-5.2 Ma; Haile-Selassie, 2001; Haile-Selassie and WoldeGabriel, 2009) and *Ardipithecus ramidus* (4.4 Ma; White et al., 2004; 2009), of which the ARA-VP-6/500 partial skeleton provides the most informative postcranial evidence. ARA-VP-

6/500 is remarkably complete but unfortunately does not preserve the articular ends of most long bones and the pelvic bones are highly fragmented. The lower body morphology shows several features associated with bipedalism, including shorter and medially-rotated iliac blades, a well-developed anterior inferior iliac spine, a shortened greater trochanter, thinner cortex on the superior margin of the femoral neck, lateral midfoot rigidity, and evidence of regular dorsiflexion at the metatarsal-phalangeal joints (White et al., 2009; Lovejoy et al., 2009c). This morphology is combined with several features considered advantageous for arboreality: a grasping hallux with no dorsal doming, a long ischium, long, curved manual and pedal phalanges, as well as several features described as distinct from extant apes and more like Early Miocene apes, including short metacarpals but relatively long pollex, a simple ‘carpometacarpal complex’, and long tarsus (Lovejoy et al., 2009b; Selby et al., 2016; Simpson et al., 2019). Collectively, this suite of postcranial features is interpreted as indicating facultative, terrestrial bipedalism combined with the primitive retention of arboreal capabilities including palmigrade above-branch quadrupedalism and ‘careful climbing’ (White et al., 2009; Lovejoy et al., 2009b, c). Critically, the initial interpretations highlighted a distinct absence of any great ape-like morphology related to orthogrady, suspension, vertical climbing, and knuckle-walking, implying that shared morphologies among extant great apes must be homoplasies (White et al., 2009; 2015; Lovejoy et al., 2009a).

Recent studies, however, have questioned the original functional interpretations of the *Ar. ramidus* morphology and the subsequent evolutionary implications. For example, Prang et al. (2021) demonstrated that the *Ar. ramidus* hand is most similar to chimpanzees and bonobos with morphology advantageous for suspensory locomotion. Similarly, Prang (2019) interpreted the *Ar. ramidus* foot as most similar to chimpanzees and gorillas, and suggested that the elongated tarsus could have increased propulsion during bipedalism. A morphological and cladistic analysis of foot morphology by DeSilva et al. (2019) further highlighted distinct morphs within the *Ardipithecus* sample (see also Simpson et al., 2019) as well as the Burtele foot (Haile-Selassie et al., 2012) and StW 573 (Kidd and Oxnard, 2005; Crompton et al., 2021; see below), which they interpreted as evidence of different hominin taxa engaging in different forms of bipedal walking or arboreality. This conclusion is further supported by morphometric and kinematic modeling of the hominin pelvis showing that *Ar. ramidus* had human-like hip extension for bipedal walking but also powerful, ape-like hip extension for vertical climbing, while *Au. afarensis* and *Au. africanus* had a reduced mechanical advantage for climbing (Kozma et al., 2018). Multiple forms of bipedality (and climbing) in early hominins further complicate interpretations of trait polarity and functional significance in reconstructions of australopith bipedalism.

Orrorin tugenensis (6 Ma) from Lukeino Formation, Kenya preserves three femora, a distal humerus and manual phalanges (Senut et al., 2001; Gommery and Senut, 2006). The two most preserved femora show features interpreted as indicators of habitual bipedality, including a femoral neck that is elongated and anteroposteriorly compressed, and has thicker cortex inferiorly than superiorly, the presence of an obturator externus groove, and a well-developed gluteal tuberosity (Senut et al., 2001; Pickford et al., 2002; Galik et al., 2004). These morphological features were originally inferred to suggest *Orrorin* was a habitual, and perhaps obligate biped, but with upper limb morphology that indicated effective climbing abilities (Senut et al., 2001). The preserved external shape of the *Orrorin* proximal femur has been described as more hominin-like rather than ape-like but the asymmetric cortical bone distribution in the femoral neck has received particular attention as arguably one of the key traits indicative of bipedality in *Orrorin* (Pickford et al. 2002, Galik et al. 2004; Richmond and Jungers, 2008). Some have questioned the methodology employed and the quality of the CT scans used to demonstrate the inferiorly thicker femoral neck cortex of *Orrorin* (Ohman et al. 2005, White 2006), while others have criticized the usefulness of the trait in general, regardless of its presence in *Orrorin*, as an indicator of habitual or obligate bipedality (Andrews and Harrison, 2005). A more recent study of the cortical thickness topographic distribution of the *Orrorin* femoral shaft confirms a human-like cortical distribution consistent with habitual terrestrial bipedalism (Puymerail et al., 2017).

Arguably the most controversial of the early putative hominins, *Sahelanthropus tchadensis* (~7 Ma) from Toros-Menalla, Chad, was inferred to be bipedal based initially on basicranial morphology (Brunet, 2002, Brunet et al., 2005; Zollikofer et al., 2005) and only recently on postcranial evidence (Daver et al., 2022). In their analyses of the external and internal morphology of the *Sahelanthropus* femoral shaft, Daver et al. (2022) show an anteroposteriorly compressed femoral neck, the presence of a linea aspera and calcar femorale, and human-like cross-sectional geometry of the diaphysis. The ulnae, however, show a suite of morphological features reflecting arboreality, including high degree of shaft curvature and orangutan-like cross-sectional geometry (Daver et al., 2022). Taken together, Daver et al. (2022) concluded that *Sahelanthropus* engaged in habitual bipedalism, likely on the ground, and arboreal ‘cautious climbing’ behaviors. However, others have questioned the association of the postcrania with the *Sahelanthropus* cranium (Beauvilain, 2008). Independent analyses of the external morphology and cross-sectional shape reveal greater similarities with *Pan* and features that are distinct from the femoral shaft morphology of *Orrorin* or later hominins (Macchiarelli et al., 2020). Moreover, a calcar femorale can be present in extant great apes and absent in some bipedal hominins, indicating that this feature is not necessarily indicative of bipedal locomotion (Cazenave et al., 2022). At ~7 Ma, so close to the panin-hominin divergence, a full suite of bipedal features in *Sahelanthropus* is an unrealistic expectation, creating an unclear threshold of ‘how many bipedal features does one need to be considered a fully terrestrial biped or a hominin’? This fundamental problem is further confounded by the challenge of identifying bipedalism in a potential hominin with a different body plan, which would elicit distinct, site-specific biomechanics and therefore distinct internal bone structure response. As Macchiarelli et al. (2020) highlight, even if *Sahelanthropus* is not bipedal, it does not diminish its importance in our understanding of hominid evolution.

Although a minority of researchers view some of the above hominin taxa as ‘chronospecies’ leading to *Au. afarensis* (White, 2003; White et al., 2006, 2009), most paleoanthropologists recognize a far bushier and perhaps reticulated hominin evolutionary tree (e.g., Holliday, 2003; Harrison, 2010; Wood and Harrison, 2011; Strait et al., 2015; Wood and Boyle, 2016; Slon et al., 2018). Importantly, paleoanthropologists must acknowledge that some or all of these early, putative hominins could instead fall within the panin clade or any number of extinct clades, and that homoplasy will undoubtedly be rampant and confounding (Wood and Harrison, 2011; Daegling, 2022). Thus, although there are now many more fossils within the 7–4 Ma ‘black box’ than there were at the time of Hunt’s (1994) functional interpretation of *Au. afarensis* postcranium, any potential clarity on the polarity or functional significance of australopith morphology is overshadowed by new and complex questions about early hominin evolution and phylogenetic relationships. As Wood and Harrison (2011:p. 348) aptly question: “Should the discovery of a purported fossil hominin overturn predictions about an ancestral morphotype based on a wealth of comparative data from extant taxa, or should one defer to the hypothetical morphotypes that best fit the comparative evidence and critically reassess the phylogenetic placement of fossil taxa that contradicts such an hypothesis?”

4. New fossil evidence: Australopiths in a complex taxonomic context

As highlighted by Hunt (1994), inferences about positional behaviors and their energetic costs in fossil taxa are only possible for species represented by sufficient postcranial remains. However, the rarity of unambiguously associated craniodental and postcranial remains complicates the already difficult task of drawing functional inferences from fragmentary and/or incomplete axial or appendicular skeletal remains (e.g., Susman et al., 2001; Wood and Constantino, 2007; Domínguez-Rodrigo et al., 2013; Hlusko et al., 2015; Lague, 2015; Wood and Boyle, 2016). This is especially true in the Plio-Pleistocene in which hominin taxic diversity has increased and become more complex with recent fossil discoveries (e.g., Berger et al., 2010; Wood and Boyle, 2016; Clarke and Kuman, 2019; Zipfel et al., 2021), and which possibly may be underestimated (e.g., Cofran and Thackeray, 2010; Zanolli et al., 2019; Pickering et al., 2021; Zipfel et al., 2021). Nonetheless, intense fieldwork has unveiled relatively complete hominin skeletons or sufficient associated remains to satisfactorily reconstruct a body plan and to provide more robust functional inferences (e.g., Brown et al., 2004; Alemseged et al., 2006; Berger et al., 2010, 2015; Haile-Selassie et al., 2010; Clarke and Kuman, 2019; see sections 4.2 and 4.3).

These relatively complete hominin skeletons each reflect committed bipedalism, but also differing mosaics of anatomical features that suggest biomechanical variation in bipedal gait, and that arborealism or climbing continued to be a significant component of behavior for some hominins, including into the Pleistocene (e.g., Stern, 2000; Ward, 2002, 2013; Larson et al., 2009; Lovejoy et al., 2009a,b,c; Haile-Selassie et al., 2012; Barak et al., 2013; Berger et al., 2015; Kivell et al., 2015; Harcourt-Smith, 2016; Ruff et al., 2016, 2018; Zeininger et al., 2016; McNutt et al., 2021). This new evidence departs from Hunt's (1994) vision of a single, unique, adaptive morphotype for both terrestrial and arboreal bipedal foraging in hominins that may have remained relatively unchanged even in *Homo habilis*. However, Hunt's (1994) hypothesis accommodated the arboreal features of the *Au. afarensis* upper body because he considered them functionally significant (i.e., via stabilizing selection), with the underlying assumption of correspondence between the presence of a morphology and the use of that morphology in a biological role. New fossil discoveries and new analyses of old fossils have revealed that Hunt's (1994) functional interpretation remains valid. We outline this evidence below.

