

Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/authorsrights>



Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

News and views

The female *Homo* pelvis from Gona: Response to Ruff (2010)Scott W. Simpson^{a,b,c,*}, Jay Quade^d, Naomi E. Levin^e, Sileshi Semaw^{f,g,h}^a Department of Anatomy, Case Western Reserve University School of Medicine, 10900 Euclid Avenue, Cleveland, OH 44106-4930, USA^b Institute for the Science of Origins, Case Western Reserve University, Cleveland, OH 44106, USA^c Laboratory of Physical Anthropology, Cleveland Museum of Natural History, Cleveland, OH 44106, USA^d Department of Geosciences, University of Arizona, Tucson, AZ, USA^e Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore, MD, USA^f Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Sierra de Atapuerca s/n, 09002 Burgos, Spain^g The Stone Age Institute, 1392 West Dittmore Road, Gosport, IN 47433, USA^h CRAFT, Indiana University, Bloomington, IN 47405, USA

ARTICLE INFO

Article history:

Received 19 January 2012

Accepted 10 December 2013

Available online 18 February 2014

Ruff (2010a, b) challenged the taxonomic attribution of the Gona fossil pelvis (BSN49/P27 (Simpson et al., 2008)) to *Homo erectus* based on the premise that its acetabulum is too small and outside the range of currently known early *Homo*. Ruff's alternative taxonomic suggestion is that the pelvis may belong to another species, notably *Australopithecus (Paranthropus) boisei*. We reject these proposals for the reasons outlined below.

Morphology

A number of morphological differences that distinguish between *Australopithecus* and *Homo* pelves were not considered by Ruff (2010a, b). These features include breadth of the m. obturator internus groove (acetabulo-tuberous sulcus) (Broom and Robinson, 1950; McHenry, 1975; Gommery et al., 2002; Simpson et al., 2008; Haile-Selassie et al., 2010; although see; Kibii et al., 2011), anterior inferior iliac spine size and shape, iliac pillar robusticity, deep groove for the m. iliopsoas, size of the gluteal fossa and ischial tuberosity, details of the sacrum including dorsal alar tubercle presence and size and auricular surface breadth, and angulation of the ilio-pubic ramus (Lovejoy, 2005; Kibii et al., 2011). The lateral iliac flaring is phenetically distinguishable between the BSN49/P27 pelvis and *Australopithecus* (Kibii and Clarke, 2003; Berge and Goularas, 2010), which have very obliquely oriented ilia associated with a greater anterior projection of the anterior portion of the

ilium. This latter trait is pronounced in *Au. (P.) robustus* (e.g., SK50, TM 1605) (Robinson, 1972).

Other taxonomically useful traits found in *Homo* pelves that were not included in Ruff's taxonomic attribution were a well-developed anterior horn of the acetabulum, increased antero-posterior breadth of the birth canal, position of the obturator canal margins, as well as derived delayed formation of the tall, narrow pubic symphyseal face, a trait seen only in humans (and also the ca. 1 Ma Buia UA-466 pubis (Bondioli et al., 2006)), and is a correlate of maintaining obstetrically necessary mobility at the interpubic joint (Lovejoy, 2005; Simpson et al., 2008).

The fossil data set

Only 36 fossil specimens were included in Ruff's analysis (2010a, b). No specimens attributable to *Au. (P.) boisei* were included in this analysis. Nine of the 36 specimens predate 2.5 Ma.

Ruff (2010a, b) included only those fossils that had a reasonably complete acetabulum or femoral heads due to their use as a reasonable proxy of body mass, femoral length, and stature. This excludes other cranial or post-cranial elements that provide information about body size (e.g., Reno et al., 2003). For example, numerous other smaller-bodied skeletal elements are known for *Homo*, such as OH62 and perhaps OH8, as well as those from Dmanisi (D3479, D4111, D3442) that provide body mass estimates of about 40.0 kg – much smaller than the 52.6 kg based on the femoral head of the largest individual from Dmanisi (Lordkipanidze et al., 2007). Thus, the survey of early hominin body size is incomplete and excludes substantial amount of fossil evidence resulting in a biased estimate of body size variation in the early hominins.

