



Contents lists available at ScienceDirect

## Comptes Rendus Palevol

[www.sciencedirect.com](http://www.sciencedirect.com)



Human Palaeontology and Prehistory

### Adaptation to bipedal gait and fifth metatarsal structural properties in *Australopithecus*, *Paranthropus*, and *Homo*

### *Adaptation à la marche bipède et propriétés structurales du cinquième métatarse chez Australopithecus, Paranthropus et Homo*

Mark R. Dowdeswell<sup>a</sup>, Tea Jashashvili<sup>b,c,d,\*</sup>, Biren A. Patel<sup>e,f,d</sup>, Renaud Lebrun<sup>g</sup>,  
Randall L. Susman<sup>h</sup>, David Lordkipanidze<sup>c</sup>, Kristian J. Carlson<sup>e,d,i,j</sup>

<sup>a</sup> School of Statistics and Actuarial Science, University of the Witwatersrand, Johannesburg, South Africa

<sup>b</sup> Molecular Imaging Center, Department of Radiology, USC Keck School of Medicine, University of Southern California, Los Angeles, USA

<sup>c</sup> Department of Geology and Palaeontology, Georgian National Museum, Tbilisi, Georgia

<sup>d</sup> Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa

<sup>e</sup> Department of Cell and Neurobiology, Keck School of Medicine, University of Southern California, Los Angeles, USA

<sup>f</sup> Human and Evolutionary Biology Section, Department of Biological Sciences, University of Southern California, Los Angeles, USA

<sup>g</sup> Institut des Sciences de l'Evolution de Montpellier – UMR 5554, Montpellier, France

<sup>h</sup> Department of Anatomical Sciences, Stony Brook University, Stony Brook, USA

<sup>i</sup> School of Geosciences, University of the Witwatersrand, Johannesburg, South Africa

<sup>j</sup> Department of Anthropology, Indiana University, Bloomington, USA

#### ARTICLE INFO

##### Article history:

Received 11 August 2016

Accepted after revision 24 October 2016

Available online xxx

Handled by Roberto Macchiarelli

##### Keywords:

Bone functional adaptation

Foot loading

Lateral column

Hominoids

Visualization

#### ABSTRACT

Humans, unlike African apes, have relatively robust fifth metatarsals (Mt5) presumably reflecting substantial weight-bearing and stability function in the lateral column of the former. When this morphological difference emerged during hominin evolution is debated. Here we investigate internal diaphyseal structure of Mt5s attributed to *Australopithecus* (from Sterkfontein), *Paranthropus* (from Swartkrans), and *Homo* (from Olduvai, Dmanisi, and Dinaledi) placed in the context of human and African ape Mt5 internal diaphyseal structure. 'Whole-shaft' properties were evaluated from 17 cross sections sampling 25% to 75% diaphyseal length using computed tomography. To assess structural patterns, scaled cortical bone thicknesses (sCBT) and scaled second moments of area (sSMA) were visualized and evaluated through penalized discriminant analyses. While the majority of fossil hominin Mt5s exhibited ape-like sCBT, their sSMA were comparatively more human-like. Human-like functional loading of the lateral column existed in at least some fossil hominins, although perhaps surprisingly not in hominins from Dmanisi or Dinaledi.

© 2016 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

#### RÉSUMÉ

Contrairement aux grands singes, les humains ont un cinquième métatarse (Mt5) robuste. Cette morphologie particulière est liée au fait qu'une plus grande partie du poids du corps repose sur la partie latérale du pied. La date de l'émergence de ce caractère au cours de l'évolution humaine est toujours sujette à débats. Nous étudions ici la structure interne de la diaphyse du Mt5 chez les genres *Australopithecus* (de Sterkfontein), *Paranthropus*

##### Mots clés :

Adaptation fonctionnelle de l'os

Répartition du poids sur le pied

Partie latérale du pied

Hominoides

Visualisation

\* Corresponding author at: Molecular Imaging Center, Department of Radiology, USC Keck School of Medicine, University of Southern California, Los Angeles, USA.

E-mail address: [tjashashvili@yahoo.fr](mailto:tjashashvili@yahoo.fr) (T. Jashashvili).

<http://dx.doi.org/10.1016/j.crpv.2016.10.003>

1631-0683/© 2016 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

(de Swartkrans) et *Homo* (d'Olduvai, de Dinaledi et de Dmanisi), que nous comparons à l'homme moderne ainsi qu'aux grands singes africains. Nous avons utilisé la tomographie afin d'évaluer les propriétés des diaphyses dans leur ensemble à partir de 17 sections transversales de celles-ci, effectuées entre 25 % et 75 % de la longueur totale de l'os. Afin d'évaluer les patrons structurels de ce métatars, l'épaisseur calibrée de l'os (sCBT) ainsi que l'épaisseur calibrée des moments quadratiques (sSMA) ont été mesurées, puis comparées au sein de l'échantillon par analyse discriminante pondérée. Alors que la majorité des fossiles d'hominidés ont des valeurs de sCBT pour Mt5 similaires à celles observées pour les grands singes actuels, les valeurs de sSMA sont proches de celles de l'homme actuel. Chez certains hominidés fossiles au moins, à l'instar de l'homme moderne, la partie latérale du pied supportait une fraction importante du poids du corps, bien que, de manière peut-être surprenante, ce ne soit pas le cas pour les hominidés de Dmanisi et de Dinaledi.

