

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevolSpatial and temporal variation of body size among early *Homo*Manuel Will ^{a, b, *}, Jay T. Stock ^b^a Department of Early Prehistory and Quaternary Ecology, University of Tübingen, Schloss Hohentübingen, Tübingen, 72070, Germany^b PAVE Research Group, Department of Archaeology and Anthropology, University of Cambridge, Cambridge, CB2 3QG, United Kingdom

ARTICLE INFO

Article history:

Received 7 January 2014

Accepted 10 February 2015

Available online 26 March 2015

Keywords:

Postcranium
Human evolution
Homo habilis
Homo ergaster
Body mass
Stature
Early *Homo*

ABSTRACT

The estimation of body size among the earliest members of the genus *Homo* (2.4–1.5 Myr [millions of years ago]) is central to interpretations of their biology. It is widely accepted that *Homo ergaster* possessed increased body size compared with *Homo habilis* and *Homo rudolfensis*, and that this may have been a factor involved with the dispersal of *Homo* out of Africa. The study of taxonomic differences in body size, however, is problematic. Postcranial remains are rarely associated with craniodental fossils, and taxonomic attributions frequently rest upon the size of skeletal elements. Previous body size estimates have been based upon well-preserved specimens with a more reliable species assessment. Since these samples are small ($n < 5$) and disparate in space and time, little is known about geographical and chronological variation in body size within early *Homo*.

We investigate temporal and spatial variation in body size among fossils of early *Homo* using a ‘taxon-free’ approach, considering evidence for size variation from isolated and fragmentary postcranial remains ($n = 39$). To render the size of disparate fossil elements comparable, we derived new regression equations for common parameters of body size from a globally representative sample of hunter-gatherers and applied them to available postcranial measurements from the fossils.

The results demonstrate chronological and spatial variation but no simple temporal or geographical trends for the evolution of body size among early *Homo*. Pronounced body size increases within Africa take place only after hominin populations were established at Dmanisi, suggesting that migrations into Eurasia were not contingent on larger body sizes. The primary evidence for these marked changes among early *Homo* is based upon material from Koobi Fora after 1.7 Myr, indicating regional size variation. The significant body size differences between specimens from Koobi Fora and Olduvai support the cranial evidence for at least two co-existing morphotypes in the Early Pleistocene of eastern Africa.

Crown Copyright © 2015 Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Introduction

Body size is one of the most important biological characteristics of an animal. It plays a central role in the overall biology and adaptive strategy of organisms, correlating with numerous physiological, energetic, behavioural, and life history traits (Peters, 1983; Calder, 1984; Damuth and MacFadden, 1990; Brown and West, 2000). Studies of body size have focused on many hominin genera and species (McHenry, 1975; Foley, 1987; Aiello and Wood, 1994; McHenry and Coffing, 2000), including *Paranthropus*, *Australopithecus* (Wolpoff, 1973; McHenry, 1974, 1991, 1992; Olivier, 1976; Feldesman and Lundy, 1988; Jungers, 1988a; McHenry and Berger, 1998), and fossil *Homo* (Feldesman et al., 1990; McHenry,

1991, 1992; Hartwig-Scherer, 1993, 1994; Ruff and Walker, 1993; Ruff et al., 1997; Ruff, 2010; Holliday, 2012; Carretero et al., 2012; Dingwall et al., 2013).

In this study, we focus on body size variation of the earliest members attributed to the genus *Homo*, which first appear around 2.4–1.8 Myr (million years ago) in the fossil record of eastern and southern Africa (Wood, 1992; Schrenk et al., 1993, 2007; Kimbel, 2009; Antón, 2012). In this time frame, three species are recognized by many (though not all) scholars: *Homo habilis*, *Homo rudolfensis*, and *Homo ergaster* (or African *Homo erectus*). Differences in cranial morphology of non-*H. ergaster* finds in eastern Africa, best exemplified by the specimens KNM-ER 1813 (*H. habilis* sensu stricto) and KNM-ER 1470 (*H. rudolfensis*), support the existence of three contemporary early *Homo* taxa (Groves and Mazák, 1975; Wood, 1992, 1999; Rightmire, 1993; Lieberman et al., 1996; Schrenk et al., 2007; Spoor et al., 2007; Antón, 2012; Leakey et al., 2012; Antón et al., 2014). We refer to these three species

* Corresponding author.

E-mail address: manuel.will@uni-tuebingen.de (M. Will).

with the informal term 'early *Homo*' in a slightly expanded time range of 2.4–1.5 Myr.

Body size has been implicated as a factor contributing to both brain evolution (McHenry, 1994; Kappelman, 1996; McHenry and Coffing, 2000) and the first hominin dispersals into Eurasia (Antón et al., 2001; Antón and Swisher, 2004; Wells and Stock, 2007; Fleagle et al., 2009; Pontzer, 2012). More detailed knowledge of the spatial and temporal variation in hominin body size evolution can improve interpretations of the origins and adaptive strategies of the genus *Homo* (Kimbel, 2009; Antón and Snodgrass, 2012; Carretero et al., 2012; Pontzer, 2012). New information on body size variation also helps to address the question of whether or not there were two separate lineages in the Early Pleistocene fossil record of eastern Africa in addition to *H. ergaster* and whether the sizes of these species are more similar to taxa within the *Australopithecus* or *Homo* grade (Wood, 1992; Lieberman et al., 1996; Suwa et al., 1996; Wood and Collard, 1999; Blumenschine et al., 2003; Haeusler and McHenry, 2004; Leakey et al., 2012; Antón et al., 2014).

Previous studies of body size among early *Homo* suggest that *H. habilis* and *H. rudolfensis* remain close in body mass and stature to the australopithecines (Feldesman and Lundy, 1988; McHenry, 1991, 1992; Hartwig-Scherer, 1993; McHenry and Coffing, 2000; but see; Holliday, 2012). *Homo habilis* in particular is often interpreted as exhibiting small body size and plesiomorphic body proportions, characterized by lower limbs that were short relative to the upper limbs, similar to *Australopithecus* (Johanson et al., 1987; Hartwig-Scherer and Martin, 1991; McHenry and Berger, 1998; Richmond et al., 2002; but see Haeusler and McHenry, 2004, 2007). Many of these interpretations rest on the partial skeleton OH 62, with an estimated stature of 100–120 cm (Feldesman and Lundy, 1988; Jungers, 1988b) and a body mass of 20–37 kg (McHenry, 1992; Hartwig-Scherer, 1993). Partly based on these results, some scholars have even challenged the placement of *H. habilis* into the genus *Homo* (e.g., Wood and Collard, 1999; Wood, 2009; Berger et al., 2010). The origin of *H. ergaster* at ~1.8 Myr is often considered a major adaptive shift in human evolution (Feldesman and Lundy, 1988; McHenry, 1988, 1991; Ruff and Walker, 1993; Wood and Collard, 1999; Antón, 2003; Lieberman, 2007; Ruff, 2010; but see; Antón, 2012; Antón and Snodgrass, 2012; Pontzer, 2012), based largely upon evidence for an increase in stature and mass (to around 160–185 cm and 50–70 kg) and the evolution of modern human-like limb proportions with lower limbs that are long relative to upper limbs. Scholars usually link these developments to changes in locomotion (Stuedel-Numbers and Tilkens, 2004; Stuedel-Numbers, 2006; Ruff, 2009; Pontzer et al., 2010), as well as foraging behaviour and diet (Foley, 2001, 2002; Antón et al., 2002; Antón, 2003; Antón and Swisher, 2004). The notion of apomorphic body size and proportions in *H. ergaster* is based primarily on the well-preserved specimens KNM-WT 15000 at 1.47 Myr (Walker and Leakey, 1993; Ruff and Burgess, 2015) and KNM-ER 1808 at 1.60 Myr (Leakey and Walker, 1985; McDougall et al., 2012).

The prevailing views on body size evolution have been challenged by the recovery of postcranial remains that indicate smaller body sizes (Simpson et al., 2008, 2014) and small-sized cranial remains (Spoor et al., 2007) from eastern Africa that are attributed to *H. ergaster* (but see Ruff, 2010) as well as the discovery of small-bodied early *Homo* in Dmanisi, currently the oldest hominin fossils outside of Africa (~1.77 Myr; Gabunia et al., 2000, 2001; Lordkipanidze et al., 2007, 2013; Ferring et al., 2011). The Dmanisi fossils exhibit a mixture of plesiomorphic and derived traits in their postcranial morphology, raising issues about their taxonomy and dispersal capacities. While elongated lower limbs are suggestive of adaptations to locomotor efficiency, their estimated body size and leg length, as well as their metatarsal morphology, are less derived

compared with *H. ergaster* (Lordkipanidze et al., 2007; Pontzer et al., 2010).

The most recent studies to estimate and compare body size within early *Homo* were conducted over 20 years ago (McHenry, 1991, 1992; Ruff and Walker, 1993; summarized in McHenry and Coffing, 2000; but see; Ruff, 2010). These landmark studies have provided widely used methods and estimates of body size for early *Homo* (see McHenry, 1994; Kappelman, 1996; Wood and Collard, 1999; McHenry and Coffing, 2000; Aiello and Key, 2002; Ruff, 2002; Stuedel-Numbers and Tilkens, 2004; Stuedel-Numbers, 2006; Robson and Wood, 2008; Klein, 2009; Carretero et al., 2012; Holliday, 2012; Pontzer, 2012; Dingwall et al., 2013; Antón et al., 2014). Estimates of the stature of fossil *Homo* have primarily been based upon regression equations (McHenry, 1974; Feldesman and Lundy, 1988; Ruff and Walker, 1993; Carretero et al., 2012; Dingwall et al., 2013), but some researchers used a generic femur-stature ratio (Feldesman et al., 1990; McHenry, 1991). Body mass estimates most commonly employ mechanical methods (McHenry, 1988; Hartwig-Scherer, 1993, 1994; Ruff, 2010) based on the relationship between linear measurements of the skeleton and known living body mass from reference individuals (Ruff et al., 1991; McHenry, 1992; Grine et al., 1995; Auerbach and Ruff, 2004; Holliday, 2012).¹ Table 1 provides a summary and methodological overview of previous studies that have estimated the body size of early *Homo* specimens that are also included in this study.

Practical and methodological problems

Studies of the evolution of body size in early *Homo* face several practical and methodological challenges. In order to investigate taxonomic variation of body size, species designation of the postcranial material used in the estimation is crucial. At present, however, there is no consensus on morphological traits that characterize the postcrania of early *Homo*, which frequently results in multiple taxonomic attributions for individual fossils (Wood, 1992; McHenry, 1994; Wood and Collard, 1999; Haeusler and McHenry, 2004; see also Table 2). The often fragmentary and isolated nature of the postcranial fossil record for early *Homo* complicates this situation (Wood, 1992; Hartwig-Scherer, 1993; Reno et al., 2005; Rightmire and Lordkipanidze, 2009; Antón, 2012; Dusseldorp et al., 2013). Without associated craniodental remains, palaeoanthropologists often assign isolated postcrania to species based on the size of the skeletal element (cf. Wood, 1992; Antón, 2012). This procedure, however, introduces circularity: as most large elements are assigned to *H. ergaster*, the specimens from this taxon will naturally yield the largest values when used to estimate body size.

There is also no consensus on the hypodigms for any of the early *Homo* species. Their taxonomy remains one of the most controversial issues in palaeoanthropology (for more details of the discussions in the last two decades see Wood, 1992, 2009, 2014; Grine et al., 1996; Lieberman et al., 1996; Suwa et al., 1996; Wood and Collard, 1999; Blumenschine et al., 2003; Schrenk et al., 2007; Kimbel, 2009; Jiménez-Arenas et al., 2011; Antón, 2012; Van Arsdale and Wolpoff, 2013; Antón et al., 2014), as exemplified by recent discoveries in Koobi Fora (Leakey et al., 2012) and Dmanisi (Lordkipanidze et al., 2013; Spoor, 2013; Schwartz et al., 2014; Wood, 2014; Zollikofer et al., 2014). Even when postcranial bones are associated with craniodental remains, there are only a small number of specimens with an unambiguous taxonomic assignment. Since early *Homo* was sympatric with *Australopithecus* and

¹ McHenry (1992) derived body mass from estimated stature based on a power curve, although power functions are not considered to be sufficiently strong for this procedure (Porter, 2002).

Table 1Main studies of stature and body mass estimation in hominins that included specimens of early *Homo* also analysed in this study.

Study	Focus	Early <i>Homo</i> ^a	Reference sample	Method	Line fitting	Variables ^b	Analysis	95% CI? ^c
<i>Stature</i>								
McHenry, 1974	<i>Australopithecus</i>	4	Modern humans	Regression	OLS	20	Taxonomic	No
Feldesman and Lundy, 1988	Hominins (3.0–1.0 Myr)	7	Modern humans	Regression	(OLS) MA	3	Taxonomic	Yes
Feldesman et al., 1990	<i>Homo erectus</i> – <i>Homo sapiens</i>	1	Modern humans	Femur-stature ratio	–	1	Taxonomic	No
McHenry, 1991	Hominins (3.1–0.7 Myr)	12	Modern humans	Femur-stature ratio	–	1	Taxonomic Chronologic	No
Ruff and Walker, 1993	<i>Homo ergaster</i>	7	Modern humans	Regression	OLS	1	Taxonomic	No
Lordkipanidze et al., 2007	Dmanisi <i>Homo</i>	3	Modern humans	Regression	OLS	4	Taxonomic	Yes
Carretero et al., 2012	<i>Homo heidelbergensis</i>	5	Modern humans	Regression	RMA	6	Taxonomic Chronologic	Yes
<i>Body mass</i>								
McHenry, 1988	Hominins (3.1–1.4 Myr)	7	Hominoid	Mechanical	OLS	1	Taxonomic Chronologic	Yes
McHenry, 1992	Hominins (4–1.4 Myr)	21	Hominoid and modern human	Mechanical	OLS, MA, RMA	13	Taxonomic	No
Hartwig-Scherer, 1993	Hominins (3.3–1.4 Myr)	10	'taxon-independent'	Mechanical	RMA	7	Taxonomic	Yes
Hartwig-Scherer, 1994	Pleistocene <i>Homo</i>	7	Modern humans	Mechanical	RMA	10	Taxonomic	Yes
Ruff et al., 1997	Pleistocene <i>Homo</i>	5	Modern humans	Mechanical	OLS	2	Chronologic	Yes
Lordkipanidze et al., 2007	Dmanisi <i>Homo</i>	3	Modern humans	Mechanical	OLS	7	Taxonomic	Yes
Ruff, 2010	Hominins (6.0–0.26 Myr)	5	Modern humans	Mechanical	OLS	2	Taxonomic	No

^a Number of early *Homo* specimens that are also included in this study.^b Number of linear measurements used for estimating body mass.^c Are 95% confidence intervals given?

Paranthropus at the principal fossil sites in eastern and southern Africa, this issue also applies to the genus level (McHenry, 1992; Wood, 1992; McHenry and Coffing, 2000; Spoor et al., 2007; Wood and Lonergan, 2008; Wood and Leakey, 2011; Dingwall et al., 2013; Dusseldorp et al., 2013).

Two examples highlight these problems. In 1986, Alexeev proposed the taxon *H. rudolfensis* for fossil material from Koobi Fora dating to >1.8 Myr. Since the definition of this taxon, both its integrity as an independent species and the composition of its hypodigm have been controversial (Tobias, 1991; Wood, 1992, 1999; Rightmire, 1993; Lieberman et al., 1996; Suwa et al., 1996; Blumenschine et al., 2003; Jiménez-Arenas et al., 2011; Antón, 2012; Antón et al., 2014). At present, no postcranial remains are directly and unequivocally associated with *H. rudolfensis* (Wood, 1992; Lieberman et al., 1996; Kimbel, 2009; Rightmire and Lordkipanidze, 2009; but see; McHenry and Coffing, 2000; Haeusler and McHenry, 2004). In southern Africa, taxonomic attribution for early *Homo* is even more problematic for the isolated postcrania found in cave sites such as Swartkrans. Here, assigning postcranial remains to either *Paranthropus* or *Homo* has been hampered by the lack of direct association with craniodental remains. Scholars attributed specimens to early *Homo* mainly on the basis of morphological affinities to modern humans or eastern African *Homo* fossils (e.g., Napier, 1959; Day, 1976; Susman, 1989; Susman et al., 2001; Grine, 2005; Pickering et al., 2011; Dusseldorp et al., 2013).

In summary, an accurate analysis of taxonomic variation in body size based on postcranial remains alone is problematic. While the studies summarized in Table 1 may provide accurate estimates of body size variables for species, the small sample sizes used are prone to the effects of outliers (Harmon and Losos, 2005; Smith, 2005; Schillaci and Schillaci, 2009; Plavcan, 2012) and limit the potential for statistical analyses (Siegel and Castellan, 1988; Sokal and Rohlf, 1995; Zar, 1996; Pontzer, 2012).

Apart from these practical caveats, there are a number of methodological problems in creating regression equations to

estimate the body size of extinct *Homo*. Choosing an appropriate reference sample for the estimation of body size in early *Homo* can be problematic as Plio-Pleistocene fossils are not members of any extant species. While various models have been used (see Table 1), most studies have found modern humans to be most appropriate for Plio-Pleistocene *Homo* (e.g., McHenry, 1991, 1992; Ruff et al., 1997; for more details see Hartwig-Scherer, 1993, 1994). When using modern humans as a reference sample, the inclusion of small-bodied individuals is essential as the size of the target specimens compared with the reference sample directly affects the accuracy of the prediction equations (Stuedel, 1985; Dagosto and Terranova, 1992; Hens et al., 2000; Porter, 2002; Kurki et al., 2010). In addition, the body proportions of the comparative sample should be similar to the fossil taxa (Trotter and Gleser, 1952; Ruff, 1994, 2002; Holliday and Ruff, 1997).

For fragmented and isolated postcranial bones, measurements normally used for body size estimation (e.g., long bone length) are frequently not preserved. In such circumstances, other linear measurements must be employed (e.g., Byers et al., 1989; Meadows and Jantz, 1992; Hartwig-Scherer, 1993; McHenry and Berger, 1998; De Groote and Humphrey, 2011). Fossils that exhibit both cranial and postcranial bones, such as KNM-WT 15000, KNM-ER 1808, and OH 62, are the most reliable individuals to assess body size because the performance of several estimators can be compared (McHenry, 1992; Walker and Leakey, 1993; Hartwig-Scherer, 1994).

