Chimpanzee ankle and foot joint kinematics: Arboreal versus terrestrial locomotion

Nicholas B. Holowka1,2 | Matthew C. O’Neill3 | Nathan E. Thompson4,5 | Brigitte Demes5

Abstract
Objectives: Many aspects of chimpanzee ankle and midfoot joint morphology are believed to reflect adaptations for arboreal locomotion. However, terrestrial travel also constitutes a significant component of chimpanzee locomotion, complicating functional interpretations of chimpanzee and fossil hominin foot morphology. Here we tested hypotheses of foot motion and, in keeping with general assumptions, we predicted that chimpanzees would use greater ankle and midfoot joint ranges of motion during travel on arboreal supports than on the ground.

Methods: We used a high-speed motion capture system to measure three-dimensional kinematics of the ankle and midfoot joints in two male chimpanzees during three locomotor modes: terrestrial quadrupedalism on a flat runway, arboreal quadrupedalism on a horizontally oriented tree trunk, and climbing on a vertically oriented tree trunk.

Results: Chimpanzees used relatively high ankle joint dorsiflexion angles during all three locomotor modes, although dorsiflexion was greatest in arboreal modes. They used higher subtalar joint coronal plane ranges of motion during terrestrial and arboreal quadrupedalism than during climbing, due in part to their use of high eversion angles in the former. Finally, they used high midfoot inversion angles during arboreal locomotor modes, but used similar midfoot sagittal plane kinematics across all locomotor modes.

Discussion: The results indicate that chimpanzees use large ranges of motion at their various ankle and midfoot joints during both terrestrial and arboreal locomotion. Therefore, we argue that chimpanzee foot anatomy enables a versatile locomotor repertoire, and urge caution when using foot joint morphology to reconstruct arboreal behavior in fossil hominins.

KEYWORDS
biomechanics, climbing, foot morphology, human evolution, primate locomotion

1 INTRODUCTION

Chimpanzees are our closest living relatives, but possess a dramatically different locomotor behavioral repertoire from us. Whereas humans are obligate terrestrial bipeds, chimpanzees frequently travel on arboreal substrates in the wild (Doran, 1992a, 1992b, 1993, 1997; Doran and Hunt, 1994; Hunt, 1992; Sarringhaus et al., 2014). This includes time spent climbing and walking quadrupedally on tree trunks, branches, and other arboreal supports. As such, chimpanzee postcranial features that differ from those of humans are often assumed to be related to chimpanzees’ reliance on arboreal locomotion. Among these, features of the foot and ankle have received considerable attention due to the remarkable dissimilarity in pedal anatomy between humans and chimpanzees, and the implications of these differences for understanding the evolution of human bipedalism (e.g., Elftman and Manter, 1935a, 1935b; Morton, 1922, 1924; Susman, 1983; Weidenreich, 1923; Wood Jones, 1917).

The ankle joint complex, which can be thought of as including both the talocrural and subtalar joints (Elftman and Manter, 1935b), is a common focus of comparative investigations of hominid functional
The talocrural joint, located between the talus proximally and the calcaneus distally, mainly allows inversion–eversion and abduction–adduction motions in humans and chimpanzees (Close et al., 1967; Inman, 1976; Lewis, 1980b), and complements the plantarflexion–dorsiflexion at the talocrural joint in controlling the three-dimensional position of the foot relative to the leg. Chimpanzees possess a more curved posterior subtalar facet than humans (Deloison, 1985; Latimer and Lovejoy, 1989; Prang, 2016), which is thought to be indicative of a greater range of subtalar joint motion. This mobility has been argued to represent an arboreal locomotor adaptation that enables chimpanzees to position their feet at highly inverted angles when climbing or traveling atop arboreal supports (Lewis, 1980b; Zipfel et al., 2011), thereby enhancing pedal grasping by exposing a greater surface area of the foot to the substrate (Cartmill, 1985).

Chimpanzees are also thought to possess highly mobile midfoot joints that are adapted to enable the foot to better conform to arboreal supports. The joints expected to yield the greatest mobility are those of the midfoot joint complex, which consists of the calcaneocuboid and talonavicular joints (the transverse tarsal joints), and the cuboid–metatarsal joints (Bojsen-Møller, 1979; DeSilva, 2010; Elftman and Manter, 1935b; Lewis, 1980b). The calcaneocuboid joint of humans and chimpanzees differs in the morphology of the calcaneal process of the cuboid. This process is large and medially located in humans, which restricts motion due to the overhanging congruent articular surface of the calcaneus. This provides a stable, close-packed position during joint inversion (Bojsen-Møller, 1979; Lewis, 1980b). In contrast, the process is smaller and more centrally located in chimpanzees, resulting in unrestricted inversion–eversion motion about a central pivot point. Chimpanzees also possess more curved (concavo-convex) cuboid–metatarsal joint surfaces than humans, which are thought to afford a greater range of joint motion (DeSilva, 2010; Proctor, 2013). The heightened mobility of these midfoot joints is believed to enhance pedal grasping in chimpanzees, but it has also been argued to influence foot kinematics during pushoff in terrestrial walking: Following heel lift, chimpanzees have been observed to exhibit a “midtarsal break,” in which the joints of the midfoot dorsiflex as the foot is lifted from the ground (DeSilva, 2010; Elftman and Manter, 1935a; Holowka et al., 2017; Susman, 1983). This mobility, in comparison to that of humans, may represent an adaptation for proficient arboreal locomotion in chimpanzees (Bojsen-Møller, 1979; Elftman and Manter, 1935b; Langdon et al., 1991).

Researchers have used the above-described differences in human and chimpanzee joint morphology and their suspected relationships to arboreal substrate use in reconstructions of fossil hominin locomotor behavior. Several studies have argued that the talocrural joint morphology of early fossil hominins, including Australopithecus afarensis and Australopithecus africanus, resembled that of humans and would therefore have prevented the range of foot dorsiflexion and abduction angles necessary for chimpanzee-like vertical climbing (DeSilva, 2009; Latimer et al., 1987; but see Venkataraman et al., 2013). Other studies have argued that human-like subtalar joint morphology signals reduced reliance on arboreal locomotion in A. afarensis (Latimer and Lovejoy, 1989; Prang, 2016), but that chimpanzee-like morphology in Australopithecus sediba reveals a subtalar joint adapted for inversion during climbing (Prang, 2016; Zipfel et al., 2011). Among the midfoot joints, the presence of flattened, human-like cuboid-metatarsal joint surfaces has been interpreted as indicating reduced midfoot mobility—and, therefore, reduced reliance on arboreal locomotion—in many early hominin species, including A. afarensis and A. africanus (DeSilva, 2010; Proctor, 2013; Ward et al., 2011).

