News and views: Response to 'Non-metric dental traits and hominin phylogeny' by Carter et al. (2013), with additional information on the Arizona State University Dental Anthropology System and phylogenetic 'place' of *Australopithecus sediba*

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Introduction

Here we respond to Carter and colleagues' (2013) remarks 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. (2013), 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. (2013) 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) was conducted. Larger samples are needed to document intra- and inter-species variability, so pooling was effected (i.e., *Paranthropus boisei + P. robustus*; *Homo habilis/rudolfensis + H. 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 method were used ([PAUP 4.0b10 (Swofford, 2002)]). Gap weighting at 10, 20, and 26 states (max in PAUP) each produced one most parsimonious tree (MPT). Nodes and topography of all three MPTs are identical (Fig. 2). Although varying from Figure 1, the following clades are retained: East African australopithecines-*Paranthropus*, *A. sediba-A. africanus*, and the modern *Homo* samples.

Insert Figures 1 and 2 approximately here

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. (2013:pp) 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. (2013:pp) 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 and colleague's (2013) Figure 1. It may be possible to quantify the relationship between 'fossil' and 'extant' characters, but their Venn-like diagram is entirely speculative. That said, ASUDAS traits do not "capture the [full] range of variability" (Carter et al., 2013:pp). We acknowledged this statement (Irish et al., 2013: S1), though further explained that most ASUDAS traits recorded in fossil hominins are useful for comparing species. Regarding Carter et al.'s (2013) 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 response to not using what are said to be more phylogenetically informative traits is presented below.

4: Fossil hominins likely had the potential for polymorphism in ASUDAS traits (i.e., homoplasy), which can be an issue in cladistic study.

Carter et al. (2013:pp) go on to say that "independent acquisition of traits in different populations of recent hominins (e.g., independent acquisition of shoveling in NE Asians and Neandertals; Denton, 2011) calls into question the phylogenetic use of these characters." First, we are aware of shoveling homoplasy. As reported (Irish, 1998; Irish and Guatelli-Steinberg, 2003), Mizoguchi (1985) records three forms: Type 1, in some Plio-Pleistocene hominins and modern Africans; Type 2, in Neandertals; and Type 3, in Northeast Asians and other Sinodonts (Turner, 1990). We recorded only Type 1 (Irish it al., 2013), which Mizoguchi (1985) considers ancestral. Second, the overall likelihood of homoplasy was discussed in detail in our paper; ASUDAS traits are less likely to be susceptible to homoplasy than many of the more standard characters used in paleoanthropological study (Irish et al., 2013: S1–S2).

5: Characters were treated as ordered, which gives more weight to those with more states and non-sequential transformations.

Their concerns are based on the oft-cited paper by Hauser and Presch (1991). Yet, in an equally well-cited paper, Wilkinson (1992) promotes treating multistate characters as ordered, a standard strategy (Skelton and McHenry, 1992; Strait et al., 1997; Strait and Grine, 2004; Smith and Grine, 2008; Berger et al., 2010). Unordered characters have less explanatory power, and

"hypotheses of unorder are less restrictive than hypotheses of order . . . [so] they would seem to be less bold and harder to falsify" (Wilkinson, 1992: 382). Greater explanatory power with ordering is evident when a non-sequential jump does occur at a node (e.g., 0-3 instead of 0–1); additional support is lent to that node (two more steps). Of course that tree becomes longer and less parsimonious.

However, our primary reason for ordering ASUDAS characters is that, following Smith and Grine (2008: 687), the dental states appear to belong on an "evolutionary trajectory." Based on derivation (e.g., Gregory and Hellman, 1926), distribution (Scott and Turner, 1997), and expression (i.e., multiple genes acting in an additive manner in these quasi-continuous traits) (Grüneberg, 1952; Scott and Turner, 1997), most characters appear to have changed from their primitive states in a sequential manner. Evidence is seen today. In support of the African origin model, a primitive-to-derived cline of ASUDAS frequencies emanates from that continent. In parallel with migration routes, gradual increases in derived frequencies are documented in North Africa, Europe, Asia and, finally, the Americas and Oceania (Irish, 1998; Irish and Guatelli-Steinberg, 2003; Hanihara, 2008, 2013). There is no evidence for traits jumping from state to state out of sequence. That said, one ASUDAS trait should have been unordered. States for LP4 lingual cusp number appear "discrete and independently evolve[d]," with "no *a priori* expectation" that a primitive state of two equal lingual cusps evolved into a form where the mesial cusp is larger, to reach a point where the latter cusp is smaller (Smith and Grine (2008: 687).