Sex assignment of the fossils

Of the 36 fossils included in Ruff's analysis, only 15 are assigned to a sex (Ruff, 2010a: Table 1): seven of which are from the Middle Pleistocene of Europe (Arago and Atapuerca) and are

* Corresponding author.

E-mail address: sws3@cwru.edu (S.W. Simpson).

inappropriately assigned to *H. erectus* (Rightmire, 2008; Hublin, 2013). Of the remaining sex assignments, one is from 'archaic *Homo sapiens*', one of the four included 'early *Homo*', one of seven for *Au. africanus*, two (of two) from African *H. erectus*, and two (of two) from *Au. afarensis*. None of the fossils assigned to *Au. (P.) robustus* ($n = 6$), *Au. sp.* ($n = 3$), or *Orrorin* ($n = 1$) is assigned to sex. Of the more immediately relevant Pliocene and Early Pleistocene specimens ($n = 24$), only six are assigned to a sex and of that small sample, only *Au. afarensis* has reasonably assigned male and female elements without taxonomic ambiguity.

To assess sexual dimorphism in Pleistocene *Homo*, we concluded the OH28 os coxa fragment was from a male based on its very large size (the largest known from Pleistocene Africa) and robust (very thick iliac pillar, and large anterior inferior iliac spine) morphology. We also examined the greater sciatic notch in OH28 and concluded that, while it is quite wide, it was a male (Simpson et al., 2008; Fig. S9). Ruff (2010a), accounting for damage to its ischial spine he thought we had overlooked, concluded that the morphology of the greater sciatic notch indicated OH28 pelvis is from a female. In a reassessment the OH28 specimen, we again get a similar measurement as we published previously, which is very different from that of Ruff. Since all of our data were measured in the same fashion, we stand by our original assessment as presented in Simpson et al. (2008; Fig. S9). Using the standard criteria for assessing greater sciatic notch form in modern humans (e.g., Walker, 2005), the OH28 innominate would score either a 2 or a 3 on the 1 (female) to 5 (male) scale. In a study of sex assessment of a sample of modern humans, Walker (2005) noted that the probability of being a male with these scores is high (2: 0.66%; 3: 0.88%) and the probability of being assigned as female is correspondingly low (2: 0.34%; 3: 0.12%). Thus, while OH28 has a wide greater sciatic notch, its morphology is consistent with that of a male. When we rely on the total morphological form, and include other criteria, such as the 'composite arch' (Bruzek, 2002), posterior angle (Takahashi, 2006), and absence of a preauricular sulcus, we conclude that the OH28 os coxa fragment was from a male.

The larger-sized *H. erectus* specimen KNM-ER 1808 is identified by Ruff as female due to the similarity of its greater sciatic notch form to OH28. As we showed above, the sole criterion used by Ruff and Walker (1993) to identify OH28 as a female (shape of the greater sciatic notch) is unreliable and we agree with McHenry (1991) that KNM-ER 1808 is a male.

Other large pelvis fragments are known from the Early Pleistocene, especially the ca. 1 Ma UA-173 (+UA-405) and UA-466 specimens from Buia, Eritrea. The original assessment of these remains suggested that they derived from a single individual (Machiarelli et al., 2004). More recently, a more cautious approach was taken and their association is now unclear, despite similarities in preservation and stratigraphic propinquity. Future discoveries at that locality may resolve this issue. The anatomy of the UA-466 pubis appears male (Bondioli et al., 2006). In the original description (Machiarelli et al., 2004), the other large sized os coxa fragment (UA-173+405) was noted to have a wide greater sciatic notch relative to modern humans and was thought to be a female. However, its large size, similar to that of OH28, and possible association with the male UA-31 cranium suggests that the UA 173+405 specimen was a male. We continue to suggest that the breadth of the greater sciatic notch in ancient *Homo* differs in characteristic ways from modern humans (Simpson et al., 2008).