To address the problems associated with taxonomy and the small numbers of fossils for which size estimates are available (Aiello and Wood, 1994; Smith, 2005; Schillaci and Schillaci, 2009), we pursue a 'taxon-free' approach to analyse variation in body size among early *Homo*. Instead of focussing on taxonomy, this study examines two parameters that are easier to control: geography and chronology. Previous studies have rarely examined these dimensions of body size variation in early *Homo* since they used small samples of fossils that are disparate in space and time. Such an approach, however, is important as body size constitutes a highly plastic trait with multifactorial inheritance that is influenced by not

Table 2The early *Homo* database, encompassing 47 individual specimens with published metric data.^a

Specimen	Taxonomy	Element	Dating/Layer ^b	Locality	Key references
KNM-WT 15000	<i>Homo ergaster</i>	Partial skeleton	1.47/Natoo Formation	Koobi Fora	Brown et al., 1985; Walker and Leakey, 1993
KNM-ER 164	<i>Homo ergaster</i> ; <i>Homo sp.</i>	Partial skeleton	1.65/KBS Member	Koobi Fora	Leakey, 1971a; 1972; Day and Leakey, 1974
KNM-ER 736	<i>Homo ergaster</i>	Femur	1.58/Okote Member	Koobi Fora	Leakey, 1971a; Day, 1976; Geissmann, 1986
KNM-ER 737	<i>Homo ergaster</i> ; <i>Homo sp.</i>	Femur	1.60/Okote Member	Koobi Fora	Leakey, 1971a; Day and Leakey, 1973
KNM-ER 741	<i>Homo ergaster</i> ; <i>Australopithecus sp.</i>	Tibia	1.60/Okote Member	Koobi Fora	Leakey, 1971a; Leakey et al., 1972
KNM-ER 803	<i>Homo ergaster</i>	Partial skeleton	1.50/Okote Member	Koobi Fora	Leakey et al., 1972; Day and Leakey, 1974
KNM-ER 1808	<i>Homo ergaster</i>	Partial skeleton	1.60/KBS Member	Koobi Fora	Leakey, 1973; Leakey and Walker, 1985
KNM-ER 1812 ^c	<i>Homo ergaster</i> ; <i>Homo habilis</i>	Partial skeleton	1.60/KBS Member	Koobi Fora	Leakey, 1974; Leakey et al., 1978
KNM-ER 5428	<i>Homo ergaster</i> ; <i>Paranthropus sp.</i>	Talus	1.65/KBS Member	Koobi Fora	Walker and Leakey, 1993; DeSilva, 2009
OH 7 ^c	<i>Homo habilis</i> ; <i>Paranthropus boisei</i> ?	Partial skeleton	1.75/Bed I	Olduvai	Leakey et al., 1964; Susman and Stern, 1982
OH 8	<i>Homo habilis</i> ; <i>Paranthropus boisei</i> ?	Foot bones	1.75/Bed I	Olduvai	Day and Napier, 1964; Leakey et al., 1964; Susman, 2008
OH 10 ^c	<i>Homo habilis</i> ; <i>Homo sp.</i>	Foot phalanx	1.75/Bed I	Olduvai	Day and Napier, 1966; Day, 1976
OH 35	<i>Homo habilis</i> ; <i>Paranthropus sp.</i> ?	Tibia, Fibula	1.75/Bed I	Olduvai	Leakey, 1960; Davis, 1964; Susman and Stern, 1982
OH 43 ^c	<i>Homo habilis</i> <i>Homo sp.</i>	Metatarsus	1.75/Bed I	Olduvai	Day, 1978
OH 48	<i>Homo habilis</i>	Clavicle	1.75/Bed I	Olduvai	Leakey, 1960; Wood, 1974; Day, 1978
OH 49	<i>Homo habilis</i> ; <i>Homo sp.</i>	Radius	1.75/Bed I	Olduvai	Wood, 1974
OH 53	<i>Homo habilis</i> ?	Femur	1.75/Bed I	Olduvai	McHenry 1991; Haeusler and McHenry, 2004
OH 62	<i>Homo habilis</i>	Partial skeleton	1.75/Bed I	Olduvai	Johanson et al., 1987; Haeusler and McHenry, 2004
KNM-ER 813	<i>Homo habilis</i> ?; <i>Homo ergaster</i> ?; <i>Homo sp.</i>	Talus, Tibia	1.85/KBS Member	Koobi Fora	Leakey, 1972; Leakey and Wood, 1973; Wood, 1976
KNM-ER 1472	<i>Homo rudolfensis</i> ; <i>Homo habilis</i> ; <i>Homo ergaster</i>	Femur	2.00/Upper Burgi	Koobi Fora	Leakey et al., 1972; Day et al., 1975
KNM-ER 1473	<i>Homo sp.</i> ; <i>Homo rudolfensis</i>	Humerus	2.00/Upper Burgi	Koobi Fora	Day et al., 1976; Leakey et al., 1978
KNM-ER 1475	<i>Homo sp.</i>	Femur	2.00/Upper Burgi	Koobi Fora	Leakey, 1973; Day et al., 1975
KNM-ER 1481	<i>Homo sp.</i> ; <i>Homo rudolfensis</i> ; <i>Homo ergaster</i>	Femur, Tibia, Fibula	1.95/Upper Burgi	Koobi Fora	Leakey et al., 1972; Day et al., 1975
KNM-ER 3228	<i>Homo rudolfensis</i> ; <i>Homo ergaster</i>	Pelvis	1.9 0/Upper Burgi	Koobi Fora	Rose, 1984; McHenry and Coffing, 2000
KNM-ER 3728	<i>Homo habilis</i> ; <i>Homo rudolfensis</i> ; <i>Paranthropus boisei</i>	Femur	1.90/Upper Burgi	Koobi Fora	Leakey and Walker, 1985; Walker and Leakey, 1993
KNM-ER 3735	<i>Homo habilis</i> ; <i>Homo sp.</i>	Partial skeleton	1.90/Upper Burgi	Koobi Fora	Leakey and Walker, 1985; Leakey et al., 1989
KNM-ER 5881	<i>Homo sp.</i>	Femur, Pelvis	1.90/Upper Burgi	Koobi Fora	Leakey and Walker, 1985; Ward et al., 2011
KNM-ER 5882	<i>Homo sp.</i>	Femur	1.90/Upper Burgi	Koobi Fora	Leakey and Walker, 1985; Ruff, 1995
Omo 323–76–898	<i>Homo sp.</i>	Talus	2.20/Shungura Frm. G	Omo	Deloison, 1997; Gebo and Schwartz, 2006
Stw 311	<i>Homo aff. H. habilis</i> ; <i>Paranthropus</i> ?	Femur	1.7–1.4/Member 5	Sterkfontein	Kuman and Clarke, 2000; Ruff, 2010
Stw 567	<i>Homo ergaster</i> ; <i>Homo aff. H. habilis</i>	Tibia	1.7–1.4/Member 5	Sterkfontein	Kuman and Clarke, 2000; DeSilva, 2009
Stw 571	<i>Homo aff. H. habilis</i> ; <i>Homo ergaster</i>	Ulna	2.6–2.0 or 1.8–1.5/Stw 53 infill	Sterkfontein	Kuman and Clarke, 2000
SK 18b	<i>Homo cf. erectus</i> ; <i>Homo sp.</i>	Radius	1.8–1.5/Member 1 HR	Swartkrans	Brain, 1978; Day, 1978; Susman, 1993
SK 84	<i>Homo erectus</i> ; <i>Paranthropus robustus</i>	Metacarpus	1.8–1.5/Member 1 HR	Swartkrans	Broom and Robinson, 1949; Napier, 1959
SK 85	<i>Homo cf. erectus</i>	Metacarpus	1.8–1.5/Member 1 HR	Swartkrans	Napier, 1959; Susman, 1993; Susman et al., 2001
SK 853 ^c	<i>Homo cf. erectus</i>	Vertebra	1.8–1.5/Member 1 HR	Swartkrans	Broom and Robinson, 1949; Napier, 1959
SK 1896	<i>Homo cf. erectus</i> <i>Homo sp.</i>	Femur	1.8–1.5/Member 1 HR	Swartkrans	Susman et al., 2001
SKX 2045	<i>Homo cf. erectus</i> ; <i>Homo sp.</i>	Radius	1.7–1.1/Member 2	Swartkrans	Susman et al., 2001
SKX 3342	<i>Homo cf. erectus</i> ?; <i>Homo sp.</i>	Vertebra	1.7–1.1/Member 2	Swartkrans	Susman, 1989; Susman et al., 2001
SKX 34805	<i>Homo cf. erectus</i> ; <i>Paranthropus robustus</i>	Humerus	1.8–1.5/Member 1 LB	Swartkrans	Susman, 1989; Susman et al., 2001
SKX 42695	<i>Homo cf. erectus</i> ; <i>Paranthropus robustus</i>	Talus	1.8–1.5/Member 1 LB	Swartkrans	Susman et al., 2001; Zipfel et al., 2011
SKW 2954	<i>Homo sp.</i>	Metacarpus	1.7–1.1/Member 2	Swartkrans	Susman, 1989; Curnoe, 2010
SKW 3646 ^c	<i>Homo sp.</i>	Metacarpus	1.7–1.1/Member 2	Swartkrans	Susman, 1989; Curnoe, 2010
'D2600' ^d	<i>Homo ergaster</i> ; <i>Homo habilis</i>	Partial skeleton	1.80/Stratum B1	Dmanisi	Lordkipanidze et al., 2007; Pontzer et al., 2010
'D2700/D2735' ^{c,d}	<i>Homo ergaster</i> ; <i>Homo habilis</i>	Partial skeleton	1.80/Stratum B1	Dmanisi	Lordkipanidze et al., 2007; Pontzer et al., 2010
D3479 ^c	<i>Homo ergaster</i> ; <i>Homo habilis</i>	Metatarsus	1.80/Stratum B1	Dmanisi	Lordkipanidze et al., 2007; Pontzer et al., 2010
D4111/D3442	<i>Homo ergaster</i> ; <i>Homo habilis</i>	Metatarsus	1.80/Stratum B1	Dmanisi	Lordkipanidze et al., 2007; Pontzer et al., 2010.

^a For the estimation of body size, 39 fossils of early *Homo* could be included. Specimens are ordered by their spatiotemporal groups (see also Table 3).^b Dates in Myr. For information on the stratigraphic placement and dating see: Koobi Fora and Omo (Brown and Feibel, 1985; Feibel et al., 1989, 2009; Isaac and Behrensmeyer, 1997; Brown et al., 2006; Gathogo and Brown, 2006; McDougall and Brown, 2006; Lepre and Kent, 2010; Brown and McDougall, 2011; Joordens et al., 2011, 2013; Wood and Leakey, 2011; McDougall et al., 2012), Olduvai (Leakey, 1971b; Tobias, 1991; Wood, 1991), South African cave sites (Brain, 1993; Kuman and Clarke, 2000; Curnoe et al., 2001; Susman et al., 2001; Balter et al., 2008; Herries et al., 2009; Pickering and Kramers, 2010; Herries and Shaw, 2011; Dusseldorp et al., 2013—but note the very complicated stratigraphy and associated dating problems), and Dmanisi (Lordkipanidze et al., 2007, 2013; Ferring et al., 2011; Lordkipanidze et al., 2013).^c Not included in the estimation procedures as the specimens were clear subadults or matching measurements in the reference sample were lacking.^d 'D2600' and 'D2700/2735' refer to the postcranial specimens associated with these cranial elements (see Lordkipanidze et al., 2007).

just taxonomy but also ontogeny, diet, resource availability, climate, and environment (e.g., Wells and Stock, 2011; Antón and Snodgrass, 2012; Kuzawa and Bragg, 2012; Plavcan, 2012). Geography and chronology constitute two key elements of these influences. A temporal analysis also allows investigation of the tempo and mode of body size evolution in early *Homo*.

We examined temporal and spatial variation in body size among fossils of early *Homo* by developing new regression equations to estimate size variables using isolated and more fragmentary postcranial fossil evidence. The central assumption of our analysis is that all linear skeletal measurements will, to some extent, be correlated with body size. However, the direct size comparison of different elements of the skeleton is impossible without determining the relationship of their size to common size variables. After identifying which measurements were available for the fossil material, we used the same measurements to derive regression equations for body size estimation using a globally representative sample of modern human hunter-gatherers. Equations that provided significant correlations with estimates of body size for these skeletons were then used to predict body size for fragmentary fossils of early *Homo*, including specimens for which no such predictions have yet been published. Using an expanded dataset of body size estimates, we address the following questions: a) Was there a general temporal increase in body size within early *Homo*?, b) Were there spatial differences in body size within early members of the genus?, and c) Is there evidence for an increase in body size prior to the first appearance of the genus *Homo* at Dmanisi?

Methods and materials

The challenge of interpreting size variation from fragmentary fossil remains is one of ‘extracting’ the size information of different specimens and using this to estimate common size variables that can be directly compared. To accomplish this, we compiled published and unpublished postcranial metric data of fossils purported to represent *Homo* between 2.2 and 1.5 Myr from the literature (Supplementary Online Material [SOM] Appendix 1). We included specimens if their taxonomic designation to the genus *Homo* was considered the ‘most probable.’² The postcranial database represents 47 fossils (Table 2) and 420 linear measurements (see SOM Table 3). We gathered these data from approximately 100 journal publications and book chapters, 15 monographs, and personal communications with two researchers (J. DeSilva and R. Susman). For each specimen, the sources of these measurements were noted and the quality of the gathered data evaluated (see SOM Appendix 1 and SOM Tables 1–3). Since the omission of raw measurements in publications has proven a real problem to this study, we provide all data in a supplementary Excel spreadsheet (SOM EarlyHomoPostcrania.xlsx). We categorized the fossils into five spatiotemporal groups (Table 3; Fig. 1), rank ordered by age (1 is the youngest, 5 the oldest). These units constitute artificial constructions but they exhibit clear boundaries and allow for a taxon-free analysis of geographical and chronological variation in body size among early *Homo*.

While using the more fragmented material enlarges the available sample size for postcranial remains of early *Homo*, many of the measurements that are usually employed to estimate body size are not preserved. For these fossils, substitute measurements that show a statistically significant correlation with parameters of body

Table 3

Geographical and chronological description of the spatiotemporal groups together with the specimens included in each.^a

Spatiotemporal group	Description	Specimens
1	Koobi Fora, <1.7 Myr	KNM-ER 164, 736, 737, 741, 803, 1808, 1812, 5428; KNM-WT 15000 ^b
2	South African caves, 1.8–1.4 Myr	Stw 311, 567, 571; SK 18b, 84, 85, 853, 1896; SKX 2045, 3342, 34805, 42695; SKW 2954, 3646
3	Olduvai, 1.75 Myr	OH 7, 8, 10, 35, 43, 48, 49, 53, 62
4	Dmanisi, 1.8 Myr	<i>D2600</i> , <i>D2700/D2735</i> , <i>D3479</i> , <i>D4111/3442</i>
5	Koobi Fora, >1.8 Myr	KNM-ER 813, 1472, 1473, 1475, 1481, 3228, 3728, 3735, 5881, 5882; Omo 323-76-898

^a *Italicized* specimens could not be included in further analyses due to their unequivocal subadult status.

^b Adult body size estimates were used for the juvenile KNM-WT 15000, following Ruff and Burgess (2015).

size were used, including postcranial elements rarely utilised in body size estimations (e.g., vertebrae or metacarpals). We identified reliable predictors of body size by deriving regression equations from modern human populations for the same measurements and analysing their performance (by p-value; R^2 , %SEE, and %PE; see below).

The modern human populations used as a reference sample were predominantly hunter-gatherers, representing a wide range of body proportions and sizes. Hunter-gatherer groups constitute a particularly appropriate reference sample because their locomotor and subsistence strategies are most similar to extinct *Homo*. They also lack the positive secular (post-industrial) growth effects that are nearly ubiquitous among modern human populations (Trotter and Gleser, 1958; Ruff, 1994), which have been commonly used to construct regression equations for body mass and stature applied to extinct hominins. The modern human data included 828 adult individuals from 17 populations that span five continents and cover a time range from the African Late Pleistocene (~20,000 BC) until the recent past. All linear measurements were taken by one of the authors (JTS). The populations inhabited several different climatic zones, including both high-latitude and equatorial areas (Fig. 1; see SOM Table 4). The reference populations also include small-bodied foragers from the Andaman Islands and the Late Stone Age (LSA) of southern Africa (Stock and Pfeiffer, 2001). We found a total of 95 corresponding linear measurements for creating regression equations from this reference sample applicable to the early *Homo* specimens (SOM Table 6). By this selection of measurements, we could estimate adult body size for 39 specimens of early *Homo*.

Although we use a globally representative sample of modern humans for estimating body size, equations deriving exclusively from tropical populations might yield more accurate results for the eastern African early *Homo* specimens as they inhabited the same latitudes (see Ruff, 1994, 2002; Holliday and Ruff, 1997; Holliday, 2012). To control for this potential bias, we also calculated regression equations from the sub-sample of tropical populations in our reference database and applied them to fossils from eastern Africa. Subsequently, we compared the predictions of body size for each specimen between the tropical and global regression equations.

While using an osteological sample from hunter gatherers carries several advantages over living humans, the main drawback is that neither body mass nor stature is known for these individuals. The stature of each reference population was estimated by population-specific regression equations (see SOM Appendix 1 and SOM Table 7). We chose femoral head diameter (FHD) as the best indirect indicator of body mass because the hip joint is the major weight-bearing articulation (Ruff et al., 1991, 1997; McHenry, 1992;

² For some of the included specimens, genera other than *Homo* have been proposed. Since this study takes all its taxonomic information from the literature, the principle of majority rule was applied. ‘Most probably’ in this context means that only fossils that are frequently (and by many different authors) assigned to *Homo* are included in the database.

