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Lucy's back: Reassessment of fossils associated with the A.L. 288-1 vertebral column

Marc R. Meyer [a, *], Scott A. Williams [b, c], Michael P. Smith [d], Gary J. Sawyer [d]

[a] Department of Anthropology, Chaffey College, Rancho Cucamonga, CA 91737, USA
[b] Center for the Study of Human Origins, Department of Anthropology, New York University, 25, New York, NY 10003, USA
[c] New York Consortium in Evolutionary Primatology, New York, NY 10024, USA
[d] Division of Anthropology, American Museum of Natural History, New York, NY 10024, USA

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ABSTRACT

The *Australopithecus afarensis* partial skeleton A.L. 288-1, popularly known as "Lucy" is associated with nine vertebrae. The vertebrae were given provisional level assignments to locations within the vertebral column by their discoverers and later workers. The continuity of the thoracic series differs in these assessments, which has implications for functional interpretations and comparative studies with other fossil hominins. Johanson and colleagues described one vertebral element (A.L. 288-1am) as uniquely worn amongst the A.L. 288-1 fossil assemblage, a condition unobservable on casts of the fossils. Here, we reassess the species attribution and serial position of this vertebral fragment and other vertebrae in the A.L. 288-1 series. When compared to the other vertebrae, A.L. 288-1am falls well below the expected size within a given spinal column. Furthermore, we demonstrate this vertebra exhibits non-metric characters absent in hominoids but common in large-bodied papionins. Quantitative analyses situate this vertebra within the genus *Theropithecus*, which today is solely represented by the gelada baboon but was the most abundant cercopithecoid in the KH-1s deposit at Hadar where Lucy was discovered. Our additional analyses confirm that the remainder of the A.L. 288-1 vertebral material belongs to *A. afarensis*, and we provide new level assignments for some of the other vertebrae, resulting in a continuous articular series of thoracic vertebrae, from T6 to T11. This work does not refute previous work on Lucy or its importance for human evolution, but rather highlights the importance of studying original fossils, as well as the efficacy of the scientific method.

1. Introduction

Associated partial skeletons are rare in the hominin fossil record. One of the most remarkable and famous ones, an *Australopithecus afarensis* partial skeleton, A.L. 288-1, popularly known as Lucy, was discovered 40 years ago (Johanson and Taieb, 1976; Johanson et al., 1982). The full description of the A.L. 288-1 postcrania included nine vertebrae, which were given provisional serial assignments (positions in the vertebral column; Table 1). Excluding the oddly worn upper thoracic neural arch (A.L. 288-1am) and the lumbar vertebrae, the remaining thoracic vertebrae were arranged to form an incomplete series, from the sixth thoracic vertebra (T6) to its caudal end (T12), with the seventh thoracic vertebra (T7) missing. Cook et al. (1983:85; their Table 1) subsequently modified and augmented some of the serial assignments, suggesting that the T9 was absent rather than T7. Here, we readdress the serial assignments and associations of the A.L. 288-1 vertebrae.

We pay special attention to two partial neural arch fragments, A.L. 288-1ai, a right pars interarticularis, superior and inferior articular facets, pedicle, and transverse process of a transitional (or diaphragmatic) vertebra, and A.L. 288-1am, an upper thoracic neural arch with preserved articular facets and left pedicle (Fig. 1). In describing A.L. 288-1am, Johanson et al. (1982:432) noted that this specimen was unusual, and although they do not provide a figure illustrating it, they suggested that it differed from the other fossils as it was "polished or even 'water-worn' and is the only specimen from A.L. 288 to display these characters" (Supplementary Online Material [SOM] Fig. S1).

A.L. 288-1 was discovered in the KH-1s deposit, a sheet of sandstone between the Kada Hadar Tuff and Confetti Clay

* Corresponding author.
E-mail address: marc.meyer@chaffey.edu (M.R. Meyer).

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Table 1
Previous and current level assignments for the nine vertebral elements of the A.L. 288-1 partial skeleton. In addition to proposing that one thoracic vertebra does not belong to Lucy, we suggest that the remaining thoracic vertebrae form a continuous series and reassign the lumbar vertebrae.

A.L. 288-1	Johanson[a]	Cook et al.	This study
am	T1/2/3/4	T3/T4	N.H.[b]
ae/ah	T6	T6	T6
af	T8	T7	T7
ag/aj	T9	T8	T8
ad	T10	T10	T9
ac	T11	T11	T10
ai	T12	T12	T11
ab	N/A	L3/L4	L2
aa/ak/al	L3	L2	L3

[a] Johanson et al. (1982). Ranges are sometimes given, but the preferred element diagnosis is listed here.
[b] Non-hominin: we refer the neural arch A.L. 288-1am to fossil *Theropithecus darti*.