Two size morphs are recognized in the ca. 1.77 Ma Dmanisi, Republic of Georgia hominin collections (Lordkipanidze et al., 2007, 2013). The complete femur (D4167) is perhaps from a male as it is recognized as belonging to the large individual (Lordkipanidze et al., 2007) and it is nearly identical in femoral head diameter as the smallest early *Homo* specimen (KNM-ER 1472) from Africa. As

smaller sized fossils from 1.8 to 2.0 Ma of Africa are known, all three of the African 'early *Homo*' specimens (KNM-ER 1472, KNM-ER 1481, KNM-ER 3228) are reasonably considered to be males (McHenry, 1992). In fact, of the five 0.7–2.0 Ma African *Homo* fossils included in Ruff's analysis, all five could be males. Since it is possible that no females are present in this sample, the degree of sexual dimorphism is unknown. Thus, we lack the ability to reliably assess sex related size variation in this small, perhaps single-sex, sample. We could assume that *Homo* was skeletally monomorphic but this is at odds with the known fossil remains (e.g., KNM-OL 45500 (Potts et al., 2004); KNM-ER 42700 (Spoor et al., 2007), Dmanisi (Lordkipanidze et al., 2013)).

The inconsistencies in the assignment of sex in the Ruff paper (2010a) impact the assessments of the coefficient of variation (CV) and male-female size differences. In Ruff's Early Pleistocene *Homo* sample, of the five specimens listed in Table 1, only three are assigned to sex. However, later in the same paper (Table 4), all five are assigned a sex without error as male and female body mass estimates are provided based on those specimens. Similarly for *Au. africanus*, all seven specimens were assigned to sex when in Table 1 only one was assigned to sex. For *Au. (P.) robustus*, Table 4 assigns sex to all of the specimens, yet in Table 1, none is assigned a sex. The accuracy of a ratio of the male and female means relies on accurate assessments of sex in the fossil record, something that has not been demonstrated by previous workers and has not been improved upon by Ruff. Thus, the ratio of the means provided in Ruff's Table 4, cannot be considered reliable.

In summary, there are numerous problems and inconsistencies in sex assignment of the 36 specimens included in the Ruff analysis. The sample sizes are small, the justification for sex assignment is not provided, and sample composition is biased. Until sex and taxonomic allocations are reliably demonstrated for these hip fossils, we cannot rely on the individual sex assignments, the sample means, CV, or ratio of the means provided by Ruff.

Finally, Ruff proposed that the Gona pelvis could possibly have been a representative of a species outside of the genus *Homo*, such as *Au. (P.) boisei*. Unfortunately, no fossils were allocated to this species in his analysis. No pelvis of *Au. (P.) boisei* is known and no *Australopithecus* have been discovered from the Afar region that are younger than 2.5 Ma. Fossils representing the 'robust' group were all from Swartkrans and assignable to *Au. (P.) robustus*. While assigning the Gona pelvis to *Au. (P.) boisei* might seem like a possibility, the absence of any known comparative material makes this assignment untestable as it is not based on comparative data.

Homo sample

Although the focus is on African Early Pleistocene *Homo*, a number of European, Asian, and African Middle Pleistocene fossils (Jinniushan, Arago, Atapuerca, and Kabwe) were included. Of those included, the only one that is assigned reliably to *H. erectus* is KNM-WT 15000. Only two *Homo* fossils (OH 28 and KNM-WT 15000: both males) from Africa are included from the 1.6–0.6 Ma span. The young date of the OH28 specimen (<0.780 Ma (Tamrat et al., 1995)) raises the possibility that it is not *H. erectus* but may be the more derived larger bodied *Homo rhodesiensis/heidelbergensis*.

In addition, the taxonomic assignment by Ruff (2010a, b) of the Atapuerca, Arago, and Kabwe specimens to *H. erectus* is at odds with all other contemporary researchers (Arsuaga et al., 1999; Rosenberg et al., 2006; Antón, 2013; Hublin, 2013; Rightmire, 2013), who recognize their morphological similarity with Neandertals, or assign them to either *H. heidelbergensis* or *H. rhodesiensis*, both of which are very derived in cranial form and body size relative to *H. erectus*. Inclusion of the Sima de los Huesos fossils into *H. erectus* artificially and inappropriately inflates the *H. erectus*

sample in space, body size, and sample size. Thus, any summary values presented in the Ruff paper to *H. erectus* (e.g., male and female body mass estimates [Table 1], CV, ratio of means [Table 4]) are invalid as 10 (perhaps 11) of the 12 specimens are demonstrably not assignable to *H. erectus*.