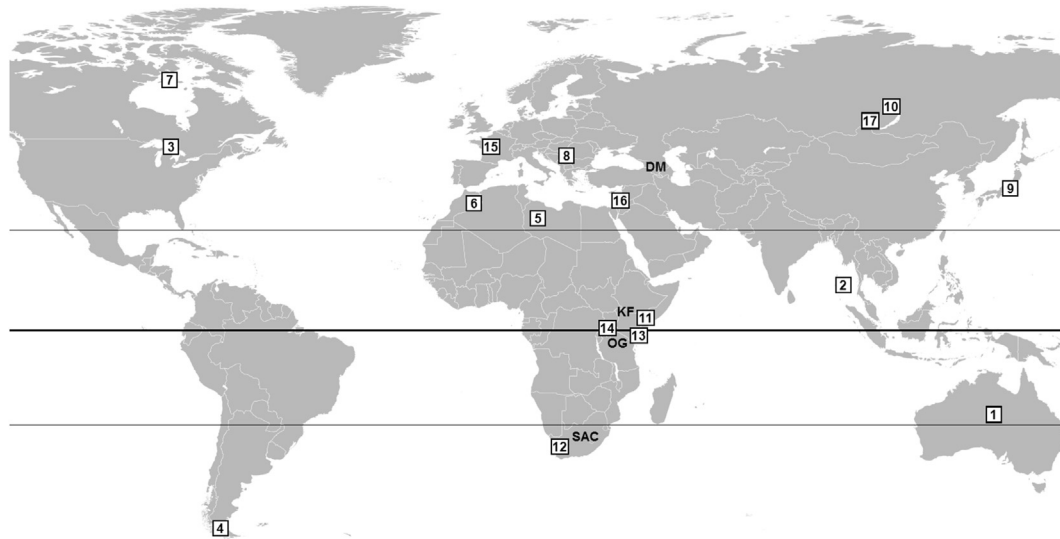


Figure 1. World map depicting the origin of the reference populations and the location of the spatiotemporal groups of early *Homo*. Reference populations: 1) Australian Aborigine; 2) Andaman Islanders; 3) Great Lakes (Archaic Period); 4) Fuegian (Yaghan); 5) Libya (Garamantean); 6) North Africa (Iberomarusian); 7) Inuit; 8) Iron Gates (Mesolithic); 9) Japan (Jomon); 10) Siberia (Kitoi); 11) Kenya (LSA); 12) South Africa (LSA); 13) Tanzania (LSA); 14) Tanzania (Masai); 15) France/Croatia (Mesolithic); 16) Israel (Natufian); 17) Siberia (Serovo/Glazkovo). Spatiotemporal groups: DM – Dmanisi; KF – Koobi Fora; OG – Olduvai Gorge; SAC – South African caves. Thick black line = equator; Thin black lines = Tropic of Cancer; Tropic of Capricorn.

Ruff, 2010). Femoral head diameter is also preserved in many individuals of the reference population, enabling direct calculation of regression equations for the estimation of FHD from other variables. In subsequent analyses, we assessed body mass of early *Homo* fossils in a two-step procedure: first by the predicted FHD for each specimen and second by the estimation of body mass from this predicted FHD. The latter procedure follows the methodology of Ruff (2010; for description of the method see SOM Appendix 1, Procedure of body mass calculation from FHD in early *Homo*).

We want to emphasize that the body mass and stature estimations applied here include multiple steps of prediction and thus generate cumulative error (Feldesman and Lundy, 1988; Porter, 2002). Therefore, the resulting absolute values should be treated with utmost caution (Smith, 1996). Taking these problems into account, we follow Steudel (1985) and directly compare our body size estimates with one another, which are all based on the same estimation procedures and assumptions. Thus, our comparisons focus on relative differences (e.g., specimen a > specimen b > specimen c) and not on absolute values.

The three main procedures of line fitting to create estimation equations from a bivariate dataset are ordinary least squares (OLS), major axis (MA), and reduced major axis (RMA) regression analysis. Anthropologists are divided between using and recommending OLS (Jungers, 1988a; Ruff and Walker, 1993; Ruff et al., 1997; Koenigsberg et al., 1998; Smith, 2009; Holliday, 2012; Dingwall et al., 2013), RMA (Sjøvold, 1990; Aiello, 1992; Hartwig-Scherer, 1994; Carretero et al., 2012), or MA (Feldesman and Lundy, 1988; Martin and Barbour, 1989) for estimating body size. The choice of a line-fitting model depends upon the biological relationship between the dependent and independent variables, as well as the context and aim of the study (Aiello, 1992; Smith, 2009; Carretero et al., 2012).

We generated OLS linear regression equations for the estimation of FHD and stature from measurements of the modern human reference sample. Since information on sex is rarely available for the early *Homo* specimens, the regression equations are based on pooled sex data. We transformed all linear measurements logarithmically to base 10 to ensure normal distribution,

homoscedacity, linearity between dependent and independent variables, and to reduce the effect of outliers (Smith, 1980; Martin and Barbour, 1989). All \log_{10} - \log_{10} linear regressions were performed on one independent variable (univariate). We used OLS as the method of line fitting, as the main purpose of the regressions is one-way prediction of body size from measurements of the post-cranial skeleton. Furthermore, due to the careful choice of the reference samples, the various body size estimates (e.g., FHD) of early *Homo* fall within the general size range of the reference populations (SOM Table 5). Hence, either no, or very little, extrapolation is required, allowing the use of OLS (Jungers, 1988a; Aiello, 1992; Auerbach and Ruff, 2004; Smith, 2009; Kurki et al., 2010). As size estimations often have (large) error margins it is best practice to state the 95% confidence intervals of estimates whenever this is possible (Steudel, 1985; Smith, 1996; Porter, 2002).

We used a total of 95 regression equations to predict stature and FHD (body mass) for the early *Homo* specimens. Our choice of the best regression equation for the prediction of each specimen is based on the equations that provided the lowest percent standard error of estimate (%SEE; Trotter and Gleser, 1958; Smith, 1980, 1984; Dagosto and Terranova, 1992). While the regression equations in the reference sample are exclusively based on adult individuals, some early *Homo* remains are either clearly adolescent (KNM-WT 15000; KNM-ER 1812; 'D2700/2735'; SK 853) or might be (OH 8; Susman, 2008; Susman et al., 2011; but see DeSilva et al., 2010). With the exception of KNM-WT 15000 and OH 8, these individuals were excluded from the estimation procedure. For KNM-WT 15000, we used the average values of the most recent estimates of adult body size by Ruff and Burgess (2015). Regarding OH 8, we choose to follow the adult assessment of DeSilva et al. (2010).

To control for the potential unreliability of single estimators of body size in our database (e.g., reconstructed or multiple measurements), we compared the mean values of all different estimates per specimen with the best prediction. All estimates were divided into those derived from lower limb variables and those derived from the remainder of the skeleton. This accounts for the possibility that upper and lower limbs scale differently to body size in early *Homo* compared with modern humans (Johanson et al., 1987;

Hartwig-Scherer and Martin, 1991; McHenry and Berger, 1998; Ruff, 2009). Previous studies found lower limb variables to be the most reliable and accurate estimators of stature and body mass (e.g., McHenry, 1991, 1992), hence more confidence is attributed to these results. However, since many early *Homo* fossils do not preserve lower limb elements, using values from the entire skeleton carries the advantage of increasing sample size considerably.

Some of the measurements used to estimate body size in the reference populations have low sample sizes (see SOM Tables 8 and 9), potentially influencing the accuracy of the regression equations. This applies particularly to talar measurements ($n < 30$). In order to control for potential bias when using these equations to estimate body size in early *Homo*, we checked whether the exclusion of talus specimens ($n = 5$; KNM-ER 813; KNM-ER 5428; OH 8; Omo 323-76-898; SKX 42695) had an impact on the temporal and spatial results. The use of diaphyseal areas to estimate body mass in fossil *Homo* ($n = 6$ in our sample) poses a more general problem. As early *Homo* probably had wider femoral diaphyses relative to body size than modern humans, the body mass equations based on our reference sample potentially overestimate true values (Trinkaus and Ruff, 2012; C. Ruff, Personal communication). In order to control for the magnitude of this effect, we predicted FHD from femoral midshaft and subtrochanteric diaphyseal areas (mediolateral * anteroposterior dimensions) in specimens that preserve both measurements.

To assess whether body size in early *Homo* varies across time and space, we pooled the best estimates of body size for individual specimens by spatiotemporal groups and analysed them relative to chronological and geographical categories. Non-parametric Kruskal–Wallis tests were used to investigate significant differences ($p < 0.05$) between more than two groups where sample sizes permitted. Post-hoc comparisons among groups were made using Mann–Whitney *U*-tests with Bonferroni correction to protect against Type I errors (Siegel and Castellan, 1988; Sokal and Rohlf, 1995; Zar, 1996). We conducted univariate linear regressions with time as the dependent variable on FHD (body mass) and stature to analyse chronological trends in more detail and test for significant correlations. All calculations and statistical analyses were performed using Microsoft Excel 2007 and SPSS 19.0 for Windows.

Results

Regression equations and body size estimates of individual early Homo specimens

The univariate \log_{10} – \log_{10} linear regression equations created for stature and FHD from the reference sample indicate that 79 of 95, and 89 of 95 estimator variables, respectively, reach significant correlation ($p < 0.05$; SOM Tables 8 and 9). Measurements that correlate significantly with stature ($n = 79$) exhibit %SEEs and %PEs below a maximum of ~6%, with the majority falling in a %SEE range of 3–5%. The 89 measurements significantly correlated with FHD show %SEEs and %PEs below a maximum of 11% and 9%, respectively. The high number of significant correlations and the low maximum %PEs and %SEEs suggest that from a mathematical point of view, most of the employed metric traits can be used to estimate stature or FHD (body mass) in the early *Homo* specimens. Having said this, there is still the potential that systematic differences in body proportions between early and modern *Homo* bias the predictions (see below).

Tables 4 and 5 provide the estimates of stature and FHD from the best predictor variables per individual early *Homo* specimen. When FHD is preserved, the direct measurement was used. The 95% confidence intervals indicate the (sometimes large) error ranges associated with the estimation process. Individual estimates of

body mass (Table 6) are based on the best predictions of FHD, with indication of the range based on the 95% CI of the FHD estimates. The range of stature (133.82–173.19 cm) and FHD (31.92–52.05 mm) estimates fall within or only slightly below the ranges of the reference sample (SOM Table 5). In terms of sample sizes, stature, FHD, and body mass were estimated for a total of 39 specimens, with 27 values deriving from lower limb predictors. To the best of our knowledge, more than a dozen of these early *Homo* specimens had no previously published stature (KNM-ER 813, 1473, 1475, 1812, 5428, 5881, 5882; OH 48, 49; Omo 323–76–898; Stw 311, 567, 571; SK 84, 85; SKX 2045, 34805, 42695; SKW 2954, 3646) or body mass estimates (KNM-ER 5881, 5882; Omo 323–76–898; Stw 567, 571; SK 84, 85; SKX 2045, 34805; SKW 2954, 3646).

We examined the effect of using only tropical populations from our reference sample to estimate body size in early *Homo* specimens from eastern Africa (SOM Appendix 1). For stature, individual differences between global and tropical equations mostly amount to $\pm 2\%$, with rare deviations up to 7% (SOM Table 12). There is, however, no consistent trend of over- or underestimation. FHD values from the tropical equations show that the global sample generally overestimates body mass, but again most differences fall in a range of $\pm 2\%$ (SOM Table 13). Considering the lower sample sizes for all measurements in the tropical sample—and the fact that some measurements are completely missing in this sub-set—we chose to use the estimates from the global equations for all further analyses.

An individual level test for differences in body proportions that might bias the body size predictions is possible for five adult specimens of early *Homo*. Upper limb (and axial) variables tend to overestimate stature and body mass compared with the hindlimb estimators for OH 62 and KNM-ER 3735 and to a lesser extent in the Dmanisi specimen (Figs. 2 and 3), indicating diverging upper limb morphology from the modern human reference sample. No such systematic difference exists for KNM-ER 803 and 1808. These findings suggest that estimates of body size that derive from measurements of the lower limb are more accurate predictors for the entire early *Homo* sample compared with upper limb and axial variables.

The control of body size estimates within single specimens was based on the percentage difference (%diff) between the best and mean predictions from lower limb variables only (Tables 4 and 5). In general, most predictions show %diff below 5%, indicating that the best values provide comparable results. For a few specimens, the %diff falls above 5% (stature: $n = 2$; FHD: $n = 3$). However, only for KNM-ER 1808 does this apply to both variables. In summary, most of the best estimators from the lower limbs compare well with the mean values and are thus consistent measurements to predict stature and FHD (body mass) in early *Homo*.

For FHD, the accuracy of the employed regressions could be further controlled by comparing estimated values in specimens that preserve the actual FHD. The majority of measurements predict actual FHD reasonably well, lying below 10% divergence (SOM Table 14). Although rare deviations above 20% occur, the majority of regression equations perform within an appropriate level of accuracy (cf. Aiello and Wood, 1994). Only three adult early *Homo* specimens allowed prediction of FHD from diaphyseal areas. For one specimen, femoral midshaft and subtrochanteric diaphyseal areas underestimate FHD (2–7%), but for two fossils these measures overestimate FHD (3–9%; SOM Table 14). These results suggest that using diaphyseal areas sometimes overestimates body mass when applied to early *Homo* (see Trinkaus and Ruff, 2012), but the effect appears to be small and applies to only six specimens in our sample. Furthermore, there are not enough data on fossil hominins at this point to adequately derive regression equations to standardize our estimates by.

Table 4
Best and mean estimates for stature (cm) in early *Homo*, including 39 specimens.

Fossil	<i>n</i> ^a	Estimator ^b	Best estimate	Mean estimate	%diff ^c	95% CI ^d
KNM-WT 15000 ^e	9	Ruff and Burgess	178	–	–	171.00–185.00
KNM-ER 164	3	C7DHT	160.85	162.31	+0.91	146.09–177.35
KNM-ER 736	7	F1	172.58	168.53	–2.35	166.49–178.49
KNM-ER 737	10	F1	167.41	166.02	–0.83	161.53–173.14
KNM-ER 741	2	T1	158.29	158.06	–0.15	152.80–163.22
KNM-ER 803	12	F1T1	156.65	160.75	+2.62	152.43–160.73
KNM-ER 1808	8	F2	173.19	159.60	–7.85	167.00–178.54
KNM-ER 5428	2	Ta6	162.65	167.65	+3.07	153.91–171.73
OH 8	3	Ta6	133.82	136.41	+1.94	123.63–144.72
OH 35	2	T1	137.13	142.22	+3.71	132.33–141.47
OH 48	1	C1	161.73	161.73	–	150.64–174.21
OH 49	1	R9	156.73	156.73	–	144.80–170.33
OH 53	4	F1	143.40	151.34	+5.54	138.34–148.34
OH 62	9	F1	148.37	148.00	–0.25	143.15–153.46
KNM-ER 813	3	Ta6	147.92	150.76	+1.92	139.29–156.94
KNM-ER 1472	16	F2	153.73	155.90	+1.41	148.25–158.47
KNM-ER 1473	1	H16	162.91	162.91	–	150.77–175.69
KNM-ER 1475	5	FemArea (ST)	156.74	157.05	+0.20	145.50–170.08
KNM-ER 1481	17	F2	152.47	156.68	+2.76	147.04–157.17
KNM-ER 3228	5	Oc8	168.06	165.84	–1.32	155.78–181.10
KNM-ER 3728	11	F2	151.20	153.30	+1.39	145.82–155.87
KNM-ER 3735	3	T16	149.62	150.59	+0.65	139.47–160.21
KNM-ER 5881	3	FemArea (MS)	152.57	153.22	+0.43	141.01–164.36
KNM-ER 5882	3	FemArea (MS)	153.78	154.19	+0.27	142.14–165.65
Omo 323–76–898	2	Ta6	153.05	145.69	–4.81	144.65–161.80
D2600	11	F1T1	146.69	151.97	+3.60	142.72–150.52
D4111/D3442	2	Mtl6	152.65	151.02	–1.07	135.85–171.36
Stw 311	1	F16	149.48	149.48	–	138.56–160.93
Stw 567	1	T25	156.50	156.50	–	143.49–170.86
Stw 571	3	UlnaArea (P)	158.71	159.12	+0.26	144.89–174.09
SK 18b	2	R1	151.49	153.24	+1.16	144.53–159.45
SK 84	4	Mcl1	141.44	150.21	+6.20	130.52–153.80
SK 85	1	Mcl1	139.37	139.37	–	127.91–152.65
SK 1896	1	F32	153.07	153.07	–	141.53–165.48
SKX 2045	1	R15	159.36	159.36	–	147.91–171.77
SKW 2954	4	Mcl1	135.80	134.49	–0.96	124.44–148.97
SKX 3342	4	T7XHT	145.80	144.79	–0.69	129.01–165.02
SKX 34805	4	H31	148.02	156.22	+5.54	137.90–158.98
SKX 42695	1	Ta12	150.59	150.59	–	140.52–161.66

^a Denotes the total number of measurements per specimen.

^b Abbreviations of estimator variables are explained in SOM Table 6. Exact numerical values used for each estimator are given in SOM Table 2.

^c ((mean estimate – best estimate)/best estimate)* 100.

^d The 95% confidence interval applies to the best estimates only.

^e Estimated adult stature after Ruff and Burgess (2015).

Body size by chronology

To investigate chronological trends in body size we plotted estimates for individual fossils of early *Homo* on a time axis with indication of spatiotemporal group membership (Fig. 4). Univariate linear regressions for body size parameters with time as the dependent variable are significant for FHD ($p = 0.046$), but not for body mass ($p = 0.062$) and stature ($p = 0.077$), and show low R^2 -values (0.120–0.151). The use of quadratic regressions increases R^2 -values slightly (0.267–0.282), and yields significant results for stature, FHD, and body mass ($p = 0.019$ –0.024). The resulting curves of the quadratic regressions appear to be strongly driven by the small Olduvai specimens in the middle of the studied period. Removing the Olduvai group from the analyses supports this assertion (Fig. 5), as linear regression of body size with time as the dependent variable become significant for stature, FHD, and body mass ($p = 0.028$ –0.044; $R^2 = 0.180$ –0.210) and provide a better fit than a quadratic curve. Univariate regressions with group means instead of individual estimates provide principally the same results. As indicated by the spatiotemporal group membership on Figs. 4 and 5, the sample size and chronological duration are too low to analyse temporal trends within groups.