The underlying arguments of these studies reveal the pervasive assumption that chimpanzee foot and ankle joint morphology reflects adaptation to arboreal locomotion. However, behavioral studies indicate that most chimpanzee locomotion in the wild actually occurs on the ground. Although chimpanzees forage and sleep in the trees, travel between sites is almost exclusively terrestrial (Doran and Hunt, 1994; Hunt, 2016). During infancy, chimpanzee locomotion occurs mainly on arboreal substrates, but by adolescence terrestrial quadrupedalism is the primary locomotor behavior (Doran, 1992b; Sarringhaus et al., 2014). Across different field sites, the vast majority of adult chimpanzee travel has been reported to consist of terrestrial quadrupedalism (Doran, 1992a, 1992b; Doran and Hunt, 1994; Hunt, 1992, 2016). Thus, if behavioral frequencies drive trait adaptation, we might expect that chimpanzee foot and ankle morphology reflects terrestrial locomotion as well, albeit in ways that differ from the bipedal adaptations of the human foot.

Understanding the relationship between pedal morphology and locomotion requires a detailed understanding of chimpanzee foot kinematics in vivo during travel on different substrate types. However, relatively little of the data that are needed to evaluate this relationship have been collected thus far. Although several recent studies have reported measurements of chimpanzee ankle (O’Neill et al., 2015;
Pontzer et al., 2014) and midfoot (DeSilva, 2010; Holowka et al., 2017) motion during terrestrial walking, only one study has attempted to quantify the motion of a foot joint in chimpanzees during arboreal locomotion. DeSilva (2009) measured peak ankle dorsiflexion angles in wild chimpanzees climbing trees, but used two-dimensional images from video recordings. Arboreal locomotion is expected to involve considerable nonsagittal plane motion at the ankle and midfoot joints, and thus three-dimensional (3-D) kinematic data are necessary to fully evaluate hypotheses concerning foot joint function in chimpanzees. Additionally, although vertical climbing is the most common arboreal locomotor behavior of chimpanzees in the wild, above-branch quadrupedalism is also used frequently (Doran, 1992a, 1993; Doran and Hunt, 1994), and therefore must also be considered in studies of chimpanzee foot function.

To address these issues, we collected 3-D kinematic data from the ankle and midfoot joints of two chimpanzees in a controlled, laboratory setting during three locomotor modes: terrestrial quadrupedalism on a flat runway, above-branch arboreal quadrupedalism on a horizontally oriented tree trunk, and climbing on a vertically oriented tree trunk. We sought to test the hypothesis that arboreal modes (i.e., climbing, above-branch quadrupedalism) require greater ankle and midfoot joint mobility than overground locomotion. Specifically, we predicted that chimpanzees would use higher maximum ankle dorsiflexion angles during arboreal modes than on the ground, based on the measurements of DeSilva (2009), and on the presumed relationship between chimpanzee talocural joint morphology and climbing (DeSilva, 2009; Latimer et al., 1987; Lewis, 1980a). We also predicted that chimpanzees would use greater coronal plane ranges of motion and higher maximum inversion angles at the subtalar joint during arboreal modes based on qualitative observations that chimpanzees use inverted foot postures when traveling on arboreal supports (DeSilva, 2009; Weidenreich, 1923; Wood Jones, 1917), and the presumption that this inversion occurs largely at the subtalar joint (Elftman and Manter, 1935b; Lewis, 1980b; Morton, 1924; Rose, 1986). Finally, we predicted that chimpanzee midfoot joints would have greater ranges of motion and use greater maximum and minimum angles on arboreal substrates than on the ground to allow the foot to conform to the support and thereby enhance pedal grasping (Bojsen-Møller, 1979; DeSilva, 2010; Elftman and Manter, 1935b; Lewis, 1980b).

2 | METHODS

2.1 | Data collection

We collected 3-D kinematic data from two male chimpanzees (7.5 ± 0.3 years, 40.8 ± 2.5 kg), hereafter referred to as Chimp A and Chimp B. Subjects were housed and trained in a large multiroom enclosure with ropes, poles, and other surface types to provide a varied and stimulating environment. All experimental procedures involving chimpanzee subjects were approved by Stony Brook University’s Institutional Animal Care and Use Committee.

During all experiments, subjects were video recorded at 150 Hz using a four-camera motion capture system (Xcitex Inc., Woburn, MA, USA). For all arboreal locomotion experiments, we used a smooth-barked beech tree trunk that was 4 m long and 15 cm in diameter. The support diameter is between the size ranges that Susman et al. (1980) used to define branches and boughs, and was selected to reflect the size of an arboreal substrate that wild chimpanzees use frequently for both climbing and above-branch quadrupedalism (DeSilva, 2008; Doran, 1992a; Hunt, 1992). During climbing experiments, the support was oriented vertically and securely bracketed to the ceiling and floor; for arboreal quadrupedalism experiments, it was oriented horizontally and elevated 0.5 m above the ground. In both cases, the support was immobile when subjects were travelling on it. Using one support for both locomotor modes allowed us to control for the influence of support diameter on foot kinematics, but we acknowledge that our study design did not allow us to capture the full range of foot postures that could be required on different supports, and we interpret our results within this limitation. Nevertheless, the support used here should simulate the basic mechanical challenges of arboreal versus terrestrial locomotion, and therefore reveal fundamental differences in how the chimpanzee foot functions on these different substrate types.

For terrestrial quadrupedalism experiments, subjects were video recorded walking on a flat 11 m long runway. In all experiments, subjects were encouraged by an animal trainer offering positive reinforcement. Subjects traveled at self-selected speeds in all experiments.

