Craniodental continuity and change between Iron Age peoples and their descendants

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The appearance of the Iron Age of southern Africa early in the first millennium AD is associated with the migration of Bantu speakers who were broadly ancestral to present-day Bantu speakers. While there is sufficient genetic, physical anthropological and cultural evidence to support general continuity into contemporary populations, the extent to which events since colonialism have affected morphological variation is poorly understood. We used dental anthropological techniques and three-dimensional craniomandibular metrics to examine biological relationships among Iron Age farmers, a historical 19th-century Ndebele sample and 20th-century Bantu speakers. We show that, although Iron Age and modern morphologies are generally similar, there are differences. Moreover, the historical sample falls between the precolonial and modern samples, suggesting increased genetic exchange from the 19th century onwards. These results suggest that recent historical events altered the genetic make-up of Bantu speakers and that, as a result, extrapolations from modern groups to the past should be done with caution as morphological variability is relative to historical context.

Introduction

In southern Africa over the last 2000 years, there have been several significant demographic shifts that imply gene flow or exchange at several different geographical scales. Early in the first millennium AD, the Iron Age appears rapidly in this region and is identified archaeologically through a 'package' of agropastoralist elements associated with permanent and semi-permanent settlements.[1-4] These elements include a distinctive ceramic style (the Chifumbaze complex) that is widespread in East and southern Africa, and metallurgical skill. The archaeological and linguistic evidence indicates that the abrupt introduction of this 'Iron Age package' is associated with the migration of farmers who spoke Bantu languages and that there is a general continuity through to Bantu speakers in present-day southern Africa. This scenario is also supported by genetic evidence from modern-day descendants, which indicates recent and common origins throughout much of southernmost Africa.[5-8]

Debate concerning the cultural continuity between the Early Iron Age (EIA) and historical Bantu speakers[5,9,10] considers that EIA people did not arrive and develop in isolation; the evidence for intermarriage and cultural exchange with Stone Age hunter–gatherers is clear.[5,11] Additionally, the shift in ceramic style between the EIA and Later Iron Age (LIA) early in the second millennium AD[12] is associated with further migration from east Africa. Blackburn ceramics (ancestral Nguni speakers) appear in KwaZulu-Natal from around 1100 AD and Moloko ceramics (ancestral Sotho–Tswana speakers) appear north of the Soutpansberg from around 1300 AD.[12-15] Furthermore, Sotho–Tswana and Nguni ancestors colonised the southern grasslands, south of the Vaal River[16], and the Eastern Cape from the 16th century[12]. Once again, linguistic, cultural and genetic evidence shows considerable interaction with San hunter–gatherers. Significant shifts among agropastoralists, especially Nguni diasporas from northern KwaZulu-Natal from the 16th century AD, may have been prompted by climatic change and the introduction of maize via the Portuguese.[12]

Demographic movement increased from the early 19th century as colonial expansion intensified from the southeast African coast and from the Cape. This expansion contributed to the early 19th-century mfecane/difaqane (troubled times) during which there was considerable demographic movement and change.[12] Colonial encroachment and intensified trade demands for ivory and labour contributed to agropastoralist political centralisation in the west, the development of large Tswana towns[17] and the establishment of the Zulu state in northern KwaZulu-Natal[18,19]. These events exacerbated a demographic 'swirl' and Nguni speakers, for example, moved into southwestern Zimbabwe as well as northern Malawi and southern Tanzania. Despite the colonial characterisation of this period as savage and chaotic, the movement of people and the negotiation of new political arrangements elsewhere simply continued from previous political processes that underpinned inclusiveness. The *Land Act of 1913* and the establishment of apartheid homelands during the 20th century collapsed identity into an immutable package of race, culture and language.

While the historical and archaeological record indicates overall continuity through the EIA and into the present there has been gene flow from both closely related groups and more distantly related ones (e.g. Khoesan, colonists) and this is likely to have influenced the biological composition of these peoples over time.[8,20] Although studies of the remains of Iron Age peoples have the potential to contribute to our understanding of biological continuity (or change) over time, to date the contribution of physical anthropology to the question of temporal continuity is limited. Analyses of morphological variability within and between Iron Age human samples, as well as between Iron Age and later samples, are rare (but see Ribot et al.[21]). Because Iron Age human burials are typically dispersed within a settlement (in a patterned way according to gender and status), it is unlikely that more than a few burials are discovered and excavated per site.[22] The exceptions are the burials excavated from the early second millennium AD Mapungubwe and K2 capitals, which have been analysed and shown to be within the range of variation expected in modern Bantu speakers.[22-25] These specimens have since been reburied.[26]

Additionally, a number of studies have looked at skeletal variation in modern Bantu-speaking peoples. A large-scale study on variability between Bantu speakers, using linguistic identity as a proxy for 'tribal' affiliation was conducted by De Villiers[27], based on cranial metric and non-metric analyses[27]. Her study showed that there is low variation between recent historical South African Bantu speakers and that many features were similar between these groups and the Khoesan (suggesting admixture). This finding was supported by a more recent study using geometric morphometrics.[28] Dental anthropology on modern Bantu groups conducted by Jacobson[29] and Irish[30,30] also support conclusions of low inter-population variability[29-31]. These conclusions are supported by the genetics[32], although later research suggests that the level of admixture varies between groups, indicating that differences between southern Bantu and more northern populations result from the intensity of interaction and intermarriage with Khoesan[28,33].

