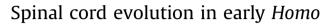
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# ABSTRACT

The discovery at Nariokotome of the Homo erectus skeleton KNM-WT 15000, with a narrow spinal canal, seemed to show that this relatively large-brained hominin retained the primitive spinal cord size of African apes and that brain size expansion preceded postcranial neurological evolution. Here we compare the size and shape of the KNM-WT 15000 spinal canal with modern and fossil taxa including H. erectus from Dmanisi, Homo antecessor, the European middle Pleistocene hominins from Sima de los Huesos, and Pan troglodytes. In terms of shape and absolute and relative size of the spinal canal, we find all of the Dmanisi and most of the vertebrae of KNM-WT 15000 are within the human range of variation except for the C7, T2, and T3 of KNM-WT 15000, which are constricted, suggesting spinal stenosis. While additional fossils might definitively indicate whether H. erectus had evolved a human-like enlarged spinal canal, the evidence from the Dmanisi spinal canal and the unaffected levels of KNM-WT 15000 show that unlike Australopithecus, H. erectus had a spinal canal size and shape equivalent to that of modern humans. Subadult status is unlikely to affect our results, as spinal canal growth is complete in both individuals. We contest the notion that vertebrae yield information about respiratory control or language evolution, but suggest that, like H. antecessor and European middle Pleistocene hominins from Sima de los Huesos, early Homo possessed a postcranial neurological endowment roughly commensurate to modern humans, with implications for neurological, structural, and vascular improvements over Pan and Australopithecus.

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## 1. Introduction

The most complete early hominin skeleton ever discovered, KNM-WT 15000, dated to 1.6 million years ago, was discovered at Nariokotome, West Lake Turkana, Kenya (Brown et al., 1985; Walker and Leakey, 1993). Belonging to a young *Homo erectus* male, it preserves an almost complete series of vertebrae from last cervical to the last sacral element. As such, it serves as the reference axial skeleton of the species. In contrast to *Pan troglodytes* and *Australopithecus*, the KNM-WT 15000 (Nariokotome) skeleton demonstrates relatively large vertebral bodies. This is combined with modern human-like adaptations to bipedalism, including a well-developed lumbar lordosis with wedge-shaped vertebrae, a caudally increasing width of the lumbar vertebral bodies and laminae, and an increasing obliquity of the articular facets (Robinson, 1972; Latimer and Ward, 1993; Shapiro, 1993b; Sanders,

\* Corresponding author. E-mail address: marc.meyer@chaffey.edu (M.R. Meyer). 1998; Meyer, 2005; Whitcome et al., 2007). In addition, recently discovered vertebral and rib material confirms that the Nariokotome skeleton exhibits an essentially humanlike orientation of the articular facets and a modern segmentation pattern of the vertebral column with twelve thoracic and five lumbar vertebrae (Haeusler et al., 2002, 2011, 2012). Its spinal canal, however, has been a point of contention since the initial discovery. Like the modern human brain, the human spinal canal is expanded relative to that of the great apes to accommodate an enlarged spinal cord (MacLarnon, 1987). Since the cross-sectional area of the cervical and thoracic spinal canal among primates is highly correlated with the size of the enclosed spinal cord (MacLarnon, 1995, 1996a), Nariokotome offered the first opportunity to assess spinal cord size in early *Homo* (MacLarnon, 1993).

Brown et al.'s (1985) initial report of the Nariokotome skeleton described the spinal canal as small, which MacLarnon (1993) confirmed and attributed to the primitive retention of a small, chimpanzee-sized spinal cord. Because Nariokotome possessed a much larger brain than its *Australopithecus* predecessors and the African great apes, this suggests that brain expansion preceded







spinal cord expansion in the human lineage. This has functional implications, as spinal canal dimensions of extinct taxa have been used to infer spinal cord size, and by extension, the neurological potential of the limbs among extinct diapsids and synapsids (e.g., Giffin, 1995), as well as in extinct primates (e.g., MacLarnon, 1987, 1995, 1996a). In humans, an enlarged thoracic spinal cord has been related to increased breathing coordination relative to nonhuman primates by virtue of a size increase of the anterior horns of the thoracic spinal cord. This results in augmented innervation of the intercostal and abdominal wall muscles (MacLarnon, 1993) involved in precision motor control during respiration (Campbell, 1968, 1974). Since spoken language involves long, complex modulated utterances (Draper et al., 1959; Hixon and Weismer, 1995), it has been hypothesized that a greater neurological commitment to the abdominals and intercostals compared with nonhuman primates explains the advent of human speech (MacLarnon and Hewitt, 1999, 2004). Since other hominins such as Australopithecus exhibit small thoracic spinal canals relative to those in humans, a small spinal cord was inferred. By extension, it has been argued that early hominins lacked fine control of breathing for speech, and therefore, lacked the ability to produce complex vocalizations necessary for spoken language (MacLarnon and Hewitt, 1999).

Despite being the only representative preserving vertebrae for *H. erectus* at the time, the small spinal canal size in Nariokotome relative to humans also suggested a small spinal cord and less fine motor control of the abdominal and intercostal muscles. Thus, it was suggested that Nariokotome "would only have been capable of short, unmodulated utterances, like those of extant nonhuman primates" and was incapable of spoken language (MacLarnon and Hewitt, 1999:341). However, it has been proposed that Nariokotome's axial skeleton exhibits multiple congenital pathologies, including spinal stenosis, and inferences for H. erectus biology and behavior that are based on this specimen might therefore be compromised (Latimer and Ohman, 2001; Ohman et al., 2002; Meyer, 2003), although recent studies rejected this interpretation, arguing instead that KNM-WT 15000 reflects normal variation for the species (Haeusler et al., 2011, 2012, 2013; Schiess and Haeusler, 2013; Schiess et al., 2014; Villamil, 2014).