In conclusion, our analyses found both significant and non-significant linear correlations between time and measures of

body size, depending on the sample of early *Homo* specimens included. While there is an increase in body size through time when considering the start and end points, with very large body sizes only occurring at the end of the studied period (Koobi Fora <1.7 Myr), small-bodied individuals occur throughout 1.9–1.5 Myr. The low R^2 -values of the linear regressions suggest that factors other than chronology also influenced body size in our sample of early *Homo*.

Body size by geography

We performed three separate analyses to compare estimates of body size in early *Homo* by their geographical origin, taking into account chronological information when necessary. This approach allowed for the application of statistical methods to investigate spatial differences. First, given that the samples are separated by less than 1000 km, we examined whether there is significant regional variation in body size of early *Homo* within eastern Africa. To answer this question, we used Kruskal–Wallis tests to compare the best estimates of body size from both the lower limb variables and the entire skeleton between Koobi Fora (>1.8 Myr), Olduvai Gorge (~1.8 Myr), and Koobi Fora (<1.7 Myr). The results of all four tests indicate significant differences between the three groups for stature and FHD ($n = 21$; $p = 0.001$ –0.004). Pairwise post-hoc

Table 5Best and mean estimates for FHD (mm) in early *Homo*, including 39 specimens.

Fossil	<i>n</i> ^a	Estimator ^b	Best estimate	Mean estimate	%diff ^c	95% CI ^d
KNM-WT 15000 ^e	22	Ruff and Burgess	52.50	–	–	–
KNM-ER 164	2	C7SBr	43.11	38.88	–9.81	39.09–53.89
KNM-ER 736	8	FemArea (ST)	52.05	49.81	–4.30	46.56–58.27
KNM-ER 737	10	F6	51.15	48.94	–4.32	45.89–56.97
KNM-ER 741	2	T1	43.05	42.94	–0.26	36.63–50.84
KNM-ER 803	18	F6	47.43	44.94	–5.25	42.57–52.81
KNM-ER 1808	15	FemArea (ST)	51.54	45.01	–12.67	46.09–57.68
KNM-ER 5428	2	Ta6	43.81	45.98	+4.95	39.51–48.39
OH 8	3	Ta8	36.14	34.53	–4.45	31.10–40.31
OH 35	2	T16	37.85	37.00	–2.25	33.07–43.21
OH 48	1	C1	45.66	45.66	–	39.71–52.27
OH 49	1	R9	42.46	42.46	–	37.56–48.02
OH 53	4	FemArea (ST)	39.80	39.42	–0.95	35.61–44.53
OH 62	14	FemArea (ST)	34.88	37.25	+6.79	31.18–39.05
KNM-ER 813	5	Ta6	38.76	39.35	+1.52	35.04–43.50
KNM-ER 1472	16	F16 ^f	40.00 ^e	41.83	+4.58	40.00
KNM-ER 1473	1	H16	47.06	47.06	–	43.38–51.09
KNM-ER 1475	5	F19	42.83	42.73	–0.23	38.88–47.14
KNM-ER 1481	17	F16 ^f	43.70 ^e	41.77	–4.42	43.70
KNM-ER 3228	5	F16 ^f	46.10	47.19	2.36	46.10
KNM-ER 3728	11	F19	45.17	40.38	–10.60	41.00–49.71
KNM-ER 3735	8	F28	35.36	39.60	+11.99	31.85–39.05
KNM-ER 5881	3	FemArea (MS)	39.47	40.06	+1.49	35.12–44.46
KNM-ER 5882	3	FemArea (MS)	40.22	40.56	+0.85	35.78–45.29
Omo 323-76-898	3	Ta6	40.50	38.35	–5.31	36.58–44.97
D2600	16	F16 ^f	40.00 ^e	41.14	+2.85	40.00
D4111/D3442	3	Mtl6	38.22	36.81	–3.69	31.63–46.05
Stw 311	1	F16 ^f	36.40 ^e	36.40	–	36.40
Stw 567	1	T25	41.51	41.51	–	36.30–47.35
Stw 571	3	U14	38.09	43.30	+13.68	33.25–43.71
SK 18b	2	R15	41.40	40.98	–1.01	36.59–46.70
SK 84	3	Mcl1	33.64	34.39	+2.23	29.66–38.18
SK 85	1	Mcl1	33.57	34.39	+2.44	28.56–39.48
SK 1896	1	F32	39.87	39.87	–	35.11–46.02
SKX 2045	1	R15	44.21	44.21	–	39.08–49.88
SKW 2954	4	Mcl1	31.92	30.48	–4.51	27.08–37.64
SKX 3342	7	T7XHT	33.10	35.10	+6.04	26.82–40.78
SKX 34805	4	H31	37.08	42.14	+13.65	33.46–41.06
SKX 42695	1	Ta12	39.72	39.72	–	35.01–44.98

^a Denotes the total number of measurements per specimen.^b Abbreviations of used estimator variables are explained in SOM Table 6. Exact numerical values used for each estimator are given in SOM Table 2.^c ((mean estimate – best estimate)/best estimate) * 100.^d The 95% confidence interval applies to the best estimates only.^e Estimated adult FHD after Ruff and Burgess (2015).^f Indicates measures of actually preserved FHD of early *Homo* specimens.

comparisons show significant differences between Koobi Fora (<1.7 Myr) and Olduvai Gorge ($p = 0.001$ – 0.005), but also between the two groups from Koobi Fora ($p = 0.031$ – 0.042). In both cases, specimens from Koobi Fora (<1.7 Myr) are significantly larger in body size. We performed further analyses of regional differences by combining the two Koobi Fora groups and comparing them with Olduvai Gorge. The Mann–Whitney *U*-test demonstrates that the combined Koobi Fora group is significantly larger in stature and FHD (body mass) than the Olduvai Gorge specimens ($p = 0.001$ – 0.030).

In a further test of geographical patterns within the entire sample of early *Homo* we employed Kruskal–Wallis tests to analyse the difference between body size estimates of the combined eastern African groups, the southern African fossils, and the Dmanisi specimens. We used both the best estimates from the lower limbs and the entire skeleton. The results suggest that there are no significant differences between the groups for stature and FHD based on the lower limb estimates ($p = 0.486$; $p = 0.329$). The same applies to stature from all estimates ($p = 0.066$), but differences for FHD are significant ($p = 0.008$). In this analysis, the eastern African group is significantly larger than the southern African group ($p = 0.007$).

A potentially confounding factor in this analysis is the lumping of three separate groups into the ‘eastern Africa group,’ as they exhibit significant differences in stature and FHD from one another. To account for this, the differences between southern and eastern Africa were analysed in more detail. We compared the southern African group to Koobi Fora (<1.7 Myr) and both Olduvai and Koobi Fora (>1.8 Myr). The Mann–Whitney *U*-test demonstrates that Koobi Fora (<1.7 Myr) yields significantly larger stature ($p < 0.006$) and FHD ($p < 0.006$) estimates compared with the southern African group. In the second part of the analysis, Kruskal–Wallis and Mann–Whitney *U*-tests show no significant pairwise differences between southern African specimens and both Olduvai and Koobi Fora (>1.8 Myr) for estimated stature or FHD values ($p > 0.111$). Hence, the geographical difference between eastern and southern Africa is mainly driven by the large Koobi Fora group (<1.7 Myr).

A third analysis examined body size differences among early *Homo* before and after the earliest dispersals out of Africa. To this end we performed individual Mann–Whitney *U*-tests between the two potential source populations in eastern Africa that predate Dmanisi and the eastern African group that postdates these expansions. For all estimates of stature and FHD neither Olduvai

Table 6
Best estimates for body mass (kg) in early *Homo*, including 39 specimens.^a

Fossil	FHD best	Body mass best	95% CI ^c
KNM-WT 15000 ^b	—	81	80–83
KNM-ER 164	43.11	60	51–84
KNM ER 736	52.05	80	67–93
KNM ER 737	51.15	78	66–91
KNM-ER 741	43.05	60	42–78
KNM-ER 803	47.43	69	59–82
KNM-ER 1808	51.54	79	66–92
KNM-ER 5428	43.81	61	52–72
OH 8	36.14	41	30–54
OH 35	37.85	45	34–60
OH 48	45.66	65	52–81
OH 49	42.46	58	44–72
OH 53	39.80	53	40–63
OH 62	34.88	38	30–51
KNM-ER 813	38.76	50	39–61
KNM-ER 1472	40.00 ^d	53	42–64
KNM-ER 1473	47.06	68	60–78
KNM-ER 1475	42.83	59	51–68
KNM-ER 1481	43.70 ^d	61	49–73
KNM-ER 3228	46.10 ^d	66	53–79
KNM-ER 3728	45.17	64	55–75
KNM-ER 3735	35.36	39	31–51
KNM-ER 5881	39.47	52	39–63
KNM-ER 5882	40.22	54	40–64
Omo 323-76-898	40.50	54	42–64
'D2600'	40.00 ^d	53	42–64
D4111/3442	38.22	46	31–66
Stw 311	36.40 ^d	42	34–50
Stw 567	41.51	56	41–69
Stw 571	38.09	45	35–61
SK 18b	41.40	56	42–68
SK 84	33.64	35	27–46
SK 85	33.57	35	24–52
SK 1896	39.87	53	39–66
SKX 2045	44.21	62	51–76
SKW 2954	31.92	32	21–44
SKX 3342	33.10	34	20–55
SKX 34805	37.08	43	35–55
SKX 42695	39.72	53	38–64

^a Body mass is calculated based on the best value of the predicted FHD.

^b Adult body mass estimates after Ruff and Burgess (2015).

^c 95% confidence intervals are based on the 95% CI of the best FHD estimation. Body mass values for specimens with preserved FHD are calculated by $\pm 20\%$ (Ruff, 2010).

^d Indicates measures of actually preserved FHD of early *Homo* specimens.

($p > 0.267$) nor Koobi Fora (>1.8 Myr; $p > 0.273$) are significantly different from the Dmanisi specimens. In contrast, there is a complete separation without overlap between fossils from Koobi Fora (<1.7 Myr) and Dmanisi when looking at individual body size estimates. These differences are significant for stature and FHD when estimates from the entire skeleton are used ($p = 0.044$) and near-significant for estimates from the lower limbs only ($p = 0.056$), despite the very small sample sizes ($n = 9$).

For illustrative purposes, Tables 7–9 and Figs. 6–8 summarize the mean values of the best estimates for stature, FHD, and body mass, organised by the five spatiotemporal groups. For all three parameters of body size the same relative pattern from largest to smallest emerges when lower limb predictors are used ($n = 27$): Koobi Fora (<1.7 Myr), Koobi Fora (>1.8 Myr), southern Africa (1.8–1.4 Myr), Dmanisi (~ 1.8 Myr), Olduvai Gorge (1.75 Myr). Using predictor variables from the entire skeleton ($n = 39$) yields a similar pattern but with markedly larger ranges for most groups. The sample of fossils from Koobi Fora (<1.7 Myr) shows by far the highest estimates of body size for all predictors.

Finally, we performed all spatial and chronological analyses without estimates of body size derived from talar measurements ($n = 5$), due to the small sample sizes of the original regression

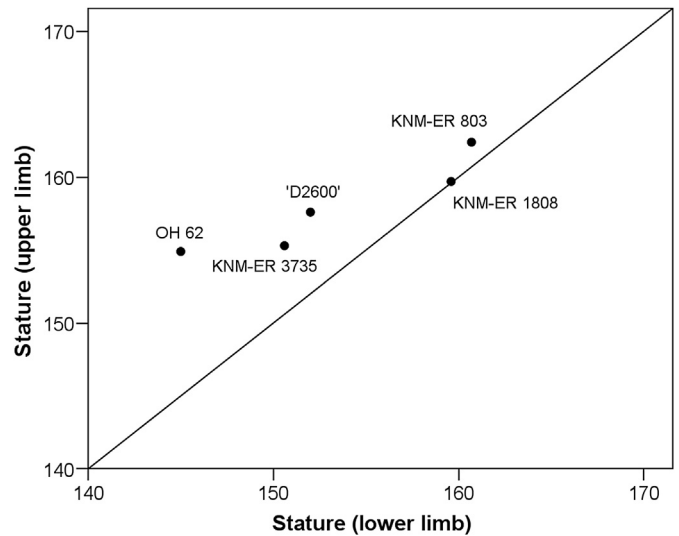


Figure 2. Comparison of the mean upper versus lower limb stature estimates (in cm) for individual early *Homo* specimens. The line indicates whether upper limbs generally overestimate (point above the line) or underestimate (point below the line) stature.

equations. In so doing, the chronological regressions provide principally the same picture as before, with the exception that the linear correlation between stature and time becomes non-significant ($p = 0.058$) when excluding the Olduvai specimens from the analyses. The relative pattern of all three parameters of body size for the five spatiotemporal groups also remains constant, with slight fluctuations in average values. The only change in the spatial analyses concerns the differences between Koobi Fora (<1.7 Myr) and Dmanisi, which become partially non-significant ($p = 0.044$ – 0.056) in the Mann–Whitney *U*-test. This result, however, is entirely contingent upon the lower sample sizes in the non-parametric statistical analyses, as the body size values of both groups are still non-overlapping. Thus, the exclusion of talar body size estimates does not change any of the results in a substantial manner.

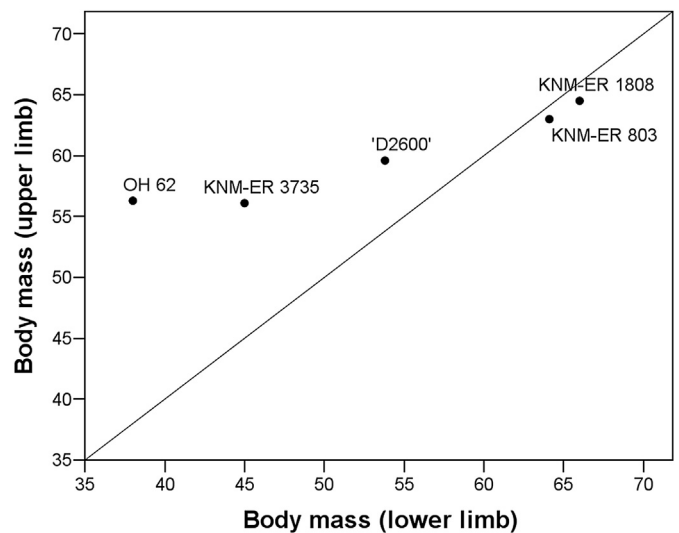


Figure 3. Comparison of the average upper versus lower limb body mass estimates (in kg) for individual early *Homo* specimens, estimated from FHD. The line indicates whether upper limbs generally overestimate (point above the line) or underestimate (point below the line) body mass.

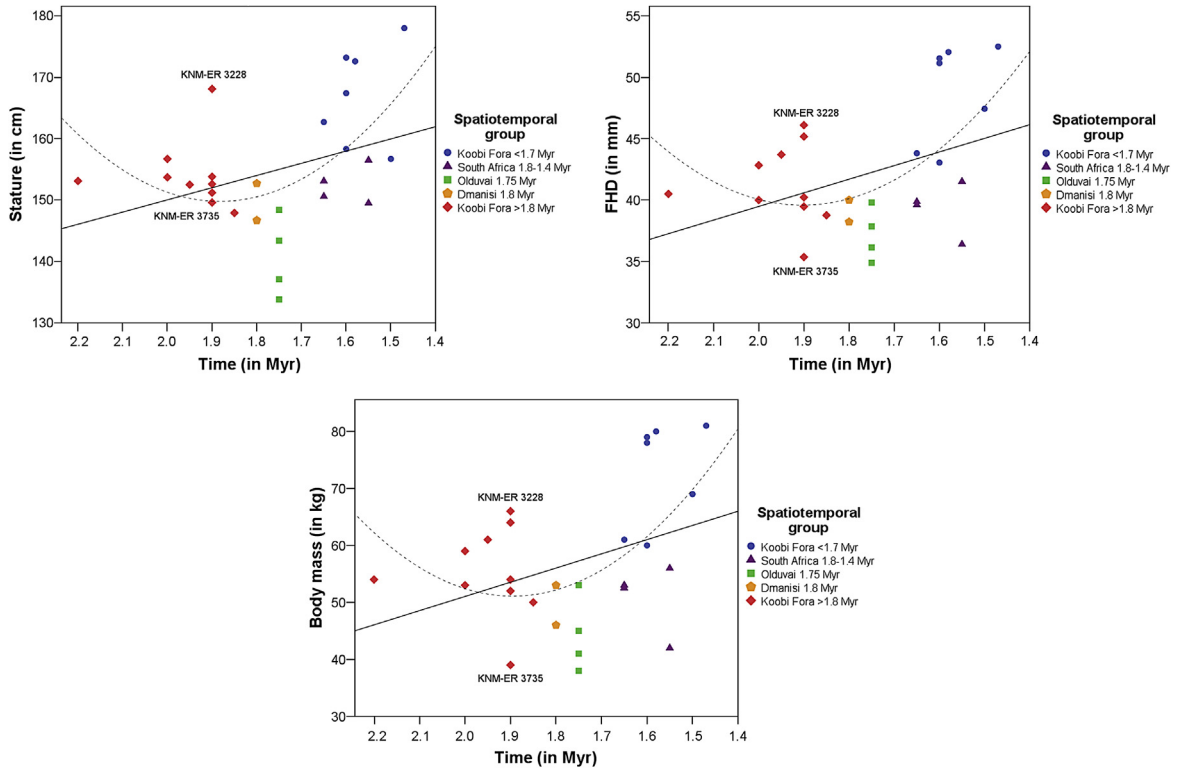


Figure 4. Scatter plots of the three body size variables on a timescale (in Myr), deriving from lower limb estimates for the entire sample for early *Homo*. Individual points mark early *Homo* specimens with indication of their spatiotemporal group membership. OLS best-fit lines are matched to each scatter plot. From top left to bottom: stature ($R^2 = 0.120$; $p = 0.077$), FHD ($R^2 = 0.151$; $p = 0.046$), body mass ($R^2 = 0.132$; $p = 0.062$). Note that the line of the quadratic regression describes the observed variation in body size through time slightly better.

