Journal of Human Evolution 63 (2012) 552–556

Contents lists available at SciVerse ScienceDirect

Journal of Human Evolution

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

News and views

Modern or distinct axial bauplan in early hominins? Comments on Haeusler et al. (2011)

Scott A. Williams

Center for the Study of Human Origins, Department of Anthropology, New York University, 25 Waverly Place, New York, NY 10003, USA

ARTICLE INFO

Article history:
Received 6 October 2011
Accepted 18 January 2012
Available online 11 March 2012

Keywords:
Diaphragmatic vertebra
Australopithecus
Homo erectus
Modern human variation
Bipedalism

The vertebral column plays a central role in the evolution and performance of positional behaviors, including upright posture and bipedal locomotion in the human lineage. The lumbar column, in particular, is associated with locomotor function. As such, its numerical composition has been a major source of contention in the paleoanthropological literature. Ever since Robinson's (1972) description and interpretation of the nearly complete thoraco-lumbar vertebral column of Sts 14 (*Australopithecus africanus*), researchers have, with few exceptions, consistently stated that early hominins possessed six lumbar vertebrae (Benade, 1990; Latimer and Ward, 1993; Shapiro, 1993; Walker and Leakey, 1993; Sanders, 1995, 1998; Tobias, 1998; Pilbeam, 2004; Rosenman, 2008; McCollum et al., 2010). In 2002, Haeusler et al. demonstrated that these reconstructions were incorrect because they were based on aberrant vertebral morphologies, conflation of multiple definitions (costal versus zygapophyseal) of thoracic and lumbar vertebrae, and the fragmentary nature and associated uncertainty of consecutiveness of fossil vertebral elements in general (see also Williams, 2011).

In a new study, Haeusler et al. (2011) describe newly identified vertebra and rib fragments associated with the KNM-WT 15000 juvenile *Homo erectus* skeleton that reinforce their previous contention (Haeusler et al., 2002) that this specimen has five instead of six lumbar vertebrae, a finding consistent with recent reconstructions of the *A. africanus* specimens Sts 14 and Stw 431 (Haeusler et al., 2002; Toussaint et al., 2003) and Cook et al.'s (1983) prediction of five lumbar vertebrae in the *A. afarensis* partial skeleton, A.L. 288-1 (but see Sanders, 1995 regarding incompleteness and uncertainty in predicting lumbar number in the latter specimen).

Importantly, Haeusler et al.'s (2011) findings also confirm that, as with Sts 14 and Stw 431, the KNM-WT 15,000 diaphragmatic vertebra, the one that bears flat, posteriorly-facing, and 'thoracic-like' prezygapophyses and curved, laterally-directed, and 'lumbar-like' postzygapophyses (Fig. 1), is cranially displaced relative to the last rib-bearing vertebra (Fig. 2), a configuration that is not the norm in modern humans or in other extant hominoids (Williams, 2011). While the new material presented in Haeusler et al. (2011) helps resolve the controversial issue of the number of lumbar vertebrae in fossil hominins, I disagree with the authors' treatment of modern human variation in the placement of the diaphragmatic vertebra and their interpretation of the functional significance of this feature in fossil hominins.

Here, I briefly review the sparse and somewhat inconsistent literature on this topic and provide my own data on a large sample ($N = 125$) of adult modern human vertebral columns and argue that: 1) comparisons among such studies are often hampered by different methodologies and/or lack of a formalized definition of zygapophyseal orientation change, 2) cranial displacement of the diaphragmatic vertebra relative to the last rib-bearing vertebra (see Fig. 2) occurs in modern humans with lower frequency, and common placement of these morphologies at greater frequency, than Haeusler et al. (2011) report, and 3) the consistent presence of six postdiaphragmatic vertebrae (i.e., presacral elements following the diaphragmatic vertebra) in early hominins is unique and likely represents a functional strategy to achieve effective lordosis in the early hominin body plan.