4.1. What we have learned about Australopithecus afarensis *since Hunt (1994)*

The *Au. afarensis* hypodigm currently includes more than 400 specimens collected from multiple sites in eastern Africa, which are thoroughly reviewed by Kimbel and Delezene (2009; see also Drapeau et al., 2005 and Ward et al., 2012). Therefore, here we do not aim to reproduce their work and instead focus on functional inferences derived from more recent morphological studies of the partial skeleton A.L. 288-1 'Lucy' and *Au. afarensis* more generally (Fig. 2a).

One of the anatomical features highlighted by Hunt (1994) was the presence of six lumbar vertebrae in *Au. afarensis*, indicating a longer, more flexible lower back than that of humans and African apes, and that australopiths were likely not adapted to vertical climbing or leaping. However, a recent re-analysis of the A.L. 288-1 lumbar vertebrae found that one vertebra (A.L. 288-1am) exhibited morphology that is absent in extant hominoids but common in large-bodied extant papionins, indicating that this vertebra is not hominin (Meyer et al., 2015). Moreover, a reassessment of the A.L. 288-1 sacral vertebrae suggests that ‘Lucy’ possessed five sacral vertebrae as in modern humans (Russo and Williams, 2015), rather than four as previously interpreted (Lovejoy et al., 2009d; McCollum et al., 2010). The juvenile *Au. afarensis* partial skeleton (DIK-1-1) from Dikika, Ethiopia provides further insights into the full vertebral column, preserving the only known complete early hominin cervical and thoracic vertebral column (Alemseged et al., 2006; Ward et al., 2017). DIK-1-1, at 3.3 Ma, preserves the earliest evidence of 12 thoracic vertebrae, rather than 13 in African apes, but a thoracolumbar transition at the 11th thoracic segment, a distinctive transitional pattern found in other early hominins but that is higher than in modern humans and extant apes (Ward et al., 2017). Collectively, this new evidence has important implications for reconstructing the trunk and lower back morphology in early hominin evolution (see reviews in Williams et al., 2016; Williams and Pilbeam, 2021).

Hunt (1994) focused on differing functional signals derived from the upper vs. lower body in *Au. afarensis*. Researchers agree that the derived traits of the australopith lower limb (and postcranial skeleton overall) are the result of selection for bipedality (reviewed in Ward, 2002, 2013). However, there has been enduring debate over australopith bipedal gait and kinematics, in particular whether they used a human-like, extended-limb striding bipedalism or a compliant, bent-hip/bent-knee gait (reviewed in Schmitt, 2003; Carey and Crompton, 2005). The recently discovered *Au. afarensis* partial skeleton (KSD-VP-1/1) from Woranso-Mille, Ethiopia (3.58 Ma) confirms key bipedal features, including a long tibia, an elliptical lateral femoral condyle, and a well-developed patellar lip that together is coherent with human-like bipedalism with a valgus knee (Haile-Selassie et al., 2010). In addition, a complete *Au. afarensis* fourth metatarsal (A.L. 333-160) recently recovered from Hadar, Ethiopia, was also interpreted as having morphology consistent with a human-like bipedal gait (Ward et al., 2011). This morphology includes torsion of the metatarsal shaft, a feature thought only to be observed in modern humans, and suggesting *Au. afarensis* possessed modern human-like transverse and longitudinal arches, which are critical to committed, terrestrial bipedalism (Ward et al., 2011). Morphological comparisons of A.L. 333-160 with a larger comparative sample show similarities between hominins and cercopithecids in torsion of the fourth metatarsal, reflecting the presence of transverse arches in terrestrial cercopithecids as well (Drapeau et al., 2013; Mitchell et al., 2012). Furthermore, other aspects of metatarsal morphology highlighted by Ward et al. (2011) are also similar to other great apes and/or highly variable, bringing into question the significance of these features for inferring midfoot stiffness and the interpretation that *Au. afarensis* was a habitual terrestrial biped, at least from its fourth metatarsal morphology alone (Mitchell et al., 2012).

Nonetheless, there are several other features of the *Au. afarensis* foot that are surprisingly human-like, especially in light of new australopith discoveries (see below; Zipfel et al., 2011; McNutt et al., 2018; DeSilva et al., 2019). These features include a robust calcaneal tuberosity and an expanded, plantarly-positioned lateral plantar process, both of which are found in the modern human heel and suggest the *Au. afarensis* foot was well adapted for incurring high forces during heel-strike (Prang, 2015a; McNutt et al., 2018). *Au. afarensis* tali have a human-like, plantarly-oriented talar head (Prang, 2016a) and more human-like overall shape relative to other australopiths (Sorrentino et al., 2020). An associated *Au. afarensis* forefoot (A.L. 333-115) demonstrates human-like dorsal doming of the lateral metatarsal heads, but the kinematics of toe push-off during the bipedal gait are interpreted as differing from that of humans based on a more mediolaterally narrow first metatarsal head compared to modern humans (Latimer et al., 1982; Latimer and Lovejoy, 1990; Fernandez et al., 2016). Moreover, the nearly completely juvenile foot from Dikika, Ethiopia (DIK-1-1f) offers a rare opportunity to assess how function and behavior may have changed throughout ontogeny in *Au. afarensis* (Alemseged et al., 2006; DeSilva et al., 2018). Compared to adult *Au. afarensis* specimens, the hallux was more mobile and the calcaneus more gracile, indicating selection for foot grasping abilities in juveniles combined with habitual bipedality (DeSilva et al., 2018).

For *Au. afarensis*, functional information from postcranial morphology can be combined with biomechanical inferences derived from the Laetoli footprints (3.66 Ma; Leakey, 1978; Leakey and Hay, 1979; White and Suwa, 1987). Novel analyses of the ‘G’ and ‘S’ tracks using extant human bipedal biomechanics as a model suggest *Au. afarensis* walked with an extended hip and knee (Raichlen et al., 2010) but potentially with a slightly more flexed limb at foot strike than that of modern humans (Hatala et al., 2016; but see McNutt et al, 2021). Comparisons of the Laetoli footprints to younger (1.5 Ma) hominin footprints from Ileret, Kenya, imply that the Laetoli hominins had a shallower and wider instep and potentially different foot proportions relative to later hominins (Bennett et al., 2009).

Regarding the *Au. afarensis* upper limb, recent analyses of the scapula support Hunt’s (1994) functional interpretation of the importance of arboreality in australopiths. The Dikika partial juvenile skeleton preserves both scapulae showing cranially-oriented glenoid fossae and obliquely-oriented scapular spines, similar to that of great apes, and suggesting an African ape-like ontogenetic trajectory (Green and Alemseged, 2012; Young et al., 2015). Shared morphology between juvenile and adult *Au. afarensis* scapulae indicates that arboreal locomotion was an important behavior throughout adulthood as well (Green and Almeseged, 2012). In contrast, others have suggested that the KSD-VP-1/1 adult partial scapula is more human-like (Haile-Selassie et al., 2010) and potentially reflects use of the upper limbs for tool-use while engaging in committed terrestrially (Melillo, 2016).

Several studies have focused on the functional inferences that can be drawn from *Au. afarensis* hand morphology, particularly in relation to the estimated intrinsic hand proportions, but these studies have typically focused on potential manipulative abilities rather than locomotor behaviors. The composite hand of *Au. afarensis* includes second to fifth metacarpals (Mc 2–5) that most likely belong to a single individual, combined with a first metacarpal and phalanges from different A.L. 333 localities (Marzke, 1983; Alba et al., 2003). The estimated intrinsic hand proportions (i.e., relative length of the thumb to the finger[s]) range from *Gorilla*-like (Rolian and Gordon, 2013) to human-like (Alba et al., 2003). Experimental evidence of human participants using simulated stone tools instrumented with force sensors highlights the high joint forces acting on the thumb, which has implications for early hominin tool use (Rolian et al., 2011; also see Williams et al., 2012; Key and Dunmore, 2015; Williams-Hatala et al., 2018). As such, some researchers suggest that *Au. afarensis* lacked the ability to produce precision grips with the same proficiency as modern humans (Rolian and Gordon, 2013) and that the gracile first metacarpal morphology could not effectively dissipate the high stress that occurs during stone tool behaviors (Rolian et al., 2011). In contrast, others have inferred a human-like pad-to-pad precision grip ability in response to or as an exaptation for a variety of manipulative behaviors, not just lithic or non-lithic tool-use (Alba et al., 2003; Almécija and Alba, 2014; Feix et al., 2015; Prang et al., 2021). These functional interpretations, however, took on new relevance with the discovery of cut marks and percussion marks in the Dikika assemblage at 3.4 Ma (McPherron et al., 2010) and the Lomekwi tool technology in Kenya at 3.3 Ma (Harmand et al., 2015) that are, at least potentially, associated with *Au. afarensis* (but see Sahlea et al., 2017; Domínguez-Rodrigo and Alcalá, 2019).

Hunt’s (1994) hypothesis aimed to accommodate the contrasting functional signals within the *Au. afarensis* upper and lower limbs. The new discoveries and analyses since this time continue to confirm the dual nature of the functional signals reflected in its postcranial morphology. New evidence suggests that the bipedal gait of *Au*. *afarensis* may have been more human-like and energetically economical than some researchers previously posited (e.g., Crompton et al., 1998; Wang et al., 2003; Carey and Crompton, 2005; Lovejoy and McCollum, 2010; Raichlen et al., 2010), and, interestingly, more human-like than other roughly contemporary or more recent australopiths (Harcourt-Smith and Aiello, 2004; Zipfel et al., 2011, DeSilva et al., 2018; see below). Although some debate still remains over the significance of arboreality in *Au. afarensis*, evidence of perimortem fractures throughout the A.L. 288-1 skeleton is interpreted as consistent with a vertical fall from a tree, unusual evidence of arborealism in *Au. afarensis* (Kappelman et al., 2016). Moreover, in contrast to previous assumptions (e.g., Marzke, 1983, 1988; Latimer, 1991; Marzke et al., 1992; Alba et al., 2003; Tocheri et al., 2008), recent hominin discoveries suggesting the possibility that *Au*. *afarensis* was a lithic stone tool user and/or capable of forceful precision dexterity are not incompatible with a significant reliance on arboreal locomotion (Kivell et al., 2015; Feuerriegel, 2016). We highlight some of this new comparative context below.