2.2 | 3-D kinematics

Our methodology for measuring 3-D joint motion followed Hamill and Selbie (2004). Prior to video recording, we painted markers (1 cm diameter circles) onto the legs and feet of our subjects using nontoxic paint while they were under general anesthesia. Marker locations were determined by palpable bony landmarks or by measuring discrete distances from palpable landmarks. These locations were confirmed by referring to measurements taken on radiographs of subjects’ legs and feet. In humans, studies comparing surface markers and bone pinned markers have determined that markers placed on the foot are less susceptible to errors than those placed on other parts of the lower limb due to the lack of significant intervening tissue between skin and bone (Leardini et al., 2005; Maslen and Ackland, 1994; Tranberg and Karlsson, 1998). Nevertheless, to further minimize measurement error due to motion of soft tissue structures relative to bone (e.g., Reinschmidt et al., 1997), we selected marker locations on the foot away from prominent subcutaneous soft tissue structures that could cause extraneous marker motion. Additionally, we used a singular value decomposition algorithm to minimize residuals in marker position caused by unpredictable error sources such as soft tissue motion (see below; Reinschmidt and van den Bogert, 1997; Söderkvist and Wedin, 1993).

We used markers to define three hind limb segments (Table 1 and Figure 1a): the “leg,” defined by three markers on the lateral side of the leg, the “rear foot,” defined by three markers on the skin overlaying the calcaneus, and the “forefoot,” defined by four markers on the skin overlaying metatarsals 2–5. The use of 3–4 noncollinear markers per segment allowed us to define local coordinate systems for each segment. To align these local coordinate systems with the lab’s global
coordinate system, we recorded a 3-D calibration shot of the leg and foot in a "neutral position," which we established using a custom-made jig while the subject was still under general anesthesia. In the jig, the subject's foot was aligned with the direction of travel, the leg was set perpendicular to the foot, and clear vinyl straps were used to ensure that the plantar surface of the foot was flat against the jig's bottom plate with the digits extended (Figure 1b). The calibration shot allowed us to align the segments' local coordinate systems with the lab coordinate system, and determine the instantaneous 3-D orientations of the segments during locomotion trials relative to "neutral position," defined by the position of the foot and leg in the jig.

This methodology enabled us to calculate 3-D motion between two segment pairs: the leg and rear foot, and the rear foot and forefoot. Leg–rear foot motion represents the net motion of the ankle joint complex (i.e., talocural and subtalar joints), and rear foot–forefoot motion represents the cumulative motion of the midfoot joints, including the transverse tarsal and tarsometatarsal joints. A similar approach is taken in many human 3-D foot kinematics studies (e.g., Carson et al., 2001; Hunt and Smith, 2004; Kidder et al., 1996) because 3-D motion cannot be accurately resolved at individual ankle or midfoot joints without the use of bone pins or fluoroscopic imaging (e.g., Nester et al., 2007).

We selected five representative steps per subject per locomotor mode for analysis. In all selected steps, subjects appeared to be traveling at a steady speed and did not exhibit any unusual foot or lower limb motions. We extracted 3-D marker coordinates from the selected steps using ProAnalyst (Xcitex Inc.), which we imported into MATLAB (The Mathworks Inc., Natick, MA) and filtered using a fourth order low-pass Butterworth filter with 5, 7, and 6 Hz cutoff frequencies for the X, Y, and Z coordinates, respectively, as determined appropriate by residual analysis (Winter, 2005). We calculated 3-D joint angles from filtered data using a custom-modified version of the KineMat MATLAB package (Reinschmidt and van den Bogert, 1997). Following International Society of Biomechanics recommendations for the human ankle (Wu et al., 2002), we calculated angles using the Joint Coordinate System method with a ZYX Cardan rotation sequence (Grood and Suntay, 1983). Although the appropriateness of this rotation sequence has not been rigorously demonstrated in chimpanzees, preliminary analyses that we carried out using different rotation sequences produced very similar results, and as the primary goal of this study was to compare kinematics in different locomotor modes, we deemed this rotation sequence to be adequate for our purposes. The Joint Coordinate System method calculates angles as rotation of the distal segment relative to the proximal segment about three axes: the mediolateral axis of the proximal segment, the vertical axis of the distal segment, and a floating axis that is orthogonal to both axes (Grood and Suntay, 1983). These rotations represent motion in the sagittal plane (plantarflexion–dorsiflexion), transverse plane (abduction–adduction), and coronal plane (inversion–eversion), respectively (Figure 2).

For each step, we calculated the instantaneous angles between segment pairs throughout the full duration of stance phase, which we defined as beginning when the foot contacted the substrate (touchdown) and ending when the toes lost contact with the substrate (liftoff) (Figure 3). These events were determined based on visual assessment from the video recordings. We then calculated the minimum and
maximum angles, and the total range of motion between segments throughout stance within each anatomical plane for each step.

2.3 | Statistics

All statistical tests were carried out in R v.3.3.1 (R Core Team, 2016). To test for significant differences in kinematic variables between locomotor modes, we used individual steps as data points, and pooled data between subjects. To account for the nonindependence of data from steps from the same subject, we created linear mixed effects regression models using the package “lme4” (Bates et al., 2015), with locomotor mode as a fixed factor and subject identity as a random factor. We created a model for each kinematic variable (e.g., maximum inversion angle between the leg and rear foot), and generated plots of model residuals versus fitted data to check for homoscedasticity and linearity, and quantile-quantile plots to check for normality. These criteria were met for all tests that we performed. We carried out Type III analyses of variance to test for differences in model variance components attributed to locomotor mode. We also used Tukey’s tests for post-hoc pairwise comparisons between locomotor modes using the “multcomp” package (Hothorn et al., 2008). The significance level for all tests was set at $p < .05$.

2.4 | Speed

To accurately track marker position and quantify 3-D foot kinematics, we used zoomed-in camera views that provided close-cropped video of the foot and leg, but precluded the measurement of locomotion speed and duty factor. However, we have previously demonstrated that locomotion speed during terrestrial quadrupedalism in chimpanzees is tightly correlated with stance phase duration (Demes et al., 1994; Fernández et al., 2016). Furthermore, stance phase duration is the primary determinant of duty factor, which Schoonaert et al. (2016) demonstrated to be correlated with speed of progression during arboreal quadrupedalism and climbing in chimpanzees’ sister species, bonobos (Pan paniscus). Therefore, for each locomotor mode, we selected steps with similar stance phase durations to minimize variation in speeds within modes.