In this study, we compared modern and archaeological Iron Age human samples, as well as an historical Ndebele sample, in order to assess the degree of morphological continuity among these broad groups. These analyses focus on cranial and dental morphology for two reasons. Firstly, in other studies on both contemporary and archaeological human samples,[23,28,33-40] both dental and cranial morphology have been shown to be population-specific indicators of identity. Secondly, teeth are better preserved in the archaeological record than the postcranial skeleton and therefore comprise a larger sample size. Our main objective in this study was to characterise cranial and dental variability within Iron Age and more contemporary Bantu speakers, and identify differences in variation that may have arisen as a result of recent historical processes influencing gene flow. As within-group variability in both the Iron Age and modern Bantu speakers has been shown to be small,[27,29,30,38,41] we considered them as cohesive entities. Significant differences between these larger temporal groups is likely to have arisen during the colonial and post-colonial periods, represented here (albeit incompletely) by the historical Ndebele (Historic Cave) sample. More broadly, this research will allow us to evaluate the assumptions that can be made of historical groups using contemporary Bantu-speaking populations.

Materials and Methods

Specimens

The sample is separated into three groups: Iron Age, historical and modern. The Iron Age specimens ($n=142$) come from a number of sites and are housed in the following institutions: University of Cape Town, the Natal Museum, the University of the Witwatersrand, the University of Pretoria, the National Museum of Cultural History (Ditsong Museums of South Africa) and the University of Botswana (in association with the Botswana National Museum). Sites from where the samples originate range from as far north as Zambia (Ingombe Ilede and Isamu Patu), east into the Kalahari of eastern Botswana (Toutswemogala sites) and along the KwaZulu-Natal (eastern) coast of South Africa. All these sites date to between 1600 and 150 BP, and consequently straddle both the EIA and LIA. Because current research suggests that morphological variability (both temporal and geographical) between groups in the Iron Age is low,[41] the Iron Age is treated as a single group for comparisons within this study. The historical specimens are Ndebele peoples from Historic Cave, located in the Makapan Valley in South Africa, and date to a historically documented siege by the Trekboers in 1854.[18] The sample consists mostly of loose teeth (166 teeth in total). While the Historic Cave sample is clearly not representative of the entire colonial period, it does provide a useful and interesting marker with which to compare the modern and Iron Age samples.

Data for the modern sample were collected from the Raymond A. Dart Collection of human skeletons at the University of the Witwatersrand. The full sample consists of 39 individuals derived from southern Bantu-speaking groups. These specimens are classified as Zulu, Sotho and Xhosa in the catalogues; however, it is important to remember that many of the specimens within the Raymond A. Dart Collection of human skeletons have been classified into these groups on the basis of language, and more specifically surnames,[42] so these affiliations may not be entirely accurate. Details for the list of specimens, including descriptions of individual specimens (Iron Age and modern) can be found in Warren[41]. Sex was not taken into account in the analyses as a large portion of the sample consists of individual teeth and there are currently no reliable metrical methods for determining sex from teeth available for South Africa. Only adult crania and teeth (including adult teeth from subadult individuals) were used for morphological and dental analyses.

Dental anthropology

Both metric and non-metric data were collected to examine dental variability among the Iron Age, historical (19th century) and modern Bantu speakers (cadavers from the Dart Collection). Non-metric dental traits were scored according to the Arizona State University Dental Anthropological System.[43] These procedures were calibrated with external researchers (Ms Wendy Black who, herself, calibrated with Dr Joel Irish) to increase accuracy to within 93%. Sample sizes varied for each trait within each group, based on presence of tooth and the visibility of the trait. The modern group ranged from 12 to 39 specimens, the historical sample from 1 to 25 specimens, and the Iron Age sample from 47 to 108 specimens. Two dental calliper measurements – buccolingual and mesiodistal lengths – were also taken on each available tooth. Statistical analyses were performed using t-tests (in Microsoft Excel) conducted between each group for all comparable traits. Chi-squared tests were performed in Microsoft Excel on the non-metric traits in order to compare trait frequencies between groups. Testing multiple hypotheses is problematic by nature. If no corrections are made for multiple comparisons, significant findings may be observed by chance – i.e. it is too easy to make a Type I error. By contrast, if corrections for multiple comparisons are made, power to detect real differences is lost – i.e. it is too easy to make a Type II error. Therefore we report both uncorrected and Bonferroni corrected p-values here, for both the chi-squared and the metric comparisons. The mean measure of divergence (MMD; Freeman Turkey transformation) was also calculated using script for R created by A. Soltysiak. MMD was calculated only between the Iron Age and modern samples; MMDs were not calculated using the Historic Cave sample, given the very small sample sizes for some traits. A principal components analysis (PCA) was performed in Statistica (version 11) in order to further illustrate variability between the modern and Iron Age samples. The t-tests were conducted on the regression scores in Excel. For the PCA analysis, Historic Cave specimens were not included because of small sample sizes.

Craniomandibular metrics

A NextEngine 3D Laser Scanner and Scanstudio HD software (version 1.1) were used to create three-dimensional scans of the available cranial and mandibular material. Three-dimensional coordinates for 34 cranial landmarks and 19 mandibular landmarks were then extracted using MeshLab v1.3.1 (Table 1), and a series of Euclidean distances were derived from these landmarks (Table 2). These distances were chosen to capture overall morphology while minimising redundancy. T-tests were performed using Microsoft Excel in order to compare the modern and Iron Age sample; Historic Cave specimens were not included as they were represented by teeth only. Again, we report both uncorrected and Bonferroni corrected p-values for these comparisons. A PCA was performed in Statistica (version 11) to visually display variation, and t-tests were conducted on the regression scores in Excel. Because of missing data, this PCA was by necessity based on only a subset of landmarks.