4.2. Recently-discovered australopiths and anatomical evidence of locomotor behaviors

Since 1994, several new australopith discoveries have expanded australopith taxic diversity (e.g., Asfaw et al., 1999; Berger et al., 2010; Haile-Selassie et al., 2012; 2015; Clarke and Kuman, 2019; reviewed in Wood and Boyle, 2016). Here we synthesize the functional morphology of partial skeletons from two *Australopithecus* species recently found in South Africa, focusing on the locomotor signals within the lower and upper limb: StW 573 from Sterkfontein caves, dated to as old as 3.67 Ma (Granger et al., 2015; Bruxelles et al., 2019) and referred to as *Australopithecus prometheus* (Clarke and Kuman, 2019), and *Australopithecus sediba* Malapa Hominin 1 (MH1) and Malapa Hominin 2 (MH2) from Malapa (Berger et al., 2010), dated to 1.977 Ma (Pickering et al., 2011).

The StW 573 partial skeleton is remarkably well preserved, including relatively complete upper and lower limbs from both sides with a complete, semi-articulated hand, as well as a thorax and partial pelvis (Stratford and Crompton, 2021; Fig. 2b). Many features of the lower limb bones, including developmentally plastic features that only form during repeated use of bipedal gaits (Frost, 1990; Duren, 1999; Hamrick, 1999; Tardieu, 2010), suggest clear evidence of habitual terrestrial bipedality (Heaton et al., 2019; Crompton et al., 2021). For example, the StW 573 femur has a relatively large head, an intertrochanteric crest reflecting a strong iliofemoral ligament, a well-developed patellar lip, flattened and asymmetrical femoral condyles, and a high bicondylar angle indicating stabilized hip and knee joints during bipedal walking (Heaton et al., 2019; Crompton et al., 2021). These features are found in combination with a more ape-like tibia morphology and fibulotalar articulation indicating greater ankle mobility than that of extant humans (Heaton et al., 2019; Crompton et al., 2021). The StW 573 foot bones were originally described as having a mosaic of features, including a human-like talus and a medially-oriented medial cuneiform-first metatarsal joint implying a more abducted hallux compared to extant humans, which would have facilitated arboreality (Clarke and Tobias, 1995). In contrast, more recent morphological studies suggest an ape-like talus and lack of hallux opposability in StW 573 (Harcourt-Smith, 2002; Crompton et al., 2021).

Morphology of the StW 573 upper limb indicates that climbing and/or suspension continued to be a part of its locomotor repertoire (Heaton et al., 2019; Carlson et al., 2021; Crompton et al., 2021). The long clavicles, the African ape-like shape of the scapulae, including a cranially-oriented glenoid fossa, as well as low humeral torsion, suggest a high, dorsally-positioned scapula that would have facilitated above-head upper limb use and body weight support (Heaton et al., 2019; Carlson et al., 2021), as well as hand-assisted bipedalism (Hunt, 1994; Thorpe et al., 2007). The humeri have widely-flaring lateral supracondylar ridges and large epicondyles that, in apes, reflect a well-developed brachioradialis muscle and long wrist and digital flexor muscles, facilitating climbing (Heaton et al., 2019; Crompton et al., 2021). StW 573 also preserves a complete (apart from one missing phalanx), articulated left hand. It has been described as having modern human-like intrinsic hand proportions (Clarke, 1998, 2002; Crompton et al., 2021) and having a *Gorilla*-like ridge on the first metacarpal facet that would help to stabilize the thumb in abducted pinch grips (Crompton et al., 2021). However, to date no quantitative analyses or detailed descriptions of any of the StW 573 hand anatomy have been published. Although the hand remains articulated within the breccia, making morphological analyses more challenging, our own study of the fossils based on caliper linear measurements (taken by T.L.K.) estimates thumb length (including the metacarpal and proximal phalanx) at 68 mm and third digit length (including the metacarpal and proximal and intermediate phalanges) as 128 mm, indicating a thumb length that is approximately 53% the length of the third digit. Thus, StW 573 indeed does have similar intrinsic hand proportions to those of modern humans (mean 54%), but shorter than *Homo naledi* (Hand 1, 58%) and, especially, *Au. sediba* (MH2, 61%; Kivell et al., 2011, 2015). The first metacarpal facet of the trapezium shows strong dorsopalmar convex curvature like that of African apes and unlike humans, but no ridge is present (T.L.K., pers. observ.).

The remarkable preservation of StW 573 offers a rare opportunity to reliably assess limb proportions in an early hominin, and like other early hominins for which these can be assessed, the StW 573 limb indices are intermediate and roughly equidistant from those of African apes and modern humans (Heaton et al., 2019). As reported by Heaton et al. (2019), the StW 573 intermembral index (85.5) is almost identical to that of A.L. 288-1 (85.6), indicating that variation in upper and lower proportions is less influenced by allometry than previously thought (Holliday and Franciscus, 2012). The humerofemoral index (86.6) in StW 573 is also similar to A.L. 288-1, as well as *Ardipithecus* (both 84.3), indicating a relatively shorter femur than that of modern humans (Heaton et al., 2019). The StW 573 brachial index shows a surprising degree of bilateral asymmetry (82.8 and 86.2) and is similar to that of *Gorilla* (mean 80.6) and *Au. sediba* (~84) but lower than A.L. 288-1 (88.6; Heaton et al., 2019).

Crompton et al. (2021) concluded that StW 573 morphology reflects active selection for both arboreal and terrestrial locomotion. They argued that relatively short upper limb length compared with African apes would have reduced its energetic economy for arboreal locomotion but would have been more economical than humans (Crompton et al., 2021). The ape-like aspects of the pectoral girdle have also been interpreted as reflecting greater selection for suspensory activities rather than enhanced manipulation (Carlson et al., 2021). The human-like bipedal morphology of the lower limb combined with relatively shorter length compared to modern humans suggest selection for walking short-to-medium distances and that bipedalism would have been used within an arboreal context as well (Crompton et al., 2021). This behavioral interpretation is also consistent with the morphology of the vestibular apparatus suggesting that StW 573 was adapted to utilizing environments requiring maintenance of head/visual stability in a variety of postures such as three-dimensionally (3D) complex arboreal environments (Beaudet et al., 2019).

The two associated partial skeletons of *Au. sediba*, one likely representing a subadult male (MH1) and the other an adult female (MH2), show a mosaic of ape-like and human-like morphology as well, but a different mosaic relative to that of StW 573 and *Au. afarensis* (Fig. 2c; Kibii et al., 2011; Kivell et al., 2011; Williams, 2011, 2012; Zipfel et al., 2011; Berger, 2013; Churchill et al., 2013; 2018; de Ruiter et al., 2013, 2017; DeSilva et al., 2013; Schmid et al., 2013; Williams et al., 2013, 2018, 2021; Prang, 2015a, b, 2016a, b; Meyer et al., 2017; Rein et al., 2017; Dunmore et al., 2020a). Partial pelvic and sacral remains from both MH1 and MH2 share several features with other australopiths, including a long pubis, relatively small sacral and acetabular joints, and a wide bi-acetabular diameter (Kibii et al., 2011; Churchill et al., 2018). However, the overall architecture of the pelvis is more similar to modern humans, including more sagittally-oriented iliac blades (i.e., less flared) with a sigmoid curvature, robust iliac pillar (acetabulo-cristal buttress, at least in MH1) and short ischium (Kibii et al., 2011; Churchill et al., 2018). Importantly, *Au. sediba* demonstrates that the derived pelvic features of *Homo* can evolve in the absence of brain encephalization (Kibii et al., 2011; Churchill et al., 2018). Newly recovered lumbar vertebrae of MH2 demonstrate morphology consistent with lumbar lordosis and other adaptations to bipedalism, although features of the vertebrae themselves show a mix of human-like and more ape-like aspects (Williams et al., 2021).

The *Au. sediba* lower limb shows a unique combination of morphologies unlike any other known australopith. As in other australopiths (Ward et al., 2015), the femoral neck is long and anteroposteriorly compressed (DeSilva et al., 2013, 2018) and, when combined with the pelvic morphology, would likely increase both the contractile force of the abductors and the hip joint reaction force that would, in turn, increase the mediolateral bending moments around the proximal femoral shaft (Ruff, 1995). The MH2 distal femur possesses australopith-like condyles, an unusually well-developed lateral patellar lip that is *Homo*-like, but lacks the anterior projection of the patellar surface (DeSilva et al., 2013, 2018). The distal tibia of MH2 (and MH4) has an ape-like mediolaterally thick medial malleolus that is thicker than other australopiths but has a human-like articulation with the talus (Zipfel et al., 2011; Desilva et al., 2018).

The *Au. sediba* foot bones, some of which were found in articulation, each reveal their own mix of human-like and ape-like features not observed in other fossil hominins. For example, the MH2 talus is human-like in having a flat trochlea, but ape-like in having a talar head and subtalar joint morphology that suggests high mobility (Prang, 2015b; 2016a; Zipfel et al., 2011). In both MH1 and MH2, the calcaneal tuberosity is gracile with an ape-like dorsally-positioned lateral plantar process, a morphology that is more basal than that characterizing *Au. afarensis* (Latimer and Lovejoy, 1989; Zipfel et al., 2011; Prang, 2015b; DeSilva et al., 2018).

Taken together, the unusual morphology of the *Au. sediba* lower limb indicates that it was clearly adapted to habitual bipedalism, but with distinct biomechanics compared with other hominins (DeSilva et al., 2013). DeSilva et al. (2013) suggest a hyperpronating bipedal gait, in which heel strike occurs on the lateral edge of an inverted foot (e.g., reflecting a gracile calcaneal tuberosity), followed by extreme pronation that would internally-rotate the tibia and femur (e.g., reflecting a well-developed patellar lip). Moreover, pronation is also an important motion during ape climbing (Stern and Susman, 1983) and thus the particular mosaic of features and gait mechanics in the *Au. sediba* lower limb may also have been advantageous for arboreal locomotion (DeSilva et al., 2013).