FIGURE 3  Stance phase during the locomotor modes investigated in this study. Touchdown occurs at 0% of stance and liftoff occurs at 100% of stance.
3 | RESULTS

Stance phase durations for the steps included in analyses differed considerably among locomotor modes, but were similar within them. The average stance phase duration for terrestrial quadrupedal steps was 0.71 ± 0.06 s, which corresponds to 0.17 ± 0.03 Froude based on the linear regression models that we previously developed specifically for the subjects used in this study (Fernández et al., 2016). Average stance phase durations were 1.0 ± 0.08 s and 1.09 ± 0.11 s for arboreal quadrupedalism and climbing, respectively.

What follows is a description of average foot kinematics in all three locomotor modes (ankle joint complex: Figure 4; midfoot joints: Figure 6). Although the absolute joint angles are offset between the individual chimpanzees in many instances (ankle joint complex: Figure 5; midfoot joints: Figure 7), the patterns of motion are generally consistent between individuals, and thus we focus on patterns of motion rather than absolute values in our descriptions. We also report differences between locomotor modes when steps for both subjects are pooled (Table 2), and describe the results of statistical tests (Table 3). Individual subject results for the ankle joint complex and the midfoot joints are presented in Tables 4 and 5, respectively.

3.1 | Ankle joint complex motion

During all three locomotor modes, chimpanzees dorsiflexed their ankle joints following touchdown, but reached peak dorsiflexion angles earlier in climbing (around 50% of stance) than during the other locomotor modes (around 70–80% of stance) (Figure 4a; see also Figure 3). They tended to touchdown with inverted ankle joint complexes during both terrestrial and arboreal quadrupedalism, but everted their joints during the first 25% of stance phase in these modes (Figure 4b; see also Figure 3). In contrast, they inverted their ankle joint complexes following touchdown in climbing, and then maintained relatively inverted and abducted postures throughout the remainder of stance (Figure 4b,c).
During arboreal quadrupedism, they steadily inverted their ankle joint complexes from about 25% of stance until liftoff. In all three locomotor modes, they plantarflexed their joints in the final 25% of stance (Figure 4a; see also Figure 3).

Chimpanzees used significantly greater peak ankle joint dorsiflexion angles during arboreal quadrupedism and climbing than during terrestrial quadrupedalism (p < .05; Tables 2 and 3), and greater peak plantarflexion angles and sagittal plane ranges of motion during climbing.

**TABLE 2** Average (±SD) maximum and minimum angles and ranges of motion (RoM) at the ankle joint complex and midfoot joints during terrestrial quadrupedalism (TQ), arboreal quadrupedalism (AQ), and climbing (C)

<table>
<thead>
<tr>
<th>Plane</th>
<th>Variable</th>
<th>Ankle joint complex</th>
<th>Midfoot joints</th>
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<tr>
<td></td>
<td></td>
<td>TQ</td>
<td>AQ</td>
</tr>
<tr>
<td>Sagittal</td>
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<td>–2 ± 5°</td>
<td>–12 ± 10°</td>
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<td></td>
<td>Max (DF)</td>
<td>21 ± 2°</td>
<td>26 ± 8°</td>
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<tr>
<td></td>
<td>RoM</td>
<td>23 ± 5°</td>
<td>38 ± 5°</td>
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<tr>
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<td>–9 ± 6°</td>
<td>–4 ± 12°</td>
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<tr>
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<td>Max (IN)</td>
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<td>20 ± 4°</td>
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<tr>
<td></td>
<td>RoM</td>
<td>9 ± 2°</td>
<td>13 ± 3°</td>
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Abbreviations: PF = plantarflexion; DF = dorsiflexion; EV = eversion; IN = inversion; AD = adduction; AB = abduction.
During both terrestrial and arboreal quadrupedalism, the chimpanzees did use significantly greater coronal plane ranges of motion than during climbing (p < .001; Tables 2 and 3). In the transverse plane, they used greater peak abduction angles during both arboreal locomotor modes than during terrestrial quadrupedalism (p < .001; Tables 2 and 3).

### Table 3: Results of statistical Type III ANOVAs and post-hoc Tukey’s pairwise comparison tests between terrestrial quadrupedalism (TQ), arboreal quadrupedalism (AQ), and climbing (C), including degrees of freedom (DF), test statistics, and p-values, with significant results (p < .05) bolded

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<td>.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Max (AD)</td>
<td>2, 26</td>
<td>45.9</td>
<td>&lt;.001</td>
<td>26</td>
<td>-0.5</td>
<td>.86</td>
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<td>&lt;.001</td>
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<tr>
<td></td>
<td></td>
<td>Range</td>
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<td>26</td>
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<td>-4.1</td>
<td>&lt;.001</td>
<td>4.4</td>
<td>&lt;.001</td>
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</table>

Abbreviations: PF = plantarflexion; DF = dorsiflexion; EV = eversion; IN = inversion; AD = adduction; AB = abduction.

### Table 4: Average (±SD) maximum and minimum angles and ranges of motion (RoM) at the ankle joint complex during terrestrial quadrupedalism (TQ), arboreal quadrupedalism (AQ), and climbing (C) in both subjects individually

<table>
<thead>
<tr>
<th>Plane</th>
<th>Variable</th>
<th>Chimp A (º)</th>
<th>Chimp B (º)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sagittal</td>
<td>Min (PF)</td>
<td>0 ± 2</td>
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</tr>
<tr>
<td></td>
<td>Max (DF)</td>
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<tr>
<td></td>
<td>RoM</td>
<td>22 ± 2</td>
<td>35 ± 3</td>
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<tr>
<td>Coronal</td>
<td>Min (EV)</td>
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</tr>
<tr>
<td></td>
<td>Max (IN)</td>
<td>4 ± 2</td>
<td>22 ± 4</td>
</tr>
<tr>
<td></td>
<td>RoM</td>
<td>18 ± 2</td>
<td>17 ± 7</td>
</tr>
<tr>
<td>Transverse</td>
<td>Min (AB)</td>
<td>2 ± 1</td>
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<td>Max (AD)</td>
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<td>-8 ± 3</td>
</tr>
<tr>
<td></td>
<td>RoM</td>
<td>8 ± 1</td>
<td>13 ± 4</td>
</tr>
</tbody>
</table>