In any event, when all ASUDAS characters were treated as unordered by Carter et al. (2013) conflicting results were reported. According to Wilkinson (1992: 383) "[d]isagreement indicates a need for further study." Yet the most parsimonious approach is to treat only requisite

characters as unordered (i.e., LP4 cusp number); doing so yielded a tree identical to that in

Figure 1, though length was reduced by one. If differential weighting is still deemed problematic,

more data ameliorate the issue, as above where states range from 0–1 to 0–5 (Strait et al., 1997;

Strait and Grine, 2004; Smith and Grine, 2008), and 0–6 (Skelton and McHenry, 1993). Lastly,

gap weighting eliminates the issue with equal state numbers for all traits.

6: The 50% majority-rule consensus tree displays several clades below the 50% threshold,

which suggests poor phylogenetic resolvability of the character matrix.

All clades are <50% except one (Irish et al., 2013) (Fig. 1). Trait number is the reason,

not trait appropriateness (ref. Carter et al., 2013:pp); eighteen traits were used in analysis after

removal of four (above). Higher bootstrap values in other studies resulted by comparing 62

(Berger et al., 2010) to 198 characters (Strait and Grine, 2004). Over 125 nonredundant

ASUDAS traits are observable in a full dentition. Of these, 92 were recorded between both *A.*

sediba specimens. If all these traits had been included clade support would have been greater;

however, only the subset of ASUDAS characters collected so far in the comparative fossil

samples (Irish and Guatelli-Steinberg, 2003) could be used.

We initially included non-ASUDAS dental data from Berger et al. (2010) to illustrate that

more traits provide greater clade resolution, before removing them in the review process. Here,

in a simple numerical exercise the 18 final traits are quadrupled to yield '72' characters. Given

these redundant data, one MPT identical to Figure 1 results (Fig. 3A). Yet a 50% majority-rule

consensus tree (Fig. 3B) shows much greater bootstrap support, including *A. sediba* and *A.*

africanus 60% (versus 48%). Gap weighting of all 22 traits at 20 states each with fewer samples

also increases resolution (Fig. 2B). Thus, again, when additional ASUDAS data are recorded in

the comparative samples greater resolution will result.

Insert Figure 3 approximately here

7: Irish et al. (2013) present a single most parsimonious tree (MPT), but there is no mention whether other marginally less parsimonious trees support conflicting evolutionary relationships.

Given the proliferation of phylogenetic and statistical software, it is increasingly easy to identify alternate trees. Out of 2,026,767 trees with lengths of 77-103, Carter et al. (2013: Fig. 3) found 253 (0.001%) with a length ≤80 not significantly different from the MPT. There is little to say other than that we employed standard non-statistical parsimony. Our MPT was accompanied with the cautionary caveat that, as above, "the phylogenetic place of *A. sediba* has not [yet] been settled" (Irish et al., 2013: 1233062–1233064). Beyond that, support is provided by the highly comparable dendrogram in Irish et al. (2013: Fig. S1) and cladogram in Berger et al. (2010: Fig. S3); the latter was based on an independent set of traits.

8: Carter et al. (2013) state that our *Gorilla* outgroup is problematic because its dental specializations may bias polarity. An outgroup of multiple species (e.g., *Pan*) is suggested.

Gorilla meets the basic criteria for an outgroup (Lehtonen et al., 2012). Furthermore, Nixon and Carpenter (1993: 423) state that it is unnecessary to use more than one outgroup, and it "need not be 'primitive' relative to the ingroup; cladistic parsimony will deal with the problem of polarity and 'primitiveness'" (Nixon and Carpenter, 1993:423). Thus, a gorilla outgroup is appropriate. Nevertheless, we now have data (Table 1) in *Pan troglodytes* (n=139) (Cameroon) to root a two-species outgroup. The same cladistic procedures (Irish et al., 2013) were followed to produce one MPT (Fig. 4A). Beyond *Pan*, topography is identical to our original tree (Irish et al., 2013) (Fig. 1). When unrooted (Fig. 4B), hominin clades remain constant.

Insert Table 1 and Figure 4 approximately here

Conclusion

Carter et al. (2013:) "feel that ASUDAS is an inappropriate metric for evaluating the phylogenetic place of *A. sediba*." We feel otherwise. The few ASUDAS traits recorded in fossil samples to date are useful in reconstructing hominin phylogenies. As explained fully elsewhere (Irish et al., 2013: S1-S2), more is understood about ASUDAS characters (scoring replicability, heritability, derivation, inter-trait correlation) than those commonly used in paleoanthropological study. Moreover, in addressing Carter et al.'s comments (2013) regarding our assumptions, methods, and outgroup composition, the initial (Irish et al., 2013) and subsequent results are concordant. When assessing the phylogenetic place of *any* fossil species, it is preferable to use more characters than less. Thus, we consider that dismissing the ASUDAS based on perceived concerns with our preliminary findings (Irish et al., 2013) is unwarranted. Further analyses using a larger ASUDAS matrix, separately or with other characters, in larger samples should be the deciding factor in assessing viability.