The fossils assigned to 'early *Homo*' in the Ruff (2010a, b) analysis include one specimen from Dmanisi and three from Koobi Fora. The Dmanisi femoral head, which is from the larger individual, is about the same size as the smallest specimen from Koobi Fora (D4167: 40.2 mm; KNM-ER 1472: 40.0 mm). In all likelihood, all four are males and the only females known from the 'early *Homo*' sample are the smaller elements from Dmanisi and Koobi Fora that are not included in Ruff's analysis.

While there is still some uncertainty about the systematics of the Dmanisi sample, a number of authors have assigned them to *H. erectus* (Rightmire et al., 2006; Lordkipanidze et al., 2006, 2013; Rightmire and Lordkipanidze, 2010), while Ruff adopts the conservative sorting to 'early *Homo*'. The large, probably male, Dmanisi individual represented by the femur (D4167) has an estimated mass of 52.6 kg, which is smaller than the smallest individual from Atapuerca, which is likely female. By omitting this collection from the *H. erectus* sample while including the Atapuerca specimens, it excludes the smaller bodied individuals from that species, thus biasing the sample of *H. erectus* towards a larger mass estimate.

Absence of evidence

Ruff (2010a) also noted that sites contemporary with BSN49 that have yielded *H. erectus*, such as the ca. 1.0 Ma Daka, Middle Awash, Ethiopia site (Gilbert and Asfaw, 2008), have not yielded individuals with a smaller body size. However, this assessment was based on consideration of only three of the nine known hominin fossils from Daka. The Daka site has produced one well-preserved cranium, small portions of two additional crania, a mandible fragment, three femur fragments, a tibia fragment, and a talus (Asfaw et al., 2008; Gilbert, 2008). The size of the fragmentary crania, mandible, and talus (four of the nine specimens) is not explicitly discussed by Gilbert and colleagues (Gilbert, 2008; Asfaw et al., 2008) although information about the size of the mandible is available in their descriptions and photos. The Daka mandible (BOU-VP-3/154) has a shallow corpus height (27–28 mm [size estimated from image in Asfaw et al. (2008) and corroborated by T.D. White, Personal communication]), a value similar to that of the small Dmanisi mandible and markedly different from the larger Dmanisi mandible (corpus depth at P3 - D211: 26.5–27.5 mm; D2600: 44.0–44.1 mm) (Rightmire et al., 2008), indicating that not all Early Pleistocene African *Homo* are large. Thus, the statement by Ruff that "there is no evidence for a temporally or geographically delimited subspecies of *H. erectus* of small body size in the Gona region; . . ." (Ruff, 2010a: 174) is inaccurate and was based on consideration of only a part of the *H. erectus* sample from Daka.

Taxonomic assignment of Gona pelvis

Ruff (2010a:173) noted that because the Gona specimen's estimated mass does not overlap with "all known Early Pleistocene specimens ($n = 5$)", it must therefore be excluded from the early *Homo* group. However, it is difficult to expect that only five individuals that span over 1 million years and two continents can reasonably reflect body size variation in a species. Thus, we stand by our original description that the data set is 'surprisingly meager' (cf. Ruff, 2010a: 173) since five specimens of uncertain sex cannot reasonably sample the hundreds of thousands (or more) *H. erectus* individuals that ever lived. The inclusion of the Ileret footprints

(Bennett et al., 2009), while an important additional observation, does not resolve the problem since the sex of the individuals is unknown. Plus, it is possible that all five of the Pleistocene *Homo* specimens studied by Ruff (D4167, KNM-ER 1472, KNM-ER 1481, KNM-ER 3228, OH28) are male and that no females are included in this analysis. Given these limitations, it is not possible using these data to assess size based variation in African *Homo* based on the femoral head. Thus, rejecting the hypothesis that the Gona pelvis based on its size is *Homo* is premature.