Abbreviations: PF = plantarflexion; DF = dorsiflexion; EV = eversion; IN = inversion; AD = adduction; AB = abduction.
Table 5  Average (±SD) maximum and minimum angles and ranges of motion (RoM) at the midfoot joints during terrestrial quadrupedalism (TQ), arboreal quadrupedalism (AQ), and climbing (C) in both subjects individually

<table>
<thead>
<tr>
<th>Plane</th>
<th>Variable</th>
<th>Chimp A TQ (°)</th>
<th>Chimp A AQ (°)</th>
<th>Chimp A C (°)</th>
<th>Chimp B TQ (°)</th>
<th>Chimp B AQ (°)</th>
<th>Chimp B C (°)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sagittal</td>
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<tr>
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<td>RoM</td>
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<td>7 ± 1</td>
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<td>8 ± 2</td>
</tr>
<tr>
<td>Coronal</td>
<td>Min (EV)</td>
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<td>−2 ± 3</td>
<td>12 ± 3</td>
<td>−7 ± 2</td>
<td>3 ± 3</td>
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<td>12 ± 2</td>
<td>13 ± 2</td>
</tr>
<tr>
<td></td>
<td>RoM</td>
<td>8 ± 1</td>
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<tr>
<td>Transverse</td>
<td>Min (AB)</td>
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<td>−7 ± 1</td>
<td>−6 ± 1</td>
<td>−2 ± 1</td>
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<td>4 ± 1</td>
<td>5 ± 2</td>
<td>5 ± 1</td>
<td>4 ± 1</td>
</tr>
</tbody>
</table>

Abbreviations: PF = plantarflexion; DF = dorsiflexion; EV = eversion; IN = inversion; AD = adduction; AB = abduction.

Figure 6  Motion at the midfoot joints in the sagittal (a, dorsiflexion+/plantarflexion−), coronal (b, inversion+/eversion−), and transverse (c, adduction+/abduction−) planes. Graphs on the left depict average motion (±SD) across stance phase, and graphs on the right depict average (±SD) minimum angle, maximum angle, and range of motion. Notice that the chimpanzees tended to use more abducted and inverted joint angles during climbing than during the other locomotor modes, but used generally similar angles in the sagittal plane.
whereas they used greater peak adduction angles during terrestrial quadrupedalism than during climbing ($p < .001$; Tables 2 and 3). During arboreal quadrupedalism they used greater ranges of transverse plane motion than during either climbing or terrestrial quadrupedalism ($p < .01$; Tables 2 and 3).

### 3.2 | Midfoot joint motion

Chimpanzees used very similar midfoot joint motion patterns during terrestrial and arboreal quadrupedalism in the sagittal and transverse planes (Figure 6a,c). They plantarflexed and adducted their midfoot joints following touchdown, dorsiflexed, and abducted them from 25% to 75% of stance, and then plantarflexed them in the final 25% of stance. However, they adopted relatively everted joints during terrestrial quadrupedalism, versus relatively inverted joints during arboreal quadrupedalism (Figure 6b). During climbing, they dorsiflexed their joints while maintaining relatively inverted and abducted joint postures across stance.

Chimpanzees used significantly greater ranges of sagittal plane midfoot motion and lower minimum dorsiflexion angles during arboreal quadrupedalism than during climbing ($p < .005$; Tables 2 and 3), but there were no differences in peak dorsiflexion angles between the locomotor modes. There were no differences in the midfoot coronal plane ranges of motion used by the chimpanzees during the different locomotor modes, but there were differences in peak joint angles (Figure 6b): Chimpanzees used greater peak eversion angles during terrestrial quadrupedalism than during either arboreal locomotor mode ($p < .001$; Tables 2 and 3), whereas they used greater peak inversion angles during climbing than during terrestrial or arboreal quadrupedalism ($p < .001$; Tables 2 and 3). They also used significantly greater peak abduction angles during climbing than during either other locomotor mode ($p < .005$; Tables 2 and 3). However, they used greater peak adduction angles and transverse plane ranges of motion during arboreal and terrestrial quadrupedalism than during climbing ($p < .001$; Tables 2 and 3).

### 4 | DISCUSSION

As our closest living relatives, and as adept arborealists, chimpanzees are frequent models in efforts to identify postcranial adaptations to arboreal behavior in extant and fossil hominoids (e.g., Bojsen-Møller, 1979; DeSilva, 2009, 2010; Elftman and Manter, 1935b; Latimer et al., 1987; Latimer and Lovejoy, 1989; Lewis, 1980a, 1980b; Rose, 1986). Studies of the chimpanzee ankle and foot often assume that features indicating high joint mobility reflect an adaptation to arboreal substrate use, but frequently neglect the possibility that high mobility might be advantageous for terrestrial locomotion as well. Here we address this issue by providing detailed 3-D kinematic data from the ankle and midfoot joints of chimpanzees traveling on both arboreal and terrestrial substrates.

In the following discussion of motion at the ankle joint complex, we assume that most plantarflexion–dorsiflexion occurs at the talocrural joint, and most inversion–eversion occurs at the subtalar joint, as suggested by previous chimpanzee cadaver studies (Lewis, 1980a,b). However, our kinematics methodology precludes us from definitively assigning motion within a given plane to a particular joint, and we therefore offer the caveat that some coronal and sagittal plane motion may occur at both joints. Nevertheless, our assumption should be appropriate for the purpose of comparing the relative amounts of joint motion in different locomotor modes.

### 4.1 | Talocrural joint motion

Based on aspects of talocroual joint morphology that are thought to be related to arboreal locomotion (DeSilva, 2009; Latimer et al., 1987; Lewis, 1980a) and expectations of more flexed limb postures on arboreal substrates (Cartmill, 1985; DeSilva, 2009), we predicted that chimpanzees would use greater ankle joint dorsiflexion angles during arboreal locomotor modes than during terrestrial quadrupedalism. This prediction was supported by our results; during arboreal quadrupedalism and climbing, subjects used $26 \pm 8^\circ$ and $27 \pm 4^\circ$ peak dorsiflexion angles, respectively, versus $21 \pm 2^\circ$ peak dorsiflexion on the ground (Table 2 and Figure 4a). In both arboreal modes, chimpanzees must resist gravitational moments that will tend to topple them off of the substrate, whether backward or laterally (Cartmill, 1985; Chadwell and Young, 2015). In both contexts, dorsiflexing the ankle should effectively reduce the functional length of the hind limb, thereby bringing the body’s center of mass closer to the substrate. Theoretically, this shortens the moment arm of the gravitational force acting on the body’s center of mass, which would reduce the gravitational moment that the animal must resist to avoid falling. However, we note that in one subject, Chimp B, dorsiflexion angles were actually slightly higher in terrestrial quadrupedalism than in arboreal quadrupedalism on average (Figure 5 and Table 4). Thus, the importance of adopting more dorsiflexed ankle postures in above branch travel than in terrestrial locomotion is not strongly supported by our results.