After reviewing published data in the literature and analyzing their own sample of subadult modern humans ($N = 37$), Haeusler et al. (2011: 580) state that cranial displacement "occurs in between 40% and 50% of all skeletons." However, their summary of the literature is biased towards producing a higher degree of cranial displacement than probably exists biologically. First, Haeusler et al. exclude data from two datasets in their 2011 study that they

E-mail address: sawilliams@nyu.edu.

0047-2484/$ – see front matter
doi:10.1016/j.jhevol.2012.01.007

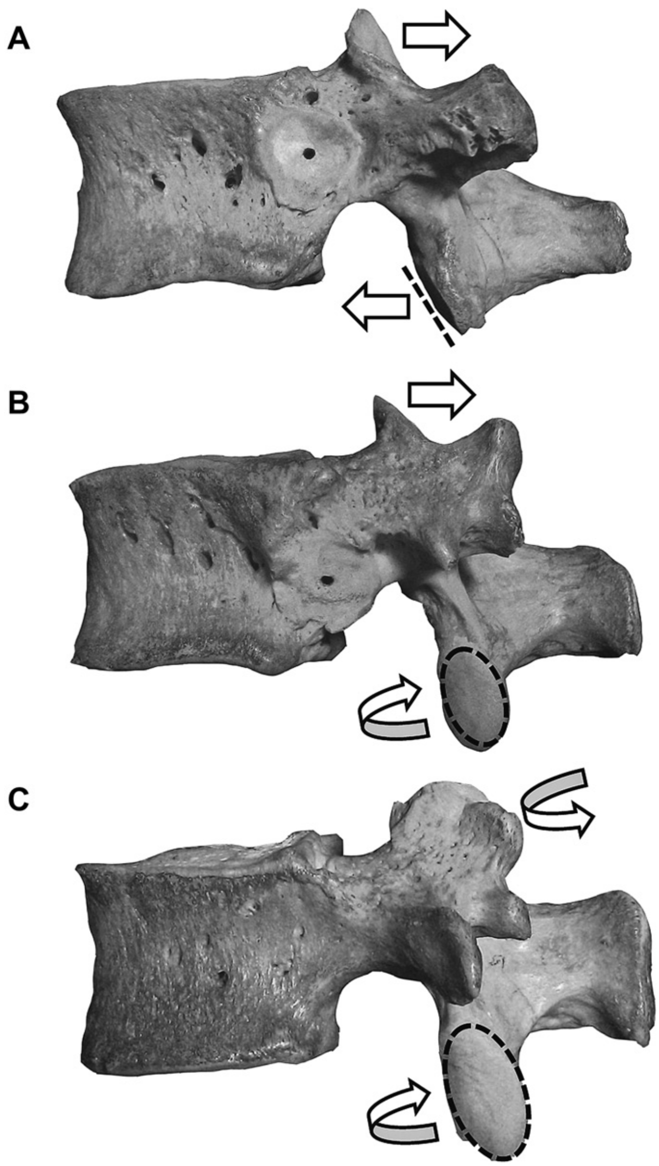

Figure 1. Typical modern human thoraco-lumbar transition, showing zygapohpysis orientation underlying prediaphragmatic (A), diaphragmatic (B), and post-diaphragmatic (C) vertebrae. The diaphragmatic vertebra bears flat, coronally-oriented prezygapophyses and curved, sagitally-oriented postzygapophyses. Here, it is also the last rib-bearing vertebra (notice that rib facets are marked by artificial foramen at their centers), although this configuration does not always occur.

previously included in their 2002 summary (compare Tables 1 and 1 in these studies), reasoning that Hasebe (1913) and Stewart (1932) "used different definitions of thoracic and lumbar type articular facets" (p. 580). I find no evidence for this contention (see page 334 in Hasebe and page 128 in Stewart). These authors used a definition of zygapophysis change – identification of the diaphragmatic vertebra – identical to that employed in Lanier (1939) and Allbrook (1955), data that Haeusler et al. (2011) include in their analysis.