Results

Dental non-metric results

Table 3 shows the frequencies and sample sizes of the non-metric dental traits for each sample (modern, historical and Iron Age). Table 4 lists the chi-squared p-values calculated for each comparison. Between the Iron Age and the modern samples, 6 out of the 25 traits (24%) are significantly different at $p<0.05$. These traits are winging (UI1), UM1 cusp 5, Carabelli's trait, protostylid (LM1), torsomolar angle and LM1 root number. Between the Iron Age and historical samples, only three traits show significant differences (12%) at $p<0.05$. These traits are winging (UI1), canine mesial ridge and LM2 cusp number. Winging is therefore the only trait that is significantly different between Iron Age samples and both the historical and modern samples. However, winging could only be observed on two Historic Cave specimens, the significance of which will be addressed in the discussion. Between the modern and

Table 1: Craniomandibular landmarks extracted from three-dimensional scans

Landmark	Description	Position
Mandible		
GNA	Gnathion	Midline
POG	Pogonion	Midline
INFRA	Infradentale	Midline
MSPIN	Superior mental spine	Midline
MNS	Mandibular symphysis	Midline
MEN	Mental foramen	Bilateral
ALV	Alveolar border of body	Bilateral
IBB	Inferior border of body	Bilateral
GON	Gonion	Bilateral
PGA	Inferior posterior ramus	Bilateral
AJUNC	Inferior anterior ramus	Bilateral
LAT	Lateral mandibular condyle	Bilateral
PSC	Posterior mandibular condyle	Bilateral
COR	Coronoid process	Bilateral
MC	Medial mandibular condyle	Bilateral
MN	Mandibular notch	Bilateral
AR	Anterior ramus	Bilateral
SA	Superior anterior ramus	Bilateral
MFO	Mandibular foramen	Bilateral
Cranium		
ALV	Alveolon	Midline
B	Bregma	Midline
BA	Basion	Midline
G	Glabella	Midline
I	Inion	Midline
INC	Incisivon	Midline
L	Lambda	Midline
N	Nasion	Midline
O	Opisthion	Midline
PR	Prosthion	Midline
NS	Subspinale	Midline
A	Alare	Bilateral
AST	Asterion	Bilateral
D	Dacryon	Bilateral
MXT	Maxillary tuberosity	Bilateral
FMO	Frontomalar orbital	Bilateral
FMT	Frontomalar temporale	Bilateral
FM	Foramen magnum	Bilateral
FMN	Frontal-maxillary-nasal junction	Bilateral
J	Jugale	Bilateral
KR	Krotaphion	Bilateral
MF	Mandibular fossa	Bilateral
MMC	Max maxillary curve	Bilateral
MAS	Mastoidale	Bilateral
OCA	Occipitocondyle (anterior)	Bilateral
OCL	Occipitocondyle (lateral)	Bilateral
ORI	Orbitale (inferior)	Bilateral
ORB	Orbitale (superior)	Bilateral
POR	Porion	Bilateral
SPH	Sphenion	Bilateral
TF	Temporal fossa (posterior)	Bilateral
JRI	Jugular ridge (inferior)	Bilateral
ZY	Zygion	Bilateral
MAX	Maxillary foramen	Bilateral

Table 2: Craniomandibular measurements

	Measurements		
Mandibular	GNA-POG	MEN_R-ALV_R	IBB_R-GON_R
	POG-MNS	INFRA-ALV_L	GON_L-PGA_L
	POG-INFRA	INFRA-ALV_R	GON_R-PGA_R
	GNA-IBB_L	ALV_L-AJUNC_L	PGA_L-PSC_L
	GNA-IBB_R	ALV_R-AJUNC_R	PGA_R-PSC_R
	IBB_L-MEN_L	IBB_L-GON_L	PSC_L-LAT_L
	IBB_R-MEN_R	LAT_L-MC_L	PSC_R-LAT_R
	MEN_L-ALV_L	MSPIN-MFO_L	COR_R-MN_R
	LAT_R-MC_R	MSPIN-MFO_R	COR_L-SA_L
	LAT_L-COR_L	MFO_L-MN_L	COR_R-SA_R
	LAT_R-COR_R	MFO_R-MN-R	SA_L-AR_L
	LAT_L-MN_L	MFO_L-GON_L	SA_R-AR_R
	LAT_R-MN_R	MFO_R-GON_R	AR_L-AJUNC_L
	COR_L-MN_L	AR_R-AJUNC_R	
Cranial	G-N	J_R-MAX_R	NS-MXT_R
	N-FMN_L	FMT_L-J_L	BA-O
	N-FMN-R	FMT_R-J_R	FM_L-O
	N-D_L	SPH_L-KR_L	FM_R-O
	N-D_R	SPH_R-KR_R	FM_L-BA
	N-NS	J_L-MF_L	FM_R-BA
	NS-PR	J_R-MF_R	FM_L-FM_R
	NS-A_L	ZY_L-JRI_L	OCA_L-FM_L
	NS-A_R	ZY_R-JRI_R	OCA_R-FM_R
	D_L-FMO_L	ZY_L-MF_L	OCA_L-OCL_L
	D_R-FMO_R	ZY_R-MF_R	OCA_R-OCL_R
	ORB_L-ORI_L	MF_L-POR_L	OCL_L-FM_L
	ORB_R-ORI_R	MF_R-POR_R	OCL_R-FM_R
	D_L-ORI_L	SPH_L-B	BA-NS
	D_R-ORI_R	SPH_R-B	PR-NS
	D_L-ORB_L	KR_L-AST_L	NS-ALV
	D_R-ORB_R	KR_R-AST_R	I-AST_L
	FMO_L-FMT_L	AST_L-MAS_L	I-AST_R
	FMO_R-FMT_R	AST_R-MAS_R	NS-MXT_L
	ORI_L-MMC_L	POR_L-MAS_L	L-I
	ORI_R-MMC_R	POR_R-MAS_R	I-O
	MMC_L-JRI_L	AST_L-L	A_R-MMC_R
	MMC_R-JRI_R	AST_R-L	J_L-MAX_L
	A_L-MMC_L	L-B	