Our results provide some support for the argument that the expanded anterior aspect of the distal tibia in the chimpanzee ankle reflects an adaptation to close-pack the talocroual joint during climbing (DeSilva, 2009). However, our subjects’ peak dorsiflexion angles during terrestrial quadrupedalism were only $6^\circ$ less, on average, than those used in climbing (Table 2 and Figure 4a), and were roughly twice those typically reported for humans during normal bipedal walking (e.g., Leardini et al., 2007). Furthermore, Barak et al. (2013) reported that chimpanzees use on average $10^\circ$ more ankle dorsiflexion during times of peak loading when walking quadrupedally than humans do when walking bipedally. Although chimpanzee climbing appears to require a greater range of dorsiflexion than terrestrial quadrupedalism, Venkataraman et al. (2013) demonstrated that differences in distal tibia morphology between humans and chimpanzees are likely not reflective of active range of motion, because humans are capable of climbing with highly dorsiflexed ankle joints as well. Nevertheless, human and chimpanzee climbing mechanics likely differ in many other ways (e.g.,

--Barak et al. (2013) define “peak loading” as the portion of stance when vertical ground reaction force is $>75\%$ of body weight.
climbing speed) that could be reflected in differences in joint morphology. Distal tibia morphology may also be associated with the relative frequency of use of highly dorsiflexed ankle postures (Venkataraman et al., 2013), and therefore may be reflective of both terrestrial and arboreal locomotion in chimpanzees.

The peak dorsiflexion angles that we measured during climbing were considerably less than those measured by DeSilva (2009), who reported angles of $46 \pm 7^\circ$ for chimpanzees climbing in the wild. The discrepancy between studies can be attributed to numerous factors, but in our view the most likely is methodology. In particular, we collected marker-based 3-D kinematics using multiple cameras under controlled lab conditions, whereas DeSilva (2009) measured angles from single-view video images taken in the wild. The latter approach introduces two major sources of error to angle measurements: difficulty in accurately identifying position and orientation of the leg and foot segments, and the inclusion of out-of-plane motion in estimates of dorsiflexion angle. An alternative explanation for the discrepancy between study results is that our two subjects simply had less flexible ankle joints than the wild subjects measured in DeSilva’s (2009). However, we measured much greater passive ranges of dorsiflexion ($42 \pm 1^\circ$) in our subjects than they used during climbing bouts (Figure 8), indicating that their active ranges of motion were not restricted by any ankle joint inflexibility, and were similar to ranges of motion previously reported for chimpanzees (i.e., Holowka and O’Neill, 2013).

### 4.2 Subtalar joint

We predicted that chimpanzees would use greater subtalar joint coronal plane ranges of motion, and in particular greater maximum inversion angles during arboreal locomotor modes than on the ground. Inverting the foot would likely allow chimpanzees to place a greater percentage of the plantar surface of the foot in contact with rounded arboreal supports (Cartmill, 1985). Contrary to our predictions we found no significant difference in peak inversion angles between modes, and we found that terrestrial and arboreal quadrupedalism involve significantly greater ranges of coronal plane motion than climbing. The latter result was driven by our subjects’ use of inverted joint postures at touchdown in terrestrial and arboreal quadrupedalism, followed by rapid eversion of their joints in the first 20% of stance (Figure 4b). In contrast, both subjects used inverted joints through virtually the entirety of stance phase during climbing. Although we were unable to collect kinetic data in this locomotor mode, it is likely that the foot experiences high substrate reaction forces during climbing, and thus the chimpanzee subtalar joint may be adapted to withstand high loads.
While inverted for climbing, while retaining the ability to withstand high loads during terrestrial quadrupedalism. This could be reflected in the highly curved posterior subtalar facet of the chimpanzee calcaneus, which is argued to indicate an adaptation for joint loading in a wide range of postures (Latimer and Lovejoy, 1989). On the other hand, Chimpanzees A and B used only 11° and 8° peak subtalar inversion angles during climbing, respectively (Figure 6 and Table 5), which is within the passive range of motion reported for humans (15°-25°; Grimston et al., 1993; Menadue et al., 2006). Thus, chimpanzees do not necessarily use exceptionally high subtalar joint inversion angles during climbing.

Beyond inversion, our results reveal that a high subtalar joint ever-sion range of motion is also important for chimpanzee locomotion; Chimp A used a peak eversion angle of 14° during terrestrial quadrupedalism, and Chimp B used a peak eversion angle of 14° during arboreal quadrupedalism (Figure 6 and Table 5). These are both near the maximum passive range of motion reported for humans (10°-15°; Grimston et al., 1993; Menadue et al., 2006), although the chimpanzee passive eversion range is likely to be higher (20°-30°; Holowka and O’Neill, 2013). Chimpanzee talocrural joint geometry naturally sets the foot at a varus position relative to the leg (Latimer et al., 1987), and thus a high subtalar eversion range of motion may be necessary to allow chimpanzees to place the whole plantar surface of the foot onto the substrate during certain behaviors. These results accord with the arguments of Morton (1924) and Elftman and Manter (1935b), who asserted that the basic mechanics of weight support will force the chimpanzee subtalar joint into an everted position during terrestrial locomotion. Further, these results counter suggestions that chimpanzees maintain inverted foot postures across stance phase during terrestrial locomotion, which would force them to support weight on the lateral edges of their feet (Gebo, 1992; Lewis, 1983; Tuttle, 1970; Weidenreich, 1923). Rather, chimpanzees possess subtalar joints that permit large ranges of both eversion and inversion to accommodate a wide variety of foot postures on different substrates. Conversely, humans are likely to have evolved reduced subtalar joint mobility, particularly in the range of eversion permitted, in favor of greater joint stability during bipedal locomotion. This reduction in joint range of motion is likely related to a thicker deltoid ligament (Gomberg, 1981) and reduced degree of curvature of the posterior subtalar facet of the calcaneus in humans compared to chimpanzees (Delloison, 1985; Latimer and Lovejoy, 1989). These lines of evidence suggest that enhanced subtalar joint stability has been selected for over the course of human evolution.