A source of inconsistency between Hasebe's (1913) study and those of Stewart (1932) and Allbrook (1955) is that the former lists the location of the diaphragmatic vertebra according to the numbered element from V1 (C1 – first cervical) to the last lumbar vertebra (usually, but not always, V24), a system referred to here as 'V-numeration,' whereas the latter studies identify its location in relation to regional numeration (e.g., although V20 is generally L1, it can also be T13 or L2, depending on the number of vertebrae that precede it). Therefore, Hasebe's data are not strictly comparable with the other studies since in around 12% of his specimens (Hasebe, 1913; Pilbeam, 2004), V20 does not correspond to L1, and therefore the relationship between the diaphragmatic and last rib-bearing vertebrae is not known in these cases. Stewart's (1932) study, however, is directly comparable with subsequent ones since he uses regional numeration (see Table 2 in Stewart, where columns with modal patterns are listed, and text on pages 129–130, where non-modal columns are discussed). Stewart does include a treatment of the V-numeration system in his Table 4, but this is listed only for comparative purposes with Hasebe's study.

While Haeusler et al. (2011) exclude Stewart's study, they include that of Lanier (1939), who used V-numeration and therefore did not list the specific relationship between diaphragmatic and last rib-bearing vertebrae in all cases (see Tables 27 and 31 in Lanier). In addition, Haeusler et al. add two studies (Singer et al., 1988; Shinohara, 1997) to their 2011 analysis that were not included in their 2002 summary. These, and particularly that of Singer et al. (1988), are the least compatible with the other studies for several reasons. First, Singer et al. (1988) use abdominal and thorax CT scans from radiological records for most ($N = 185$ of 214) of their sample. Therefore, only a subset of the vertebral column was visible and so precise identification of vertebral number is unknown in these specimens.

Second, the nature of the specimen material in Singer et al. (1988) is different than that used in previous studies (i.e., 2-D scans versus whole skeletal specimens). Haeusler et al. (2011: 580) admit that different frequencies observed between this study and previous ones "might be inherent to the method of analyzing a single axial CT scan through the facet joints rather than the orientation of the entire facet as in skeletal studies," but nonetheless include the data and interpret it as direct support for their hypothesis that early hominins and modern humans possessed the same pattern of diaphragmatic placement.

Third, Singer et al. (1988) and Shinohara (1997) categorize large percentages of their specimens as demonstrating a 'gradual' change in zygapophyseal orientation (54% and 34%, respectively), instead of identifying a single vertebra as diaphragmatic. In this regard, Haeusler et al.'s (2011) treatment of the Singer et al. (1988) dataset is particularly problematic, for they subsume within the cranial displacement category the 54% of specimens characterized by a gradual transition (Fig. 3). Based on Fig. 4 from Singer et al. (reproduced here as Fig. 3; see also Fig. 2 in Shinohara, 1997), it is far from clear that these specimens demonstrate cranial displacement. Furthermore, these authors do not specify the degree of orientation change in the gradual specimens; surely, there is a fair amount of variation in this regard.

The gradual specimens should therefore be treated on an individual basis and reclassified into either cranial displacement or common placement categories (not possible here since the original material is not available), or they should be removed from the dataset. Haeusler et al.'s (2011) lumping of the two categories (gradual and cranial displacement) in the Singer et al. (1988) dataset brings the percentage of cranial displacement from 16% (as reported in Singer et al., 1988) to 70% (recorded in Haeusler et al., 2011), with only 29% frequency of common placement. Conversely, if Haeusler et al. (2011) had grouped the gradual specimens with those demonstrating common placement, the frequency of common placement would be much higher (83%), and that of cranial displacement much lower (16%). Alternatively, if the gradual specimens are removed from the dataset, the results are much more comparable with other studies of diaphragmatic placement (Table 1). This would likely also be the case if the gradual specimens were reclassified, as suggested above.