Table 3: Sample size and frequencies for each trait for each sample

		Modern	Iron Age	Historic Cave
Winging UI1	%	16.0	2.1	0.0
(+ = ASU 1,2 and 4)	*n*	25	47	2
Shovel UI1	%	8.7	7.4	0.0
(+ = ASU 3+)	*n*	23	54	12
Double Shovel UI1	%	0.0	0.0	0.0
(+ = ASU 2+)	*n*	22	63	12
I and C td UI2	%	19.4	12.0	22.2
(+ = ASU 3+)	*n*	31	75	9
C mesial ridge UC	%	91.2	97.1	100.0
(+ = ASU 1+)	*n*	34	68	9
CDAR UC	%	73.5	70.7	85.7
(+ = ASU 2+)	*n*	34	58	7
Hypocone UM2	%	64.9	98.9	100.0
(+ = ASU 3+)	*n*	37	87	5
Cusp 5 UM1	%	84.2	83.9	87.5
(+ = ASU 1+)	*n*	38	93	8
Carabelli UM1	%	92.1	77.3	50.0
(+ = ASU 3+)	*n*	38	75	6
Parastyle UM3	%	0.0	2.8	0.0
(+ = ASU 2+)	*n*	37	108	7
Root no. UM2	%	9.4	7.7	0.0
(+ = ASU 3+)	*n*	32	91	5
P ling cusp LP2	%	0.0	1.0	0.0
(+ = ASU 2+)	*n*	38	100	7
Tome root LP1	%	0.0	1.1	0.0
(+ = ASU +)	*n*	34	88	25
Groove pattern LM2	%	0.0	0.0	0.0
(+ = ASU Y)	*n*	38	76	9
Cusp no. LM1	%	97.4	91.9	90.9
(+ = ASU 5+)	*n*	39	74	11
Cusp no. LM2	%	97.1	96.4	70.0
(+ = ASU 5+)	*n*	34	84	10
Def wrinkle LM1	%	40.0	55.7	66.7
(+ = ASU 2-3)	*n*	35	79	3
DT crest LM1	%	100.0	100.0	100.0
(+ = ASU +)	*n*	33	77	2
Protostylid LM1	%	17.6	12.5	0.0
(+ = ASU 1+)	*n*	34	56	1
Cusp 6 LM1	%	29.0	18.5	0.0
(+ = ASU 1+)	*n*	31	81	1
Cusp 7 LM1	%	91.2	84.2	50.0
(+ = ASU 2+)	*n*	34	76	2
Torso. angle	%	63.6	36.8	0.0
(+ = ASU +)	*n*	33	76	2
Root no. LM1	%	75.0	59.5	54.5
(+ = ASU 3+)	*n*	36	84	11
Root no. LM2	%	63.2	50.0	72.7
(+ = ASU 2+)	*n*	38	90	11
Peg, absent UM3	%	100.0	98.0	100.0
(+ = ASU -)	*n*	12	98	7

Table 4: Chi-squared *p*-values for non-metric dental comparisons among the modern, historical and Iron Age samples

	Iron Age/modern	Iron Age/historical	Modern/historical
Winging UI1	0.027	0.019	0.673
Shovel UI1	0.847	0.331	0.293
Double shovel UI1	—	—	—
I and C td UI2	0.323	0.390	0.850
C mesial ridge UC	0.195	0.000	0.001
CDAR UC	0.770	0.401	0.494
Hypocone UM2	0.962	0.787	0.814
Cusp 5 UM1	0.017	0.908	0.119
Carabelli UM1	0.000	0.257	0.534
Parastyle UM3	0.764	0.520	0.475
Root no. UM2	0.139	0.408	0.180
P ling cusp LP2	0.957	0.642	0.612
Tome root LP1	0.661	0.101	0.565
Groove pattern LM2	0.177	0.653	0.290
Cusp no. LM1	—	—	—
Cusp no. LM2	—	0.003	0.071
Def wrinkle LM1	0.087	0.192	0.048
DT crest LM1	0.448	0.785	0.482
Protostylid LM1	0.001	0.743	0.173
Cusp 6 LM1	0.151	0.201	0.056
Cusp 7 LM1	0.105	0.752	0.194
Torso angle	0.000	—	—
Root no. LM1	0.000	0.574	0.070
Root no. LM2	0.617	0.703	—
Peg, reduced absent UM3	0.536	0.790	—

historical samples, two traits (8%) are significantly different at $p<0.05$: LM1 deflecting wrinkle and canine mesial ridge. Of these, canine mesial ridge was also significantly different for the comparison between the Iron Age and historical material. For the trait deflecting wrinkle the historical sample was once again very small ($n=3$). Because the chance of calculating at least one significant *p*-value (0.05) between any two samples is high (72%), we further adjusted the *p*-value to the Bonferroni correction, at $p=0.002$. Four traits remain significantly different between the Iron Age and modern samples (Carabelli UM1, protostylid LM1, torsomolar angle and LM1 root number), while canine mesial ridge is still significantly different between the Historic Cave sample and both the Iron Age and modern samples. Although correcting the values confirms that the samples are different, it is nonetheless important to look at each trait (e.g. at $p=0.05$) to identify the manner in which these samples differ. The MMD (i.e. phenetic distance) between the modern and Iron Age samples is low at 0.088, again suggesting only a small amount of difference between these groups.