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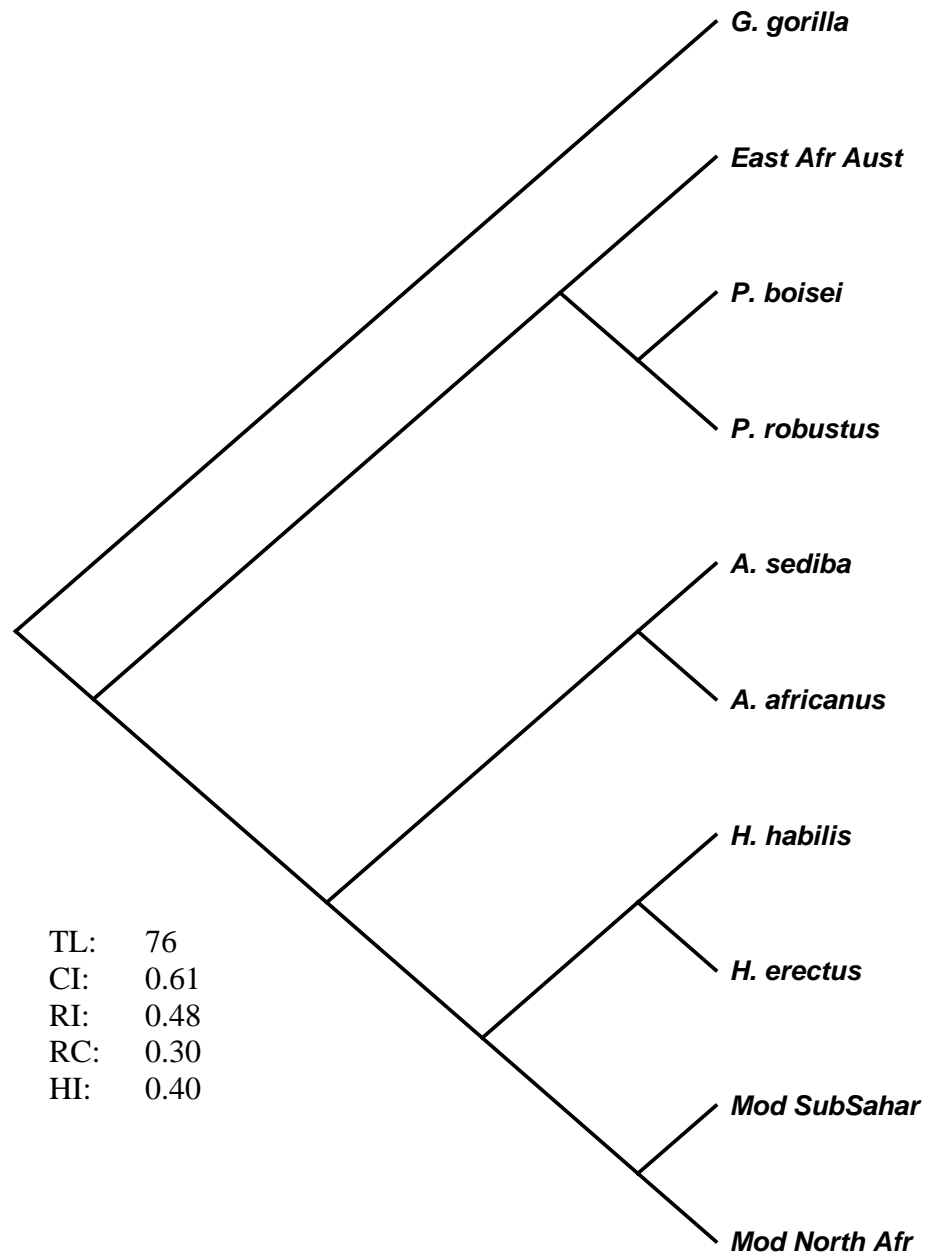
Figure Captions

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).

Figure 2. (A) Maximum parsimony cladogram of gorilla outgroup and seven pooled hominin samples based on gap weighting (20 states) of 22 ASUDAS characters. (B) 50% majority consensus tree of 10,000 bootstrapped replicate data sets. See text for details.