The overall morphology of the *Au. sediba* upper limb bones (both MH1 and MH2) is similar to other australopiths (Churchill et al., 2013, 2018). The short length and joint orientations of the clavicle, low humeral torsion, and a cranially-oriented glenoid fossa of the scapula, suggest the scapula was positioned laterally and high on the thorax and that the upper limb was habitually used in overhead arm postures (Churchill et al., 2013). The morphology of the elbow is also similar to other australopiths, with well-developed epicondyles and an elongated brachioradialis crest at the distal humerus, a well-developed insertion for the biceps brachii on the radius, and ape-like morphology of the ulnar trochlea that generally reflect powerful arm, wrist, and digital flexion that is advantageous for climbing (Churchill et al., 2013; Rein et al., 2017).

The relatively complete MH2 hand shows mosaic carpal morphology, including a radioulnarly narrow lunate, that suggests a greater range of abduction at the radiocarpal joint and perhaps less central-axis loading of the radiocarpal and midcarpal joints than is interpreted for other fossil hominins (Kivell et al., 2011, 2018a). The metacarpals are relatively gracile, including the first metacarpal, that in combination with the radial carpometacarpal region, suggests limited force production by the thumb. However, intrinsic hand proportions reveal a thumb that is surprisingly long relative to the fingers, and longer than that found in modern humans, which would have facilitated opposition of the thumb to the fingers and pad-to-pad precision gripping that is typical of later *Homo* (Kivell et al., 2011, 2018a). The MH2 proximal phalanges show moderate curvature and, unusually, both the proximal and intermediate phalanges have well-developed flexor sheath ridges that, in combination with a palmarly-projecting hamate hamulus, suggest powerful flexion and that some degree of arboreality may have been a functionally important part of the *Au. sediba* locomotor repertoire (Kivell et al., 2011, 2018a; Syeda et al., 2021).

Finally, we can assess some limb proportions in *Au. sediba*. The complete right upper limb of MH2 has a brachial index similar to A.L. 228-1, with a forearm relatively shorter than *Ardipithecus* but longer than modern humans (Churchill et al., 2013). Interlimb comparisons show that the upper limb articular size is smaller than those of the lower limb, which is typical of bipedal hominins, but the intermembral index remains intermediate between that of African apes and modern humans (Holliday et al., 2018). Relative to other hominins, *Au. sediba* joint proportions are most similar to *Au. africanus*, as well as *H. habilis* and *Homo floresiensis*, and are more ape-like than *Au. afarensis* (Prabhat et al., 2021).

Taken together, the *Au. sediba* postcrania indicate active selection for habitual, terrestrial bipedalism, albeit with a unique bipedal gait relative to other hominins, and for short to medium distances given that the lower limb is not as elongated as in early *Homo* (Kibii et al., 2011; DeSilva et al., 2013; Holliday et al., 2018). However, there likely remained stabilizing selection for arboreal competency, as indicated by the upper limb and hand morphology associated with over-head arm support that includes developmentally plastic features associated with climbing and suspension (i.e., keeled ulnar trochlear facet and curved phalanges) and mobile foot joints that are advantageous for climbing (Holliday et al., 2018; Churchill et al., 2013; DeSilva et al., 2013; Rein et al., 2017; Williams et al., 2021). We can also combine these locomotor inferences with a remarkably long thumb that would increase dexterity in *Au. sediba*, but would also enhance arboreal grasping in a hominin with relatively short fingers (Kivell et al., 2011, 2018a).

Hunt (1994) reiterated the dual-behavioral signal of A.L. 288-1 upper and lower limbs highlighted by previous analyses (e.g., Senut, 1980; Tuttle, 1981; Jungers, 1982; Jungers and Stern, 1983; Stern and Susman, 1983) and current fossil evidence still supports this functional interpretation, not only for *Au. afarensis*, but also for StW 573 and *Au. sediba*. However, the suite of anatomical features in each of these species is different, suggesting subtly or, in some cases, dramatically different locomotor biomechanics for each taxon. Although the retention of arboreal features in these early hominins, as well as other Middle to Late Pleistocene hominins

(Larson et al., 2009; Berger et al. 2015), lends strong evidence to active selection for forelimb-dominated locomotion, questions remain over how frequent and significant these behaviors were in the day-to-day life of a given hominin. How do we better understand how these hominins were interacting with different paleoenvironments and how can we better infer behavior during a hominin lifetime?

5. Advances in methodological approaches for extracting functional information from hominin fossils

5.1. Behavioral studies of wild, habituated great apes

The foundation of Hunt's (1994) small-tree postural feeding hypothesis is rooted in his observations of when, where, and for which purpose Mahale and Gombe chimpanzees used bipedalism and the functional link between bipedalism and arm-hanging. Although additional comprehensive locomotor studies of great apes since then are limited (Remis, 1994, 1998; Doran, 1997; Thorpe and Crompton, 2006; Manduell et al., 2011; Sarringhaus et al., 2014), we have gained a greater appreciation of behavioral variation within and between great ape species, populations, and different ecological settings. Moreover, we have recognized the relevance of the variation in African ape behavior, locomotor and otherwise, to our understanding of hominin evolution (e.g., Pruetz et al., 2015; Luncz et al., 2018; Thompson et al., 2018; Wessling et al., 2018).

Since Hunt's (1994) study, more recent positional behavioral investigations of chimpanzees at other sites confirm their infrequent use of bipedalism (Doran, 1997; Stanford, 2006; Sarringhaus et al., 2014; Drummond-Clarke et al., 2022). For example, in adult chimpanzees of Ngogo, Uganda, bipedalism represents less than 2% of all locomotor time and they most frequently use hand-assisted, flexed-hindlimb, bipedal walking (Sarringhaus et al., 2014). However, the behavioral context of chimpanzee bipedalism (e.g., feeding, vigilance) has only been further studied in the chimpanzees of Bwindi Impenetrable National Park, Uganda (Stanford, 2006). Bipedalism in Bwindi chimpanzees was almost always postural and arboreal, and was most commonly used during foraging, similar to Hunt's (1994, 1996) results. However, Stanford (2006) highlighted bipedal use in an arboreal, rather than a terrestrial, context for the potential emergence of bipedalism in hominins.

Based on subtle anatomical differences between chimpanzees and bonobos (e.g., more curved phalanges, longer and narrower scapula), bonobos were hypothesized to engage in more suspensory locomotion and bipedalism (Zihlman et al., 1978, 1996). Initial studies of bonobo positional behavior confirmed this hypothesis, highlighting a greater frequency of arboreality in bonobos compared with chimpanzees, including higher frequencies of leaping, arboreal bipedalism (Susman et al., 1980; Susman, 1984), and suspension (Doran, 1992, 1993). However, these initial studies focused largely on comparisons of arboreal behaviors only (i.e., without terrestrial data) and were conducted on bonobo populations (Lomako and Wamba, Democratic Republic of the Congo, DRC) that the researchers acknowledged were less habituated than their chimpanzee comparators, potentially inflating the frequency of arboreality (Susman et al., 1980; Susman, 1984; Doran, 1993). A more recent study of a habituated population (Lui Kotole, DRC), however, suggests that bonobos (when sexes are pooled) are no more arboreal than chimpanzees (56% of locomotor time on the ground and 44% in the trees) and suspensory locomotion is extremely rare (<0.1% of locomotor time; Ramos, 2014).

Bonobo bipedalism varies by population: at Lomako, bipedal locomotion ranged between 1–2% (Doran and Hunt, 1994) and 6–8% (Susman et al., 1980; Susman, 1984) of their arboreal locomotor time, whereas at Wamba bonobos rarely used bipedal postures, even during feeding (Kano and Malavwa, 1984; Hunt, 1991). At Lui Kotole, bipedalism, primarily postural, was used 6% of time spent in the trees but represented only 0.2% of total positional behavior (Ramos, 2014). Bipedal standing with arm-hanging—the foundation of Hunt's (1994) hypothesis—was rare in Lui Kotole bonobos (<0.01% of all postural time) and was used in the trees, rather than on the ground, for feeding (Ramos, 2014).

Compared with chimpanzees, investigation of orangutan (*Pongo pygmaeus*) positional behavior has also highlighted their slightly more common use of bipedal postures (7% of arboreal time vs. 0.3% in Mahale/Gombe chimpanzees) and bipedal walking (7% of arboreal locomotion vs. 7% in Mahale/Gombe chimpanzees and 3% in Taï chimpanzees; Thorpe and Crompton, 2006). However, unlike the flexed hindlimbs of chimpanzees, orangutans typically use extended hindlimbs during bipedalism, making them a potentially better model for the ecological context in which bipedalism evolved in the panin-hominin ancestor (Thorpe and Crompton, 2006; Thorpe et al., 2007; but see Begun et al., 2007).

The value of studying extant chimpanzees is also derived from the diverse landscapes they inhabit, ranging from dense, closed forest, to open, dry woodland savanna, allowing researchers to observe how locomotor (and other) behaviors may change in response to the habitat (Lindshield et al., 2021). In particular, behavioral changes as a result of a more open and dry environment are thought to have played a key role in hominin evolution and speciation (Behrensmeyer, 2006). Previous comparisons of positional behavior in bonobos and chimpanzees from different habitats, ranging from woodland/deciduous forest (Gombe, Tanzania) to evergreen rainforest (Taï, Ivory Coast) showed that there was far less variation in positional behavior between chimpanzee habitats (and subspecies) than between chimpanzees and bonobos (Doran and Hunt, 1994; see also Doran, 1996). However, as highlighted by van Leeuwen et al. (2020), the chimpanzee populations used in this comparative study all lived in forested habitats. Chimpanzees living in dry, open savanna landscapes[1] like Fongoli, Senegal (Pruetz and Bertolani, 2009; Wessling et al., 2018), Mt. Asserik, Senegal (McGrew et al., 1981), and Issa Valley, Tanzania (Fig. 3; Piel et al., 2017; Drummond-Clarke et al., 2022) represent particularly informative models for interpreting the evolutionary pressures that potentially affected hominins.