The inverted subtalar joint angles the chimpanzees used at touchdown during terrestrial quadrupedalism were consistent with previous descriptions of the inverted foot strike postures used by Pan species when walking on the ground (Elftman and Manter, 1935a; Susman, 1983; Vereecke et al., 2003). The reason these species use this foot strike posture is currently unknown, but some have suggested that it may help with shock absorption and weight bearing, as chimpanzees possess gracile calcaneal tubers that lack the large lateral plantar process found in humans (Latimer and Lovejoy, 1989). This has led some
researchers to argue that this morphology necessitates that chimpanzees bear weight on their large, robust peroneal tubercle, which is located on the lateral side of the calcaneus (Deloison, 1985; Gebo, 1992; Gill et al., 2014; Latimer and Lovejoy, 1989; Lewis, 1983). We tested this notion by painting a marker onto the skin directly overlying the peroneal tubercle, which was easily palpable in our subjects. Videos from terrestrial locomotion bouts reveal that the peroneal tubercle never comes close to contacting the substrate, even when the foot is in its most inverted position, at touchdown (Figure 9). Although chimpanzees possess gracile calcanei, dissection of a chimpanzee foot specimen by one author (NBH) revealed that there is a substantial amount of subcutaneous soft tissue in the heel, including a thick fat pad. Thus, chimpanzee feet are likely capable of absorbing impact forces and bearing weight during terrestrial quadrupedalism without additional bony reinforcement beyond the medial plantar process of the calcaneus.

4.3 | Ankle joint complex transverse plane motion

Based on their articular surface morphologies and reconstructed axes of rotation, both the talocrural and subtalar joints of chimpanzees should contribute to transverse plane motion at the ankle joint complex (Elftman and Manter, 1935b; Latimer et al., 1987; Lewis, 1980a, 1980b; Rose, 1986). At the talocrural joint, Lewis (1980a) and Latimer et al. (1987) argued that at increasing dorsiflexion angles, such as those that occur during climbing, the chimpanzee foot becomes progressively more abducted. These predictions are partly borne out by our results: our subjects used their highest abduction and dorsiflexion angles during climbing and arboreal quadrupedalism, often during similar periods in stance. However, sagittal and transverse plane motions often are not closely coordinated. For instance, during arboreal quadrupedalism, progressive dorsiflexion is coupled with progressive abduction at the ankle joint complex (Figures 4 and 5). In these cases, it is important to recognize that transverse plane motion also occurs at the chimpanzee subtalar joint, where inversion is coupled with adduction, and eversion is coupled with abduction (Elftman and Manter, 1935b; Rose, 1986). Thus, in order for chimpanzees to attain inverted and abducted foot postures, they must dorsiflex their talocrural joints while inverting their subtalar joints; in this position, adduction at the subtalar joint is canceled out by abduction at the talocrural joint. Our chimpanzees assumed this ankle joint complex position for much of stance phase in both arboreal locomotor modes (Figures 4 and 5).

4.4 | Midfoot joint motion

We predicted that chimpanzees would use greater ranges of midfoot motion when traveling on arboreal supports than on the ground to allow the foot to better conform to the underlying substrate, enhancing pedal grasping. This was not the case. In neither arboreal quadrupedalism nor climbing, did our subjects use greater ranges of midfoot motion in any of the three anatomical planes than during terrestrial quadrupedalism. However, they did use greater maximum inversion angles during both arboreal modes, providing limited support for our prediction of greater peak joint angles on arboreal supports. Climbing especially required the maintenance of both highly inverted and abducted midfoot joints through the full duration of stance, indicating that these joint postures assist in pedal grasping (Figures 6 and 7). It should be noted that only Chimp B used higher maximum abduction angles on average during climbing than during the other locomotor modes (Table 5). However, unlike in arboreal and terrestrial quadrupedalism, both Chimps A and B maintained abducted midfoot joints throughout stance phase in climbing, indicating the relative importance of this motion to this locomotor mode. On the ground, the relatively high evasion angles our subjects used during terrestrial quadrupedalism further suggest that midfoot coronal plane motion allows chimpanzees to easily adjust their foot postures to different substrate types. These interpretations are supported by a previous investigation where we measured passive ranges of motion of the transverse tarsal joints in the same chimpanzees used in this study (Thompson et al., 2014). Although our approach in that study only allowed us to measure 2-D motion, we inferred a large coronal plane range of motion at the transverse tarsal joint complex based on the presence of large disparities in talonavicular and calcaneocuboid joint passive motion range. Comparative anatomical investigations of calcaneocuboid joint morphology have also implicated the transverse tarsal joint complex as a potential site of substantial inversion–eversion in the chimpanzee foot (Bojsen-Møller, 1979; Lewis, 1980b; Rose, 1986). Relative to that
of humans, the calcaneal process of the chimpanzee cuboid is small and centrally located, thereby permitting unrestricted rotation against the congruent articular surface of the calcaneus. In contrast, the calcaneal process is larger and more medially located in humans, restricting motion when the cuboid is inverted against the overhanging congruent articular surface of the calcaneus. The cuboid–metatarsal joints are also likely sites of some component of the midfoot motion measured in this study. These joints present articular surfaces that are more dorsoplantarly concavo–convex in chimpanzees than in humans, and have consequently been implicated mainly in sagittal plane motion (DeSilva, 2010; Greiner and Ball, 2014; Proctor, 2013). They could potentially contribute to the midfoot abduction and inversion motions that we measured in this study as well, but establishing the mobility of these joints outside of the sagittal plane requires further investigation.