Dental metric results

The 32 dental metric comparisons are shown in Table 5. Between the Iron Age and modern samples, 11 measurements (34%) show significant differences at $p<0.05$. For buccolingual measurements, the first and second molars (upper and lower) are all significantly different. For mesiodistal length, the premolars (upper P1 and P2, lower P1 and P2), the lower canines, the lower first molar and upper first incisor are significantly different. Between the Iron Age and historical samples, 5 of the 30 measurements (17%) were significantly different at $p<0.05$. These measurements are buccolingual lengths of the upper first premolar, lower first and second incisors, lower M2, and the mesiodistal length of the upper P2. Of these, mesiodistal length of the upper second premolar and buccolingual length of the lower second molars are also significantly different for the Iron Age versus modern comparison. Between the historical and modern comparisons, four measurements (13%) are significantly different at $p<0.05$: mesiodistal measures of the upper canine and second premolar and the lower canine and lower second premolar. Of these, mesiodistal measurement of the lower canine and lower second premolar are also significant for the Iron Age versus modern comparison. Mesiodistal length of the upper second premolar is significant for all three comparisons.

Although the use of $p=0.05$ for significance is useful when comparing individual traits, the chances of calculating one significant *p*-value when the samples are actually similar is as high as 80%. In order to detect any real difference between the samples themselves (and not just the traits), the *p*-value was corrected to 0.0016. When this correction was done, only a single measurement differed significantly between the modern and Iron Age samples (buccolingual LM1), and between the Historic Cave and modern samples (mesiodistal UP2). There is no significant difference between the Historic Cave and Iron Age samples. Whether this finding is a result of a small sample size, close biological relationships or a combination of both, is unknown.

Figure 1 shows the dental metric covariance PCA for factor 1 versus factor 2 for the Iron Age and modern specimens. Coefficient ellipses (95%) surround each group. PC1 shows loadings that are all positive, ranging from only 0.030 (mesiodistal lower first premolar) to 0.179 (buccolingual upper second molar), indicating that PC1 is a size variable. PC1 includes 67% of the variance and PC2 includes 7% of the variance (total 74%). The greatest contributions to the first PC are from the buccolingual upper second molar (0.179 loading proportion) and mesiodistal lower second molar (0.159). The smallest contributions to

Table 5: The *p*-values for *t*-tests for each dental metric comparison

	t-test	Modern/Iron Age	Iron Age/historical	Historical/modern
Buccolingual	I1	0.529	0.742	0.739
upper	I2	0.761	0.173	0.402
	C	0.129	0.886	0.380
	P1	0.137	0.043	0.308
	P2	0.395	0.954	0.519
	M1	0.026	0.333	0.980
	M2	0.022	0.080	0.538
	M3	0.572	0.126	0.545
Mesiodistal	I1	0.013	0.655	0.305
upper	I2	0.150	0.739	0.082
	C	0.057	0.156	0.023
	P1	0.006	0.386	0.556
	P2	0.002	0.006	0.000
	M1	0.142	0.994	0.746
	M2	0.627	0.218	0.510
	M3	0.552	0.344	0.440
Buccolingual	I1	0.180	0.018	0.293
lower	I2	0.149	0.029	0.352
	C	0.387	0.963	0.780
	P1	0.244	0.136	0.273
	P2	0.684	0.599	0.698
	M1	0.000	0.141	0.536
	M2	0.005	0.010	0.237
	M3	0.867	—	—
Mesiodistal	I1	0.326	0.876	0.602
lower	I2	0.901	0.306	0.400
	C	0.007	0.089	0.003
	P1	0.034	0.474	0.060
	P2	0.006	0.457	0.031
	M1	0.014	0.924	0.508
	M2	0.103	0.816	0.572
	M3	0.149	—	—

PC1 come from the buccolingual (0.043) and mesiodistal (0.03) lower first premolars. For PC2, the mesiodistal upper second molar contributes the largest proportion (0.613), with buccolingual and mesiodistal upper first premolars contributing the least (less than 0.01). Figure 1 indicates that although there is much overlap between the modern and Iron Age samples, there are some differences in both size and shape, as indicated by the placement of modern specimens at the lower right of the graph. The *t*-tests on the regression scores indicate that the two samples are significantly different for PC1, 2 and 6 (size and two shape factors) at $p<0.05$. At the Bonferroni corrected value of $p<0.005$, differences for PC2 are still significant, indicating shape differences between the Iron Age and modern samples.

Craniomandibular metric results

Table 6 shows the results of *t*-tests between the Iron Age and modern samples for a series of craniomandibular measurements (there were no complete adult cranial or mandibular historical specimens from Historic Cave, only isolated teeth). The table shows the measurements used, sample sizes for each measurement for each category and the mean measurement (in millimetres) for each sample. Sample sizes vary between measurements, depending on preservation and visibility of the landmarks. For the modern sample, each measurement was taken on between 33 and 40 specimens (Table 6). For the Iron Age sample, each measurement was taken on between 25 (NS-PR and INFRA-ALV) and