Although the anatomy and 'Bauplan' of hominins differed from those of extant apes, chimpanzees (and other primates) offer the opportunity to test hypotheses about how a large-bodied, semi-arboreal ape may adapt its physiology or behavior to ecological constraints similarly faced by hominins. For example, Fongoli chimpanzees experienced more physiological stress due to heat and dehydration compared with fluctuating seasonal availability in food, suggesting the importance of thermoregulatory selective pressures on hominins living in similar environments (Wessling et al., 2018). A preliminary study of postural and locomotor bipedalism at Fongoli found that bipedalism is still rare in Fongoli chimpanzees but they do it more often (2.3% of all positional behavior time) than chimpanzees at Taï (1.2%, Doran, 1993), as well as Mahale, Gombe and Bwindi, and used bipedalism most often during feeding, both in arboreal and terrestrial contexts (Tourkakis, 2009). Issa chimpanzees living in a mosaic environment of savanna woodland and riparian forest also change the frequencies of their locomotor behaviors and substrate use in their different habitats (Drummond-Clarke et al., 2022). Interestingly,

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[1] These include trees with a mostly open canopy, as defined by Lindshield et al. (2021) and van Leeuwen et al. (2020).

however, Issa chimpanzees do not increase their frequency of bipedalism in the open savanna woodland, and in fact use just as much arboreal locomotion in the savanna woodland as chimpanzees living in densely-forested habitats, contrary to expectations based on hominin evolutionary models (Drummond-Clarke et al., 2022). Variation in habitat has also been shown to influence orangutan locomotor behavior, including higher frequencies of bipedalism in dry, lowland forests (Ketambe, Sumatra) compared with peat swamp forests (Suaq Balimbing, Sumatra and Sabangau, Borneo; Manduell et al., 2012). These studies highlight how a large-bodied semi- (or highly) arboreal ape may change the frequency of different positional behaviors and context in which they are used (e.g., feeding, vigilance) based on. variation in habitat, both across seasons and sites, which can help make more refined inferences of behavior in hominins.

5.2. Australopith locomotor economy

Given that *Au. afarensis* pelvic and lower limb morphology differs from that of later *Homo*, Hunt (1994) suggested that early hominin bipedal locomotion was less efficient (i.e., consumed more energy and caused greater muscle fatigue) relative to both modern human bipedalism and ape quadrupedalism. Over nearly the past five decades, the locomotor economy of australopith morphology has been inferred through experimental and comparative work in locomotor energetics involving humans and chimpanzees (Rodman and McHenry, 1980; Pontzer and Wrangham, 2004; Sockol et al., 2007; Pontzer et al., 2009, 2014; Pontzer, 2017). Mechanical studies have demonstrated that the long hind limbs and straight-legged walking gait of humans have greatly reduced the cost of transport during walking compared to chimpanzee quadrupedalism and bipedalism (Sockol et al., 2007; Pontzer et al., 2014). In fact, human walking is nearly twice as economical compared to that of chimpanzees (Pontzer, 2017). Researchers have further expanded this experimental research to assess the energetic cost of humans walking with bent hips and bent knees (Carey and Crompton, 2005) and crouched postures (Johnson et al., 2022) to provide more informed inferences of early hominin bipedal economy.

How does this recent experimental evidence fit with Hunt's (1994) hypothesis? Hunt (1994) focused on *Au. afarensis* lower body anatomy reflecting less efficient bipedal locomotion (i.e., consumed more energy) compared with that of modern humans, which is not surprising given that modern human bipedal functional morphology has had an additional three million years to be positively selected and refined for energetic economy. Given the similarities in chimpanzee bipedal gait kinematics compared to other nonhuman primates (D'Aout et al., 2004; Vereecke et al., 2006; Demes, 2011), it is reasonable and parsimonious to assume that the locomotor costs of the panin-hominin last common ancestor would have been similar to those of chimpanzees (Pontzer et al., 2014). Based on knowledge at the time (Ishida, 1991), Hunt (1994) suggested that early hominin bipedal locomotion would have been less economical than ape quadrupedalism. However, energetically costly does not mean a particular gait or behavior was not possible, or that it doomed a species to extinction; as Daegling (2022:p. 125) highlighted, since all bipedal traits did not appear simultaneously, "[t]here must have been a phase of hominin evolution that involved a highly inefficient manner of bipedal progression." Susman et al. (1984:p. 113) creatively articulated the same view: "Must not there have been a period of time when both the trees and the ground served as important areas for life's activities, as they do today for living great apes? Must not there have been a period of time when the human ancestor was neither as good at moving on two legs as it could become, nor as good at scrambling in the trees as it once had been? We expect that such a period of time did exist”. In addition, given the similarity in locomotor costs between chimpanzee quadrupedal and bipedal walking (Sockol et al., 2007; Pontzer et al., 2009, 2014), increasing the frequency of bipedal locomotion in early hominins would not necessarily have increased the costs of bipedalism (Pontzer et al., 2009, 2014) and, indeed, early hominin bipedalism could have been less costly than non-bipedal behaviors (Sockol et al., 2007).

The mechanics of early hominin bipedalism, as highlighted by Hunt (1994), are key to inferring locomotor costs. Recent studies of *Au. afarensis* bipedal gait from preserved morphology using a variety of modeling methods and parameters, generally agree that the energetic costs of bipedal locomotion in *Au. afarensis* were more economical than chimpanzee locomotion (Thompson et al., 2015) and potentially similar to those of modern humans (Crompton et al., 1998; Nagano et al., 2005; Sellers et al., 2005). Indeed, a slightly longer (relative to African apes) and extended hind limb paired with a stiff, non-grasping foot, and, although mediolaterally broad, a more human-like pelvis in *Au. afarensis* (Stern, 2000; Jungers, 2009), are all consistent with human-like locomotor economy (Nagano et al., 2005; Sellers et al., 2005).

Furthermore, even though Hunt’s (1994) hypothesis is still consistent with recent studies of great apes using (hand-assisted) bipedal postures and locomotion within small, terminal branches for feeding (Stanford and Nkurunungi, 2003; Thorpe et al., 2007; Crompton et al., 2008), recent research suggests that the retention of arboreal adaptations within the *Au. afarensis* forelimb may not have been more energetically economical compared to habitual bipedalism, as Hunt (1994) hypothesized. The energetics of rock climbing in mondern humans showed that variation in human limb proportions or body mass have minimal effects on the climbing costs of transport

(Kozma and Pontzer, 2021) and that human costs of climbing are similar to those of other primates (Hanna et al., 2008; Hanna and Schmitt, 2011). Experimental research on humans and nonhuman primates suggests that arboreal postcranial adaptations, such as longer forelimbs or curved digits, do not substantially decrease climbing costs (Hanna et al., 2008; Kozma and Pontzer, 2021). Thus, although the potential energetic costs and savings of the *Au. afarensis* upper and lower body may not be what Hunt (1994) originally predicted, the dual functional signals of the australopith postcranium are consistent with Sylvester's (2006) 'decoupling hypothesis' positing that early hominins should require efficient forms of both terrestrial and suspensory locomotion. That being said, energy expenditure is only one possible performance attribute among others that selection can act upon (Pontzer and Wrangham, 2004).

5.3. The study of internal bony structure

Hunt's (1994) functional interpretation of the *Au. afarensis* postcranium also included inferences about the associated bone stresses, particularly those incurred at the hip joint, during locomotion. Since that time, a considerable amount of research has been dedicated to developing analytical tools, many of which are virtual (Pandolfi et al., 2020), to improve our inferences of behavior in hominin taxa from skeletal morphology (e.g., Sellers et al., 2005; Gross et al., 2014; Dunmore et al., 2018; Karakostis et al., 2018; Ruff, 2018; DeMars et al., 2021; Profico et al., 2021). Here we discuss advancements in one of these virtual tools, namely, the analysis of internal bone structure based on the concept of bone functional adaptation, within a comparative extant primate context (Cowin, 2001; Currey, 2006; Ruff et al., 2006). Both cortical and trabecular bone model and remodel throughout life to adjust structurally to the local loading environment (Martin et al., 1998; Lieberman et al., 2003; Ruimerman et al., 2005; Currey, 2006; Ruff et al., 2006; Bonewald and Johnson, 2008; Gosman et al., 2011; Allen et al., 2014; Barak, 2020). Because trabecular bone is more metabolically active (Huiskes, 2000; Jacobs, 2000; Currey, 2006) and (re)models faster (~25% annual bone turnover) than cortical bone (~2–3%) in adults (Eriksen, 1986, 2010), it can be more responsive to changes in load magnitude, direction, or frequency (reviewed in Kivell, 2016; but see Lovejoy et al., 2003).

While many questions remain concerning the functional relationship between the 'container' (the cortical shell) and the 'contents' (the inner structural organization), both bone structures have been experimentally shown to provide functional information about site-specific loading conditions during one's life (van der Meulen et al., 1993, 1996; Ruff et al., 1994, 2006; van der Meulen and Carter, 1995; Biewener et al., 1996; Guldberg et al., 1997; Robling et al., 2002; Mittra et al., 2005; Pontzer et al., 2006; Carlson and Judex, 2007; Polk et al., 2008; Barak et al., 2011; Harrison et al., 2011; Carlson and Marchi, 2014; Christen et al., 2014). For example, experimental research on the human female tibia showed that diaphyseal cortical bone geometry in young adults retained signals of childhood/adolescent loading regardless of adult activity (Murray and Erlandson, 2021). By contrast, distal tibial trabecular bone density was found to reflect post-menarcheal loading, regardless of pre-menarcheal loading patterns (Murray and Erlandson, 2021). The last two decades have seen several technological advances in high-resolution 3D imaging (as well as access to this technology) and methods for quantifying and statistically comparing variation in internal bone structure (e.g., Pahr and Zysset, 2009; Bondioli et al., 2010; DeMars et al., 2021; Profico et al., 2021; Veneziano et al., 2021; Bachmann et al., 2022), while limiting risk to fossil specimens (e.g., Macchiarelli and Weniger, 2011; Weber, 2015; but see Le Cabec and Toussaint, 2017). This has led to a substantial increase in the number of studies investigating the potential functional signals within internal bone structure, and particularly trabeculae, in fossil hominin remains and extant hominid taxa, that can help paleontologists better distinguish ecophenotypic features from basal retentions (e.g., Puymerail et al., 2012a, b, 2013; Cazenave et al., 2017, 2019, 2021; Tsegai et al., 2013, 2018; Dunmore et al., 2019; 2020a, b; Bird et al., 2021; Su and Carlson, 2017; Georgiou et al., 2018, 2019, 2020; Sukhdeo et al., 2020; Bird et al., 2022; see Kivell, 2016 and references therein).

