News and views

News and views: Response to 'Non-metric dental traits and hominin phylogeny' by Carter et al., with additional information on the Arizona State University Dental Anthropology System and phylogenetic 'place' of *Australopithecus sediba*

Joel D. Irish [a,*], Debbie Guatelli-Steinberg [b,c], Scott S. Legge [d], Darryl J. de Ruiter [e,f], Lee R. Berger [f]

[a] Research Centre in Evolutionary Anthropology and Palaeoecology, School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool L3 3AF, UK
[b] Department of Anthropology, Ohio State University, Columbus, OH 43210, USA
[c] Department of Evolution, Ecology, and Organismal Biology, Ohio State University, Columbus, OH 43210, USA
[d] Department of Anthropology, Macalester College, St. Paul, MN 55105, USA
[e] Department of Anthropology, Texas A&M University, College Station, TX 77843, USA
[f] Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa

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Introduction

Here we respond to the remarks of Carter et al. (2014) concerning our Science article (Irish et al., 2013). The goals for that article were to: 1) further characterize *Australopithecus sediba* by describing 22 Arizona State University Dental Anthropology System (ASUDAS) traits, 2) compare the traits in *A. sediba* with those previously recorded in other hominin samples, and 3) present initial phylogenetic analyses using these data. Given the subset of traits, out of 125 possible (below), and small *A. sediba* sample, our conclusion was that the results "further define [the species'] position relative to other genera," but that "the phylogenetic place of *A. sediba* has not been settled" (Irish et al., 2013: 1233062–12330624). These goals were met, as a basis for more

comprehensive study. Below we summarize and reply to the eight objections of Carter et al. (2014) while: 1) demonstrating that there is a strong theoretical basis for using the ASUDAS in phylogenetic analyses, 2) presenting results (which corroborate previous cladistic analyses) that are congruent using different methodological approaches, and 3) introducing new results using a second outgroup, *Pan troglodytes*, that fully uphold our original analysis.

1: Carter et al. (2014) note that, implicit in the method we used (Irish et al., 2013) is the idea that much inter-group ASUDAS trait variability relates to differences in frequencies, not present/absent character states.

They are correct. Among-group ASUDAS variation is ordinarily quantified using trait frequencies (Scott and Turner, 1997; Irish, 2005, 2006). For that, suitable sample sizes are necessary, a shortcoming in fossil studies. However, the *A. sediba* sample ($n = 2$) necessitates a standard phylogenetic approach; inter-species variation is collapsed into a 'typical' state, after Skelton and McHenry (1992), Strait et al. (1997), Strait and Grine (2004) and Smith and Grine (2008).

As explained (Irish et al., 2013), when additional *A. sediba* remains are recovered, gap weighting (Thiele, 1993; Weins, 2001; Schols et al., 2004) of trait frequencies can identify species variation. Partitioning data into equally divided states (e.g., 4, 12, 21) yields increasingly fine-grained results. This method was successfully applied to ASUDAS data by Stringer et al. (1997). Frequencies of occurrence are based on the appraised morphological threshold of traits (Scott, 1973; Turner, 1985, 1987; Scott and Turner, 1997). To illustrate, gap weighting using all 22 traits from Irish et al. (2013)

* Corresponding author.
E-mail address: J.D.Irish@ljmu.ac.uk (J.D. Irish).

was conducted. Larger samples are needed to document intra- and inter-species variability, so pooling was effected (i.e., *Paranthropus boisei* + *Paranthropus robustus*; *Homo habilis/rudolfensis* + *Homo erectus*), though the *A. sediba* sample was retained. Breakpoints are from Scott and Turner (1997).

Data were gap weighted with MorphoCode (Schols et al., 2004). Like the initial tree (Fig. 1) (Irish et al., 2013), polarity was determined with an outgroup, characters were ordered, and Wagner parsimony and branch and bound methods were used ([PAUP 4.0b10 (Swofford, 2002)]). Gap weighting at 10, 20, and 26 states (maximum in PAUP) each produced one most parsimonious tree (MPT). Nodes and topography of all three MPTs are identical (Fig. 2). Although varying from Fig. 1, the following clades are retained: East African Australopithecines-*Paranthropus*, *A. sediba–Australopithecus africanus*, and the modern *Homo* samples.

2: The number of character states for ASUDAS traits do not necessarily relate to the number of genetic changes needed to yield 'meaningful differences in expression,' an important factor in phylogenetic analysis.

Carter et al. (2014: pp 123–128) state "while enamel extension UM1 is divided into 3 states of expression and Carabelli's Cusp UM1 into 7, there is no evidence that there are more than twice the genes involved in Carabelli's cusp expression." Although correct, there is no evidence that *any* morphological traits in hominin studies exhibit such correspondence (Skelton and McHenry, 1992; Strait et al., 1997; Strait and Grine, 2004; Smith and Grine, 2008; Berger et al., 2010). Parallel cases exist in these articles, including Strait and Grine's (2004) Table 3. Their SG53 character has six states (0–5), while SG56 has two (0–1); yet there is no evidence that one-third fewer genes are involved in SG56 expression. The point is that

correspondence between the numbers of character states and genetic changes "needed to produce population variability" is unknown, even in what Carter et al. (2014: pp 123–128) consider "phylogenetically informative" traits. Indeed, it is unknowable for the latter characters. However, ongoing genetic and developmental biological study of ASUDAS traits (Hunter et al., 2010; Hughes and Townsend, 2011; Guatelli-Steinberg et al., 2013) present in extinct and extant hominins could yield more refined divisions of characters into states.