The recent recovery of ca. 2.0 Ma *Australopithecus sediba* from South Africa (Berger et al., 2010; Kibii et al., 2011) provides another possible assignment of the Gona pelvis. While the *Homo*-like characteristics of the material were recognized, the final attribution was to *Australopithecus* based on similarities of the cranio-dental material, including a very small endocranial volume (~420 cc) (Carlson et al., 2011). While the authors (Kibii et al., 2011) identified a suite of traits linking it with *Australopithecus*, the two partial pelvises were recognized to have derived, *Homo*-like morphology including a narrow acetabulo-ischium groove, robust iliac body, sigmoid iliac crest, and shortened ilium among others. Examination of a high-quality cast (Ethiopian National Museum) reinforces these observations but also underscores the *Australopithecus*-like nature of the pelvis. *Homo* ilia include a taller posterior ilium and more extensive retro-auricular area with a somewhat shorter anterior ilium, while the *Au. sediba* ilia are more similar to A.L. 288-1 or Sts-14 in these areas. The iliac pillar in both specimens is substantially smaller than in any known *Homo* specimen, although it must be recognized that the MH-1 specimen is preadult. The pubis of the female MH-2 individual is similar in size and shape to A.L. 288-1 and lacks any of the dimorphic characters observed in human females (delayed fusion of symphyseal face, ventral arc, everted inferior margin of inferior pubic ramus). The *Au. sediba* pubic symphyseal face is quite narrow and exhibits a developmentally mature, well-defined and projecting inferior margin, traits not seen in other *Homo* pelvises. Like other australopithecids, the anterior inferior iliac spine is less robust and projecting than in *Homo*. In addition, the superior pubic ramus is gracile and long. While its angulation relative to the ilium, an angle difficult to assess on the MH-2 individual, may differ slightly from A.L. 288-1 or Sts-14, it is less than that of the Gona pelvis and neither *Au. sediba* pelvis shows evidence of a deep m. iliopsoas groove – a correlate of this angulation. Finally, the Malapa individuals are small in stature and the larger, juvenile individual is smaller than the BSN49/P27 individual. The numerous anatomical differences preclude generic identity for the Malapa and Gona pelvises.

Despite significant effort surveying for fossils, no specimens attributable to *Au. (P.) boisei* are known from the Afar region. The Konso, Ethiopia (Suwa et al., 1997) specimens are the northernmost representatives currently known. Currently, *Au. (P.) boisei* is not known from any deposits younger than 1.4 Ma (Suwa et al., 1997). Thus, the 0.9–1.4 Ma Gona pelvis, if it was assignable to *Au. (P.) boisei*, would be the unique representative from the Afar region and the last appearance datum for this species.

Conclusion

The basic model presented by Ruff, that *Australopithecus* is the only small hominin and that no smaller bodied *Homo* existed during the Early Pleistocene, is not supported by the available data. Hip joint size is inappropriate as the sole criterion for making taxonomic decisions in Pleistocene hominins. If acetabulum size were the only taxonomic criterion available, male gorillas could be characterized as *Homo*, female gorillas as *Australopithecus*, and Akka pygmies could not be distinguished from bonobos (McHenry, 1991).

No data have been presented that lead us to reject the hypothesis that the Gona pelvis is attributable to *Homo*. In short, while the assignment of the Gona pelvis to *Au. (P.) boisei* is an interesting suggestion, we do not think Ruff's proposal is very robust.

Acknowledgements

We thank T. White for providing information about the Daka (Middle Awash, Ethiopia) hominins, and B. Latimer, Y. Haile-Selassie, and O. Lovejoy for comments and discussions. This manuscript benefitted from the thoughtful and thorough comments by the reviewers and editors.