Figure 3. (A) Maximum parsimony cladogram of gorilla outgroup and nine hominin samples based on numerical exercise where the original data are quadrupled to yield '88' ASUDAS characters for analysis. (B) 50% majority consensus tree of 10,000 bootstrapped replicate data sets showing that greater clade support is linked with increased character numbers. See text for details.
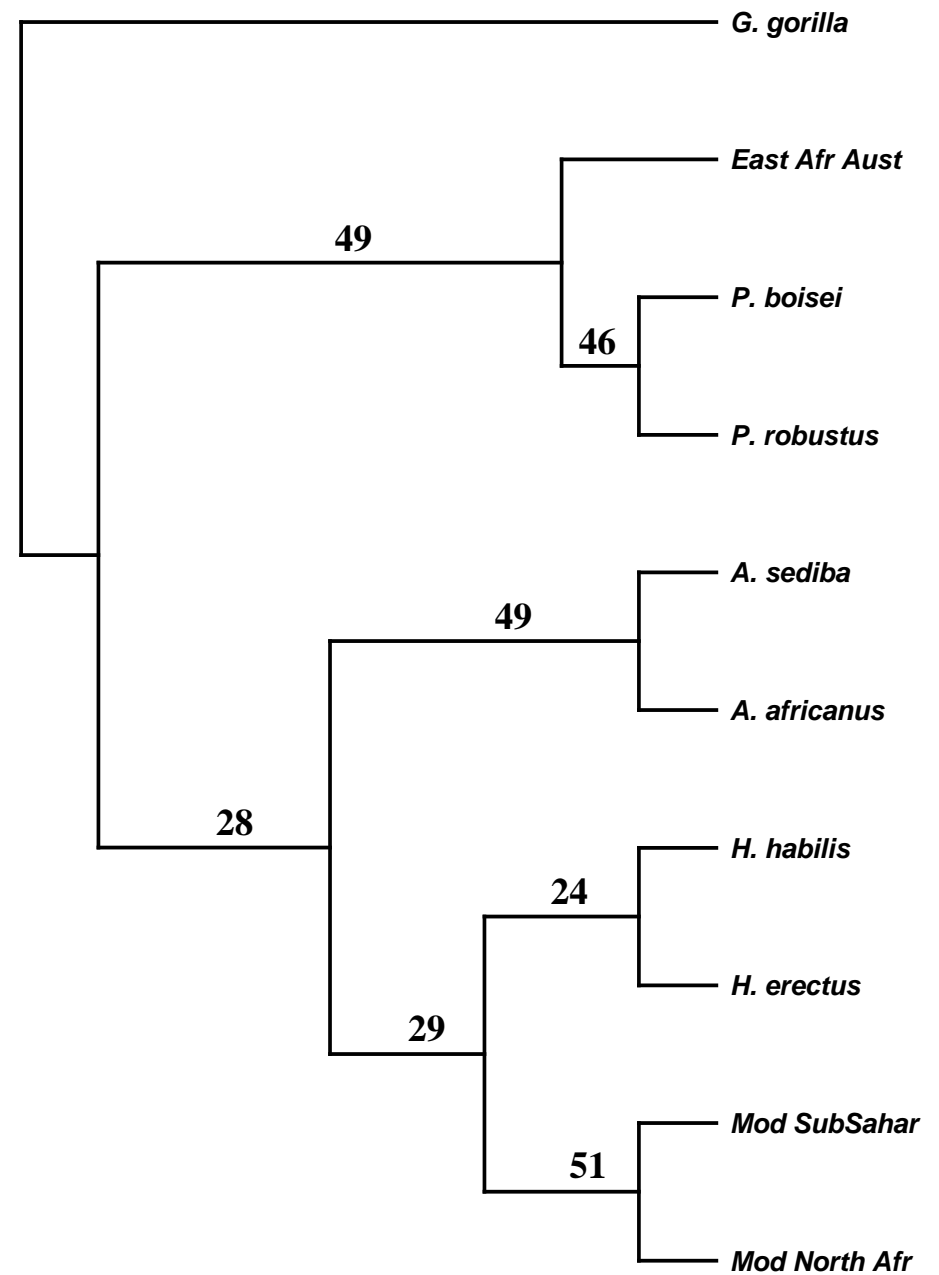
Figure 4. (A) Maximum parsimony cladogram of *Gorilla* and *Pan* outgroup and nine sample hominin ingroup based on 18 ASUDAS characters. (B) Unrooted maximum parsimony cladogram of *Gorilla*, *Pan*, and the nine hominin samples based on 18 ASUDAS characters. See text for details.
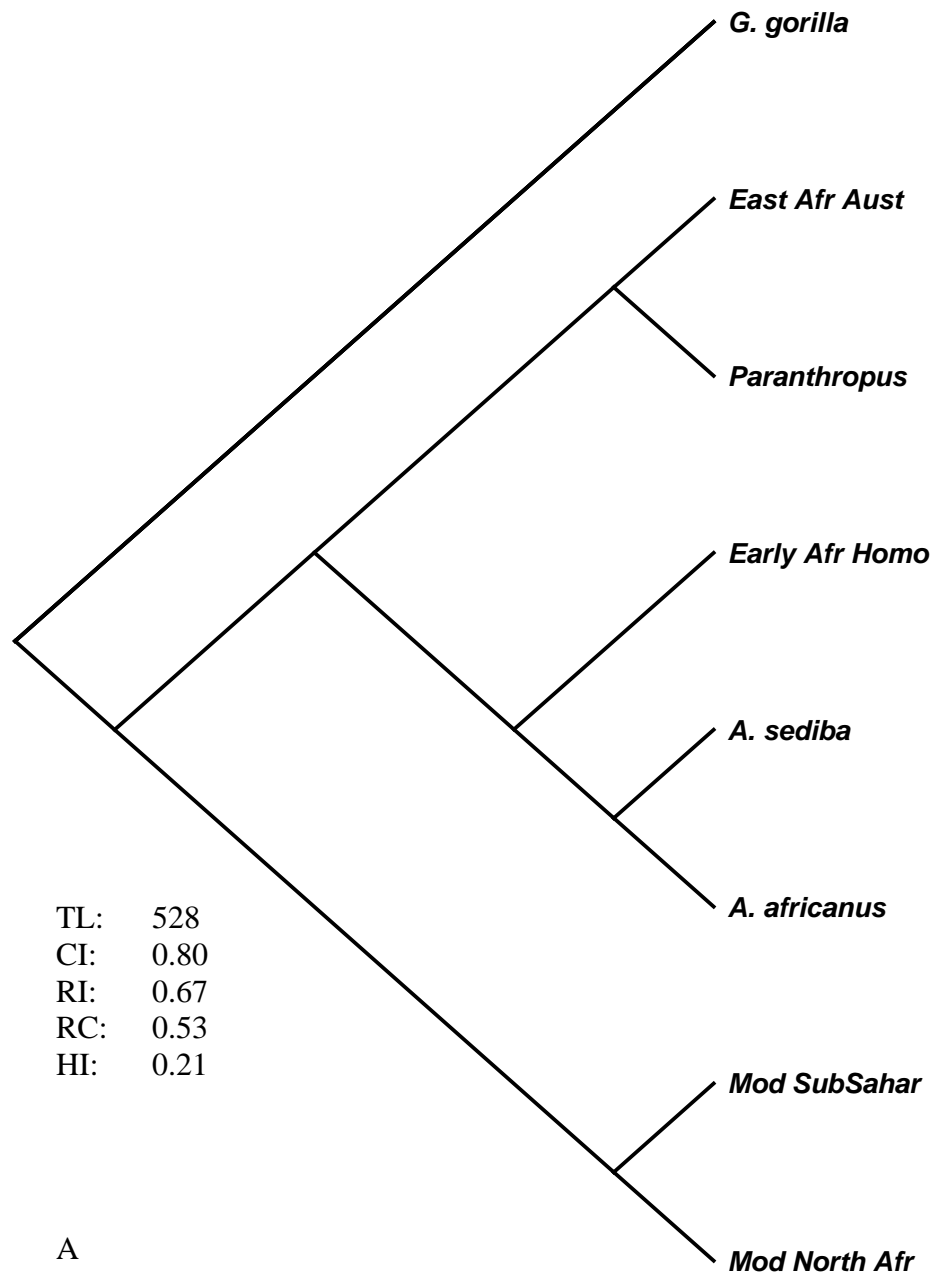
TL:	76
CI:	0.61
RI:	0.48
RC:	0.30
HI:	0.40