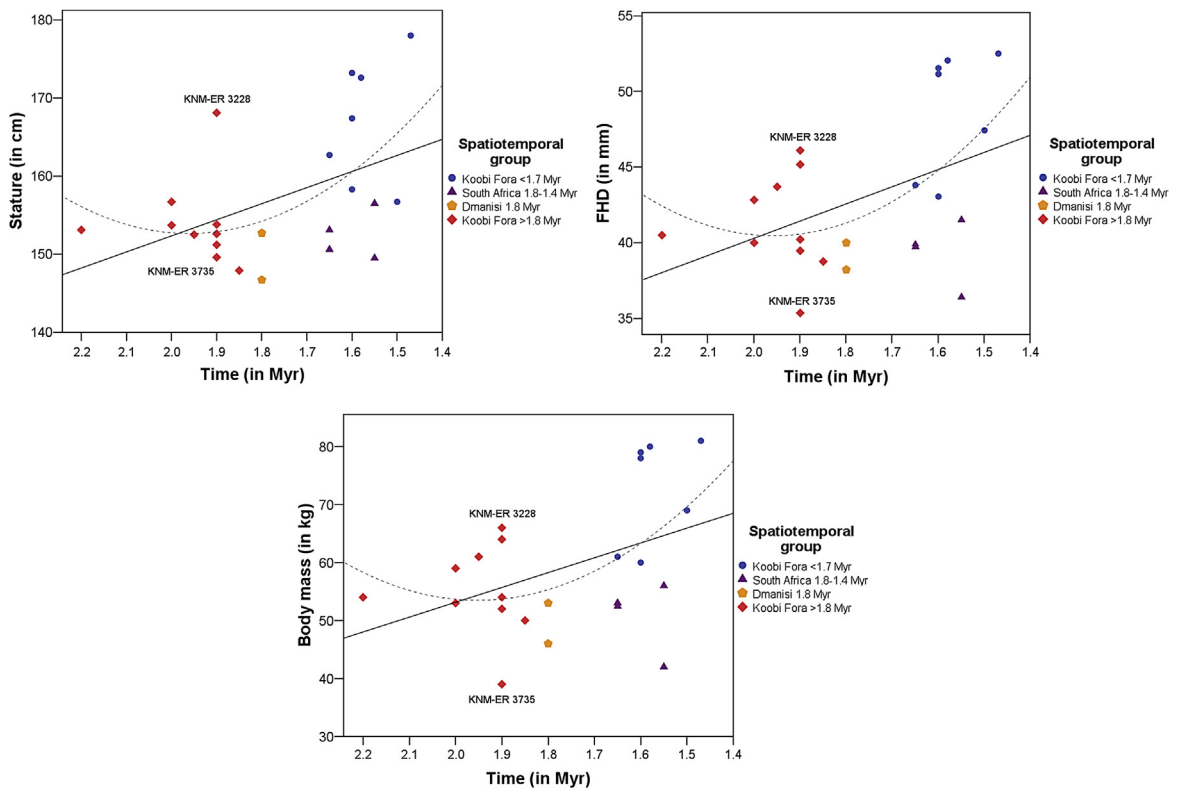


Figure 5. Scatter plots of the three body size variables on a timescale (in Myr), deriving from lower limb estimates and excluding the Olduvai specimens (1.75 Myr). Individual points mark early *Homo* specimens with indication of their spatiotemporal group membership. OLS best-fit lines are matched to each scatter plot. From top left to bottom: stature ($R^2 = 0.210$; $p = 0.028$), FHD ($R^2 = 0.195$; $p = 0.035$), body mass ($R^2 = 0.180$; $p = 0.044$). Note the steeper slope of the linear regression through time.

Table 7
Mean stature estimates (in cm) of the spatiotemporal groups.

Group	Best estimate lower limbs					Best estimate entire skeleton				
	<i>n</i>	Mean	SD	Min.	Max.	<i>n</i>	Mean	SD	Min.	Max.
Koobi Fora, <1.7 Myr	7	167.0	8.1	156.7	178.0	8	166.2	7.8	156.7	178.0
South African caves, 1.8–1.4 Myr	4	152.4	3.1	149.5	156.5	12	149.1	7.5	135.8	159.4
Olduvai, 1.75 Myr	4	140.7	6.5	133.8	148.4	6	146.9	10.9	133.8	161.7
Dmanisi, 1.8 Myr	2	149.7	4.2	146.7	152.7	2	149.7	4.2	146.7	152.7
Koobi Fora, >1.8 Myr	10	153.9	5.5	147.9	168.1	11	154.7	5.9	147.9	168.1
Total	27	154.8	10.3	133.8	178.0	39	153.9	10.0	133.8	178.0

Table 8
Mean FHD estimates (in mm) of the spatiotemporal groups.

Group	Best estimate lower limbs					Best estimate entire skeleton				
	<i>n</i>	Mean	SD	Min.	Max.	<i>n</i>	Mean	SD	Min.	Max.
Koobi Fora, <1.7 Myr	7	48.8	4.0	43.1	52.5	8	48.3	4.0	43.1	52.5
South African caves, 1.8–1.4 Myr	4	39.4	2.1	36.4	41.5	12	37.6	3.9	31.9	44.2
Olduvai, 1.75 Myr	4	37.2	2.1	34.9	39.8	6	39.5	4.1	34.9	45.7
Dmanisi, 1.8 Myr	2	39.1	1.3	38.2	40.0	2	39.1	1.3	38.2	40.0
Koobi Fora, >1.8 Myr	10	41.2	3.2	35.4	46.1	11	41.7	3.5	35.4	47.1
Total	27	42.1	5.2	34.9	52.5	39	41.3	5.3	31.9	52.5

Table 9
Mean body mass estimates (in kg) of the spatiotemporal groups.

Group	Best estimate lower limbs					Best estimate entire skeleton				
	<i>n</i>	Mean	SD	Min.	Max.	<i>n</i>	Mean	SD	Min.	Max.
Koobi Fora, <1.7 Myr	7	72.6	9.1	60	81	8	71.0	9.6	60	81
South African caves, 1.8–1.4 Myr	4	51.0	6.2	42	56	12	45.5	10.3	32	62
Olduvai, 1.75 Myr	4	44.3	6.5	38	53	6	50.0	10.5	38	65
Dmanisi, 1.8 Myr	2	49.5	4.9	46	53	2	49.5	4.9	46	53
Koobi Fora, >1.8 Myr	10	55.2	7.8	39	66	11	56.4	8.4	39	68
Total	27	57.0	12.3	38	81	39	54.7	13.0	32	81

Discussion

Spatial and temporal variation in the body size of early Homo

In our analysis of spatial and temporal variation of body size among early *Homo*, we did not find simple geographical or chronological trends. Regarding geography, eastern Africa includes the two groups with the largest estimates of body size (both at Koobi Fora) but also the one with the lowest (Olduvai). The southern

African and Eurasian groups lie in between. Having said that, closer consideration of the variation between groups of different regions, based on the identification of statistically significant differences within an expanded sample size, demonstrates that there are geographical patterns of body size among early *Homo*. We found consistent and significant regional variation in stature and FHD (body mass) within early *Homo* of eastern Africa. Specimens at Koobi Fora (<1.7 Myr) are significantly larger in body size than both the individuals from Olduvai and Koobi Fora (>1.8 Myr). We did not

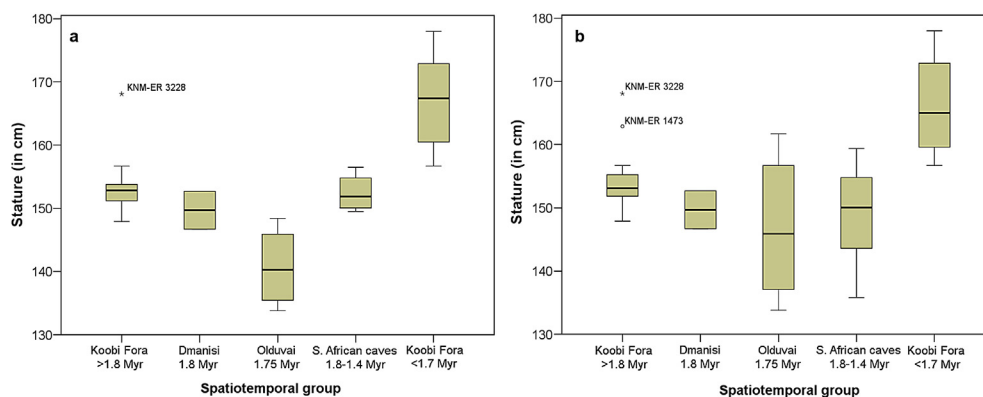


Figure 6. Box plots for estimated stature (in cm) by spatiotemporal group. a) Best estimates from lower limb variables; b) Best estimates from variables of the entire skeleton.

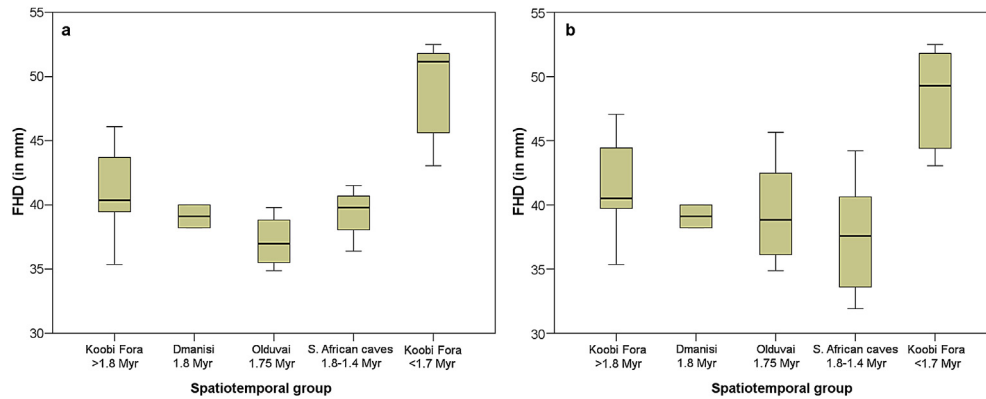


Figure 7. Box plots for estimated FHD (in mm) by spatiotemporal group. a) Best estimates from lower limb variables; b) Best estimates from variables of the entire skeleton.

find significant differences between the older Koobi Fora (>1.8 Myr) and Olduvai fossils. Our results also indicate the existence of significant differences in body size between eastern and southern Africa. Specimens from southern Africa are significantly smaller than the roughly contemporaneous early *Homo* fossils from Koobi Fora (<1.7 Myr) but not different from the earlier specimens from Koobi Fora (>1.8 Myr), Dmanisi (~1.8 Myr), and Olduvai (1.75 Myr).

The size variation within the entire sample of early *Homo* specimens does not conform to a uniform increase through time. Larger body size estimates occur at the beginning (~1.9 Myr) and particularly the end (~1.6–1.5 Myr) of the analysed period, while specimens in between—particularly the very small Olduvai fossils at ~1.75 Myr—show lower values. The possibility that several species of early *Homo*, with marked variations in body size, are included constitutes a potential confounding factor when using the entire sample of early *Homo* (e.g., Wood and Collard, 1999; Schrenk et al., 2007; Spoor et al., 2007; Ruff, 2009; Antón, 2012; Leakey et al., 2012). When removing the Olduvai specimens from the temporal analysis—which are consistently the smallest group—there is a stronger signal of a linear increase in body size through time in the remaining sample of early *Homo* (Fig. 5) that also reaches statistical significance. The most marked temporal change in the studied period is the dramatic increase in body size of Koobi Fora specimens that post-date 1.7 Myr (see also Ruff and Burgess, 2015). Interestingly, smaller-bodied individuals persist throughout 1.9–1.5 Myr (Fig. 4), even when excluding the Olduvai fossils (Fig. 5).

Regarding the earliest dispersals from Africa to Eurasia, we found significant differences and no overlap between the ranges of body size parameters for specimens from Koobi Fora (<1.7 Myr) and

Dmanisi. On the other hand, potential source populations in eastern Africa that predate Dmanisi are not significantly different in their estimated body sizes. They are either smaller (Olduvai) or larger (Koobi Fora, >1.8 Myr). Marked body size increases in eastern Africa during the Early Pleistocene appear to take place only *after* the dispersals to Eurasia, with the notable exception of KNM-ER 3228 (see below). The confidence that we ascribe to these findings derives from their general consistency and repeatability under various conditions, including the use of different analytical methods, estimators, and body size parameters.

How can we explain the observed variations in body size? Apart from the potential impact of nutrition or local environmental factors, sexual dimorphism might play a role (e.g., Jungers, 1988b; McHenry, 1994; Plavcan and Cope, 2001; Antón, 2003, 2012; Plavcan, 2012). However, almost all studied spatiotemporal groups include smaller and larger individuals and assessing sex based on the isolated and fragmentary postcranial remains of early *Homo* is nearly impossible (cf. Antón, 2012; Plavcan, 2012). Yet, there is no reason to expect systematic bias towards any sex within the spatiotemporal groups. While sexual differences remain an important source of variation, available data are inappropriate for such an analysis.

Taxonomic differences may actually explain a significant amount of the observed variation. Although we set out explicitly for a ‘taxon-free’ approach, this study provides contextual information on size variation between potential lineages. The body size estimates of the taxonomically controversial Dmanisi hominins, which have been linked to either *H. ergaster*, *H. habilis*, *Homo georgicus*, or even *H. erectus ergaster georgicus* (Vekua et al., 2002; Rightmire et al., 2006; Lieberman, 2007; Lordkipanidze et al., 2007, 2013;

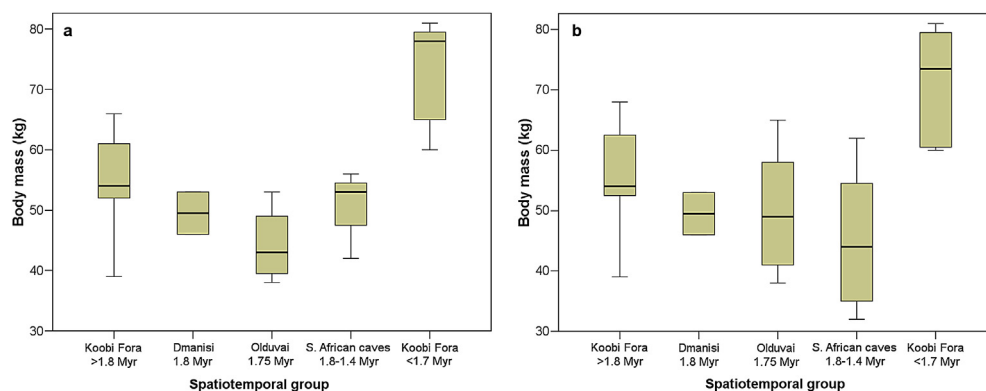


Figure 8. Box plots for estimated body mass (in kg) by spatiotemporal group. a) Best estimates from lower limb variables; b) Best estimates from variables of the entire skeleton.

Pontzer et al., 2010; Jiménez-Arenas et al., 2011; Bermúdez de Castro, 2014; Zollikofer et al., 2014), lie closest to the small-bodied Olduvai specimens at ~1.75 Myr and fall outside the range of Koobi Fora fossils younger than 1.7 Myr. Based on a larger sample of early *Homo* specimens and the application of statistical tests, our study supports the ancestral status of body size in the Dmanisi individuals (Lordkipanidze et al., 2007; Pontzer et al., 2010), which is important for taxonomic attributions of these fossils.

The significant differences in size between fossils at Olduvai Gorge ~1.75 Myr and Koobi Fora after 1.7 Myr might reflect taxonomic differences between *H. habilis* and *H. ergaster*, respectively (e.g., Leakey et al., 1964; Brown et al., 1985; Leakey and Walker, 1985; Johanson et al., 1987; Wood, 1992; Walker and Leakey, 1993). The small body sizes at around 1.75 Myr in Olduvai and the differences in the estimates from upper and lower limbs (Figs. 2 and 3) could support previous conclusions that *H. habilis* is not part of the same evolving lineage as *H. ergaster* (Wood and Collard, 1999; Ruff, 2009; Wood, 2009, 2014; Berger et al., 2010). When excluding the Olduvai specimens from the chronological analyses, the trajectory of body size evolution in early *Homo* also conforms better to the hypothesis of a consistent increase through time (e.g., Foley, 1987). Nevertheless, the previously described taxonomic ambiguities and potential circularities of attributing postcranial specimens to any early *Homo* species must be taken into account. In addition, the finding of significant differences in body size between older and younger fossils from Koobi Fora remains an enigmatic aspect in this scenario if one does not invoke an additional species such as *H. rudolfensis* (e.g., Alexeev, 1986; Wood, 1992; McHenry and Coffing, 2000; Spoor et al., 2007; Antón, 2012; Leakey et al., 2012; Antón et al., 2014). Particularly in the latter case, our results do not necessarily need to reflect taxonomic differences, but could also indicate that intra-species variation in body size through time (e.g., at Koobi Fora) is larger than previously recognized (see also Antón et al., 2014). To answer this question, future studies will need to assess the potential extent of intra- versus inter-species variation in body size of extinct hominins.

Recent size estimates for the adult specimen of *Australopithecus sediba* (MH 2) based on the preserved FHD (32.7 mm) and estimated body mass (33.3 kg; Berger et al., 2010; Kibii et al., 2011) fall outside and below the range of the entire sample of early *Homo* in this study. This might inform current debates about whether or not this species, dated to ~1.977 Myr, is a direct ancestor of the genus *Homo* (Pickering et al., 2011; Irish et al., 2013; Kimbel, 2013).

Several postcranial specimens deserve individual discussion to contextualize and evaluate the findings from our analyses. The attribution to *Homo* is challenged for some of the fossils included in the sample, particularly for southern African specimens such as SK84, SKX 34805, and SKX 42695 (e.g., Susman, 1989; Trinkaus and Long, 1990; Zipfel et al., 2011). Susman (1989) initially classified the distal humerus SKX 34805 to *Paranthropus* but subsequently re-assigned the specimen to *Homo* based on comparisons of an expanded sample of distal humeri at Swartkrans (Susman et al., 2001). Only further morphological studies and comparisons with distal humeri definitely associated with *Homo* can clarify the taxonomy of this specimen. In terms of its estimated body size values, SKX 34805 falls close to the mean of its southern African group. The same applies to the fragmentary femur KNM-ER 3728 within the Koobi Fora group >1.8 Myr, which could be either *Homo* (McHenry, 1991; Walker and Leakey, 1993) or *Paranthropus boisei* (Howell, 1978; Feldesman and Lundy, 1988; Wood, 2011a). Since these fossils lie close to the mean of their respective spatiotemporal groups, their potential exclusion does not change the main findings of this study. Nevertheless, if these specimens are indeed *Paranthropus* there would be a large overlap in body size with early *Homo* in southern and eastern Africa. Since it is difficult to securely attribute

much of the southern African fossil material to a genus, the results for this spatiotemporal group should be treated with caution.