References

- Antón, S.C., 2013. *Homo erectus* and related taxa. In: Begun, D.R. (Ed.), *A Companion in Paleoanthropology*. Blackwell Publishing Ltd, West Sussex, pp. 497–516.
- Arsuaga, J.-L., Lorenzo, C., Carretero, J.-M., Gracia, A., Martínez, I., García, N., Bermúdez de Castro, J.-M., Carbonell, E., 1999. A complete human pelvis from the Middle Pleistocene of Spain. *Nature* 399, 255–258.
- Asfaw, B., Gilbert, W.H., Richards, G.D., 2008. *Homo erectus* cranial anatomy. In: Gilbert, W.H., Asfaw, B. (Eds.), *Homo erectus: Pleistocene Evidence from the Middle Awash*. University of California Press, Berkeley, pp. 265–327.
- Bennett, M.R., Harris, J.W.K., Richmond, B.G., Braun, D.R., Mbua, E., Kiura, P., Olago, D., Kibunjia, M., Omuombo, C., Behrensmeier, A.K., Huddart, D., Gonzalez, S., 2009. Early hominin foot morphology based on 1.5-million-year-old footprints from Ileret, Kenya. *Science* 323, 1197–1201.
- Berge, C., Goullaras, D., 2010. A new reconstruction of Sts 14 pelvis (*Australopithecus africanus*) from computed tomography and three-dimensional modeling techniques. *J. Hum. Evol.* 58, 262–272.
- Berger, L.R., de Ruiter, D.J., Churchill, S.E., Schmid, P., Carlson, K.J., Dirks, P.H., Kibii, J.M., 2010. *Australopithecus sediba*: a new species of *Homo*-like australopithecine from South Africa. *Science* 328, 195–204.
- Bondioli, L., Coppa, A., Frayer, D.W., Libsekal, Y., Rook, L., Macchiarelli, R., 2006. A one-million-year-old human pubic symphysis. *J. Hum. Evol.* 50, 479–483.
- Broom, R.A., Robinson, J.T., 1950. Man contemporaneous with the Swartkrans ape-man. *Am. J. Phys. Anthropol.* 8, 151–155.
- Bruzek, J., 2002. A method for visual determination of sex, using the human hip bone. *Am. J. Phys. Anthropol.* 117, 157–168.
- Carlson, K.J., Stout, D., Jashashvili, T., De Ruiter, D.J., Tafforeau, P., Carlson, K., Berger, L.R., 2011. The endocast of MH1, *Australopithecus sediba*. *Science* 333, 1402–1407.
- Gilbert, W.H., 2008. Daka Member hominid postcranial bones. In: Gilbert, W.H., Asfaw, B. (Eds.), *Homo erectus: Pleistocene evidence from the Middle Awash*. University of California Press, Berkeley, pp. 373–396.
- Gilbert, W.H., Asfaw, B., 2008. *Homo erectus: Pleistocene Evidence from the Middle Awash*. University of California Press, Berkeley.
- Gommery, D., Sénut, B., Keyser, A., 2002. A fragmentary pelvis of *Paranthropus robustus* of the Plio-Pleistocene site of Drimolen (Republic of South Africa). *Geobios* 35, 265–281.
- Haile-Selassie, Y., Latimer, B.M., Alene, M., Deino, A.L., Gilbert, L., Melillo, S.M., Saylor, B.Z., Scott, G.R., Lovejoy, C.O., 2010. An early *Australopithecus afarensis* postcranium from Woranso-Mille, Ethiopia. *Proc. Natl. Acad. Sci.* 107, 12121–12126.
- Hublin, J.J., 2013. The Middle Pleistocene record: On the ancestry of Neandertals, modern humans and others. In: Begun, D.R. (Ed.), *A Companion in Paleoanthropology*. Blackwell Publishing Ltd., West Sussex, pp. 517–537.
- Kibii, J.M., Clarke, R.J., 2003. A reconstruction of the Stw 431 *Australopithecus* pelvis based on newly discovered fragments. *S. Afr. J. Sci.* 99, 225–226.
- 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.
- Lordkipanidze, D., Vekua, A., Ferring, R., Rightmire, G.P., Zollikofer, C.P.E., Ponce de León, M., Agustí, J., Kiladze, G., Mouskhelishvili, A., Mioradze, M., Tappen, M., 2006. A fourth hominin skull from Dmanisi, Georgia. *Anat. Rec.* 288A, 1146–1157.
- Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de León, M.S., Zollikofer, P.E., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhsianidze, M., Agustí, J., Kahlke, R., Kiladze, G., Martinex-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., Margvelashvili, A., Rak, Y., Rightmire, G.P., Vekua, A., Zollikofer, P.E., 2013. A complete skull from Dmanisi, Georgia, and the evolutionary biology of early *Homo*. *Science* 342, 326–331.
