Journal of Human Evolution 104 (2017) 32–49

Contents lists available at ScienceDirect

Journal of Human Evolution

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

The cervical spine of *Australopithecus sediba*

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ARTICLE INFO

Article history:
Received 3 December 2015
Accepted 4 January 2017
Available online 9 February 2017

Keywords:
Vertebrae
Hominin evolution
Head carriage
Lordosis
Spinal cord

ABSTRACT

Cervical vertebrae are rare in the early hominin fossil record, presenting a challenge for understanding the evolution of the neck and head carriage in hominin evolution. Here, we examine the cervical vertebrae of *Australopithecus sediba*, which unlike other South African taxa is known from associated cervical vertebrae. The *A. sediba* cervical vertebrae exhibit human-like values for wedging, pedicle cross-sectional areas, and articular facet heights, indicating reduced ventral loading relative to African apes. These features combine with a pattern of vertebral body bone distribution and caudally progressive size expansion suggesting a mode of cervical lordosis, load mitigation, and head carriage similar to humans and distinct from the cantilevered mode of head carriage of the extant African great apes. Yet these derived features in *A. sediba* are accompanied by ape-like vertebral body and dorsal pillar sizes, articular facet orientation, and uncinate process morphology signaling reduced lateral and rotational coupled movements between vertebral elements and indicate a considerably stiffer neck than in humans. A primitively long and horizontally-oriented C7 spinous process is likely related to a prognathic viscerocranium, although the complimentary C3 spinous process is short, implying large moments emanating from scapular and shoulder elevators rather than large muscles of head stabilization. Cross-sectional spinous process shape and robust anterior tubercles similarly signal increased arm elevation consistent with climbing behavior in corroboration with arboreal signatures previously observed in the shoulder, arms, and hand of *A. sediba*. Spinal canal shape and size suggests that *A. sediba* lacked the cervical spinal cord enlargement of *Homo* that confers humans with enhanced motor control to the upper limbs. The cervical spine of *A. sediba* thus presents a mosaic of primitive and derived characters, with anatomical features relating to neck posture and head carriage mirroring humans juxtaposed with most other aspects of functional anatomy that resemble chimpanzees.

1. Introduction

The human head is supported by a vertical, lordotic, and highly flexible neck consisting of seven cervical vertebrae. Despite sharing the same number of cervical vertebrae, the cantilevered mode of head carriage of African great apes (*Gorilla* and *Pan*) mandates a cervical functional and postural morphology unlike that of humans. Analyses of head posture generally focus on the cranial base (Dart, 1925; Dean and Wood, 1982; Kimbel et al., 2004, 2014; Zollikofer et al., 2005; Kimbel and Rak, 2010; Russo and Kirk, 2013), as cranial material is more commonly preserved in the fossil record, and because multiple vertebrae function together and interact with both the cranial base and wedged intervertebral discs to produce dorsal curvature of the neck (cervical lordosis). The fact that cervical vertebrae are often found in isolation, coupled with the complicated nature of how cervical vertebrae contribute to head and neck posture, has prevented researchers from interpreting much from early hominin cervical vertebrae. While middle Pleistocene and later members of the genus *Homo* are fairly well-represented by cervical fossils (McCown and Keith, 1939; Radovčić et al., 1988;

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http://dx.doi.org/10.1016/j.jhevol.2017.01.001
0047-2484/

Gómez-Olivencia et al., 2007, 2013a, b), early hominin cervical remains are sparsely represented. Fragmentary cervical vertebrae are known but yet undescribed for *Ardipithecus ramidus* (White et al., 2009) and *Australopithecus anamensis* from Asa Issie (White et al., 2006). An entire cervical column is known from a young *Australopithecus afarensis* individual (Alemseged et al., 2006), but detailed descriptions and interpretations are still pending. While "Lucy" (A.L. 288-1) does not preserve any cervical vertebrae, two adult cervical vertebrae from A.L. 333, an isolated axis (C2) and C6 vertebrae, are known for *A. afarensis* (Lovejoy et al., 1982), as are several fragmentary cervical vertebrae from the KSD–VP-1/1 *A. afarensis* individual (Haile-Selassie et al., 2010; Meyer, 2016a).

Although *Australopithecus africanus* is known from two partial skeletons (Sts 14 and StW 431), neither preserves cervical vertebrae. Two isolated, partial cervical vertebrae are known from Swartkrans, a C2 (SK 854) and a C3 (SKW 4776; Robinson, 1972; Susman, 1993), likely representing *Paranthropus robustus* or *Homo erectus*. Two subadult *H. erectus* individuals preserve cervical vertebrae, C2–C3 (D2673 and D2674) from Dmanisi (Meyer, 2005) and a C7 from Nariokotome (Latimer and Ward, 1993; Walker and Leakey, 1993). Newly discovered vertebrae of *Homo naledi* represent a number of cervical fragments, none of which are substantially complete (Berger et al., 2015; Williams et al., 2017). Here, we describe the first associated cervical vertebrae of an early hominin from South Africa, those of *Australopithecus sediba* (Berger et al., 2010; Williams et al., 2013).