The discovery of axial skeleton remains associated with the subadult D2700 H. erectus cranium from Dmanisi, Georgia, allows for a reevaluation of the narrowness of Nariokotome's spinal canal and its functional and pathological implications (Fig. 1; Vekua et al., 2002; Lordkipanidze et al., 2007). Both specimens are similar in their individual age: the skeletal age of Nariokotome equals that of 13.5–15 year old modern humans (Ruff and Walker, 1993; Smith, 1993; Tardieu, 1998), while the dental age is 8-9 years (Dean et al., 2001; Zihlman et al., 2004; Dean and Smith, 2009). This compares to 14-17 years for the skeletal age and 11-13 years for the dental age, respectively, of the Dmanisi youth D2700 (Lordkipanidze et al., 2007). Geologically, however, at 1.8 million years the Dmanisi vertebrae are more ancient. They also derive from a smaller individual (141 cm and 41 kg versus 157 cm and 48 kg; Ruff and Walker, 1993; Lordkipanidze et al., 2007; although see Ohman et al., 2002) and exhibit a fully human-sized spinal canal (Meyer, 2005; Meyer et al., 2006). Yet, no study so far has systematically examined the entirety of the cervical, thoracic, and lumbar column in either the Nariokotome or Dmanisi skeleton. In this study, we analyze spinal canal size and shape across the entire preserved spine of these H. erectus fossils using improved methodological criteria and a complete series of comparative analyses.

# 2. Materials and methods

Data were collected from original fossils unless otherwise noted. *H. erectus* is represented by KNM-WT 15000 from Nariokotome,

West Lake Turkana, Kenya, which includes the entire series between C7 and L5 except for T5 and T8 (Latimer and Ward, 1993; Haeusler et al., 2011). Identification of the vertebrae from the Nariokotome skeleton is according to Haeusler et al. (2011). Spinal canal cross-sectional area for the partial L1 and L2 (KNM-WT 15000 AA/AV and Z/BW, respectively) were reconstructed in Photoshop by mirroring the more complete sides, allowing for modeling of the whole spinal canal (Fig. 1). Although we may reliably assess the cross-sectional area of the spinal canal of these vertebrae, we did not use the reconstructions for our shape analyses. The second H. erectus individual comes from the D2700 vertebral series from Dmanisi, Georgia (Meyer, 2005; Lordkipanidze et al., 2007). In accordance with Meyer (2005), we attribute the Dmanisi vertebrae to the C2, C3, T3, T11, and L2 levels (Lordkipanidze et al. [2007] mistakenly identified the latter two vertebrae as T10 and L1, respectively).

The fossil comparative material includes VC10 (=AT-1557, C3), a European middle Pleistocene hominin from Sima de los Huesos, Sierra de Atapuerca, Spain (Carretero et al., 1999; Gómez-Olivencia, 2005; Gómez-Olivencia et al., 2007) and Homo antecessor from the TD6 level at Gran Dolina represented by ATD6-75 (Carretero et al., 1999). In accordance with Gómez-Olivencia (2005), our analyses are based on a reassignment of ATD6-75 specimen to the C7 level rather than to C3 or C4 as originally suggested by Carretero et al. (1999). Data from these two specimens were collected from published scaled photographs. Australopithecus sediba is represented by the partial skeletons MH1 and MH2 from Malapa, South Africa (Williams et al., 2013). The Australopithecus africanus sample comes from Sterkfontein. South Africa. and includes Sts 14 (T3-L5: Robinson, 1972; Haeusler et al., 2002), Sts 73 (T12; Robinson, 1972; Benade, 1990), Stw 8/41 (T11-L4; Sanders, 1998), Stw 431 (T8-L5; Tobias, 1992; Haeusler et al., 2002; Toussaint et al., 2003), Stw 572 (probably L2; undescribed), and from published scaled images of Stw 600 (L5; Partridge et al., 2003). Australopithecus afarensis is represented by the partial skeleton A.L. 288-1 from Hadar, Ethiopia (Johanson et al., 1982) and was assigned anatomical positions in accordance with Meyer et al. (2015). Paranthropus robustus is represented by two vertebrae from Swartkrans, South Africa: SK 854 (L2 or L3) and SK 3981a (probably T12; Robinson, 1972).

Human vertebrae used in this study derive from individuals 12–50 years of age at the time of death (N = 59; including 22 individuals aged 12-18). The majority of these come from the Hamann-Todd Osteological Collection housed at the Cleveland Museum of Natural History, in addition to San and Bantu individuals from the Ditsong National Museum of Natural History and the Dart collection, University of the Witwatersrand (N = 6), Kikuyu from the National Museums of Kenya (N = 11), and Natufians from El Wad and Kebara curated at the Peabody Museum at Harvard University (N = 5). Additional data come from 18 spinal columns of subadult modern humans aged 6-11 years from the Hamann-Todd Osteological Collection. To avoid confounding influences such as cold-adaptation somatotype, the majority of the sample consists of African-American individuals, while individuals of European ancestry only constitute 8% of our comparative sample. Pan troglodytes (N = 19) is represented by wild-shot adults from the Hamann-Todd Osteological Collection. The sex ratio across taxa was nearly equal for each taxon. None of the vertebrae in the extant comparative sample exhibits obvious pathological, developmental, traumatic, or degenerative malformations.

Spinal canal area and shape are traditionally described by linear measurements (dorsoventral and transverse spinal canal diameters), approximating the spinal canal with an oval. However, this introduces a significant degree of error because the spinal canal is often reniform, pentagonal, triangular, or heart-shaped rather than oval. For example, use of the mathematical formula for an Download English Version:

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