- Lovejoy, C.O., 2005. The natural history of human gait and posture. Part 1. Spine and pelvis. *Gait Posture* 21, 95–112.
- Macchiarelli, R., Bondolini, L., Checchi, M., Coppa, A., Fiore, I., Russom, R., Vecchi, F., Libsekal, Y., Rook, L., 2004. The late Early Pleistocene human remains from Buia, Danakil Depression, Eritrea. *Rivista Italiana di Paleontologia e Stratigrafia* 110, 133–144.
- McHenry, H.M., 1975. A new pelvic fragment from Swartkrans and the relationship between the robust and gracile australopithecines. *Am. J. Phys. Anthropol.* 43, 245–262.
- 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.
- Potts, R., Behrensmeier, A.K., Deino, A., Ditchfield, P., Clark, J., 2004. Small mid-Pleistocene hominin associated with East African Acheulean technology. *Science* 305, 75–78.
- Reno, P.L., Meindl, R.S., McCollum, M.A., Lovejoy, C.O., 2003. Sexual dimorphism in *Australopithecus afarensis* was similar to that of modern humans. *Proc. Natl. Acad. Sci.* 100, 9404–9409.
- Rightmire, G.P., 2008. *Homo* in the Middle Pleistocene: hypodigms, variation, and species recognition. *Evol. Anthropol.* 17, 8–21.
- Rightmire, G.P., 2013. *Homo erectus* and Middle Pleistocene hominins: Brain size, skull form, and species recognition. *J. Hum. Evol.* 65, 223–252.
- Rightmire, G.P., Lordkipanidze, D., 2010. Fossil skulls from Dmanisi: A paleodeme representing earliest *Homo* in Eurasia. In: Fleagle, J.G., Shea, J.J., Grine, F.E., Baden, A.L., Leakey, R.E. (Eds.), *Out of Africa I: The First Hominin Colonization of Eurasia*. Springer, Dordrecht, pp. 225–243.
- 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.
- Rightmire, G.P., Van Arsdale, A.P., Lordkipanidze, D., 2008. Variation in the mandibles from Dmanisi, Georgia. *J. Hum. Evol.* 54, 904–908.
- Robinson, J.T., 1972. *Early Hominid Posture and Locomotion*. University of Chicago Press, Chicago.
- Rosenberg, K.R., Zúniz, L., Ruff, C.B., 2006. Body size, body proportions, and encephalization in a Middle Pleistocene archaic human from northern China. *Proc. Natl. Acad. Sci.* 103, 3552–3556.
- Ruff, C.B., 2010a. Body size and body shape in early hominins – implications of the Gona pelvis. *J. Hum. Evol.* 58, 166–178.
- Ruff, C.B., 2010b. Body size and body shape in early *Homo* – implications of the Gona pelvis. *Am. J. Phys. Anthropol.* 50 (Suppl.), 203.
- Ruff, C., Walker, A., 1993. Body size and body shape. In: Walker, A., Leakey, R. (Eds.), *The Nariokotome *Homo erectus* Skeleton*. Harvard University Press, Cambridge, pp. 234–265.
- Simpson, S.W., Quade, J., Levin, N.E., Butler, R., Dupont-Nivet, G., Everett, M.A., Semaw, S., 2008. A female *Homo erectus* pelvis from Gona, Ethiopia. *Science* 322, 1089–1092.
- 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.
- Suwa, G., Asfaw, B., Beyene, Y., White, T.D., Katoh, S., Nagaoka, S., Nakaya, H., Uzawa, K., Renne, P., WoldeGabriel, G., 1997. The first skull of *Australopithecus boisei*. *Nature* 389, 489–492.
- Takahashi, H., 2006. Curvature of the greater sciatic notch in sexing the human pelvis. *Anthropol. Sci.* 114, 187–191.
- Tamrat, E., Thouveny, N., Taïeb, M., Opdyke, N.D., 1995. Revised magnetostratigraphy of the Plio-Pleistocene sedimentary sequence of the Olduvai Formation (Tanzania). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 114, 273–283.
- Walker, P.L., 2005. Greater sciatic notch morphology: sex, age, and population differences. *Am. J. Phys. Anthropol.* 127, 385–391.