© 2016 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

## 1. Introduction

The foot is functionally comprised of medial and lateral columns (Morton, 1935), the latter of which includes the fourth and fifth rays (e.g., metatarsals along with their associated phalanges). Proximally, fourth and fifth metatarsals (Mt4 and Mt5, respectively) articulate with the cuboid, which in turn articulates with the calcaneus. Greater rigidity in the lateral column, including within metatarsophalangeal, tarsometatarsal, and calcaneocuboid joints, is a functionally distinguishing characteristic of the modern human foot that is correlated with the presence of longitudinal and transverse arches, all of which enable the human foot to serve more effectively and efficiently as a stiff lever during the last half of stance phase in terrestrial gaits (DeSilva, 2010; Elftman and Manter, 1935a,b; Hicks, 1954; Jones, 1941; Ker et al., 1987; Lewis, 1980b; Morton, 1922, 1924; Susman, 1983). Apes, on the other hand, exhibit less arching and tend to exhibit greater sagittal plane movement in mid-foot joints during the last half of stance phase in terrestrial gaits (Elftman and Manter, 1935a; Gebo, 1992; Nowak et al., 2010; Susman, 1983; Vereecke et al., 2003). This joint movement has been referred to as a “mid-tarsal break” (Bojsen-Møller, 1979; Nowak et al., 2010) or “mid-foot break” (DeSilva, 2010). Greater mid-foot joint mobility in apes presumably reflects selection for greater conformity of the foot to substrates, particularly arboreal ones (Gebo, 1992).

The modern human foot experiences the highest loads during stance phase in its medial column (e.g., first metatarsal, Mt1), while loads lessen progressively in increasingly more lateral metatarsals (Stokes et al., 1979; Wearing et al., 2001). Within-individual load variability applied to lateral metatarsals also has been shown to be less than that applied to medial metatarsals in humans (Wearing et al., 2001). Using a theoretical approach, Preuschoft (1969) reasoned that dorsoplantar and medio-lateral oriented bending moments differentiated Mt1 and Mt5 loading, respectively. In comparisons of plantar pressure associated with terrestrial quadrupedal and bipedal gaits, and specifically the path of the centre of pressure over the course of stance phase, some of these findings have been corroborated by different pressure distributions and patterns beneath the foot of humans and apes (D'Août et al., 2004; Vereecke et al., 2003). Bonobos exhibit a centre of pressure that remains more laterally-positioned

over a longer period of stance phase during terrestrial quadrupedal and bipedal gaits compared to that of bipedal humans, and also a centre of pressure that fluctuates more in the mediolateral direction than typically observed in humans (De Cock et al., 2008; Hayafune et al., 1999; Nagel et al., 2008; Vereecke et al., 2003). Chimpanzees exhibit a relatively more laterally-positioned centre of pressure than humans during late stance phase and push-off (Elftman and Manter, 1935b). And gorillas, while less well-studied than other African apes, appear to exhibit relatively more laterally-positioned high plantar pressure than humans during stance phase (Crompton et al., 2012). Collectively, these studies of terrestrial gaits provide strong evidence of loading differences between the medial and lateral columns of modern humans versus those of apes.

Several external features of non-hallucal metatarsals highlight important functional differences between the lateral column of modern human and ape feet. For example, African apes show more internal torsion (inversion) of Mt3, Mt4, and Mt5 heads, while humans show more external torsion (eversion) of Mt3, Mt4, and Mt5 heads (Drapeau and Harmon, 2013). African apes exhibit plantar angulation of metatarsal diaphyses relative to the base in the lateral column whereas humans exhibit a dorsal angulation (Lewis, 1980a). Humans emphasize dorsal doming of metatarsal heads coupled with transverse guttering separating the subchondral surface of the head from the diaphysis, whereas apes exhibit a flatter dorsal surface without transverse guttering (Fernández et al., 2015, 2016; Latimer and Lovejoy, 1990; Susman, 1983). Finally, humans tend to exhibit an Mt5 that is second in robustness to Mt1, whereas apes tend to exhibit Mt5s with the lowest diaphyseal robusticity within the metatarsus (Archibald et al., 1972; Day and Napier, 1964; Marchi, 2010; Pontzer et al., 2010; Susman, 1988). All of these features combine to demonstrate selective pressures on modern human foot adaptations favouring obligate terrestrial bipedalism.

In contrast to comparisons of external morphology, internal structural comparisons between modern human and ape metatarsal diaphyses are comparatively less well-documented. This is despite internal properties, such as cortical bone thickness and second moments of area, that exhibit good correspondence with comparative foot biomechanics in humans and apes (Jashashvili et al., 2015; Marchi, 2005, 2010). When these internal evaluations have been made, typically they have been theoretical

Download English Version:

<https://daneshyari.com/en/article/5787816>

Download Persian Version:

<https://daneshyari.com/article/5787816>

[Daneshyari.com](https://daneshyari.com)