OH 62 and KNM-ER 3735 are important specimens as they constitute the only fossils included here that are directly identified as *H. habilis* (Johanson et al., 1987; Leakey et al., 1989; Holliday, 2012). Based on their reconstructed body size (e.g., OH 62 at 100–120 cm; 20–37 kg) and proportions, some scholars have considered *H. habilis* to be an australopithecine grade hominin (Johanson et al., 1987; Feldesman and Lundy, 1988; McHenry, 1992; Hartwig-Scherer, 1993; Wood and Collard, 1999; Ruff, 2009). These conclusions have subsequently been criticized due to the highly fragmentary nature of the fossils (Korey, 1990; Richmond et al., 2002; Reno et al., 2005; Holliday, 2012), and recent studies have reached different conclusions (Haeusler and McHenry, 2004, 2007; Pontzer, 2012). For our predictions, we used the midpoint value of the estimated femur length for OH 62 (354–404 mm) suggested by Haeusler and McHenry (2004). While some researchers rightly criticise this value as being speculative due to the incomplete nature of the specimen (cf. Korey, 1990; Richmond et al., 2002; Reno et al., 2005; Holliday, 2012), body size estimates from our study based upon six different femoral measurements available from this fossil produce corresponding estimates, which are all distinctly larger than those of previous studies. Our estimates place OH 62 slightly above the mean of the entire Olduvai group for its estimated stature, but with a smaller FHD and body mass than the other specimens in this group. While this fossil falls at the lower end of the range of body size variation for the entire sample of early *Homo*, it is not atypically small. Interestingly, KNM-ER 3735 exhibits almost the same values for the estimated parameters of body size (contra Leakey et al., 1989; Haeusler and McHenry, 2007). With these estimates, KNM-ER 3735 represents by far the smallest individual of the Koobi Fora specimens >1.8 Myr, and can be seen as an outlier for this group concerning FHD and body mass (Fig. 4).

KNM-ER 3228 constitutes an important fossil for the examination of body size evolution in early *Homo*. Researchers are divided between allocating this fossil to *H. rudolfensis* (McHenry and Coffing, 2000) or *H. ergaster* (Rose, 1984; Antón, 2003; Wood, Personal communication). The importance of KNM-ER 3228 derives from its early age (~1.9 Myr) and its relatively modern pelvic morphology with adaptations to obligate bipedality (Rose, 1984). Apart from its species allocation, KNM-ER 3228 is at present the only fossil of early *Homo* that provides evidence for large body size before the earliest dispersals out of Africa at ~1.8 Myr. This is reflected in the outlier position for stature in the chronological analysis (Fig. 4). The taxonomic attribution of KNM-ER 3228 thus remains crucial for scenarios regarding the earliest dispersals into Eurasia and the antiquity of large-sized *H. ergaster*.

Evolutionary implications

The earliest dispersals of hominins into Eurasia ('Out of Africa 1,' see Wells and Stock, 2007; Fleagle et al., 2009) are often explained by an increase in body size and lower limb length of *H. ergaster* in association with changes in foraging behaviour (higher quality diet, such as meat). According to this 'ecomorphological model,' *H. ergaster* was the first hominin to colonize other continents due to its energetically efficient bipedal locomotion, long distance travel abilities, large home range sizes, and habitat tolerance (Antón et al., 2001, 2002; Foley, 2001, 2002; Antón and Swisher, 2004). In this view, *H. ergaster* evolved in eastern Africa around 1.8 Myr and dispersed rapidly into Eurasia (but see Dennell and Roebroeks, 2005; Wood, 2011b). Having said that, our findings support previous interpretations of the Dmanisi fossils as being in the lower range of variation among early *Homo* in terms of body mass and stature (Lordkipanidze et al., 2007) and lower limb length (Pontzer

et al., 2010). According to the postcranial evidence for body size presented in this study, the marked increase of body size variables in early *Homo* took place after 1.8 Myr in eastern Africa (see also Ruff and Burgess, 2015). By this point, the dispersals had already happened, suggesting that migrations into Eurasia were possible without a significant increase in body size and possibly lower limb length. It is also important to note that no postcranial material older than 1.8 Myr has been unequivocally assigned to *H. ergaster*.

If we set the issue of the taxonomic relationship of the Dmanisi specimens to the African early *Homo* species aside, the small body size of the Dmanisi material fits well within the range found among some of the contemporaneous fossils within Africa (i.e., Olduvai Gorge). As body size is both heritable and plastic relative to life history (Wells and Stock, 2011; Kuzawa and Bragg, 2012), it remains difficult to interpret the significance of the large size of a single individual such as KNM-ER 3228. The species attribution of this fossil, however, is crucial for the 'ecomorphological model' of dispersal. If the specimen is classified as *H. ergaster*, it is the single postcranial specimen of this taxon which suggests that increased body size may have been established prior to the dispersal, but it raises more taxonomic questions about the Dmanisi specimens. However, as pointed out above, KNM-ER 3228 could also be part of a single evolving lineage with much higher intra-species variability over time than previously assumed. With our data, we cannot unambiguously differentiate between these interpretations.

Our observations also have implications for questions regarding the taxonomy of early *Homo*. We found marked and significant differences in body size and proportions among the roughly contemporaneous groups of Koobi Fora and Olduvai Gorge that cannot be explained by either geography or time. While we cannot rule out the existence of extremely high intra-species variation in body size, our results are in agreement with the independent cranial evidence for at least two co-existing morphotypes in the Early Pleistocene of eastern Africa (Wood, 1992, 1999; Rightmire, 1993; Lieberman et al., 1996; Schrenk et al., 2007; Antón, 2012; Leakey et al., 2012; Antón et al., 2014).

Limitations and future studies

We believe that a clear statement concerning the limitations of this study is important in order to improve future research into the body size of early *Homo*. While we considerably increased the sample of early *Homo* for which size has been estimated ($n = 39$) by including more fragmentary and isolated fossils, an even finer resolution is required for improved geographical and chronological investigations. Variation between species can only be studied once the number of taxonomically secure postcranial fossils increases and the status of important specimens (e.g., KNM-ER 3228) is re-evaluated.

Arguably the most crucial limitation of this study is the utilisation of estimated stature and FHD (as indirect body mass measurement) to create all regression equations because actual values of body height and weight were not available for the comparative populations. We justified this approach based on the fact that hunter-gatherer groups, including very small and large individuals, constitute a more adequate reference sample for early *Homo* than (post-) industrial modern humans. While these issues do not compromise the analyses of strictly relative differences, more reliable absolute estimates could be obtained from reference samples of known or reconstructed stature and body mass. Another potential methodological limitation is the use of OLS as a line-fitting technique. Although it is more appropriate than MA/RMA in the context of this study, 'inverse calibration' could be an additional option (Koenigsberg et al., 1998; Hens et al., 2000).

Many of the linear measurements collated for the early *Homo* database carry potential errors (see SOM Table 2). The sources of

these errors include the estimation of bone lengths, diverging values obtained by several researchers on the same specimen, different measuring techniques (analog versus digital), and disagreement about definitions of measurements. These potential errors are intrinsic in the published data, however, and could not be overcome by us. While the error margins are particularly large for some of the elements that are usually not used in the estimation of body size (e.g., SKX 3342; OH 49), at present there is no other means of estimating size from these specimens.

In a similar way, different body proportions in some of the early *Homo* specimens (e.g., *H. habilis*) compared with the reference sample of modern humans might introduce systematic errors. While we tried to factor this into our analyses by focussing on estimates from the lower limbs only, there is still the possibility that some species had relatively smaller lower limbs compared with modern humans. As we do not know the body proportions for the vast majority of included specimens, and discussion about body proportions in early *Homo* species is still ongoing (McHenry, 1992; Hartwig-Scherer, 1993; Wood and Collard, 1999; Richmond et al., 2002; Haeusler and McHenry, 2004; Reno et al., 2005; Ruff, 2009; Holliday, 2012; Pontzer, 2012), we could not completely circumvent this problem in the study.

In light of the above stated limitations, this study should be considered as a first step to render the size of early *Homo* postcranial fossils more broadly comparable through space and time, which can be improved on both methodological and empirical grounds (cf. Plavcan, 2012). In order to obtain more accurate regression equations that yield better absolute estimates of body size, anatomical reconstruction of stature (Raxter et al., 2006; Auerbach and Ruff, 2010) coupled with morphometric estimation of body mass (Ruff, 2000; Auerbach and Ruff, 2004) could be employed on a global sample of well-preserved skeletons of pre-industrial hunter-gatherer populations. These reference populations could also include a larger sample of all climatic zones in order to test for the magnitude of latitudinal effects on the resulting estimation equations.

In the absence of more securely dated fossils representing an expanded geographic range (Grine and Fleagle, 2009; Kimbel, 2009), the quality and quantity of data on the postcranial remains could be increased by applying new data capture techniques and virtual reconstructions of fragmentary fossils (e.g., Wood, 2010). Furthermore, the use of more linear measurements with larger sample sizes—such as from the tarsals, carpals, foot/hand phalanges, and scapula—would enable the creation of more reliable regressions of body size estimations in an even greater number of purported early *Homo* specimens. Finally, future studies could include broadly contemporaneous australopithecine specimens to evaluate body size differences between larger samples of early *Homo* as well as *Australopithecus* and *Paranthropus* or analyse spatial and temporal variation in fossil *Homo* throughout the entire Pleistocene (see Ruff et al., 1997; Holliday, 2012; Pontzer, 2012).

Conclusion

In order to compare body size among specimens of early *Homo*, we developed regression equations to estimate stature and body mass from a wide range of isolated and fragmented postcranial remains ($n = 39$). With this approach, we rendered the size of different skeletal elements comparable through estimates of common size parameters. Our analyses of these estimates suggest that:

- There is abundant temporal and spatial variation but no consistent unilinear temporal or geographical trend in the evolution of body size when looking at the entire sample of fossils currently attributed to early *Homo*.

- The general pattern of temporal variation in early *Homo* shows increasing body size through time when considering the start and end point of this study (2.2–1.5 Myr). Pronounced body size increases in early *Homo* were established only after the dispersals out of Africa (<1.8 Myr) in the eastern African fossil record.
- The Olduvai fossils produce estimates of body size that are distinctly smaller compared with the other spatiotemporal groups, raising questions with respect to their taxonomic status. Without the Olduvai specimens, the trajectory of body size evolution in early *Homo* conforms better to the hypothesis of a consistent increase in body size through time.
- The earliest hominins outside Africa (Dmanisi, 1.77 Myr) fall in the lower range of variation in the entire early *Homo* sample, supporting interpretations that the earliest migrations into Eurasia were not contingent upon a marked increase in body size.
- The primary evidence for pronounced increases in body size among early *Homo* comes from Koobi Fora, suggesting regional variation in size. The eastern African specimens comprise the two groups with the largest body sizes at >1.8 Myr and <1.7 Myr (both Koobi Fora) but also the one with the lowest at ~1.75 Myr (Olduvai Gorge). The statistically significant differences in body size between these groups are consistent with the cranial evidence for at least two separate and co-existing lineages in the Early Pleistocene of eastern Africa. This study presents the first application of statistical tests to examine geographical variation in body size among early *Homo*.

Despite various problems and limitations that complicate studies of body size estimation in extinct hominins (e.g., Steudel, 1985; Martin and Barbour, 1989; Aiello, 1992; Dagosto and Terranova, 1992; McHenry, 1994; Ruff, 1994, 2002, 2009; Smith, 1996, 2009; Koenigsberg et al., 1998; Hens et al., 2000; Porter, 2002; Kurki et al., 2010; Carretero et al., 2012; Plavcan, 2012; Dingwall et al., 2013; Ruff and Burgess, 2015), we encourage the search for new approaches of estimating and analysing this important biological variable. A better understanding of body size—even on strictly relative grounds—is crucial to obtain a more complete and coherent picture of the origin, adaptive strategies, and evolution of the genus *Homo*. We consider our contribution as a small part of this process.

Acknowledgements

We would like to thank Jeremy DeSilva and Randall Susman, who kindly provided their raw measurements for early *Homo* specimens (J. DeSilva for Stw 567, KNM-ER 1481, KNM-ER 5428, OH 8, and OH 43; R. Susman for OH 7 and OH 8) as well as thoughtful comments. We are also indebted to Christopher Ruff, Bernard Wood, and the anonymous reviewers for helpful comments and suggestions on earlier drafts, which have greatly improved this manuscript. MW thanks Rie Goto for her patience and help concerning the statistical analyses. JTS would also like to acknowledge generous funding from the Natural Environment Research Council, UK, (Grant Number: NE/M/S/2003/00069) for supporting this research. Final thanks go to Colin Shaw and Asier Gómez-Olivencia for critical discussions and providing ideas concerning the methodology and presentation of results.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2015.02.009>.

References

- Aiello, L.C., 1992. Allometry and the analysis of size and shape in human evolution. *J. Hum. Evol.* 22, 127–147.
- Aiello, L.C., Key, C., 2002. Energetic consequences of being a *Homo erectus* female. *Am. J. Hum. Biol.* 14, 551–565.
- Aiello, L.C., Wood, B.A., 1994. Cranial variables as predictors of hominine body mass. *Am. J. Phys. Anthropol.* 95, 409–426.
- Alexeev, V.P., 1986. *The Origin of the Human Race*. Progress Publishers, Moscow.
- Antón, S.C., 2003. Natural history of *Homo erectus*. *Yearb. Phys. Anthropol.* 46, 126–170.
- Antón, S.C., 2012. Early *Homo*: who, when, and where. *Curr. Anthropol.* 53, S278–S298.
- Antón, S.C., Smongrass, J.J., 2012. Human biology and the origins of *Homo*. *Curr. Anthropol.* 53, S479–S496.
- Antón, S.C., Swisher, C.C., 2004. Early dispersals of *Homo* from Africa. *A. Rev. Anthropol.* 33, 271–296.
- Antón, S.C., Aziz, F., Zaim, Y., 2001. Dispersal and migration in Plio-Pleistocene *Homo*. In: Tobias, P.V., Raat, M.A., Moggi-Cecchi, J., Doyle, G.A. (Eds.), *Humanity from African Naissance to Coming Millennia – Colloquia in Human Biology and Palaeoanthropology*. Florence University Press, Florence, pp. 97–108.
- Antón, S.C., Leonard, W.R., Robertson, M., 2002. An ecomorphological model of the initial hominid dispersal from Africa. *J. Hum. Evol.* 43, 773–785.
- Antón, S.C., Potts, R., Aiello, L.C., 2014. Evolution of early *Homo*: an integrated biological perspective. *Science* 345, 1236828. <http://dx.doi.org/10.1126/science.1236828>.
- Auerbach, B.M., Ruff, C.B., 2004. Human body mass estimation: a comparison of “morphometric” and “mechanical” methods. *Am. J. Phys. Anthropol.* 125, 331–342.
- Auerbach, B.M., Ruff, C.B., 2010. Stature estimation formulae for indigenous North American populations. *Am. J. Phys. Anthropol.* 141, 190–207.
- Balter, V., Blichert-Toft, J., Braga, J., Telouk, P., Thackeray, F., Albarède, F., 2008. U–Pb dating of fossil enamel from the Swartkrans Pleistocene hominid site, South Africa. *Earth Planet. Sci. Lett.* 267, 236–246.
- Berger, L.R., de Ruiter, D.J., Churchill, S.E., Schmid, P., Carlson, K.J., Dirks, P.H.G.M., Kibii, J.M., 2010. *Australopithecus sediba*: a new species of *Homo*-like australopithecine from South Africa. *Science* 328, 205–208.
- Bermúdez de Castro, J.M.B., Martinon-Torres, M., Sier, M.J., Martín-Frances, L., 2014. On the variability of the Dmanisi mandibles. *PLOS ONE* e88212.
- Blumenshine, R.J., Peters, C.R., Masao, F.T., Clarke, R.J., Deino, A., Hay, R.L., 2003. Late Pliocene *Homo* and hominid land use from western Olduvai Gorge, Tanzania. *Science* 299, 1217–1221.
- Brain, C.K., 1978. Some aspects of the South African australopithecine sites and their bone accumulations. In: Jolly, C.J. (Ed.), *Early Hominids of Africa*. Gerald Duckworth and Co. Ltd., London, pp. 131–164.
- Brain, C.K. (Ed.), 1993. *Swartkrans – a cave’s chronicle of early man*. Transvaal Museum Monograph 8, Pretoria.
- Broom, R., Robinson, J.T., 1949. A new type of fossil man. *Nat. London* 163, 322–333.
- Brown, F.H., Feibel, C.S., 1985. Stratigraphical notes on the Okote Tuff Complex at Koobi Fora, Kenya. *Nature* 316, 794–797.
- Brown, F.H., McDougall, I., 2011. Geochronology of the Turkana Depression of northern Kenya and southern Ethiopia. *Evol. Anthropol.* 20, 217–227.
- Brown, F.H., Harris, J., Leakey, R., Walker, A., 1985. Early *Homo erectus* skeleton from west Lake Turkana, Kenya. *Nature* 316, 788–792.
- Brown, F.H., Haileab, B., McDougall, I., 2006. Sequence of tuffs between the KBS Tuff and the Chari Tuff in the Turkana Basin, Kenya and Ethiopia. *J. Geol. Soc. London* 162, 185–204.
- Brown, J.H., West, G.B. (Eds.), 2000. *Scaling in Biology*. Oxford University Press, New York.
- Byers, S.N., Akoshima, K., Curran, B., 1989. Determination of adult stature from metatarsal length. *Am. J. Phys. Anthropol.* 79, 275–279.
- Calder, W.A., 1984. *Size, Function and Life History*. Harvard University Press, Cambridge.
- Carretero, J.-M., Rodríguez, L., García-González, R., Arsuaga, J.-L., Gómez-Olivencia, A., Lorenzo, C., Bonmatí, A., García, A., Martínez, I., Quam, R., 2012. Stature estimation from complete long bones in the Middle Pleistocene humans from the Sima de los Huesos, Sierra de Atapuerca (Spain). *J. Hum. Evol.* 62, 242–255.
- Curnoe, D., 2010. A review of early *Homo* in southern Africa focusing on cranial, mandibular and dental remains, with the description of a new species (*Homo gautengensis* sp. nov.). *HOMO* 61, 151–177.
- Curnoe, D., Grün, R., Taylor, L., Thackeray, J.F., 2001. Direct ESR dating of a Pliocene hominin from Swartkrans. *J. Hum. Evol.* 40, 379–391.
- Dagosto, M., Terranova, C.J., 1992. Estimating the body size of Eocene primates: a comparison of results from dental and postcranial variables. *J. Int. Primatol.* 13, 307–344.
- Damuth, J., MacFadden, B.J. (Eds.), 1990. *Body Size in Mammalian Paleobiology. Estimation and Biological Implications*. Cambridge University Press, Cambridge.
- Davis, P.R., 1964. Hominid fossils from Bed I. Olduvai Gorge, Tanganyika. *Nature* 201, 967–968.
- Day, M.H., 1976. Hominid postcranial remains from the East Rudolf Succession. In: Coppens, Y., Howell, F.C., Isaac, G.L., Leakey, R.E.F. (Eds.), *Earliest Man and Environment in the Lake Rudolf Basin – Stratigraphy, Paleoecology, and Evolution*. University of Chicago Press, Chicago, pp. 507–521.