Analysis of internal bone structure in different associated elements of the skeleton, especially concurrently from the upper and lower limbs, can reveal complementary evidence essential to reconstructing actual habitual behavior of early fossil hominins characterized by a mosaic postcranium. However, such analyses are rare for several reasons, including: 1) the paucity of associated, relatively complete skeletons in the early hominin fossil record, 2) the inherent methodological challenges of accessing imaging technology, especially high-resolution imaging, and the time-consuming nature of some analyses (e.g., segmentation of bone from matrix or the computational power required to quantify complex internal structures in 3D), and 3) lack of access to particular fossil specimens or, when accessible, the lack of adequate preservation of internal structures. Below we consolidate the functional inferences that have been drawn from analysis of the cortical or trabecular structures in gracile and robust australopiths (Fig. 4) to highlight the value that internal analyses can bring to understanding the dual nature of the upper- and lower-limb external morphology that Hunt's (1994) hypothesis aimed to accommodate.

Australopithecus afarensis Relative differences in cortical bone cross-sectional geometry between the upper and lower limb bones can provide information about the significance of forelimb-dominated vs. bipedal locomotion. Analysis of the cross-sectional geometry of A.L. 288-1 shows femoral/humeral diaphyseal strength proportions that are intermediate between those of chimpanzees and modern humans, indicating more mechanical loading of the forelimb than in humans, which is consistent with significant use of arboreal locomotor behaviors (Ruff et al., 2016). Moreover, relative femoral head size, femoral neck cortical bone distribution, and cross-sectional shape of the proximal shaft suggest a bipedal gait involving more lateral deviation of the body's center of mass over the support limb than is typical of a modern human gait, which would have increased the costs of terrestrial locomotion (Ruff et al., 2016).

Trabecular analysis of *Au. afarensis* metacarpals also shows a pattern of trabecular distribution that is intermediate between that of modern humans and other extant apes, and distinct from other australopiths, suggesting the use of powerful flexed-fingered grasping during both arborealism and manipulation (Kivell et al., 2018b; Dunmore et al., 2020b). Future analyses of other *Au. afarensis* skeletal elements will likely provide a more refined reconstruction of *Au. afarensis* behavior, although preservation of internal bone structures in the Pliocene remains of East Africa is limited.

<u>*Australopithecus africanus*</u> The internal structure of the *Au. africanus* lower limbs has been thoroughly investigated, providing subtle, complementary information to the external morphology that can be used to reconstruct the locomotor behavior in this taxon. One of the first analyses used a series of calibrated radiographs to comparatively describe the trabecular architecture of several adult and juvenile *Au. africanus* ilia (Macchiarelli et al., 1999, 2001). The trabecular structures suggest that the *Au. africanus* pelvis underwent a loading regime commensurate with a bipedal gait, but somewhat different from that typical of modern humans (Macchiarelli et al., 1999, 2001). A volume-of-interest analysis of the trabecular structure within multiple *Au. africanus* femoral head specimens revealed a pattern more similar to that of modern humans and Pleistocene *Homo* than to the typical extant ape condition, which is also consistent

with a human-like bipedal gait, including the habitual use of a more extended hip (Ryan et al., 2018). Similarly, a ‘whole-bone’ analysis of the trabecular structure in *Au*. *africanus* femoral head specimen StW 522 also revealed a human-like pattern of loading at the hip joint and that *Au*. *africanus* likely did not climb (i.e., habitually load its hip joint in a flexed posture) at the frequencies seen in extant nonhuman apes or other Sterkfontein hominins (Georgiou et al., 2020).

In line with these results, the cortical distribution at the femoral neck confirmed a bipedal gait in *Au*. *africanus*, but somewhat different from that typical of modern humans. Sterkfontein *Au*. *africanus* specimens have relatively more symmetric superior and inferior femoral neck cortices at the mid-neck than modern humans, but a more human-like pattern at the base of the neck, suggesting greater superioinferior bending loads during bipedal locomotion in *Au. africanus* (Ruff and Higgins, 2013; Ruff et al., 2016). The orientation of trabecular struts in *Au. africanus* distal tibiae indicates that *Au*. *africanus* primarily loaded its ankles in a relatively extended posture (plantarflexed) like that of modern humans and unlike chimpanzees, indicating a human-like gait with an efficient, extended lower limb (Barak et al., 2013). Indeed, the trabecular bone orientation of the distal tibia implies the use of talocrural joint plantarflexion, which humans use at the end of the push-off phase—a distinctive feature of the biomechanics of bipedalism (Sockol et al., 2007; Pontzer et al., 2009; Barak et al., 2013).

While the investigation of the ilium, femur, and tibia internal bone structure generally agree that *Au. africanus* engaged in habitual, terrestrial bipedalism with a slightly altered gait compared with modern humans, the results of the trabecular and cortical distribution in the foot bones are more puzzling. For example, *Au. africanus* tali show that trabecular strut orientation in the antero-medial region is ape-like, implying that this hominin may not have had the derived human-like medial weight shift during the last half of stance phase (Su and Carlson, 2017). Trabecular bone density distribution in the calcaneum (StW 352) suggests that the *Au*. *africanus* heel experienced more variable loading than modern humans but less so than African apes, consistent with a large range of foot movements with locomotor kinematics that are unlike those of extant humans or apes (Zeininger et al., 2016). Finally, the cortical diaphysis of the *Au. africanus* fifth metatarsal shows a human-like dorsoplantar reinforcement for resisting dorsoplantar loading, but which is achieved via cortical thickening rather than increased dorsoplantar external dimensions, as seen in extant humans (Dowdeswell et al., 2016).

Reconstruction of the locomotor behavior in *Au. africanus* from upper limb internal bone structure has focused on the humerus and hand bones. Functional inferences from the trabecular structure within the *Au*. *africanus* StW 328 humeral head are limited due to the fragmentary preservation of this specimen, but its high trabecular bone volume and more isotropic trabecular structure is most similar to nonhuman hominoids (Kivell et al., 2018c). This pattern indicates higher magnitude and more diverse loading of the humeral head than that of modern humans and suggests *Au*. *africanus* may still have used its forelimbs for arboreal locomotion (Kivell et al., 2018c). *Australopithecus africanus* metacarpal trabecular structure shows a pattern that is intermediate between that of humans and other apes (Skinner et al., 2015; Dunmore et al., 2020b). Although the metacarpals show a high *Pan*-like trabecular density, the asymmetrical distribution of trabeculae within the metacarpal heads is similar to that of modern humans, suggesting habitual, and potentially forceful, opposition of the thumb towards the fingers (Skinner et al., 2015). However, an analysis of the cortical bending stiffness of the *Au. africanus* StW 418 first metacarpal relative to that of the ulnar rays was more similar to great apes (Dunmore et al., 2020b). Future study of the *Au. africanus* distal humerus (Arias-Martorell et al., 2021), and radius and ulna internal bone structure, will provide further clarity on arm loading and use in this taxon.

Paranthropus robustus and *Paranthropus boisei* Investigation of internal bone structure in *Paranthropus* shows that it presents a similar picture to that outlined above for *Au. africanus*. Indeed, many studies have grouped gracile and robust australopiths together because the functional signals are similar, including in the ilium (Macchiarelli et al., 1999, 2001), femoral head (Ryan et al., 2018), femoral neck (Ruff and Higgins, 2013; Ruff et al., 2016), and first metacarpal (Skinner et al., 2015). Functional interpretations from *P. robustus* lower limb cortical and trabecular structure confirm habitual, terrestrial bipedal locomotion but with a slightly different gait compared with modern humans (Macchiarelli et al., 1999, 2001; Bleuze, 2010; Ruff and Higgins, 2013; Ruff et al., 2016), including a more limited range of habitual hip joint postures (Ryan et al., 2018) and increased mechanical loading of the proximal femoral diaphysis (Ruff et al., 1999).

However, recent studies of cortical distribution and trabecular organization of the femoral neck in five *P. robustus* specimens from Swartkrans reveal distinct internal features in *P. robustus* that are not observed in modern humans or *Pan* (Cazenave et al., 2019, 2021). The functional significance of this specific configuration in the *P. robustus* femoral neck or their presence in other australopiths may support a somewhat different locomotor repertoire in *P. robustus* compared with *Au. africanus,* a hypothnesis that requires further investigation. Analysis of the trabecular distribution throughout the femoral head in two Sterkfontein specimens, one attributed to *Au. africanus* (StW 522) and one possibly attributed to *P. robustus* (or *Homo*; StW 311), indicates distinctly different loading regimes despite overall similarity in external morphology (Georgiou et al., 2020). The possible *P. robustus* specimen shows an ape-like pattern of femoral head loading in both flexed- and extended-hip postures, consistent with regular bouts of climbing and terrestrial bipedalism (Georgiou et al., 2020).

Trabecular structure within the *P. robustus* (TM 1517) and presumed *P. boisei* tali (KNM-ER 1464) show a human-like pattern in the antero-medial subregion (in contrast to the ape-like pattern in *Au. africanus*), suggesting *Paranthropus* may have had a human-like medial weight shift during the last half of stance phase (Su et al., 2013; Su and Carlson, 2017). This is one of the few studies identifying functional differences between *P. robustus* and *Au. africanus* (see also Beaudet et al., 2019; Braga et al., 2021). The trabecular structure of the *P. robustus* first metatarsal (SKX 5017 from Swartkrans Member 1) suggests hyper-dorsiflexion at the metatarsophalangeal joint, which is distinct from the trabecular pattern found in SK 1813, another (juvenile) first metatarsal from Swartkrans that is not attributed to a specific taxon (Komza and Skinner, 2019). Evidence for consistent loading in hyper-dorsiflexion in SKX 5017 suggests terrestrial bipedal gait with a toe-off that is beyond the range of motion typically found in modern humans (Komza et al., 2019). Like *Au. africanus*, the *P. robustus* fifth metatarsal also shows dorsoplantar cortical thickening to resist human-like dorsoplantar loading but does not exhibit distal shaft tapering in cortical thickness, which is found in modern humans and *Au. africanus* (Dowdeswell et al., 2016).