TL: 528
CI: 0.80
RI: 0.67
RC: 0.53
HI: 0.21

A

B

G. gorilla

East Afr Aust

P. boisei

P. robustus

A. sediba

A. africanus

H. habilis

H. erectus

Mod SubSahar

Mod North Afr

TL: 308
CI: 0.61
RI: 0.47
RC: 0.29
HI: 0.41

A

G. gorilla

East Afr Aust

69

P. boisei

57

P. robustus

A. sediba

60

A. africanus

43

H. habilis

44

H. erectus

55

Mod SubSahar

75

Mod North Afr

B

G. gorilla

P. troglodytes

East Afr Aust

P. boisei

P. robustus

A. sediba

A. africanus

H. habilis

H. erectus

Mod SubSahar

Mod North Afr

TL: 81
CI: 0.58
RI: 0.52
RC: 0.32
HI: 0.42

A

P. robustus

P. boisei

P. troglodytes

G. gorilla

East Afr Aust

A. sediba

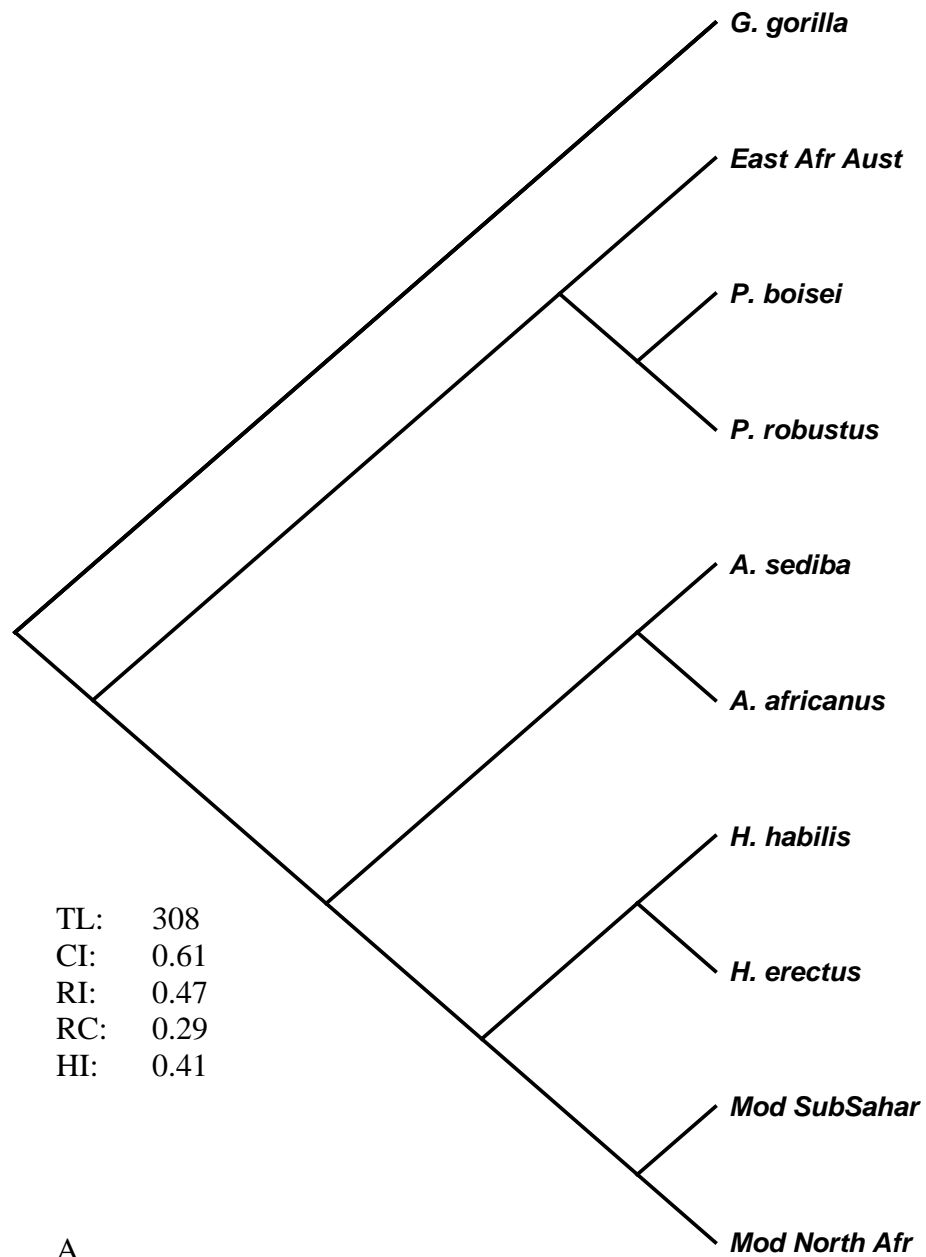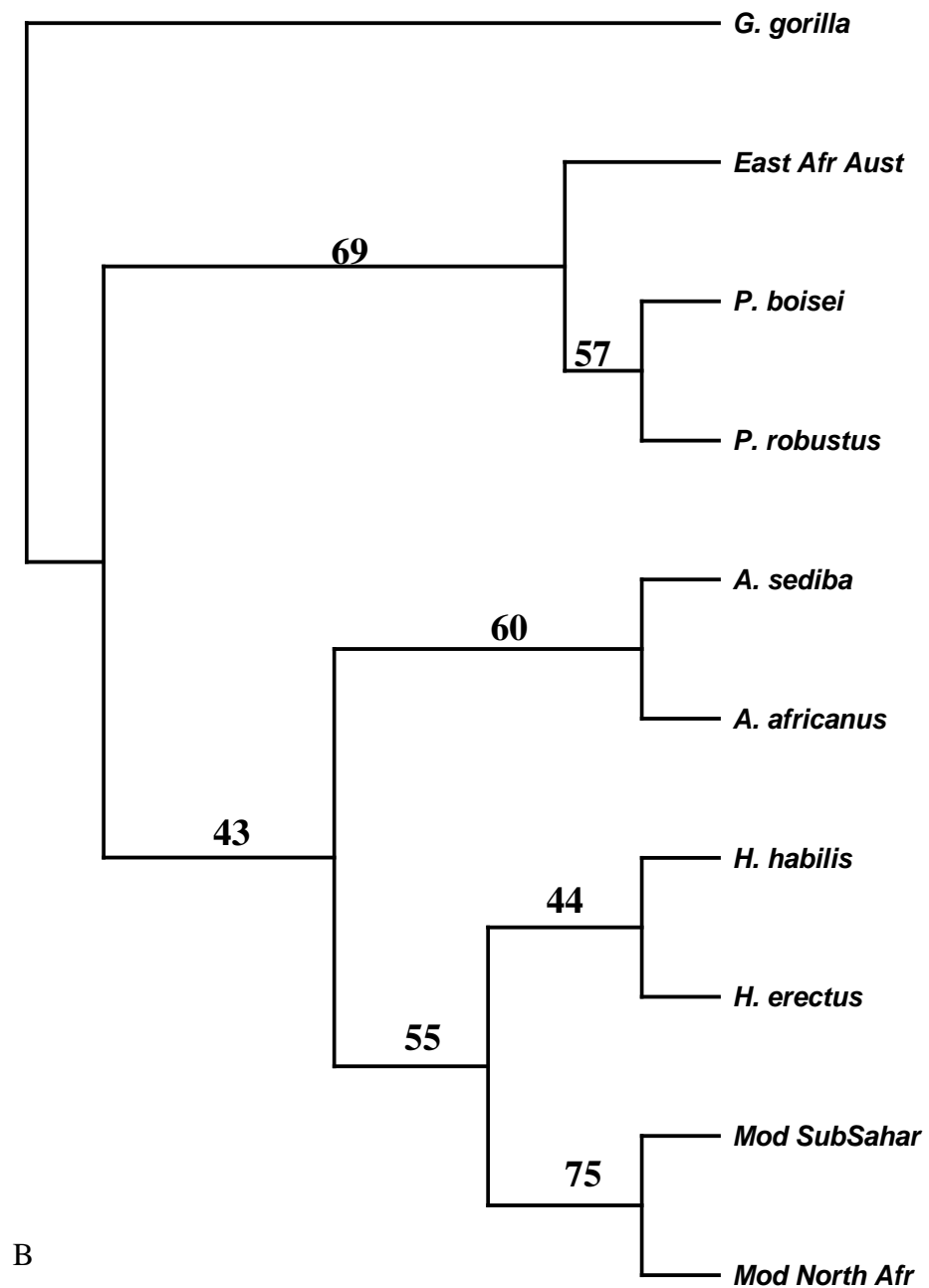Mod North Afr