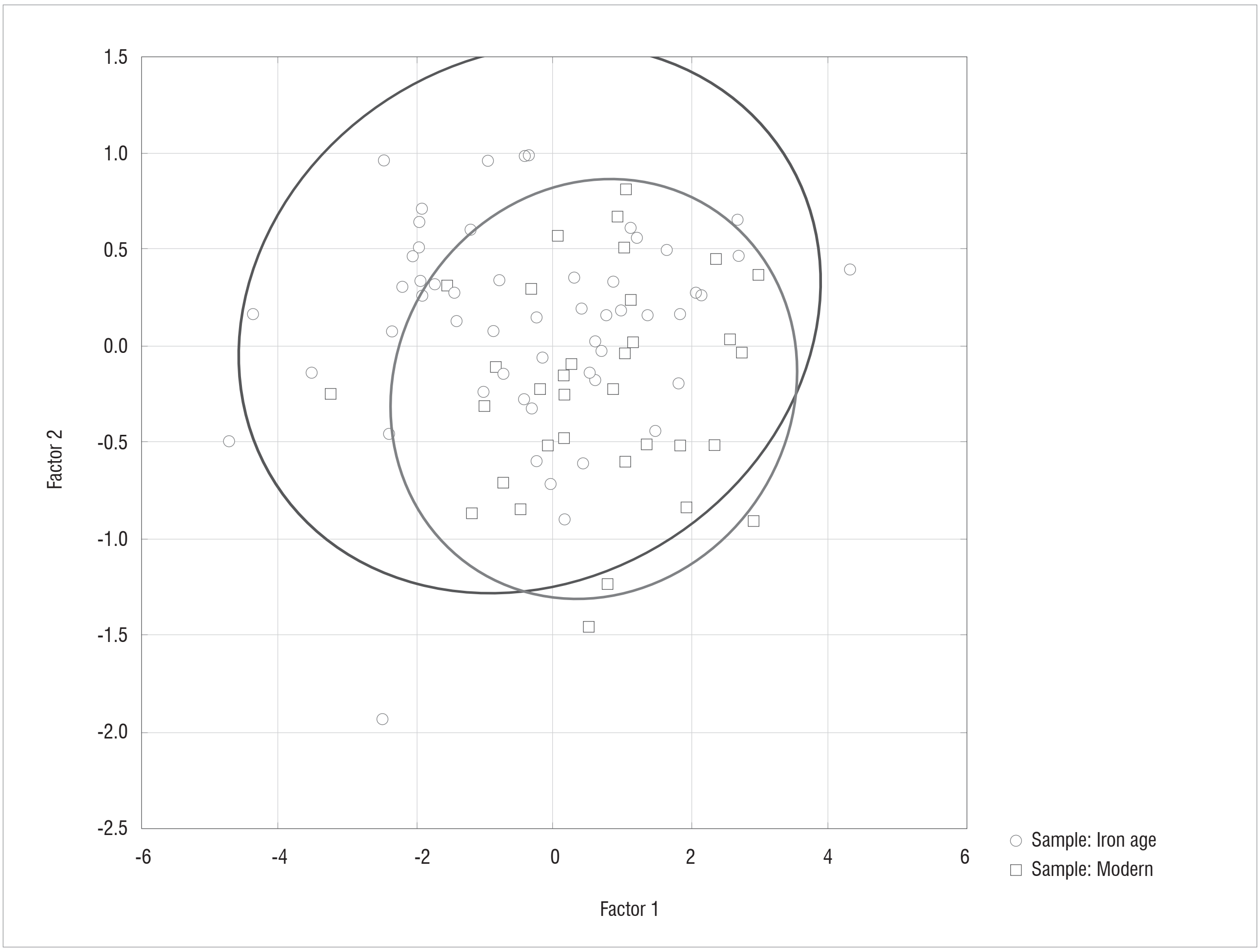

Figure 1: Principal components analysis of dental metric results: scatterplot of factor 1 (67% variance) against factor 2 (7% variance).

61 (SA-AR and AR-AJUNC) specimens. Out of the 62 measurements, 22 (35%) are significant at $p<0.05$ and 17 (27%) are significant at $p<0.01$. Although only 22 measurements are mandibular, 16 of these measurements (73%) show significant differences ($p<0.05$).

Figure 2 shows the results of the craniomandibular metric PCA. To maximise sample size, only 13 measurements, mostly mandibular, were used in this analysis. The first three PCs account for 27%, 18% and 16% of the variance, respectively (total 61%). The other PCs each contribute less than 10% of the variance. For the first component, mandibular ramus (SA-AR; 0.361) and mandibular foramen to gonion (0.197) contribute the most. Gnathion to pogonion, pogonion to the inferior posterior ramus, coronoid process to mandibular notch and mandibular foramen to poronion measurements contribute the least to PC1 (less than 0.005). For PC2, the inferior border of the body to the gonion contributes the most (0.366) and pogonion to mandibular symphysis, coronoid process to mandibular notch and mandibular foramen to poronion contribute the least (less than 0.005). PC3 has large contributions from gonion to inferior posterior ramus (0.254) and mandibular foramen to gonion (0.296). Figure 2a shows PC1 against PC2 for modern and Iron Age specimens. Although there is much overlap, modern specimens are more concentrated on the left of the graph and Iron Age specimens on the right (i.e. along PC1). Figure 2b (PC2 against PC3) illustrates complete overlap between the Iron Age and modern samples for either PC2 or PC3, although the Iron Age sample does appear to be more variable than the modern one (this pattern is also seen in Figure 2a). The *t*-tests conducted on the factor scores derived from the craniomandibular measurements of the specimens reveal that PC1 (size) and PC4 show significant difference between the Iron Age and modern samples at $p<0.05$. PC1 remains significantly different when the Bonferroni *p*-value is adjusted to 0.004, showing that differences between these groups are statistically meaningful.

Discussion

The results indicate that there is a large amount of phenotypic (and presumably underlying genetic) similarity among the Iron Age, historical and modern samples. This finding is consistent with archaeological research as well as previous genetic and linguistic work that support continuity between precolonial and modern Bantu-speaking peoples and/or cohesion among modern Bantu-speaking peoples.[7,20,27-29,32,45] Continuities through the ceramic sequence suggest that ancestral forms of Shona were spoken in the first millennium AD[12], and, more specifically, the archaeology shows direct cultural continuity between second millennium AD agropastoralists and historical Sotho–Tswana[15] and Nguni speakers[13]. Despite these overall continuities, significant regional demographic shifts resulted in linguistic and cultural entanglements, and the creation of new identities (e.g. a Venda identity emerged in the 16th century AD from intermarriage between Shona and Sotho speakers[46]).