For the upper limb, only the internal structure of the distal humerus of *Paranthropus* has been investigated, showing a clear dichotomy between *P. robustus* and modern humans and *Homo erectus* in the morphology and cortical bone distribution, including thicker cortex in *P. robustus* (Cazenave et al., 2017). The distal humerus of *P. boisei* also shows high bending strength comparable to that of extant great apes (as well as *Au. afarensis* and *H. habilis*) and considerably higher than that observed in later *Homo*, indicating powerful upper limbs and habitual climbing behavior (Lague, 2019).

6. Where is the field and future directions

What have we learned about australopiths since Hunt (1994)? Over the last two and half decades, more paleoanthropologists have accepted that australopiths were both committed bipeds and adept climbers. This greater consensus has stemmed from additional fossil evidence that has made clear that the dual-functional signal of the *Au. afarensis* skeleton is common to all known australopiths (and other hominins). Moreover, this dual-functional signal comprises different combinations of anatomical features across australopiths, the consequences of which are biomechanical variation in bipedal posture and gait and likely overall positional behavior. Thus, the australopith ‘lower-body biped’ and ‘upper-body arborealist’ (be it arm-hanging or climbing) ‘Bauplan’ that was the anatomical basis for Hunt’s (1994, 1996) postural feeding hypothesis is still upheld, but with greater variation across all regions of the skeleton and perhaps greater variation temporally than originally imagined. Indeed, recent fossil evidence and new analyses suggest *Au. afarensis* had more human-like morphology and was a more committed terrestrial biped than geologically younger australopiths (e.g., *Au. africanus*, *Au. sediba*) and even some *Homo* taxa (e.g., Ward et al., 2011; Prang et al., 2015a,b, 2016b; Boyle et al., 2018; DeSilva et al., 2019; Prabhat et al., 2021). Current debates are perhaps less divisive than in the 1980s since new fossil discoveries urged more researchers to move closer to the ‘compromise camp’ approach. Instead, debates center on more detailed biomechanical implications of australopith anatomical variation, including the specifics of bipedal gait or climbing strategy, within and between species. Such debates will likely continue as future fieldwork will undoubtedly reveal more surprise morphologies in temporal periods or geographical regions we currently would not predict. A greater understanding of human and great ape anatomy, positional behavior, and locomotor kinematics and kinetics, as well as a greater appreciation of anatomical and biomechanical variability within extant taxa, has allowed researchers to better test functional hypotheses about fossil hominin morphology and offer more refined locomotor reconstructions.

6.1. Are extant primates good models for reconstructing past behaviors and, in turn, hominin evolution?

As Washburn (1967:p. 21) aptly summarized, "[t]he understanding of human evolution comes from three different sources: from general evolutionary theory, from the fossils, and from the behavior and biology of the living primates". Over the last 50+ years, we have improved our knowledge of all three sources and, in turn, have a much deeper appreciation of the complexity of human evolutionary history. Hypotheses about the origins of bipedalism are contingent on the reconstructed positional behavior of the panin-hominin last common ancestor and that of early hominins, for which there are two general approaches; one which directly relies on morphofunctional interpretations of the fossil record (i.e., the 'bottom-up' or 'worm's eye' approach) and the other founded in the behavior and biomechanics of living primates, notably *Pan* (i.e., the 'top-down' or 'bird's eye' approach; e.g., Diogo et al., 2017; Pilbeam and Lieberman, 2017; Almécija et al., 2021). Each approach offers valuable, complementary information and both are needed to understand the earliest stages of human evolution, as well as those of African apes. However, the hominid fossil record of the Late Miocene and earliest hominin radiation is both scanty and heterogeneous, especially for the postcranial elements. In addition, extant apes represent a restricted and biased sample of a much larger Middle-to-Late Miocene ape radiation that very likely displayed a much greater variety of locomotor solutions (e.g., Pina 2016; Böhme et al., 2019).

Thus, any additional information we can learn about how African apes, and primates in general, adapt, behave, or interact within their varying ecological settings provides potential natural experimental evidence for improving our understanding of the behavior and selective pressures in the past (in addition to improved conservation efforts to ensure we have more time to learn from the many endangered primate species). We support the perspective of Pontzer et al. (2014:p. 79) that understanding the relationship between locomotor form and function in African apes "is important, not because *Pan* is a perfect model of the earliest hominins, but because it enables us to test biomechanical models of locomotor performance in a large-bodied semi-arboreal primate". This perspective reaches beyond biomechanical models and beyond just chimpanzees: it is only through the (ethical) investigation of living primates that we can test hypotheses of how behavior is reflected in external and internal bone structure to more accurately interpret past behavior. Although we must remember that modern humans and extant great apes are not ideal models with which to compare fossil hominin taxa (Daegling, 2002), experimental or behavioral studies of primates in captivity (e.g., Schmitt, 2003; Hanna et al., 2008; Pontzer et al., 2014; O'Neill et al., 2015; Samuel et al., 2018) or in natural settings (e.g., DeSilva, 2009; Thompson et al., 2018; Neufuss et al., 2018; Ostrofsky et al., 2019; Thompson et al., 2018;Wessling et al., 2018), 3D imaging of human bone structure (e.g., Schipilow et al., 2013; Macintosh et al., 2017; Pomeroy et al., 2019), and recent advances in primate archaeology (e.g., Luncz et al., 2016; Proffitt et al., 2016, 2018) are excellent examples of the utility of studying living primates and their impact on our interpretation of the hominin paleontological or archaeological record.

6.2. Do we need more fossils?

In 2000, White questioned: "[w]ill our textbooks ever be illustrated with skeletons rather than scraps?" (White, 2000:p. 290). Many others have recognized the need to find more, and more complete, fossil evidence. For instance, Wood and Leakey (2011:p. 264) stated that "[t]he early hominin fossil record is too meager to do anything other than offer very provisional statements about hominin taxonomy and phylogeny". Foley et al. (2016:p. 6) concluded that "[i]t might seem that modeling, ancient genomes and three-dimensional morphometrics are the keys to the future, but all these depend on the continuing accumulation of new fossils and the discovery of new archaeological and palaeontological sites".

In 2022, this review has highlighted only a few of the many incredible paleontological discoveries of the last two decades, including several near-complete skeletons of different hominin species (e.g., White et al., 1994; Brown et al., 2004; Lordkipanidze et al., 2007; Berger et al., 2015; Williams et al., 2018; Stratford and Crompton, 2021) that have challenged previous knowledge based on isolated and/or more fragmentary specimens. These discoveries allow us to robustly estimate body proportions or the overall Bauplan and to provide more holistic functional inferences about behavior, including from both the upper and lower limbs. These discoveries have also brought to light intriguing combinations of morphologies in hominin individuals that paleoanthropologists could not have predicted (e.g., Brown et al., 2004; Berger et al., 2010, 2015; Stratford and Crompton, 2021). But to interpret these morphologies, these discoveries also highlight the importance of using and developing new tools that allow us to extract more accurate and refined functional information from the fossils themselves. These discoveries show that we will always need more fossils, ideally representing both sexes and a variety of ontogenetic stages, and that each will add both clarity and complexity to our understanding of hominin evolution.

Evolutionary questions, however, inherently rely on the phylogenetic relationships among fossils. Therefore, more fossils will not necessarily or automatically provide better resolution of evolutionary questions. Chronology alone cannot be used as a proxy for phylogeny as fossils sample only snap-shots in time, older lineages can persist through time and retain ancestral character states, and homoplasy (via parallelisms or reversals) will be pervasive. With each fossil discovery, new hominin phylogenetic reconstructions and the subsequent interpretations that are drawn from them should be considered one of many possible hypotheses and homoplasy is a given (Wood and Harrison, 2011; Daegling, 2022).

6.3. Do we need more tools to investigate the fossil record?

The need for more fossils is undeniable and when we find them, there are few opportunities to appropriately extract the specimens and to exhaustively document their immediate context before irrevocably altering the ‘crime scene’ (e.g., Flannery, 1982; White, 2000; Foley, 2016). New developments in geochemistry (e.g., Passey et al., 2010), paleoproteomics (e.g., Welker et al., 2016), and ancient DNA (e.g., Massilani et al., 2022) have demonstrated that valuable evolutionary information can be derived from sources that only a few years ago would have likely been discarded or ignored. Thus, any methodological effort to improve or preserve the resolution of fossils in situ should be encouraged, especially in anticipation of future methodological developments to answer functional and evolutionary questions.

Regarding the reconstruction of behavior in the past, recent advances in biomechanical modeling, including musculoskeletal modeling and the use of finite element analysis (e.g., O'Higgins et al., 2017), have provided more nuanced interpretations of fossilized morphology. These methods are time-consuming and require living participants (e.g., O'Neill et al., 2015) or anatomical specimens (Synek et al., 2019) to ensure models are biologically realistic, but they have the potential ability to more accurately infer function from variation in form (e.g., O'Neill et al., 2015; Püschel and Seller, 2016; Püschel et al., 2018; Bucchi et al., 2020; Pina et al., 2020; Synek et al., 2020).

Paleoanthropological research has also greatly benefited from the development of nondestructive investigative technologies based on high-resolution computed tomography (μCT) and synchrotron radiation microtomography that are able to render at micrometric scale the external and internal structures of the mineralized tissues for detailed quantitative analyses. Importantly, the recent use of neutron microtomography for high-resolution imaging of highly-mineralized fossil specimens has been able to reveal internal structures that were not accessible via μCT X-rays (e.g., Zanolli et al., 2020). It is thus probable that future analyses will increasingly combine information derived from both the external and internal fossil morphology. Although access to high-resolution imaging technology and freeware development offer researchers the ability to analyse the 'hidden evidence' from inside fossils, there is still a long way to go in terms of the infrastructure and accessibility of these resources in the countries for which almost all hominin fossils are discovered. Moves toward greater open-access data sharing in ways that support the curatorial institutions are a welcome improvement (e.g., The Human Fossil Record and Morphosource.org).