A. africanus

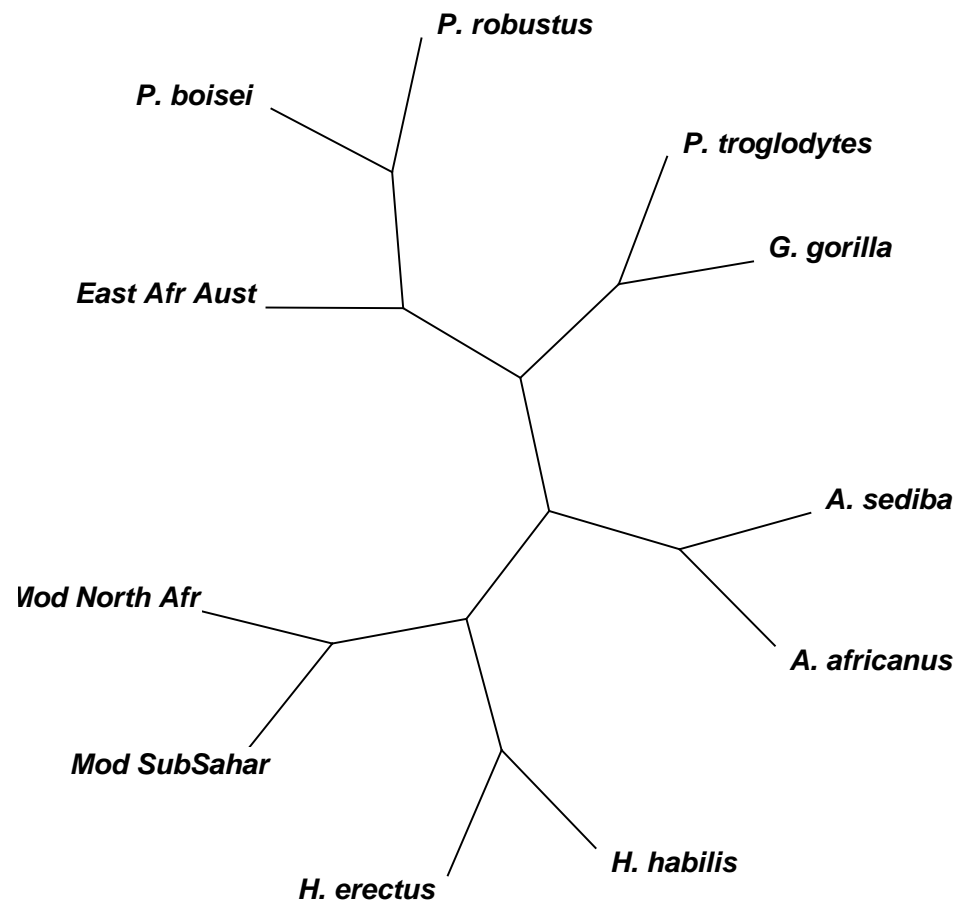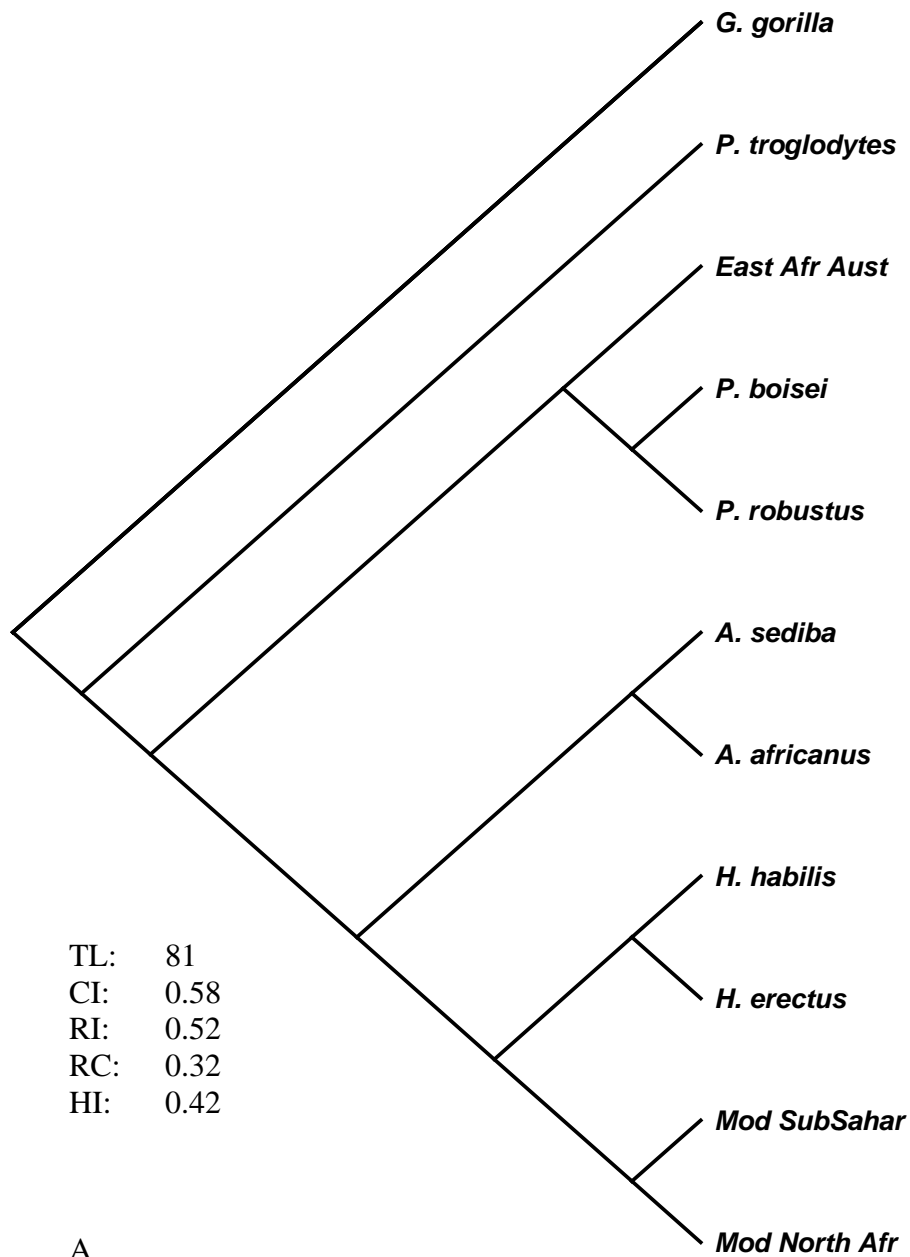Mod SubSahar

H. erectus

H. habilis

B

Table 1. 22 ASUDAS traits and distribution of their states[1] in *Pan troglodytes* outgroup.

Labial Curvature UI1	Moderate		Tome's Root LP3	Two Roots
	3			5
Shovel UI1	Absent		Lingual Cusp No. LP4	Two, Mesial Cusp Larger
	0			3
Double Shovel UI1	Absent		Anterior Fovea LM1	Weak
	0			2
Bushman Canine UC	Absent		Cusp No. LM1	Five
	0			5
Distal Acc. Ridge UC	Absent		Protostylid LM1	Curved Mesial and Distal Grooves
	0			3
Root No. UP3	Two		Cusp 7 LM1	Faint
	2			1
Carabelli's Cusp UM1[1]	Lingual Cingulum		Root No. LM1	Two
	0			2
Cusp 5 UM1	Faint Cuspule		Groove Pattern LM2	Y
	1			0
Enamel Extension UM1	Absent		Cusp No. LM2	Five
	0			5
Hypocone UM2	Very Large Cusp		Root No. LM2	Two
	5			2
UM3 Agenesis	Absent		Torsomolar Angle LM3	Minimal
	0			1

[1]See Irish et al. (2013) for definitions and comparative data.