It is not surprising that the data in this study indicate homogeneity in the measured traits between the Iron Age and historical samples. The violent nature of the mfecane early in the 19th century led to the dispersal of people, the fragmentation of polities and the reformulation of people into new political units. The small group of Ndebele, estimated to be about 300, who left KwaZulu-Natal under the leadership of Mzilikazi, increased to about 20 000 in the late 1820s – in the early years of the Ndebele state in the present-day Rustenburg area.[47] This example underpins that while the initial numbers were low, Mzilikazi ‘accumulated’ people as his settlement focus shifted further to the west and included a significant number of Sotho–Tswana speakers. While the scale of these

Table 6: Craniomandibular measurements, associated sample sizes and means (in mm) of the modern and Iron Age samples

	Modern (*n*)	**Iron Age (*n*)**	**Mean, modern**	**Mean, Iron Age**
G-N	40	40	8.9	9.8
N-FMN	40	40	6.3	6.4
N-D	40	41	11.7	11.6
N-NS	38	33	50.2	49.3
NS-PR	34	25	17.7	18.9
NS-A**	37	39	19.4	18.3
D-FMO**	40	39	42.7	44.2
ORB-ORI	40	41	35.6	35.7
D-ORI	40	41	33.8	33.5
D-ORB	40	40	27.5	27.8
FMO-FMT	40	38	6.7	6.8
ORI-MMC	39	47	22.1	23.2
MMC-JRI	39	49	12.2	11.8
A-MMC	38	45	27.3	28.4
J-MAX*	38	30	13.5	15.5
FMT-J	40	35	22.3	21.8
SPH-KR	36	43	9.1	8.9
J-MF**	40	34	42.8	45.5
ZY-JRI*	40	26	36	40.2
ZY-MF	40	26	24.8	25.4
MF-POR	40	51	13.7	14.1
SPH-B	37	40	92.4	91.3
KR-AST	36	41	84	86.4
AST-MAS	40	45	46.4	48
POR-MAS	40	52	31.3	31.6
AST-L	39	42	86.9	85.4
L-B	39	41	112.6	113.3
L-I	39	44	63.2	66.5
I-O	40	38	45.3	44.2
NS-ALV	35	27	45.3	46.6
I-AST*	40	47	66.3	63.4
NS-MXT	35	34	54.4	55.8
BA-O	40	32	39.6	40.3
FM-O	40	33	27.1	30.2
FM-BA	40	34	24.4	27.5
FM-FM	40	33	31.8	34.8
OCA-FM	39	36	19.8	22.7
OCA-OCL	38	40	15.1	15.3
OCL-FM	39	36	13	16.7
BA-NS	38	25	92.2	94.5
GNA-POG**	38	58	8.7	9.5
POG-MNS	37	56	14.7	14.3
POG-INFRA*	34	30	22.6	24
GNA-IBB	38	52	25.6	25.5
IBB-MEN**	38	65	13.8	14
MEN-ALV**	37	52	15.5	16.3
INFRA-ALV	33	25	26.7	27.2
ALV-AJUNC**	33	47	33.1	34
IBB-GON**	38	60	59.5	61.9
GON-PGA	38	62	18.7	17.4
PGA-PSC**	38	40	37.4	40.3
PSC-LAT	35	36	14.9	14.6
LAT-MC**	34	31	19	20.1
LAT-COR**	35	38	32.1	34.5
LAT-MN*	35	37	20.5	21.6
COR-MN**	38	52	19.6	20.7
COR-SA	38	58	12.4	13.8
SA-AR**	38	61	10.4	13.8
AR-AJUNC**	34	61	20	15.9
MSPIN-MFO**	38	48	74	74.8
MFO-MN**	38	52	21.9	22.7
MFO-GON**	38	60	21.5	23.2

$*p<0.05$; $**p<0.01$

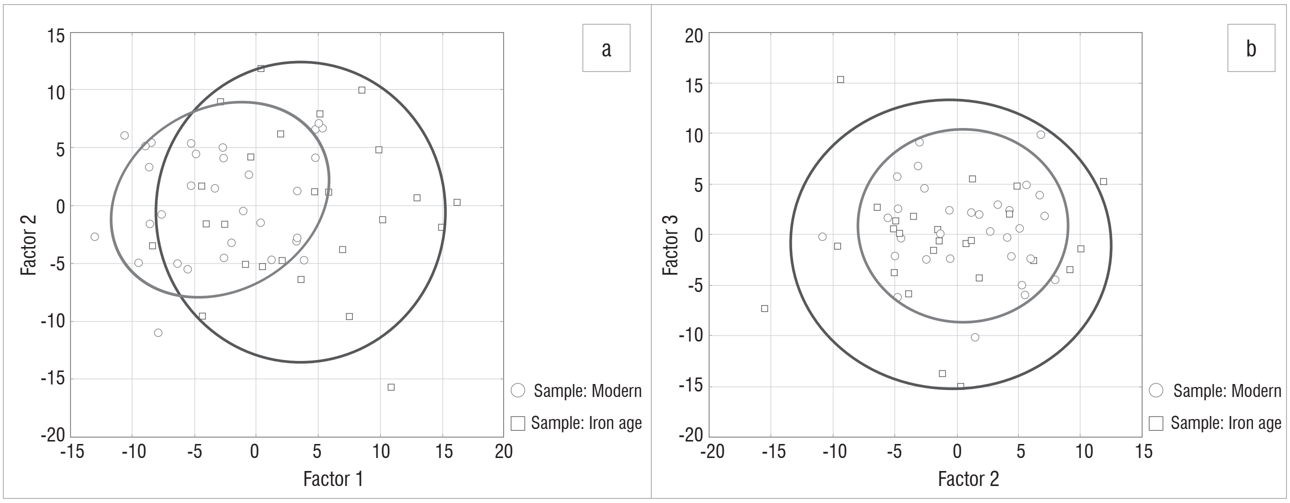

Figure 2: Principal components analysis of craniomandibular dental metric results: (a) scatterplot of factor 1 (27% variance) versus factor 2 (18% variance) and (b) factor 2 versus factor 3 (16% variance).