A partial C3 vertebra and an intact C7 were assigned to the juvenile male MH1 based on shared provenience (although ex situ), the absence of high-energy taphonomic movement (i.e., water, scavengers; Val, 2014), and developmental morphology (Fig. 1, Tables 1 and 2). Two adult vertebrae, a mostly complete C3 and C6, were similarly recovered ex situ in the "Scapula fragment block" and associated with a series of articulated arm, leg, and thoracic remains found in the same clastic calcified sediment block assigned to the female MH2 (Val, 2014). Despite a minimum number of individuals at Malapa for *A. sediba* estimated at six, only these two individuals (MH1 and MH2) appear to preserve multiple complete elements and accumulated as whole individuals in a natural death trap. Four other individuals were discovered in different depositional facies and are represented by only a few fragments, of which two belong to infants (Val, 2014; Val et al., 2015). Other researchers have made similar associations based on morphology and development in accordance with these attributions (L'Abbé et al., 2015). For these reasons, we examined the two cervical vertebrae each associated with MH1 and MH2 and carried out a comparative study with known and available fossil hominins and extant African apes. Our goal was to examine the cervical spine of *A. sediba* for characters that may shed light on functional anatomy, postcranial neurology, cervical posture, and head carriage relative to the African great apes, humans, and East African australopiths. We were especially interested to investigate whether the cervical region of *A. sediba* reflects a kinematic signal corroborating the terrestrial adaptation observed in the lower limbs (Zipfel et al., 2011; Berger, 2013), the arboreal signatures previously observed in the upper limb (Kivell et al., 2011; Churchill et al., 2013; Schmid et al., 2013; Kivell, 2015), or whether the cervical region presents a mosaic of

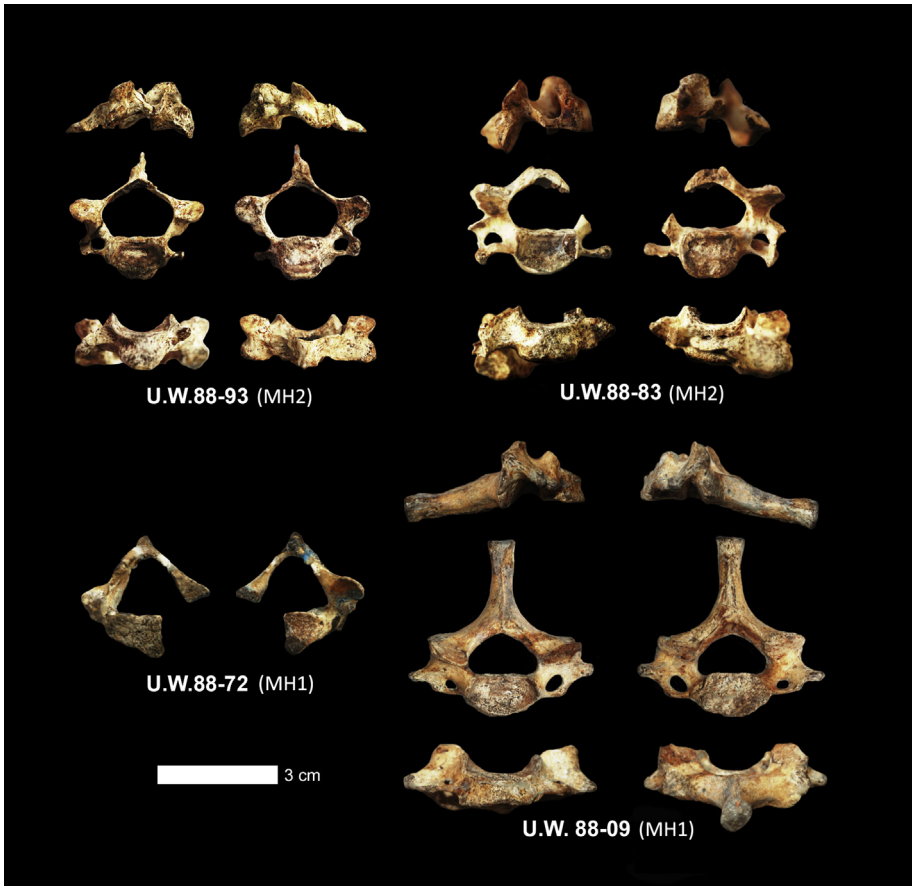

Figure 1. The four most complete cervical vertebrae for *A. sediba*. Top left: U.W. 88-93 C3 vertebra attributed to the MH2 female. Top right: U.W. 88-83 C6 vertebra also attributed to MH2. Bottom left: U.W. 88-72 C3 partial vertebra attributed to the MH1 male subadult. Bottom right: U.W. 88-09 C7 vertebra also attributed to MH1. Orientations from left to right: top rows, lateral right, lateral left; middle rows, superior and inferior; bottom rows, anterior, posterior. U.W. 88-72 C3 shown in superior and inferior views.