3: There is no indication that the ASUDAS accommodates the range of variation among fossil hominins given, for example, that some traits (e.g., Bushman canine) are monomorphic, and others deemed 'phylogenetically informative' were not included.

Before addressing this comment, we question Carter et al.'s (2014) Fig. 1. It may be possible to quantify the relationship between 'fossil' and 'extant' characters, but their Venn-like diagram is entirely speculative. That said, we do not deny that ASUDAS traits do not capture the full range of morphological variability. In fact, we acknowledged that in our previous paper (Irish et al., 2013: S1). However, we further explained that most ASUDAS traits recorded in fossil hominins are useful for comparing species. Regarding Carter et al.'s (2014) comment that some traits are monomorphic in fossil hominins, all but one was removed from the cladistic study; thus, they are a non-issue (Irish et al., 2013). Bushman canine is monomorphic among these taxa, but not all fossil species (Stringer et al., 1997; Irish, 1998). Also, use of the ASUDAS in paleoanthropology (Stringer et al., 1997; Bailey, 2002, 2008; Martinón-Torres et al., 2007, 2013; Bailey and Hublin, 2013) is yielding evidence that the deleted traits are not 'monomorphic' [e.g., three-rooted LM1 in Asian *H. erectus* (Scott and Turner, 1997)]. Lastly, our
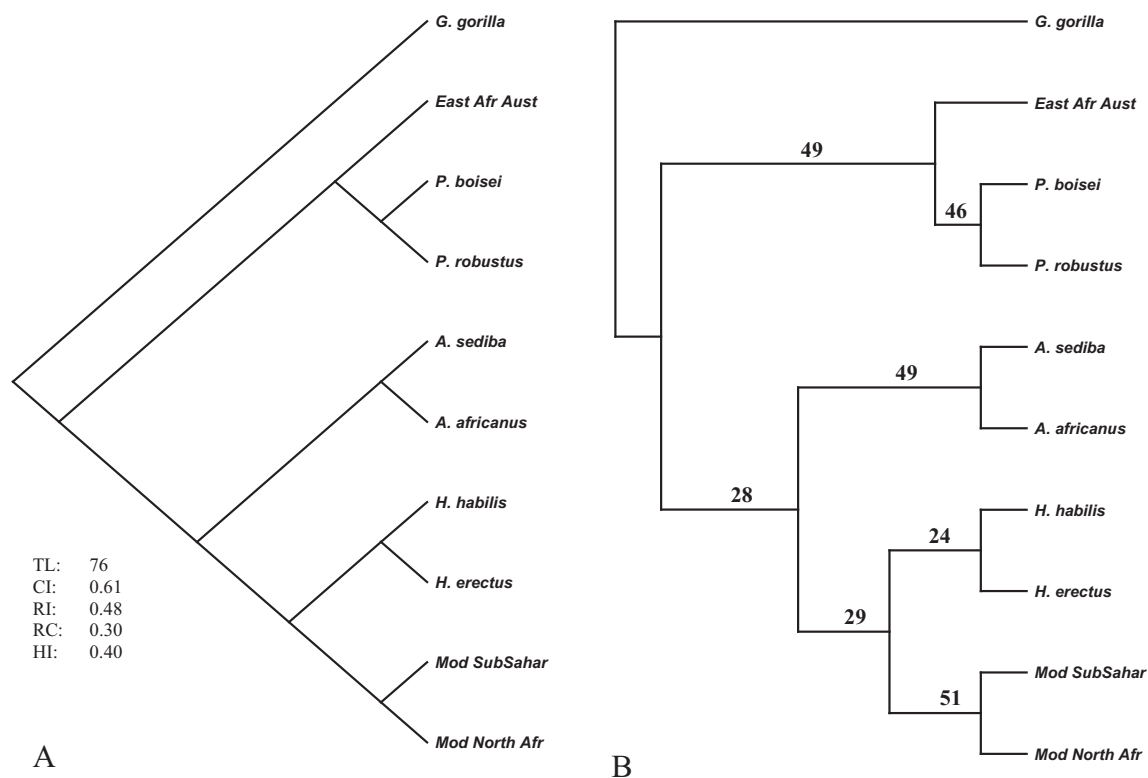

Figure 1. (A) Maximum parsimony cladogram of gorilla outgroup and nine hominin samples based on 18 ASUDAS characters. (B) Analogous 50% majority consensus tree of 10,000 bootstrapped replicate data sets; they represent the proportion of included trees that support the given node. Figure adapted from and details provided in Irish et al. (2013) (TL = tree length, CI = consistency index, RI = retention index, RC = rescaled consistency index, HI = homoplasy index).