- Day, M.H., 1978. Functional interpretation of the morphology of postcranial remains of early African hominids. In: Jolly, C.J. (Ed.), *Early Hominids of Africa*. Gerald Duckworth and Co. Ltd., London, pp. 311–346.
- Day, M.H., Leakey, R.E.F., 1973. New evidence of the genus *Homo* from East Rudolf, Kenya I. *Am. J. Phys. Anthropol.* 39, 341–354.
- Day, M.H., Leakey, R.E.F., 1974. New evidence of the genus *Homo* from East Rudolf, Kenya III. *Am. J. Phys. Anthropol.* 41, 367–380.
- Day, M.H., Napier, J.R., 1964. Hominid fossils from Bed I. Olduvai Gorge, Tanganyika. *Nature* 201, 968–970.
- Day, M.H., Napier, J.R., 1966. A hominid toe bone from Bed I, Olduvai Gorge, Tanzania. *Nature* 211, 929–930.
- Day, M.H., Leakey, R.E.F., Walker, A.C., Wood, B.A., 1975. New hominids from East Rudolf, Kenya I. *Am. J. Phys. Anthropol.* 42, 461–476.
- Day, M.H., Leakey, R.E.F., Walker, A.C., Wood, B.A., 1976. New hominids from East Rudolf, Kenya. *Am. J. Phys. Anthropol.* 45, 369–436.
- De Groot, I., Humphrey, L.T., 2011. Body mass and stature estimation based on the first metatarsal in humans. *Am. J. Phys. Anthropol.* 144, 625–632.
- Deloison, Y., 1997. Description d'un astragale fossile de primate et comparaison avec des astragales de chimpanzés, d'*Homo sapiens* et d'hominidés fossils: australopithèques et *Homo habilis*. *C. R. Acad. Sci. [IIa]* 324, 685–692.
- Dennell, R., Roebroeks, W., 2005. An Asian perspective on early human dispersal from Africa. *Nature* 438, 1099–1104.
- DeSilva, J.M., 2009. Functional morphology of the ankle and the likelihood of climbing in early hominins. *Proc. Natl. Acad. Sci.* 106, 6567–6572.
- DeSilva, J.M., Zipfel, B., Van Arsdale, A.P., Tocheri, M.W., 2010. The Olduvai Hominid 8 foot: adult or subadult? *J. Hum. Evol.* 58, 418–423.
- Dingwall, H.L., Hatala, K.G., Wunderlich, R.E., Richmond, B.G., 2013. Hominin stature, body mass, and walking speed estimates based on 1.5 million-year-old fossil footprints at Ileret, Kenya. *J. Hum. Evol.* 64, 556–568.
- Dusseldorp, G., Lombard, M., Wurz, S., 2013. Pleistocene *Homo* and the updated Stone Age sequence of South Africa. *S. Afr. J. Sci.* 109, 1–7.
- Feibel, C.S., Brown, F.H., McDougall, I., 1989. Stratigraphic context of fossil hominids from the Omo Group deposits: northern Turkana Basin, Kenya and Ethiopia. *Am. J. Phys. Anthropol.* 78, 595–622.
- Feibel, C.S., Lepre, C.J., Quinn, R.L., 2009. Stratigraphy, correlation, and age estimates for fossils from Area 123, Koobi Fora. *J. Hum. Evol.* 57, 112–122.
- Feldesman, M.R., Lundy, J.K., 1988. Stature estimates for some African Pliocene fossils hominids. *J. Hum. Evol.* 17, 583–596.
- Feldesman, M.R., Kleckner, J.G., Lundy, J.K., 1990. Femur/stature ratio and estimates of stature in Mid- and Late-Pleistocene fossil hominids. *Am. J. Phys. Anthropol.* 83, 359–372.
- Ferring, R., Oms, O., Agustí, J., Berna, F., Nioradze, M., Shelia, T., Tappen, M., Vekua, A., Zhvania, D., Lordkipanidze, D., 2011. Earliest human occupations at Dmanisi (Georgian Caucasus) dated to 1.85–1.78 Ma. *Proc. Natl. Acad. Sci.* 108, 10432–10436.
- Fleagle, J.H., Shea, J.J., Grine, F.E., Baden, A.L., Leakey, R.E. (Eds.), 2009. *Out of Africa 1 – The First Hominin Colonization of Eurasia*. Springer, Dordrecht.
- Foley, R.A.F., 1987. Another Unique Species. Longman Group, Essex.
- Foley, R.A.F., 2001. The evolutionary consequences of increased carnivory in humans. In: Stanford, C.B., Bunn, H.T. (Eds.), *Meat-eating and Human Evolution*. Oxford University Press, Oxford, pp. 305–331.
- Foley, R.A.F., 2002. Adaptive radiations and dispersals in hominin evolutionary ecology. *Evol. Anthropol. Suppl.* 1, 32–37.
- Gabunia, L., Vekua, A., Lordkipanidze, D., Swisher, C.C.III., Ferring, R., Justus, A., Nioradze, M., Tvalchrelidze, M., Antón, S.C., Bosinski, G., Jöris, O., de Lumley, M.A., Majsradze, G., Mouskhelishvili, A., 2000. Earliest Pleistocene hominid cranial remains from Dmanisi, Republic of Georgia: taxonomy, geological setting, and age. *Science* 288, 1019–1025.
- Gabunia, L., Antón, S.C., Lordkipanidze, D., Vekua, A., Justus, A., Swisher III, C.C., 2001. Dmanisi and dispersal. *Evol. Anthropol.* 10, 158–170.
- Gathogo, P.N., Brown, F.H., 2006. Revised stratigraphy of Area 123, Koobi Fora, Kenya, and new age estimates of its fossil mammals, including hominins. *J. Hum. Evol.* 51, 471–479.
- Gebo, D.L., Schwartz, G.T., 2006. Foot bones from Omo: implication for hominid evolution. *Am. J. Phys. Anthropol.* 129, 499–511.
- Geissmann, T., 1986. Estimation of australopithecine stature from long bones: A.L. 288-1 as a test case. *Folia Primatol.* 47, 119–127.
- Grine, F.E., 2005. Early *Homo* at Swartkrans, South Africa: a review of the evidence and an evaluation of recently proposed morphs. *S. Afr. J. Sci.* 101, 43–52.
- Grine, F.E., Fleagle, J.G., 2009. The first humans: a summary perspective on the origin and early evolution of the genus *Homo*. In: Grine, F.E., Fleagle, J.G., Leakey, R.E. (Eds.), *The First Human: Origin and Early Evolution of the Genus Homo*. Springer, Dordrecht, pp. 197–208.
- Grine, F.E., Jungers, W.L., Tobias, P.V., Pearson, O.M., 1995. Fossil *Homo* femur from Berg Aukas, northern Namibia. *Am. J. Phys. Anthropol.* 97, 151–185.
- Grine, F.E., Jungers, W.L., Schultz, J., 1996. Phenetic affinities among early *Homo* crania from East and South Africa. *J. Hum. Evol.* 30, 189–225.
- Groves, C.P., Mazák, V., 1975. An approach to the taxonomy of the Hominidae: gracile Villafranchian hominids of Africa. *Caspos. Miner. Geol.* 20, 225–247.
- Hausler, M., McHenry, H.M., 2004. Body proportions of *Homo habilis* reviewed. *J. Hum. Evol.* 46, 433–465.
- Hausler, M., McHenry, H.M., 2007. Evolutionary reversals of limb proportions in early hominids? Evidence from KNM-ER 3735 (*Homo habilis*). *J. Hum. Evol.* 53, 383–405.
- Harmon, L.J., Losos, J.B., 2005. The effect of intraspecific sample size on type I and type II error rates in comparative studies. *Evolution* 59, 2705–2710.
- Hartwig-Scherer, S., 1993. Body weight prediction in early fossil hominids: towards a taxon-“independent” approach. *Am. J. Phys. Anthropol.* 92, 17–36.
- Hartwig-Scherer, S., 1994. Body weight prediction in fossil *Homo*: new estimates and their limits. In: Franzen, J.L. (Ed.), *100 years of Pithecanthropus – the Homo erectus problem*. Cour. Forsch.-Inst. Senckenberg 267–279.
- Hartwig-Scherer, S., Martin, R.D., 1991. Was “Lucy” more human than her “child”? Observations on early hominid postcranial skeletons. *J. Hum. Evol.* 21, 439–449.
- Hens, S.M., Königsberg, L.W., Jungers, W.L., 2000. Estimating stature in fossil hominids: which regression model and reference sample to use? *J. Hum. Evol.* 38, 767–784.
- Herries, A.I.R., Shaw, J., 2011. Palaeomagnetic analysis of the Sterkfontein palaeocave deposits: implications for the age of the hominin fossils and stone tool industries. *J. Hum. Evol.* 60, 523–539.
- Herries, A.I.R., Curnoe, C., Adams, J.W., 2009. A multi-disciplinary seriation of early *Homo* and *Paranthropus* bearing palaeocaves in southern Africa. *Quatern. Int.* 202, 14–28.
- Holliday, T.W., 2012. Body size, body shape, and the circumscription of the genus *Homo*. *Curr. Anthropol.* 53, S330–S345.
- Holliday, T.W., Ruff, C.B., 1997. Ecogeographic patterning and stature prediction in fossil hominids: comment on Feldesman and Fountain. *Am. J. Phys. Anthropol.* 103, 137–140.
- Howell, F.C., 1978. Hominidae. In: Maglio, V.J., Cooke, H.R.S. (Eds.), *The Evolution of African Mammals*. Harvard University Press, Cambridge, pp. 154–248.
- Irish, J.D., Guatelli-Steinberg, D., Legge, S.S., de Ruiter, D.J., Berger, L.R., 2013. Dental morphology and the phylogenetic “place” of *Australopithecus sediba*. *Science* 340, 1233062.
- Isaac, G.L., Behrensmeier, A.K., 1997. Geological context and palaeoenvironment. In: Isaac, G.L. (Ed.), *Koobi Fora Research Project vol. 5. Plio-Pleistocene Archaeology*. Oxford University Press, Oxford, pp. 12–71.
- Jiménez-Arenas, J.M., Palmqvist, P., Pérez-Claros, J.A., 2011. A probabilistic approach to the craniometric variability of the genus *Homo* and inferences on the taxonomic affinities of the first human population dispersing out of Africa. *Quatern. Int.* 243, 219–230.
- Johanson, D.C., Masao, F.T., Eck, G.G., White, T.D., Walter, R.C., Kimbel, W.H., Asfaw, B., Manega, P., Ndessokia, P., Suwa, G., 1987. New partial skeleton of *Homo habilis* from Olduvai Gorge, Tanzania. *Nature* 327, 205–209.
- Joordens, J.C.A., Vonhof, H.B., Feibel, C.S., Lourens, L.J., Dupont-Nivet, G., van der Lubbe, J.H.J.L., Sier, M.J., Davies, G.R., Kroon, D., 2011. An astronomically-tuned climate framework for hominins in the Turkana Basin. *Earth Planet. Sci. Lett.* 307, 1–8.
- Joordens, J.C.A., Dupont-Nivet, G., Feibel, C.S., Spoor, F., Sier, M.J., van der Lubbe, J.H.J.L., Kellberg Nielsen, T., Knul, M.V., Davies, G.R., Vonhof, H.B., 2013. Improved age control on early *Homo* fossils from the upper Burgi Member at Koobi Fora, Kenya. *J. Hum. Evol.* 65, 731–745.
- Jungers, W.L., 1988a. New estimates of body size in australopithecines. In: Grine, F. (Ed.), *Evolutionary History of the “Robust” Australopithecines*. Aldine de Gruyter, New York, pp. 115–126.
- Jungers, W.L., 1988b. Lucy's length: Stature reconstruction in *Australopithecus afarensis* (A.L. 288-1) with implications for other small-bodied hominids. *Am. J. Phys. Anthropol.* 76, 227–231.
- Kappelman, J., 1996. The evolution of body mass and relative brain size in fossil hominids. *J. Hum. Evol.* 30, 243–276.
- Kibii, J.M., Churchill, S.E., Schmid, P., Carlson, K.J., Reed, N.D., de Ruiter, D.J., Berger, L.R., 2011. A partial pelvis of *Australopithecus sediba*. *Science* 333, 1407–1411.
- Kimbel, W.H., 2009. The origin of *Homo*. In: Grine, F.E., Fleagle, J.G., Leakey, R.E. (Eds.), *The First Humans: Origin and Early Evolution of the Genus Homo*. Springer, Dordrecht, pp. 31–38.
- Kimbel, W.H., 2013. Hesitation on hominin history. *Nature* 497, 573–574.
- Klein, R.G., 2009. *The Human Career: Human Biological and Cultural Origins*, 3rd ed. The University of Chicago Press, Chicago.
- Koenigsberg, L.W., Hens, S.M., Jantz, L.M., Jungers, W.L., 1998. Stature estimation and calibration: Bayesian and maximum likelihood perspectives in physical anthropology. *Yearb. Phys. Anthropol.* 41, 65–92.
- Korey, K.A., 1990. Deconstructing reconstruction: the OH 62 humerofemoral index. *Am. J. Phys. Anthropol.* 83, 25–33.
- Kuman, K., Clarke, R.J., 2000. Stratigraphy, artefacts, industries and hominid associations for Sterkfontein, Member 5. *J. Hum. Evol.* 38, 827–847.
- Kurki, H.K., Ginter, J.K., Stock, J.T., Pfeiffer, S., 2010. Body size estimation of small-bodied humans: applicability of current methods. *Am. J. Phys. Anthropol.* 141, 169–180.
- Kuzawa, C.W., Bragg, J.M., 2012. Plasticity in human life history strategy: implications for contemporary human variation and the evolution of genus *Homo*. *Curr. Anthropol.* 53, S369–S382.
- Leakey, L.S.B., 1960. Recent discoveries at Olduvai Gorge. *Nature* 188, 1050–1052.
- Leakey, L.S.B., Tobias, P.V., Napier, J.R., 1964. A new species of the genus *Homo* from Olduvai Gorge. *Nature* 202, 7–10.
- Leakey, M.D., 1971b. *Olduvai Gorge: Excavations in Beds I and II 1960–1963*. Cambridge University Press, Cambridge.
- Leakey, M.G., Spoor, F., Dean, C.M., Feibel, C.S., Antón, S.C., Kiarie, C., Leakey, L.N., 2012. New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early *Homo*. *Nature* 488, 201–204.