(Johanson and Taieb, 1976; Campisano and Feibel, 2008) characterized as a sinusoidal stream deposit and crevasse splay deposit that spilled out across the floodplain (Yemane, 1997). The KH-1s deposit is typically a thin deposit, but is 3 m-thick where A.L. 288-1 was found (Campisano, 2007), suggesting a locus of increased deposition with high potential for taphonomic displacement of a small bone such as A.L. 288-1am., and potentially explains the pattern of erosion unique to this fossil.

Based on the position of the preserved superior articular facet and the orientation of the bases of the transverse processes relative to the inferior articular facets, Johanson et al. (1982) classified this vertebra to an upper thoracic position, likely in the T1-T4 range. Cook et al. (1983) identified A.L. 288-1am as a T3 or T4 based on qualitative assessments of preserved portions of the neural arch, including articular facet size and spinous process orientation. During work to produce a comprehensive reconstruction of A.L. 288-1 for the American Museum of Natural History, authors GS and MS found the fossil to be unusually diminutive relative to the other vertebrae. The anomalous size and preservation of A.L. 288-1am led us to re-examine the attribution of this fossil, and we explore the possibility that this specimen does not belong to Lucy's partial skeleton but instead to that of another individual or taxon.

Figure 1. A.L. 288-1am vertebra in dorsal view. Except for the terminal facet margins this vertebra exhibits a minimal degree of weathering inconsequential to metric analyses.

2. Materials and methods

Morphology and linear dimensions from A.L. 288-1 vertebrae were compared to those of *Pan troglodytes* (N = 22), *Gorilla gorilla* (N = 20), *Homo erectus* (N = 2), *Australopithecus sediba* (N = 2), *Australopithecus africanus* (N = 1), *A. afarensis* (N = 1), and *Homo sapiens* (N = 74). The majority of the human sample is from the Hamann-Todd Osteological Collection housed at the Cleveland Museum of Natural History, but also includes San and Bantu individuals from the Ditsong National Museum of Natural History and 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). *H. erectus* is represented by KNM-WT-15000 (Latimer and Ward, 1993) and the D2700 series from Dmanisi (Meyer, 2005), *A. sediba* is represented by vertebrae from MH1 and MH2 (Williams et al., 2013), *A. africanus* is represented by Sts-14 (Robinson, 1972), and *A. afarensis* by A.L. 333x-12 (Lovejoy et al., 1982). Measurements were taken from original specimens. The sex ratio across taxa was nearly equal, and none of the extant comparative samples exhibit pathological, developmental, traumatic, or degenerative malformations. Adults in this study are defined as individuals having completed third molar erruption (see Smith and Jungers (1997) for various definitions of "adult").

Linear measurements are in accordance with Cook et al. (1983), Ward (1991), Latimer and Ward (1993), and Meyer (2005) (SOM Table S1). Angles and areas were calculated via ImageJ version 1.49c (National Institute of Health), and statistical analyses were computed using JMP version 8.0 (SAS Institute).

A.L. 288-1am was additionally compared to *Papio* ssp. (N = 62), *Theropithecus gelada* (N = 10), and *Theropithecus brumpti* (N = 2), the latter represented by mid-thoracic neural arches from a 2.6 Ma partial skeleton (KNM-TH 46700) (Gilbert et al., 2011; C. Gilbert, unpublished data). The overall size of the A.L. 288-1am partial vertebra was calculated as the geometric mean of six linear dimensions: lamina superoinferior height and dorsoventral thickness, pars interarticularis width, interarticular facet height, and superior and inferior articular interfacet maximum transverse widths. The pars interarticularis geometric mean includes three variables from the pars interarticularis: lamina superoinferior height and dorsoventral thickness, and pars interarticularis width.

For principal component and discriminant function analyses of the taxonomic attribution of A.L. 288-1am, the five variables used were superior and inferior minimum and maximum interfacet widths, and interarticular facet height (SOM Tables S2, S3). In the analysis of the T6 and T7 centra (A.L. 288-1ae and A.L. 288-1af) dimensions for the vertebrae were derived from the original centrum margins as defined by Cook et al. (1983) with which we are in agreement.

Given modern human and fossil hominin similarities in positional behaviors (i.e., bipedalism: Ward, 2002; Lovejoy, 2005; Haile-Selassie et al., 2010), vertebral functional anatomy (i.e., spinous process geometry, wedging angles: Meyer, 2005; Williams et al., 2013; Williams and Russo, 2015; but see Sanders, 1998) and modal vertebral numbers (Haeusler et al., 2002, 2011; Williams, 2012a; Williams and Russo, 2015) to the exclusion of African great apes, we assign vertebral level attributions via a human model, which is preferred over a chimpanzee or other non-hominin model; however, we note that the transitional vertebra configuration in all hominin partial skeletons that preserve the thoraco–lumbar transition is different from that of the modal pattern in modern humans (i.e., the transitional vertebra occurs at the penultimate, rather than the ultimate, thoracic level: Haeusler et al., 2002; Williams, 2012b,c; Williams et al., 2013). In this work we refer to individual vertebrae cataloged as multiple specimens by