There were no significant differences in sagittal plane kinematics between terrestrial quadrupedalism and either of the arboreal locomotor modes; in all three modes the range of sagittal plane motion was ≤11° on average, which is similar to the range of midfoot motion that we measured in the same subjects during bipedal walking (11 ± 2°; Holowka et al., 2017). This result might seem surprising when considering that we measured ranges of 32 ± 8° of passive talonavicular joint motion and 13.5 ± 5° of calcaneocuboid joint motion in these subjects in our previous study using cineradiography (see Subjects 2 and 3 in Thompson et al., 2014). However, those range values include a substantial amount of plantarflexion, whereas maximum dorsiflexion angles, beyond what could be considered the “neutral” position, were 18.5 ± 0.5° for the talonavicular joint, and essentially 0° for the calcaneocuboid joint (Figure 3; Thompson et al., 2014). The cuboid–metatarsal joints, which we did not investigate in that study, are another possible site of substantial midfoot sagittal plane motion. Greiner and Ball (2014) quantified cuboid–metatarsal joint motion in four cadaveric chimpanzee specimens during passive manipulations and measured <9° peak dorsiflexion on average (Figure 2; Greiner and Ball, 2014). When considering that we quantified midfoot motion spanning the medial and lateral sides of the foot, it is not surprising that the peak dorsiflexion angles that we measured in this study (13–13.5° on average) are between the peak passive ranges for the medial (18.5°) and lateral (<9°) sides of the foot that can be deduced by combining the results from Thompson et al. (2014) and Greiner and Ball (2014).

4.5 Conclusions and implications for hominin foot evolution

The results of this study permit the following generalizations about chimpanzee foot kinematics during locomotion. In arboreal locomotor modes, chimpanzees dorsiflex their ankles to bring their bodies closer to the supporting substrate, and invert their subtalar and midfoot joints to increase the contact area between the foot and the substrate. Chimpanzees also abduct the ankle and midfoot joints, particularly during climbing, which may help improve pedal grasping. During terrestrial quadrupedalism, chimpanzees again use relatively high ankle dorsiflexion angles, but in contrast to arboreal locomotion, use everted subtalar and midfoot joint postures to place the whole plantar surface of the foot against the substrate. Overall, these findings reveal that chimpanzees use large foot joint ranges of motion during both arboreal and terrestrial locomotion, and thus possess feet that are well suited to a versatile locomotor repertoire.

Based on these findings, we urge researchers to exercise caution when using fossil hominin foot and ankle joint morphology to assess possible retention of arboreal adaptations. In particular, the relatively narrow anterior aspect of the distal tibia in most early hominins could reflect the habitual use of bipedal walking postures that require less ankle dorsiflexion than terrestrial quadrupedalism as well as reduced reliance on arboreal behaviors (DeSilva, 2009). Similarly, the reduced posterior subtalar facet curvature in many fossil hominins could signify a loss of joint range of motion that would negatively influence arboreal locomotor abilities (Latimer and Lovejoy, 1989; Prang, 2016), although our results suggest that a substantial inversion range of motion is not necessary to climb. Additionally, whether reduced subtalar joint curvature reflects both restricted inversion and eversion motion is not clear. If the latter, A. sediba—which possessed chimpanzee-like posterior subtalar facet curvature—may have had a subtalar joint that allowed for a large eversion range, as suggested by DeSilva et al. (2013; but see Prang, 2016).

Among the midfoot joints, early hominins present flat, human-like opposing cuboid–metatarsal joint surfaces (DeSilva, 2010; Proctor, 2013; Ward et al., 2011), which have been argued to increase midfoot rigidity during bipedalism at the expense of the foot’s flexibility on arboreal supports. However, this morphology has mainly been related to sagittal plane mobility, and we recently found that humans use a greater range of midfoot sagittal plane motion overall than chimpanzees during bipedal walking (Holowka et al., 2017). This finding runs counter to the notion that cuboid–metatarsal joint morphology is reflective of overall midfoot sagittal plane range of motion across taxa (see also Greiner and Ball, 2014), although DeSilva et al. (2015) found evidence for a relationship between this morphology and midtarsal break magnitude within humans. However, the results of this study suggest that midfoot inversion and abduction are particularly critical to arboreal locomotion, and thus, further work exploring the relationship between these motions and cuboid–metatarsal joint morphology is needed. The transverse tarsal joints, on the other hand, are believed to be important sites of coronal plane mobility in the chimpanzee midfoot (Bojsen-Møller, 1979; Lewis, 1980b; Thompson et al., 2014), making them potentially important to fossil hominin investigations. Although several studies have documented differences in human and chimpanzee talonavicular joint morphology (e.g., Effman and Manter, 1935b; Prang, 2016; Sarmiento and Marcus, 2000), more work is needed to understand how these differences are related to relative ranges of motion outside of the sagittal plane. However, for the calcaneocuboid joint, the position of the cuboid’s calcaneal process has been posited as a good indicator of the joint’s inversion–eversion range of motion (Bojsen-Møller, 1979; Lewis, 1980b). Unfortunately, cuboids are rare in the hominin fossil record; prior to the genus Homo, the only fully described hominin cuboid is that attributed to Ardipithecus ramidus, which Lovejoy et al. (2009) characterize as presenting a “centrally positioned”
calcanear process. This is similar to the morphology of chimpanzees and therefore may indicate the potential for a high range of midfoot inversion, thereby corroborating many other features in the foot of Ar. ramidus that indicate this species was well adapted for arboreal locomotion (Lovejoy et al., 2009). The only other securely dated fossil hominin cuboid prior to 500 Ka is the 1.8 Ma OH 8 specimen, which is typically attributed to Homo habilis (Harcourt-Smith and Aiello, 2004). This specimen presents human-like calcaneocuboid joint morphology (Susman, 1983), revealing a potential loss of coronal plane mobility in the midfoot. Thus, this fossil provides some evidence that at least by the time of the emergence of Homo, hominins evolved foot anatomy that may have prevented the range of midfoot postures used by chimpanzees during arboreal locomotion.

Our study demonstrates that the chimpanzee foot is a complex and versatile structure that allows for a diverse array of behaviors both on the ground and in the trees. The data presented here should aid future studies attempting to link chimpanzee foot anatomy and locomotor behavior, and will allow for formulation and testing of hypotheses about hard and soft tissue adaptations in the foot. Such studies will improve our understanding of the evolution of the human foot, and help guide the use of pedal morphology in fossil hominin locomotor behavior reconstructions.

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