



## News and views

## News and views: Non-metric dental traits and hominin phylogeny

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## Introduction

Analyses of hominin dental remains conventionally include measurements of tooth crown sizes and descriptions of occlusal morphology such as minor accessory cusps, fissure patterns, and ridges (e.g., Wood, 1981; Aiello and Dean, 1990; Bailey, 2006). Following Dahlberg (1951), Turner et al. (1991) developed a formal system for dividing these 'non-metric' aspects of dental morphology into discrete categories. This system, termed the Arizona State University Dental Anthropology System (ASUDAS), is an effective tool for discriminating among modern human populations and for assessing inter-population relationships (Scott and Turner, 1997). Other researchers later used ASUDAS to examine the evolutionary relationships of various Pleistocene hominins (Irish and Guatelli-Steinberg, 2003; Martínón-Torres et al., 2007; but see Bailey et al., 2009). Most recently, Irish et al. (2013) used ASUDAS to assess the phylogenetic position of *Australopithecus sediba*, finding support for both an *Au. sediba* + *Au. africanus* clade and a clade uniting South African australopiths with *Homo*. However, as Kimbel (2013) has argued, there are theoretical issues with applying ASUDAS to assess phylogenetic relationships from small samples of fossil hominin dental remains. Here we explore the

suitability of applying a method developed for partitioning among modern human populations to assess interspecies relationships among fossil hominins. We then discuss the ramifications of different choices made during phylogenetic estimation, including those pertaining to character weighting, clade support, and out-group composition. We find that slight alteration of phylogenetic assumptions leads to numerous equally possible evolutionary reconstructions for *Au. sediba*.

## Human populations vs. hominin species

The ASUDAS system allows researchers to assess intraspecific relationships using metrics such as 'Mean Measure of Divergence' (MMD; Scott and Turner, 1997), which allows creation of hierarchical clusters of human populations using a distance matrix of overall phenetic similarity (Irish, 2006; LeBlanc et al., 2008). It is also used to assess the affinity of unknown groups with known populations based on suites of characters (Hanihara, 1977; Irish and Turner, 1990; Aguirre et al., 2006; Pereira et al., 2012). For this technique, any individual trait is not diagnostic of a particular population; rather, it is suites of character frequencies, not the presence or absence of a single character, that determine the affinity of a population. Implicit in this method, and indeed in the samples used to create population standards, is the idea that much of the human variability in ASUDAS relates to differences in frequencies, rather than presence or absence of characters states (Scott and Turner, 1997). While Irish et al. (2013) used a genetically-informed threshold model to determine cutoff points for trait presence and absence, Scott and Turner (1997) made no claim that each successive change between ASUDAS expression levels was related to meaningful differences in genetic expression, a key factor in dividing characters into states for phylogenetic analysis (Hawkins et al., 1997; Wiens, 2001). While it is well established that dental morphology is under considerable genetic control, the number of character states is not necessarily related to the number of genetic changes needed to produce population variability. For example, 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.

A phenetic method designed to assess human population relationships may or may not use characters relevant for determining

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evolutionary relationships among species. For the same reason that traits used to differentiate among breeds of dogs would not be useful to reconstruct the phylogeny of Canidae (Bininda-Emonds et al., 1999), there is no indication that the traits used for within-

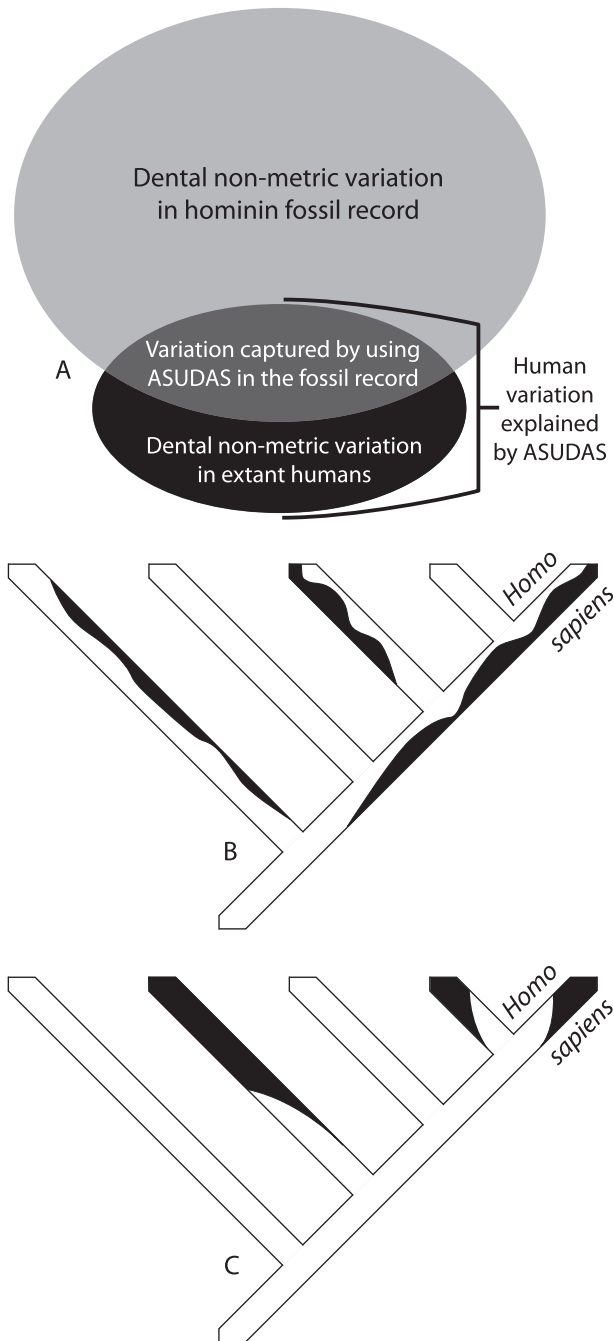
species analysis capture the range of variability expressed among species. Some of the human variability that ASUDAS samples is monomorphic among non-Neandertal fossil hominins (e.g., absence of Bushman canine, the presence of a ridge on the mesial surface of the upper canine), and ASUDAS fails to capture variation in hominins known to be phylogenetically informative, such as the degree of P4 molarization, the rotation of the P3, degree of dimorphism in the canines, and relative molar and incisor sizes (Fig. 1A) (Wood, 1981; Aiello and Dean, 1990).