7.0 Moving forward

Despite the advances described above, some enduring questions remain. Even if most researchers now recognize that commitment to bipedalism does not require the full abandonment of arboreality (c.f. e.g., Latimer and Lovejoy, 1990), determining the frequency of climbing or suspensory behaviors in the day-to-day life of a hominin is still a challenging, if not impossible, quest. The complete anatomy of any given organism does not map directly to its most frequent behavior(s), infrequent behaviors that are mechanically demanding or have a higher negative impact on fitness also influence morphology, and any given morphology can be used for a multitude of behaviors. All paleontologists must work under the assumption that morphology reflects behavior, but identifying the evolutionary significance of behavioral differences within (e.g., sex differences in positional behavior) and between hominin species will always be challenging. Such endeavors will likely require fossil samples of multiple individuals and differing ontogenetic stages, osteological or molecular data on sex (e.g., Stewart et al., 2017), independent (and detailed) ecological information (e.g., local landscape, diet), a combination of methodological approaches (e.g., biomechanical modeling, analyses of internal bone structure, extant analogues), and potentially archaeological evidence (lithic or organic; e.g., Luncz et al., 2020) to reach a robust understanding of how a particular hominin species interacted in its paleoenvironment. Advances along all of these lines of evidence make this goal more attainable.

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Figure captions

Figure 1. List of human-like derived features and ape-like features in the upper limb and axial skeleton (orange) as well as pelvic girdle and lower limb (blue) in *Australopithecus afarensis* (A.a.), '*Australopithecus prometheus*' (partial skeleton StW 573; A.p.) and *Australopithecus sediba* (A.s.). Note that if there is no specific mention of a species for a feature, it means either that the feature is absent or non-identifiable in this species for preservation and taphonomical reasons.

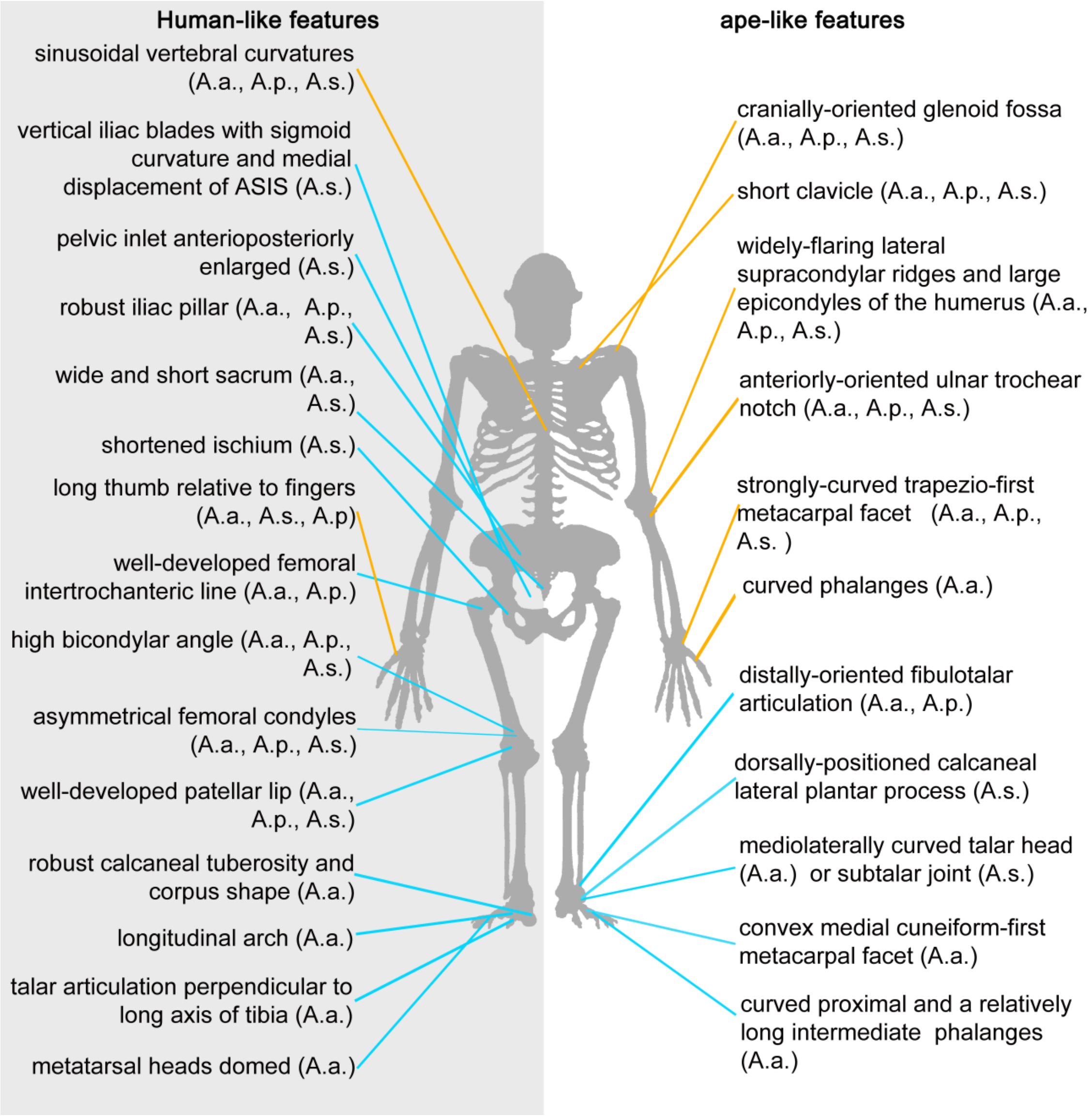

Figure 2. Partial skeletons of a) *Australopithecus afarensis* A.L. 288-1 adult female, b) StW 573 '*Australopithecus prometheus'*, likely an adult female (courtesy of Paul Myburgh), and c) *Australopithecus sediba* MH2 adult female. Images sourced from Ruff et al. (2016), Williams et al. (2018), and Palakovic (2021). Reproduced with permission of The Licensor through RightLinks.

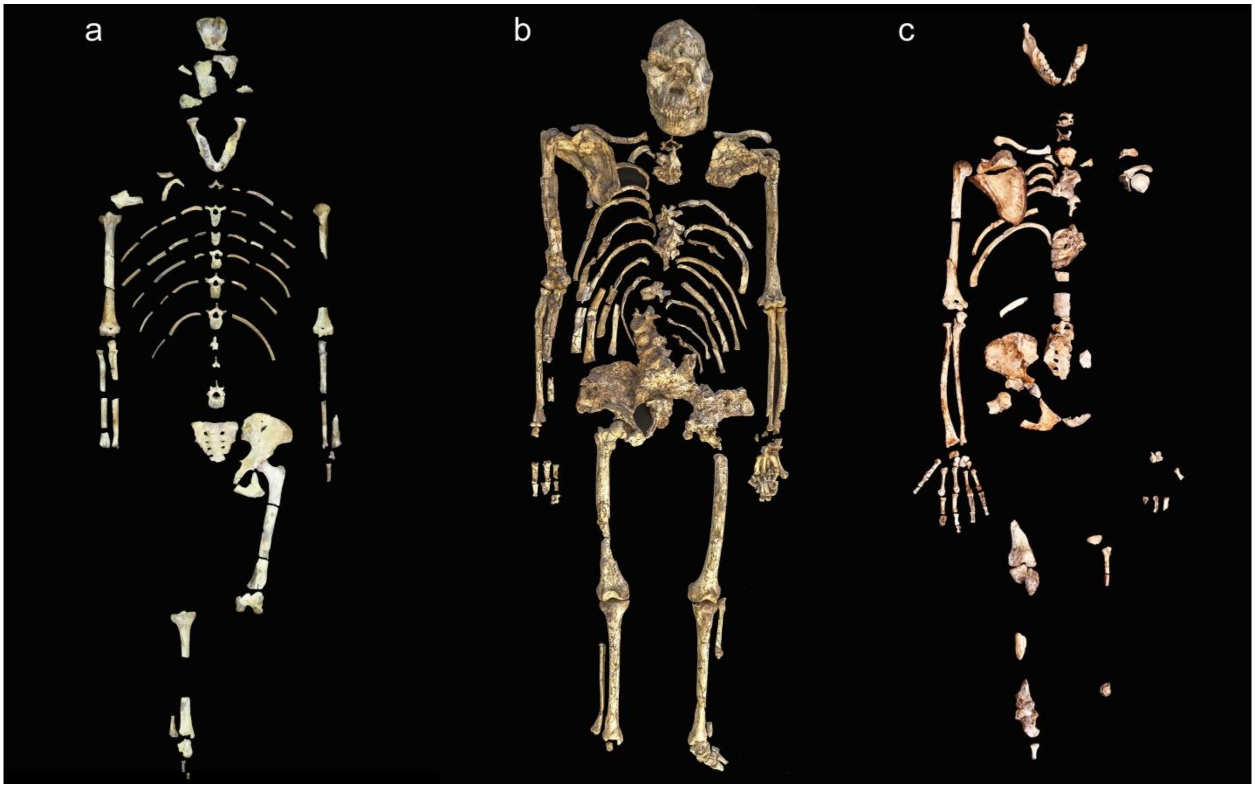

Figure 3. Chimpanzees (*Pan troglodytes schweinfurthii*) of Issa Valley, Tanzania that live in a, b) a savanna-mosaic habitat of miombo woodland and c) riparian forest similar to reconstructed paleoenvironments of early hominins. Contrary to expectations based on hominin evolutionary models, Issa chimpanzees engage more frequently in bipedalism in the forest than in the more open woodland, and use just as much arboreal locomotion in the open woodland as chimpanzees that live in more densely-forested habitats (Drummond-Clarke et al., 2021). Photo credit to Rhianna Drummond-Clarke.

Figure 4. Cortical and trabecular bone preservation and structure of different skeletal remains likely attributed to *Australopithecus africanus*, *Paranthropus robustus,* and *Paranthropus boisei*. Images sourced from Macchiarelli et al. (1999), Barak et al. (2013), Su et al. (2013), Zeininger et al. (2016), Cazenave et al. (2017, 2021), Su and Carlson (2017), Kivell et al. (2018c), Ryan et al. (2018), Komza et al. (2019), and Lague (2019). Reproduced with permission of The Licensor through RightLinks.