demographic shifts in the early 19th century may have been larger, the archaeology of both first and second millennium agropastoralists shows that regional demographic movement was essential to the political process. The examples of the origins of Venda and the earlier precolonial Nguni diasporas underpin demographic and cultural fluidity.[12]

Despite this overall pattern of similarity among the Iron Age, historical and modern samples, there are some important differences among these groups. Where dental traits do differ (both discrete and metric), the Iron Age sample tends to be more similar to the historical sample than it is to the modern one, suggesting recent, continuous gene flow from other populations in historical and modern times. This increasing gene flow could stem from a number of historical causes. For example, interaction between hunter–gatherers and farmers is observed frequently in the archaeological record,[5,12,45,48] and it is possible that admixture occurred throughout this period and may have increased because of more recent historical pressures. This scenario is supported by ongoing research on the dentition of Khoesan people that indicates that there is more similarity between a recent Khoesan sample and modern Bantu speakers than between the Khoesan sample and the Iron Age samples studied here.[41] The relationship between the Historic Cave sample and the other samples might reflect increasing population pressures and interactions through time, resulting in them being morphologically intermediate between the Iron Age sample and modern Bantu speakers. This Historic Cave sample comes from the siege of October 1854 when the Kekana (a Ndebele group) took refuge in this large cavern complex in the Makapan valley as a response to a Boer commando seeking revenge for the murder of Trekboers in the previous month.[18,49] There was substantial mortality during this siege. It is important to note that while the results do indeed indicate an intermediate position for the Historic Cave material, larger samples (and more sites) are needed in order to better evaluate this interpretation. Further research on the dentition of other colonial period peoples is necessary to advance our understanding of variation and morphological affinities at this time.

In more recent times, our expectation is that admixture increases, which again may explain the continued divergence of the modern samples from the archaeological ones. The metric and non-metric dental comparisons show a greater similarity between the Iron Age and Historic Cave samples than between the modern and Historic Cave samples, supporting increased levels of gene flow into these groups in recent times. The intensification of trade (particularly in ivory and slaves) in the second half of the 18th century and through the 19th century took place in a context of expanding European mercantile interests and both 19th-century historical contexts mentioned above were inextricably linked to this context.[18,47] Despite the negative interactions there was also admixture between Bantu speakers and Europeans, which is clearly evident in the modern sample and has also been observed in Mozambican populations.[20] This admixture is typically sex biased (European Y-chromosome haplotypes), which is not surprising given that Europeans, specifically the Portuguese, colonised the coast and parts of the interior of Mozambique from the 17th century.[50]

In addition to offering insight into the morphological effects of admixture as detailed above, this study is also important because it is the first to apply standardised dental anthropology techniques to investigate historical relationships between present-day and archaeological southern African populations. Many dental anthropological studies have focused on modern variation across broad geographical regions, with sub-Saharan Africa representing a distinct dental complex.[30,35,36,38,51] Both non-metric and metric dental studies have also focused on variation among non-sub-Saharan-African archaeological samples, indicating continuity, gene flow and morphological change in archaeological samples over time.[34,37,39,52-54] Although these studies have successfully addressed questions about variability and genetic identity using archaeological and contemporary samples, little work using these methods has been done in southern Africa. Early research by Shaw described the dentition of modern-day Bantu speakers,[55,56] but was unstandardised. Additionally, Jacobson's study which shows there is low variability among modern Bantu speakers, is difficult to compare with more recent standardised dental research.[29] Kieser et al.[57] evaluated changes in tooth size between living and recent-historical Bantu speakers drawn from the Dart Collection,[57] indicating larger mesiodistal and buccolingual lengths within the 19th century. This study, however, is the first to extend dental comparisons into archaeological samples.

Finally, this study has important implications for understanding variation within the modern sample. The research presented here – not unexpectedly – shows a degree of historical admixture in the Raymond A. Dart Collection of human skeletons. But, importantly, it also suggests that it might be possible to use archaeological samples to better understand the biological affinities of these modern specimens using skeletal indicators. This is relevant because there is not necessarily a relationship between the biological history and 'tribal' identities of specimens in the Dart Collection because they are categorised based on surnames.[42] Consequently, the biological distinction between the modern and Iron Age samples is a further reminder that modern samples do not provide a comparative baseline for the past.

Conclusion

Three important conclusions can be made from this research. Firstly, there is general similarity between Iron Age farmers, modern Bantu speakers and an historically very specific Ndebele group. This similarity supports a general genetic continuity between precolonial and historical agropastoralists and modern people in southern Africa.

Secondly, despite these similarities, there are more differences between the Iron Age and modern samples than expected, given the seeming homogeneity of both Iron Age and modern Bantu speakers indicated by previous research. This observation demonstrates gene flow between Iron Age descendants and other groups in historical and modern times, and cautions against using modern Bantu speakers as baselines for understanding variation in the past. Finally, the Historic Cave sample appears to be morphologically intermediate between the Iron Age and modern samples, once again supporting the conclusion of increasing gene flow into these groups through time, although small sample sizes reduce the value of this conclusion.

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Authors' contributions

K.A.W. collected the data, analysed samples, performed calculations and wrote the manuscript. R.R.A. conceptualised the project, provided technical and methodological input and helped write the paper. S.H. provided theoretical input and helped write the paper.

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