- Leakey, R.E.F., 1971a. Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya. *Nature* 231, 241–245.
- Leakey, R.E.F., 1972. Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya 1971. *Nature* 237, 264–269.
- Leakey, R.E.F., 1973. Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya 1972. *Nature* 242, 170–173.
- Leakey, R.E.F., 1974. Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya 1973. *Nature* 248, 653–656.
- Leakey, R.E.F., Walker, A.C., 1985. Further hominids from the Plio-Pleistocene of Koobi Fora, Kenya. *Am. J. Phys. Anthropol.* 67, 135–163.
- Leakey, R.E.F., Wood, B.A., 1973. New evidence of the genus *Homo* from East Rudolf, Kenya. II. *Am. J. Phys. Anthropol.* 39, 355–368.
- Leakey, R.E.F., Mungai, J.M., Walker, A.C., 1972. New australopithecines from East Rudolf, Kenya (II). *Am. J. Phys. Anthropol.* 36, 235–252.
- Leakey, R.E., Leakey, M.G., Behrensmayer, A.K., 1978. The hominid catalogue. In: Leakey, M.G., Leakey, R.E.F. (Eds.), *Koobi Fora Research Project, Vol. 1: The Fossil Hominids and an Introduction to their Context 1968–1974*. Clarendon Press, Oxford, pp. 86–182.
- Leakey, R.E., Walker, A., Ward, C.V., Graus, H.M., 1989. A partial skeleton of a gracile hominid from the upper Burgi member of the Koobi Fora formation, East Lake Turkana, Kenya. In: Giacobini, G. (Ed.), *Hominidae: Proceedings of the 2nd International Congress of Human Paleontology*. Jaka Books, Milano, pp. 167–173.
- Lepre, C.J., Kent, D.V., 2010. New magnetostratigraphy for the Olduvai Subchron in the Koobi Fora Formation, northwest Kenya, with implications for early *Homo*. *Earth Planet. Sci. Lett.* 290, 362–374.
- Lieberman, D., 2007. Homing in on early *Homo*. *Nature* 449, 291–292.
- Lieberman, D.E., Wood, B., Pilbeam, D., 1996. Homoplasy and early *Homo*: an analysis of the evolutionary relationships of *Homo habilis sensu stricto* and *Homo rudolfensis*. *J. Hum. Evol.* 30, 97–120.
- Lordkipanidze, D., Jashashvili, T., Vekua, V., Ponce de León, M.S., Zollikofer, C.P.E., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agustí, J., Kahlke, R., Kiladze, G., Martínez-Navarro, B., Mouskhelishvili, A., Nioradze, M., Rook, L., 2007. Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* 449, 305–310.
- Lordkipanidze, D., Ponce de León, M.S., Margvelashvili, A., Rak, Y., Rightmire, G.P., Vekua, A., Zollikofer, C.P.E., 2013. A complete skull from Dmanisi, Georgia, and the evolutionary biology of early *Homo*. *Science* 342, 326–331.
- Martin, R.D., Barbour, A.D., 1989. Aspects of line-fitting in bivariate allometric analyses. *Folia Primatol.* 53, 65–81.
- McDougall, I., Brown, F.H., 2006. Precise ⁴⁰Ar/³⁹Ar geochronology for the upper Koobi Fora Formation, Turkana Basin, northern Kenya. *J. Geol. Soc. London* 163, 205–220.
- McDougall, I., Brown, F.H., Vasconcelos, P.M., Cohen, B.E., Thiede, D.S., Buchanan, M.J., 2012. New single crystal Ar-40/Ar-39 ages improve time scale for deposition of the Omo Group, Omo-Turkana Basin, East Africa. *J. Geol. Soc. London* 169, 213–226.
- McHenry, H.M., 1974. How large were the australopithecines? *Am. J. Phys. Anthropol.* 40, 329–340.
- McHenry, H.M., 1975. Fossil hominid body weight and brain size. *Nature* 254, 686–688.
- McHenry, H.M., 1988. New estimates of body weight in early hominids and their significance to encephalization and megadontia in “robust” australopithecines. In: Grine, F. (Ed.), *Evolutionary History of the “Robust” Australopithecines*. Aldine de Gruyter, New York, pp. 133–148.
- McHenry, H.M., 1991. Femoral lengths and stature in Plio-Pleistocene hominids. *Am. J. Phys. Anthropol.* 85, 149–158.
- McHenry, H.M., 1992. Body size and proportions in early hominids. *Am. J. Phys. Anthropol.* 87, 407–431.
- McHenry, H.M., 1994. Behavioral ecological implications of early hominid body size. *J. Hum. Evol.* 27, 77–87.
- McHenry, H.M., Berger, L.R., 1998. Body proportions in *Australopithecus afarensis* and *A. africanus* and the origin of the genus *Homo*. *J. Hum. Evol.* 35, 1–22.
- McHenry, H.M., Coffing, K., 2000. *Australopithecus* to *Homo*: transformations in body and mind. *A. Rev. Anthropol.* 29, 125–146.
- Meadows, L., Jantz, R.L., 1992. Estimation of stature from metacarpal lengths. *J. Forensic Sci.* 37, 147–154.
- Napier, J.R., 1959. Fossil metacarpals from Swartkrans. *Fossil Mammals Afr.* 17, 1–18.
- Olivier, G., 1976. The stature of australopithecines. *J. Hum. Evol.* 5, 529–534.
- Peters, R.H., 1983. *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.
- Pickering, R., Kramers, J.D., 2010. Re-appraisal of the stratigraphy and determination of new U-Pb dates for the Sterkfontein hominin site, South Africa. *J. Hum. Evol.* 59, 70–86.
- Pickering, R., Dirks, P.H.G., Jinnah, Z., de Ruiter, D.J., Chruchil, S.E., Herries, A.I.R., Woodhead, J.D., Hellstrom, J.C., Berger, L.R., 2011. *Australopithecus sediba* at 1.977 Ma and implications for the origins of the genus *Homo*. *Science* 33, 1421–1423.
- Plavcan, J.M., 2012. Body size, size variation, and sexual size dimorphism in early *Homo*. *Curr. Anthropol.* 53, S409–S423.
- Plavcan, J.M., Cope, D.A., 2001. Metric variation and species recognition in the fossil record. *Evol. Anthropol.* 10, 204–222.
- Pontzer, H., 2012. Ecological energetics in early *Homo*. *Curr. Anthropol.* 53, S346–S358.
- Pontzer, H., Rolian, C., Rightmire, G.P., Jashashvili, T., Ponce de León, M.S., Lordkipanidze, D., Zollikofer, C.P.E., 2010. Locomotor anatomy and biomechanics of the Dmanisi hominins. *J. Hum. Evol.* 58, 492–504.
- Porter, A.M.W., 2002. Estimation of body size and physique from hominin skeletal remains. *HOMO* 53, 17–38.
- Raxter, M.H., Auerbach, B.M., Ruff, C.B., 2006. Revision of the Fully technique for estimating statures. *Am. J. Phys. Anthropol.* 130, 374–384.
- Reno, P.L., DeGusta, D., Serrat, M.A., Meindl, R.S., White, T.D., Eckhardt, R.B., Kuperavage, A.J., Galik, K., Lovejoy, C.O., 2005. Plio-Pleistocene hominid limb proportions: evolutionary reversals or estimation errors? *Curr. Anthropol.* 46, 575–588.
- Richmond, B.G., Aiello, L.C., Wood, B.A., 2002. Early hominin limb proportions. *J. Hum. Evol.* 43, 529–548.
- Rightmire, P., 1993. Variation among early *Homo* crania from Olduvai Gorge and the Koobi Fora region. *Am. J. Phys. Anthropol.* 90, 1–33.
- Rightmire, G.P., Lordkipanidze, D., 2009. Comparisons of early Pleistocene skulls from East Africa and the Georgian Caucasus: evidence bearing on the origin and systematics of genus *Homo*. In: Grine, F.E., Fleagle, J.G., Leakey, R.E. (Eds.), *The First Humans: Origin and Early Evolution of the Genus Homo*. Springer, New York, pp. 39–48.
- Rightmire, G.P., Lordkipanidze, D., Vekua, A., 2006. Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisi, Republic of Georgia. *J. Hum. Evol.* 50, 115–141.
- Robson, S.L., Wood, B.A., 2008. Hominin life history: reconstruction and evolution. *J. Anat.* 212, 394–425.
- Rose, M.D., 1984. A hominine hip bone, KNM-ER 3228, from East Lake Turkana, Kenya. *Am. J. Phys. Anthropol.* 63, 371–378.
- Ruff, C.B., 1994. Morphological adaptation to climate in modern and fossil hominids. *Yrbk. Phys. Anthropol.* 37, 65–107.
- Ruff, C.B., 1995. Biomechanics of the hip and birth in early *Homo*. *Am. J. Phys. Anthropol.* 98, 527–574.
- Ruff, C.B., 2000. Body mass prediction from skeletal frame size in elite athletes. *Am. J. Phys. Anthropol.* 113, 507–517.
- Ruff, C.B., 2002. Variation in human body size and shape. *A. Rev. Anthropol.* 31, 211–232.
- Ruff, C.B., 2009. Relative limb strength and locomotion in *Homo habilis*. *Am. J. Phys. Anthropol.* 138, 90–100.
- Ruff, C.B., 2010. Body size and body shape in early hominins – implications of the Gona Pelvis. *J. Hum. Evol.* 58, 166–178.
- Ruff, C.B., Burgess, M.L., 2015. How much more would KNM-WT 15000 have grown? *J. Hum. Evol.* 80, 74–82.
- Ruff, C.B., Walker, A., 1993. Body size and shape. In: Walker, A., Leakey, R. (Eds.), *The Nariokotome Homo erectus Skeleton*. Harvard University Press, Cambridge, pp. 234–265.
- Ruff, C.B., Scott, W.W., Liu, A.Y.C., 1991. Articular and diaphyseal remodeling of the proximal femur with changes in body mass in adults. *Am. J. Phys. Anthropol.* 86, 397–413.
- Ruff, C.B., Trinkaus, E., Holliday, T.W., 1997. Body mass and encephalization in Pleistocene *Homo*. *Nature* 387, 173–176.
- Schillaci, M.A., Schillaci, M.E., 2009. Estimating the probability that the sample mean is within a desired fraction of the standard deviation of the true mean. *J. Hum. Evol.* 56, 134–138.
- Schrenk, F., Bromage, T.G., Betzler, C., Ring, U., Juwayeyi, Y., 1993. Oldest *Homo* and Pliocene biogeography of the Malawi Rift. *Nature* 365, 833–836.
- Schrenk, F., Kullmer, O., Bromage, T., 2007. The earliest putative *Homo* fossils. In: Henke, W., Rothe, H., Tattersall, I. (Eds.), *Handbook of Palaeoanthropology*. Springer, Dordrecht, pp. 1611–1632.
- Schwartz, J.H., Tattersall, I., Chi, Z., 2014. Comment on “A complete skull from Dmanisi, Georgia, and the evolutionary biology of early *Homo*.” *Science* 344, 360.
- Siegel, S., Castellan, N.J., 1988. *Nonparametric Statistics for the Behavioral Sciences*, 2nd ed. McGraw-Hill, New York.
- Simpson, S.W., Quade, J., Levin, N.E., Butler, R., Dupont-Nivet, G., Everett, M., Semaw, S., 2008. A female *Homo erectus* pelvis from Gona, Ethiopia. *Science* 322, 1089–1092.
- Simpson, S.W., Quade, J., Levin, N.E., Semaw, S., 2014. The female *Homo* pelvis from Gona: response to Ruff (2010). *J. Hum. Evol.* 68, 32–35.
- Sjøvold, T., 1990. Estimation of stature from long bones utilizing the line of organic correlation. *Hum. Evol.* 5, 431–447.
- Smith, R.J., 1980. Rethinking allometry. *J. Theor. Biol.* 87, 97–111.
- Smith, R.J., 1984. Allometric scaling in comparative biology: problems of concept and method. *Am. J. Physiol.* 246, R152–R160.
- Smith, R.J., 1996. Biology and body size in human evolution: statistical inference misapplied. *Curr. Anthropol.* 37, 451–481.
- Smith, R.J., 2005. Species recognition in paleoanthropology: implications of small sample sizes. In: Lieberman, D.E., Smith, R.J., Kelley, J. (Eds.), *Interpreting the Past: Essays on Human, Primate, and Mammal Evolution in Honor of David Pilbeam*. Brill Academic Publishers, Boston, pp. 207–219.
- Smith, R.J., 2009. Use and misuse of the reduced major axis for line-fitting. *Am. J. Phys. Anthropol.* 140, 476–486.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*, 3rd ed. W.H. Freeman and Company, New York.
- Spoor, F., 2013. Small-brained and big-mouthed. *Nature* 502, 452–445.
- Spoor, F., Leakey, M.G., Gathogo, P.N., Brown, F.H., Antón, S.C., McDougall, I., Kiarie, C., Manthi, F.K., Leakey, L.N., 2007. Implications of new early *Homo* fossils from Ileret, east of Lake Turkana, Kenya. *Nature* 448, 688–691.
- Studel, K., 1985. Allometric perspectives on fossil catarrhine morphology. In: Jungers, W.L. (Ed.), *1985. Size and Scaling in Primate Biology*. Plenum Press, New York, pp. 449–476.

- Studel-Numbers, K.L., 2006. Energetics in *Homo erectus* and other early hominins: the consequences of increased lower limb length. *J. Hum. Evol.* 51, 445–453.
- Studel-Numbers, K.L., Tilkens, M.J., 2004. The effect of lower limb length on the energetic cost of locomotion: implications for fossil hominins. *J. Hum. Evol.* 47, 95–109.
- Stock, J.T., Pfeiffer, S.K., 2001. Linking structural variability in long bone diaphyses to habitual behaviors: foragers from the southern African Later Stone Age and the Andaman Islands. *Am. J. Phys. Anthropol.* 115, 337–348.
- Susman, R.L., 1989. New hominid fossils from the Swartkrans Formation (1979–1986 excavations), postcranial specimens. *Am. J. Phys. Anthropol.* 79, 451–474.
- Susman, R.L., 1993. Hominid postcranial remains from Swartkrans. In: Brain, C.K. (Ed.), *Swartkrans – A Cave's Chronicle of Early Man*. Transvaal Museum Monograph 8, Pretoria, pp. 117–136.
- Susman, R.L., 2008. Brief communication: evidence bearing on the status of *Homo habilis* at Olduvai Gorge. *Am. J. Phys. Anthropol.* 137, 356–361.
- Susman, R.L., Stern, J.T., 1982. Functional morphology of *Homo habilis*. *Science* 217, 931–934.
- Susman, R.L., de Ruiter, D., Brain, C.K., 2001. Recently identified postcranial remains of *Paranthropus* and early *Homo* from Swartkrans Cave, South Africa. *J. Hum. Evol.* 41, 607–629.
- Susman, R.L., Patel, B.A., Francis, M.J., Cardoso, H.F.V., 2011. Metatarsal fusion pattern and developmental morphology of the Olduvai Hominid 8 foot: evidence of adolescence. *J. Hum. Evol.* 60, 58–69.
- Suwa, G., White, T.D., Howell, F.C., 1996. Mandibular postcanine dentition from the Shungura Formation, Ethiopia: crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. *Am. J. Phys. Anthropol.* 101, 247–282.
- Tobias, P.V., 1991. Olduvai Gorge Volume 4. The Skulls, Endocasts and Teeth of *Homo habilis*. Cambridge University Press, Cambridge.
- Trinkaus, E., Long, J.C., 1990. Species attribution of the Swartkrans Member 1 first metacarpals: SK 84 and SKX 5020. *Am. J. Phys. Anthropol.* 83, 419–424.
- Trinkaus, E., Ruff, C.B., 2012. Femoral and tibial diaphyseal cross-sectional geometry in Pleistocene *Homo*. *PaleoAnthropology* 2012, 13–62.
- Trotter, M., Gleser, G., 1952. Estimation of stature from long bones of American whites and Negroes. *Am. J. Phys. Anthropol.* 10, 469–514.
- Trotter, M., Gleser, G., 1958. A re-evaluation of estimation of stature based on measurements taken during life and the long bones after death. *Am. J. Phys. Anthropol.* 16, 79–123.
- Van Arsdale, A.P., Wolpoff, M.H., 2013. A single lineage in Early Pleistocene *Homo*: size variation continuity in Early Pleistocene *Homo* crania from East Africa and Georgia. *Evolution* 67, 841–850.
- Vekua, A., Lordkipanidze, D., Rightmire, G.P., Agustí, J., Ferrer, R., Maisuradze, G., Mouskhelishvili, A., Nioradze, M., Ponce de León, M., Tappen, M., Tvalchrelidze, M., Zollikofer, C., 2002. A new skull of early *Homo* from Dmanisi, Georgia. *Science* 297, 85–89.
- Walker, A.C., Leakey, R.E. (Eds.), 1993. *The Nariokotome Homo erectus Skeleton*. Harvard University Press, Cambridge.
- Ward, C.V., Plavcan, J.M., Hammond, A.S., Feibel, C.F., Spoor, F., Leakey, L.S., Leakey, M.G., 2011. A new hominin pelvis and femur from Koobi Fora, Kenya. *Am. J. Phys. Anthropol.* S52, 305.
- Wells, J.C.K., Stock, J.T., 2007. The biology of the colonizing ape. *Yearb. Phys. Anthropol.* 50, 191–222.
- Wells, J.C.K., Stock, J.T., 2011. Re-examining heritability: genetics, life history and plasticity. *Trends Endocrin. Med.* 22, 421–428.
- Wolpoff, M.H., 1973. Posterior tooth size, body size, and diet in South African gracile australopithecines. *Am. J. Phys. Anthropol.* 39, 375–394.
- Wood, B.A., 1974. Olduvai Bed I post-cranial fossils: a reassessment. *J. Hum. Evol.* 3, 373–378.
- Wood, B.A., 1976. Remains attributable to *Homo* in the East Rudolf Succession. In: Coppens, Y., Howell, F.C., Isaac, G.L., Leakey, R.E.F. (Eds.), *Earliest Man and Environment in the Lake Rudolf Basin – Stratigraphy, Paleoecology, and Evolution*. University of Chicago Press, Chicago, pp. 490–506.
- Wood, B.A., 1991. Koobi Fora Research Project Vol. 4: Hominid Cranial Remains. Oxford University Press, Oxford.
- Wood, B.A., 1992. Origin and evolution of the genus *Homo*. *Nature* 355, 783–790.
- Wood, B.A., 1999. 'Homo rudolfensis' Alexeev, 1986 – fact or phantom? *J. Hum. Evol.* 36, 115–118.
- Wood, B.A., 2009. Where does the genus *Homo* begin, and how would we know? In: Grine, F.E., Fleagle, J.G., Leakey, R.E. (Eds.), *The First Humans: Origin and Early Evolution of the Genus Homo*. Springer, Dordrecht, pp. 17–30.
- Wood, B.A., 2010. Reconstructing human evolution: achievements, challenges, and opportunities. *Proc. Natl. Acad. Sci.* 107, 8902–8909.
- Wood, B.A., 2011a. Wiley-Blackwell Encyclopedia of Human Evolution. Blackwell Publishing Ltd., West Sussex.
- Wood, B.A., 2011b. Did early *Homo* migrate “out of ” or “in to” Africa? *Proc. Natl. Acad. Sci.* 108, 10375–10376.
- Wood, B.A., 2014. Fifty years after *Homo habilis*. *Nature* 508, 31–33.
- Wood, B.A., Collard, M., 1999. The human genus. *Science* 284, 65–71.
- Wood, B.A., Leakey, M.G., 2011. The Omo-Turkana Basin fossil hominins and their contribution to our understanding of human evolution in Africa. *Evol. Anthropol.* 20, 264–292.
- Wood, B.A., Lonergan, N., 2008. The hominin fossil record: taxa, grades and clades. *J. Anat.* 212, 3543–4476.
- Zar, J.H., 1996. *Biostatistical Analysis*, 3rd ed. Prentice Hall, New York.
- Zipfel, B., DeSilva, J.M., Kidd, R.S., Carlson, K.J., Churchill, S.E., Berger, L.R., 2011. The foot and ankle of *Australopithecus sediba*. *Science* 333, 1417–1420.
- Zollikofer, C.P.E., Ponce de León, M.S., Margvelashvili, A., Rightmire, G.P., Lordkipanidze, D., 2014. Response to comment on “A complete skull from Dmanisi, Georgia, and the evolutionary biology of early *Homo*.” *Science* 344, 360.