Based on the expression of ASUDAS traits across human populations, the most parsimonious interpretation of character state polymorphism is that ASUDAS characters were not fixed in the last common ancestor of all modern humans (Fig. 1B). While there are multiple processes that could produce this pattern, it is likely that fossil hominins had the genetic potential for polymorphism in most of these traits, making estimates of interspecific relationships with small sample sizes problematic. Alternative explanations, such as independent acquisition of traits in different populations of recent hominins (e.g., independent acquisition of shoveling in North-eastern Asians and Neandertals; Denton, 2011) call into question the phylogenetic use of these characters (Fig. 1C).

### Methodological choices impact phylogenetic analyses

Decisions related to character weighting schemes, branch support criteria, and outgroup composition can dramatically affect phylogenetic analysis (Nadal-Roberts and Collard, 2005; Bjarnason et al., 2011; Worthington, 2012). Irish et al. (2013) reported that all characters in their analysis were treated as being of equal weight. However, weighting nevertheless occurs as a consequence of the way character state changes are quantified. For characters with binary states, only a single change between states is possible. For multistate characters, a transition from one state to any other can occur either in a single change ('unordered') or only by traveling through all intermediate states ('ordered') (Slowinski, 1993). Irish et al. (2013) treated their characters as ordered, and combined with the unequal number of states among their sampled traits (Table 1), this resulted in characters with more states often being given more weight in their analysis. Several of the multistate characters sampled undergo non-sequential transformations (e.g., from state 0 to state 3) on their most parsimonious tree (MPT; the tree with an internal branching order that requires the fewest evolutionary events to explain the tip data). When this occurs, the hypothesis of state order implicitly gives more weight to these characters (Hauser and Presch, 1991: Figure 10, p. 260).

When character state transitions are ordered, the parsimony algorithm counts change between any intermediate states as separate evolutionary steps. In other words, twice the weight is given to a two-step change from, for example, states '1' to '3' than to any transition between binary character states. Thus a character such as Protostylid LM1, which unites *Au. sediba* and *Au. africanus* with a character state change from '1' (at the base of the clade



**Figure 1.** Theoretical problems that arise with applying ASUDAS in the fossil record. (A) ASUDAS, a method designed to partition intraspecific variation in *Homo sapiens* may not be useful for assessing interspecific variation in the fossil record as there are many phylogenetically informative characters that are not sampled (light region) and many characters which are sampled that are not phylogenetically informative (dark region). Only a small subset of phylogenetic variance is captured. Furthermore, because almost all variants of ASUDAS traits are found in all modern human populations, either (B) these traits were not fixed in the last common ancestor of modern humans or (C) these traits evolved independently in different lineages. Either explanation suggests that there are problems with using ASUDAS to estimate evolutionary relationships among fossil hominins.

**Table 1**  
Number of states exhibited by characters in Irish et al.'s (2013) matrix.

| Number of states | Number of transitions | Inverse transition weight | Count of characters | Character number  |
|------------------|-----------------------|---------------------------|---------------------|-------------------|
| 1                | 0                     | 0                         | 1                   | 18                |
| 2                | 1                     | 1                         | 7                   | 3 6 9 11 15 21 22 |
| 3                | 2                     | 0.5                       | 7                   | 2 4 5 8 10 17 19  |
| 4                | 3                     | 0.333                     | 6                   | 1 7 12 13 14 20   |
| 6                | 5                     | 0.2                       | 1                   | 16                |

Character numbers reflect the order in which characters are listed in Irish et al.'s (2013) Table 2, p. 2.

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